

Estimating Defoliation of Hardwoods Using Blade-petiole Relations

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Abstract

Prediction equations for estimating leaf blade area and dry weight from measurements of petiole thickness were used to estimate defoliation of *Populus tremuloides*, *Acer rubrum*, *Quercus rubra*, and *Q. alba*. On one tree of each species, a sample of leaves was artificially browsed in May and harvested in July. The fractions of leaf blade tissue remaining in the samples after treatment in May were compared to the fractions remaining after harvest in July, which were calculated using the blade-petiole relations. Significant differences were found between the fractions for all species except *P. tremuloides*. Late browsing treatments were applied to leaf samples of the same trees in July. Except for the remaining fraction of *Acer rubrum* blade dry weight, all fractions calculated after harvest in August were reasonably close to measured fractions after treatment, although some statistically significant differences were found.

INTRODUCTION

PURPORTED ESTIMATES of defoliation of broadleaved trees by insects are often guesses based on the appearance of leaves. This is due, in part, to the lack of methods for estimating the leaf area or dry weight consumed by the insects, especially when the normal margins of the leaves are destroyed.

Most insects consume tissue from the leaf blade only, leaving the leaf petioles unscathed. Therefore, I examined regression equations that describe dimensional relations between blade dry weight and petiole thickness, and blade area and petiole thickness in oven-dry leaves. I used the regression equations to estimate what the blade dry weights and blade areas in samples of partially browsed leaves would be if the blades were whole. With these estimates, and measurements of the actual blade dry weights and blade areas of those same browsed leaves, I estimated the remaining fractions of the total expected blade dry weight and blade area and their standard errors for each sample.

METHODS

Four tree species—quaking aspen (*Populus tremuloides*), red maple (*Acer rubrum*), red oak (*Quercus rubra*), and white oak (*Q. alba*)—were studied in three locations—Ludlow, Massachusetts; Branford, Connecticut; and Pittstown, New Jersey. Fifty leaves each were collected from three trees of each species in each location on or about June 15, July 15, and August 15, 1976. The leaves were pressed and oven-dried for at least 5 days at 80 C. Then oven-dry weights of the leaf blades were measured to the nearest 0.1 mg. Blade areas were measured with an electronic area meter to the nearest 0.1 cm. Petiole thicknesses were measured with a micrometer to the nearest 0.1 mm. The micrometer had a built-in feature that permitted application of a constant 1.75 lb•ft (2.37 N•m) torque when it was tightened about

each petiole. Thus, each petiole was measured under the same pressure.

The petiole measurements of red maple and red and white oak were taken at the petiole-blade junctions, so that each measured thickness was perpendicular to the blade surface. Pressing and oven-drying almost always produced a twist in the petiole near the petiole-blade junction of aspen leaves, and accordingly, their petiole thicknesses were measured just past the twist on the side away from the blade. The measured thickness was the minor axis of the roughly elliptical petiole cross section. If the petiole was not twisted, its thickness was measured parallel to the blade surface.

Analyses of variance were done to test whether average blade areas and dry weights for each species were significantly different for individual trees, locations, or collection dates.

Analyses of covariance were done to test whether the relations between the natural logarithms of blade dry weight and petiole thickness, and blade area and petiole thickness were significantly different among trees, locations, collection dates, or certain interactions.

After significant effects were determined, data collected in Massachusetts and Connecticut in July and August were used to estimate regression equations of the following form:

$$\log W = \beta_0 + \beta_1 \log P$$

$$\log A = \beta_0 + \beta_1 \log P$$

where, W = blade dry weight; A = blade area; and P = petiole thickness. I assumed that the relationships were not the same for the four species or the two locations. For each species, I also assumed that the intercepts for July and August would be different, but the slopes would be the same.

To test the use of the regression equations for estimating expected blade dry weight and blade area of browsed leaves, a browsing experiment was undertaken on four additional trees. A quaking aspen and a red maple were selected at the Connecticut location, and a red oak and a white oak were selected at the Massachusetts location. Each tree received an early and a late browsing treatment.

In the early treatment, 50 leaves of each tree were artificially browsed with scissors after having been photographed with a dot grid superimposed over the blades. The blades were photographed again after treatment. The blade areas of each leaf before and after treatment were obtained from the photographs. These leaves were treated about May 15 and harvested about July 15.

An identical late browsing treatment was applied about July 15 and 50 leaves of the same four trees. Pre- and post-treatment blade areas were measured in situ with a portable electronic area meter. These leaves were harvested about August 15. All the harvested leaves were pressed and oven-dried before their blade dry weight, blade area, and petiole thickness were measured.

I use a special notation to describe the data from the browsing experiment. I use lowercase letters to represent browsed leaf measurements and capital letters to represent the whole-leaf values. The following symbols refer to the i^{th} leaf in the j^{th} treatment sample:

- t_{ij} = blade area immediately after treatment,
- T_{ij} = whole blade area immediately before treatment,
- a_{ij} = blade area after harvest,
- A_{ij} = predicted whole blade area after harvest,
- w_{ij} = blade dry weight after harvest,
- W_{ij} = predicted whole blade dry weight after harvest,
- P_{ij} = petiole thickness.

The sample indexes are:

- $j = 0$ for the early treatment sample, and
- $j = 1$ for the late treatment sample.

The following symbols refer to the average blade values in the j^{th} treatment sample:

- \bar{t}_j = average blade area immediately after treatment,
- \bar{T}_j = average whole blade area immediately before treatment,
- \bar{a}_j = average blade area after harvest,
- \bar{A}_j = average predicted whole blade area after harvest,

- \bar{w}_j = average blade weight after harvest,
- \bar{W}_j = average predicted whole blade dry weight after harvest.

Estimates of $\log W_{ij}$ and $\log A_{ij}$ were made from petiole thickness measurements with the appropriate regression equations. One half of the residual variance of the regression equation was added to each estimate before it was transformed to its antilogarithm as an approximate correction for bias (see Finney 1941).

Defoliation of a given treatment sample can be defined as $1 - (\bar{w}_j/\bar{W}_j)$, $1 - (\bar{a}_j/\bar{A}_j)$, or $1 - (\bar{t}_j/\bar{T}_j)$, where (\bar{w}_j/\bar{W}_j) , (\bar{a}_j/\bar{A}_j) , and (\bar{t}_j/\bar{T}_j) are ratios of means. To determine whether the regression equations provided adequate estimates of whole leaf values, and consequently defoliation, the following differences were computed and tested for significant departure from zero with t-tests:

$$\begin{aligned} &(\bar{t}_0/\bar{T}_0) - (\bar{w}_0/\bar{W}_0), \\ &(\bar{t}_0/\bar{T}_0) - (\bar{a}_0/\bar{A}_0), \\ &(\bar{t}_1/\bar{T}_1) - (\bar{w}_1/\bar{W}_1), \\ &(\bar{t}_1/\bar{T}_1) - (\bar{a}_1/\bar{A}_1). \end{aligned}$$

I also computed the difference $(\bar{t}_0/\bar{T}_0) - (\bar{a}_0/\bar{A}_0)$ for each species. This provided a way to determine if the proportion of defoliation in the early treatment samples had changed from any cause between treatment and harvest. The differences were very small, indicating little or no change. Because of the small differences, t-tests were not done. The variances of the ratios (\bar{a}_j/\bar{A}_j) and (\bar{w}_j/\bar{W}_j) , were approximated by a formula that follows. It is given here for others who may want to estimate defoliation by my method and compute a standard error. A formula is given only for the variance of (\bar{w}_j/\bar{W}_j) . The formula for (\bar{a}_j/\bar{A}_j) is identical except that a and A are substituted for w and W , respectively. The estimator¹ is:

$$v(\bar{w}_j/\bar{W}_j) = \frac{1}{n\bar{W}_j^2} \left[v(w_j) - 2\hat{\beta}_1\bar{w}_j \text{cov}(X_j, w_j) + \hat{\beta}_1^2 v(X_j)\bar{w}_j^2 \left(\frac{\bar{W}_j^2}{\bar{W}_j^2} \right) \right] + \frac{\bar{w}_j^2 s^2}{n\bar{W}_j^2 v(X_j)} \left[\bar{X}_j^2 - \frac{2\bar{W}_j\bar{X}_j\bar{X}}{\bar{W}_j} + \frac{\bar{W}_j\bar{X}_j^2}{\bar{W}_j^2} \right] + \frac{s^4\bar{w}_j^2}{16n\bar{W}_j^2}$$

¹ This estimator was derived by Gerald S. Walton, Mathematical Statistician, Northeastern Forest Experiment Station, Hamden, CT.

where $W_{ij} = \exp(s^2/2 + \hat{\beta}_0 + \hat{\beta}_1 X_{ij})$,
 $X_{ij} = \log P_{ij}$,
 $s^2 =$ residual variance of the regression equation,
 $\overline{W_j^2} = \frac{\sum W_{ij}^2}{n}$,
 $\overline{W_j X_j} = \frac{\sum W_{ij} X_{ij}}{n}$, and
 $n =$ number of leaves in the j^{th} treatment sample.

RESULTS

From my analyses of variance of average blade areas and blade dry weights, I found that average leaf blade areas of the four species studied differ among trees in one location and among locations, but not among collection dates (Table 1). On a given tree, the average leaf blade area will not change significantly from June 15 to July 15, or from July 15 to August 15, unless a disturbance

Table 1. Level of significance for average blade areas and blade dry weights for sources of variation.

Source of variation	Species			
	Aspen	Maple	Red oak	White oak
AVERAGE BLADE AREA				
Trees within location	0.01	0.05	0.01	0.05
Locations	.01	.01	.01	.01
Collection dates	NS	NS	NS	NS
AVERAGE BLADE DRY WEIGHTS				
Trees within location	0.01	NS	0.01	NS
Locations	.01	.05	.01	.01
Collection dates	.01	NS	.05	.01

such as browsing occurs. Average leaf blade dry weights of quaking aspen and red oak differ among trees in one location, among locations, and among collection dates. Average blade dry weights of red maple differ among locations, but not among trees within one location, or collection dates. White oak average blade dry weights differ among locations and collection dates, but not among trees within locations.

From my analyses of covariance, I found that knowledge of petiole-thickness adds precision to estimates of both blade dry weight and blade area of all four species; but so does knowledge of tree, location, collection date, tree \times collection date interaction, and location \times collection date interaction.

The parameter estimates, standard errors of estimates, and coefficients of determination of the log blade dry weight, and the log blade area prediction equations are listed by species in Table 2. The performance of these equations in estimating the remaining fraction of expected blade dry weight and blade area in the early- and late-browsed samples are summarized in Table 3. This table contains the comparisons of (\bar{t}_i/\bar{T}_i) (the ratio-of-means estimate of the remaining fraction of tissue just after treatment) with (\bar{w}_j/\bar{W}_j) (the ratio-of-means estimate of the remaining fraction of blade dry weight after harvest), and (\bar{a}_i/\bar{A}_i) (the ratio-of-means estimate of the remaining fraction of blade area after harvest).

In the early-browsed treatment, $(\bar{t}_0/\bar{T}_0) - (\bar{w}_0/\bar{W}_0)$ is significantly different from zero for the samples of red maple, red oak, and white oak, and $(\bar{t}_0/\bar{T}_0) - (\bar{a}_0/\bar{A}_0)$ is significantly different from zero for the samples of red maple and red oak. In the late-browsed treatment $(\bar{t}_1/\bar{T}_1) - (\bar{w}_1/\bar{W}_1)$ differs significantly from zero for the samples of red maple and red oak, although from a practical

Table 2. Regression statistics for the blade dry weight and blade area prediction equations.

Species	Blade dry weight (g)					Blade area (cm)				
	Intercept July	Intercept August	Slope ^a	SE est.	R ²	Intercept July	Intercept August	Slope	SE est.	R ²
CONNECTICUT										
Quaking aspen	-2.731	-2.660	1.671	0.324	0.70	2.231	2.183	1.429	0.324	0.61
Red maple	-2.975	-3.065	2.242	.260	.85	2.347	2.335	1.869	.293	.76
MASSACHUSETTS										
Red oak	-2.832	-2.931	2.415	.252	.84	2.329	2.212	2.157	.295	.75
White oak	-2.732	-2.844	2.190	.266	.78	2.636	2.484	1.769	.290	.67

^a Petiole thickness measured in mm.

Table 3. Ratio of means estimates of remaining blade area immediately after treatment (\bar{t}_i/\bar{T}_i), remaining blade dry weight after harvest (\bar{w}_i/\bar{W}_i), remaining blade area after harvest (\bar{a}_i/\bar{A}_i), and the standard errors of (\bar{w}_i/\bar{W}_i), and (\bar{a}_i/\bar{A}_i). Significance levels are based on t tests using approximate standard errors of ratio differences.

Species	\bar{t}/\bar{T}	\bar{w}/\bar{W}	SE(\bar{w}/\bar{W})	\bar{a}/\bar{A}	SE(\bar{a}/\bar{A})
EARLY BROWSING TREATMENT					
Aspen	0.620	0.660NS	0.0301	0.594NS	0.0228
Maple	.608	.919**	.0457	.887**	.0393
Red oak	.611	.736**	.0329	.686*	.0303
White oak	.483	.565*	.0420	.472NS	.0318
LATE BROWSING TREATMENT					
Aspen	0.550	0.507NS	0.0345	0.492*	0.0319
Maple	.509	.631**	.0304	.544NS	.0277
Red oak	.450	.495*	.0285	.461NS	.0270
White oak	.400	.416NS	.0235	.367*	.0197

NS - ratio is not significantly different from \bar{t}_i/\bar{T}_i

* - ratio is significantly different from \bar{t}_i/\bar{T}_i at the .05 level

** - ratio is significantly different from \bar{t}_i/\bar{T}_i at the .01 level

standpoint the result for red oak is probably insignificant for most purposes, and $(\bar{t}_1/\bar{T}_1) - (\bar{a}_1/\bar{A}_1)$ differs significantly from zero for quaking aspen and white oak, but these differences may be insignificant from a practical standpoint.

The differences between (\bar{t}_0/\bar{T}_0) computed from the early-browsing treatment sample and (\bar{a}_0/\bar{A}_0) were small for all species. For quaking aspen, the difference was .015, for red maple .025, for red oak .068, and for white oak the difference was - .007.

DISCUSSION

The use of log blade dry weight or log blade area prediction equations to calculate the amount of leaf tissue a tree crown should contain could lead to erroneous defoliation estimates if insects browsed on the leaves early in the growing season but the crown was not sampled until July. Use of log blade dry weight equations might lead to significant underestimation of defoliation in red maple, red oak, and white oak. Use of log blade area equations might lead to significant underestimation in red maple and red oak.

The remaining fraction of blade area in the early-browsed samples did not change with time. My comparisons for each species of (\bar{t}_0/\bar{T}_0) with (\bar{a}_0/\bar{A}_0) suggest that petioles of leaves browsed early in the growing season do not reach the thickness they would if the blades were not browsed.

Consequently, the remaining fraction of expected tissue is overestimated and defoliation is underestimated when the equations are used.

My comparison of (\bar{t}_0/\bar{T}_0) and (\bar{a}_0/\bar{A}_0) also suggests that knowledge of mean blade-area at a given time of year would be useful in estimating defoliation. However, in my analyses of variance of these quantities, I found that average blade-area differs from tree to tree for all four species used in this study. Moreover, many insect browsers do not leave enough whole leaves on a tree for one to obtain these estimates. The leaves remaining consist of leaf petioles with attached leaf blade fragments of indeterminable length and width.

Log blade area and log blade dry weight equations perform much better for a late browsing, probably because leaves have become mature and the petioles, for the most part, have stopped growing. I did find statistically significant differences between (\bar{t}_1/\bar{T}_1) and (\bar{w}_1/\bar{W}_1) in the late browsed sample of red maple and red oak, and between (\bar{t}_1/\bar{T}_1) and (\bar{a}_1/\bar{A}_1) in quaking aspen and white oak. However, except for red maple calculated on a dry-weight basis, these differences may be small from a practical standpoint.

Small differences are to be expected when the equations are used, in light of my analyses of covariance, in which I found significant differences in the intercepts of the log dry weight and the log blade area prediction equations among trees within locations for all four species. Accordingly, it

would be better to use the log blade dry weight and log blade area prediction equations, which are derived from data from several trees, to estimate the combined defoliation of many trees. Collection of leaf samples very soon after browsing, before the leaves grow much, would probably facilitate use of blade petiole relations for estimating defolia-

tion early in the growing season. The alternative to using the equations is to guess the quantity of tissue removed or remaining.

LITERATURE CITED

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