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Foliage Weight Distribution in the Upper Crown of Balsam Fir

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Abstract

A model was developed to predict the weight of foliage at each age on a branch for a given whorl from undefoliated balsam fir (*Abies balsamea* (L.) Mill.). The normal weight of foliage by age classes can be compared to the weight of foliage remaining on a branch to estimate recent, annual defoliation by spruce budworm (*Choristoneura fumiferana* (Clem.)). One branch from each whorl was sampled in the top half of each of 22 balsam fir trees in New Hampshire and New Brunswick. The foliage was separated by age, ovendried, and weighed. A system of equations was developed to predict the total foliage weight of a branch from variables that would be minimally affected by defoliation. A ratio was developed to estimate the proportion of foliage by each age class on a branch using whorl number, needle age, and flowering effect. The estimates of total foliage weight on a branch and the proportion of each age of foliage were combined to estimate the weight of foliage for each age on a given branch.

INTRODUCTION

THE SPRUCE-FIR FORESTS of Maine and eastern Canada are periodically attacked by the spruce budworm (*Choristoneura fumiferana* (Clem.)). In the larval stages, this forest defoliator feeds primarily on the current year's shoots, buds, needles, and staminate cones of balsam fir (*Abies balsamea* (L.) Mill.) and to a lesser degree, the spruces (*Picea* spp.). When budworm populations are extremely high and the current year's foliage is depleted, the larvae will also feed on older foliage.

By removing the current year's foliage—a highly productive segment of a fir crown (Clark 1961)—the tree's photosynthetic base is reduced, resulting in a decline of tree productivity. While it is clear that increased levels of defoliation lead to decreased stem radial growth (Mott et al. 1957), it has proven difficult to relate defoliation and growth reduction in a quantitative manner. With continued epidemic budworm populations resulting in declining growth, present growth and yield data will overestimate forest productivity. If the forest manager is to make an informed decision on pest control and cutting regimes, he must be able to estimate declining spruce-fir volume growth due to budworm attack.

To relate defoliation to loss of bole volume growth, it is necessary to (a) establish the defoliation history of a small group of trees and (b) compare the growth of these trees to a standard for undefoliated trees. Conventional defoliation estimates are based on visual assessment, by broad categories, of stands of trees. Since small groups of trees are not identified in these surveys, a more specific measure of defoliation was needed for this study.

To estimate recent defoliation, we compared the distribution of foliage by age class in a defoliated crown with that in an undefoliated crown. A statistical model, based on tree characteristics that are minimally affected by budworm attack, was developed to predict the amount of foliage in each age class of an undefoliated tree and compare it with that of a defoliated tree. These year-by-year differences produce an annual defoliation index for the recent past.

This paper reports on the development of this model for estimating the age class distribution of foliage by weight on undefoliated trees and outlines the application of the model in an index of historic defoliation.

METHODS

Foliage samples were collected from 12 dominant-codominant trees during the last 2 weeks of June 1964, from Green River, New Brunswick, and from 10 dominant-codominants sampled during the third week in July 1977, from northern New Hampshire. Trees were selected from even-aged fir-spruce stands on well-drained upland sites that showed no indication of recent disturbance. The separation of samples by space (250 miles) and time (13 years) provided a data base that is not peculiar to one region or one short climatic period.

For each tree, total height, crown length, and the distance of each whorl from the top of the tree was measured to the nearest 3 cm; diameter at breast height (dbh) was recorded to the nearest 2.5 mm. A "normal" branch (one without deformities, insect attack, unusual branching, or under excessive competitive stress) was selected from each live whorl in the top half of the crown. This section of the crown contains the greatest proportion of new foliage and does not have the diversity of branching caused by stress from competing crowns. Sample branches were removed and the diameter measured at 2.5 cm from the bole of the tree. Each year's foliage was clipped, separated for each branch, ovendried, and weighed. The current year's foliage was not measured since needle growth was incomplete.

The combined data base, consisting of 251 branches from the top half of 22 balsam fir crowns, was:

Parameter	*Mean*	*Range*
Dbh (cm)	16.2	9.1 to 28.4
Height (m)	13.58	10.25 to 17.80
Crown length (m)	7.36	3.76 to 12.04
Whorls in full crown	24	16 to 35
Release age	46	36 to 60
Branch diameter (mm)	12	4 to 37
Branch foliage weight (g)	57.7	0.4 to 370.3
Density (stems/ha)	5,437	1,730 to 12,255

ANALYSIS

In order to predict the foliage weight on a branch by age, a three-step procedure was used. First, the total weight of branch foliage was estimated; second, the proportions of each age of foliage on a branch were determined; and third, the estimates of total weight and the ratios were combined to estimate the weight of each age of foliage on a branch for a given whorl.

A branch total foliage weight model

Combinations of independent variables, describing branch size and tree characteristics, were evaluated in a screening procedure to predict the total weight of foliage on a branch (Furnival and Wilson 1974). The independent variables used to describe branch size were: branch diameter, branch basal area, whorl age, and the distance of the branch from the top of the tree. Each variable has a positive, allometric relationship with foliage weight (Whitaker 1962; Loomis et al. 1966). Tree variables such as total height, dbh, crown length and width, release age, and number of whorls in the crown were also screened. Relevant branch and tree interaction variables such as branch diameter x whorl age, distance of the branch from the top ÷ crown length, total height ÷ release age were tried in the initial models.

With data from the 251 sample branches from New Hampshire and New Brunswick, the model showed no significant differences for the data between the two locations. The foliage weight model is:

$$\log W_{ij} = 0.128 + 1.467 \log (D_{ij} N_{ij}) - 0.963 \log N_j \qquad (1)$$

where

W_{ij} = total weight of foliage on a branch from the i^{th} whorl on the j^{th} tree (g)

D_{ij} = diameter of the branch from the i^{th} whorl and j^{th} tree (mm)

N_{ij} = age of the i^{th} whorl on the j^{th} tree

and

N_j = total number of whorls on j^{th} tree.

Although the model, based on the pooled data, was highly significant with an R^2 of 0.95 and a $s(\overline{\log W})$ equals 0.023, equation (1) should not be used to predict the normal foliage weight on a tree defoliated by budworm. Continued defoliation could decrease the diameter growth of a branch, thus a model was needed to predict normal branch diameter if no defoliation had occurred. The branch diameter model is:

$$D_{ij} = 8.896 + 3.148 L_{ij} + 0.229 DBH_j - 0.144 A_j \qquad (2)$$

where

L_{ij} = the length of the bole between the top of the tree and the i^{th} whorl on the j^{th} tree (m)

DBH_j = diameter at breast height of j^{th} tree (cm)

and

A_j = release age of the j^{th} tree.

The model was significant with an R^2 of 0.86 and a $s_{y.x}/\sqrt{n}$ equals 0.117.

A similar problem occurs in the branch diameter model since the distance of the whorl from the top (L_{ij}) can also be affected by budworm defoliation. The budworm often feeds on the terminal bud, eliminating or stunting the normal tree height growth, thus affecting the spatial arrangement of whorls in the crown. The data suggested that, on an undefoliated tree, the whorls are about equally spaced through the length of the crown and can be described in the form

$$L_{ij} = \beta\,(L_j/N_j)\,N_{ij} \qquad (3)$$

where L_j is the total length of the crown of the j^{th} tree (m).

The coefficient β was estimated for each tree. The mean of the β's (0.99) for the 22 trees was not significantly different from 1.0, therefore the coefficient was set equal to 1.0 in the model. The regular spacing of whorls in the crown indicates that terminal growth in defoliated trees, over the short term, can be estimated by predefoliation height growth.

The three models constitute a system of equations and the coefficients were estimated by two-stage least squares (Goldberger 1964). Distance of the i^{th} branch from the top of the tree was predicted from equation (3). The predicted distances (L^*_{ij}) were substituted for L_{ij} actual distances in the branch diameter model and the coefficients were recalculated. The last step was to substitute the predicted branch diameter (D^*_{ij}) for the actual branch diameter in the branch weight model.

Our simultaneous branch weight, branch diameter, and branch distance model is:

$$\log W_{ij} = -0.094 + 1.486 \log (D^*_{ij}\,N_{ij}) - 0.836 \log N_j \qquad (4)$$

$$D_{ij} = 8.290 + 2.751\,L^*_{ij} - 0.104\,A_j + 0.168\,DBH_j$$

$$L_{ij} = (L_j/N_j)\,N_{ij}.$$

The relationship of the branch foliage weight to tree variables that are minimally affected by defoliation was significant with an R^2 of 0.91, a $s(\overline{\log W})$ equals 0.031 and is shown in Figure 1 for various size crowns of a hypothetical tree.

Defoliation would also decrease bole diameter growth thus influencing the dbh of trees under budworm attack. Therefore "normal" dbh of a tree that has been defoliated must be estimated. Radial increments at dbh were available for the 10 New Hampshire sample trees. These data were used to evaluate the relationship between the last 5-year radial growth and the previous 5-year radial growth. The model used was

$$I_{1j} = \beta\,I_{2j}$$

where

I_{1j} = last 5-year radial increment at breast height on tree j

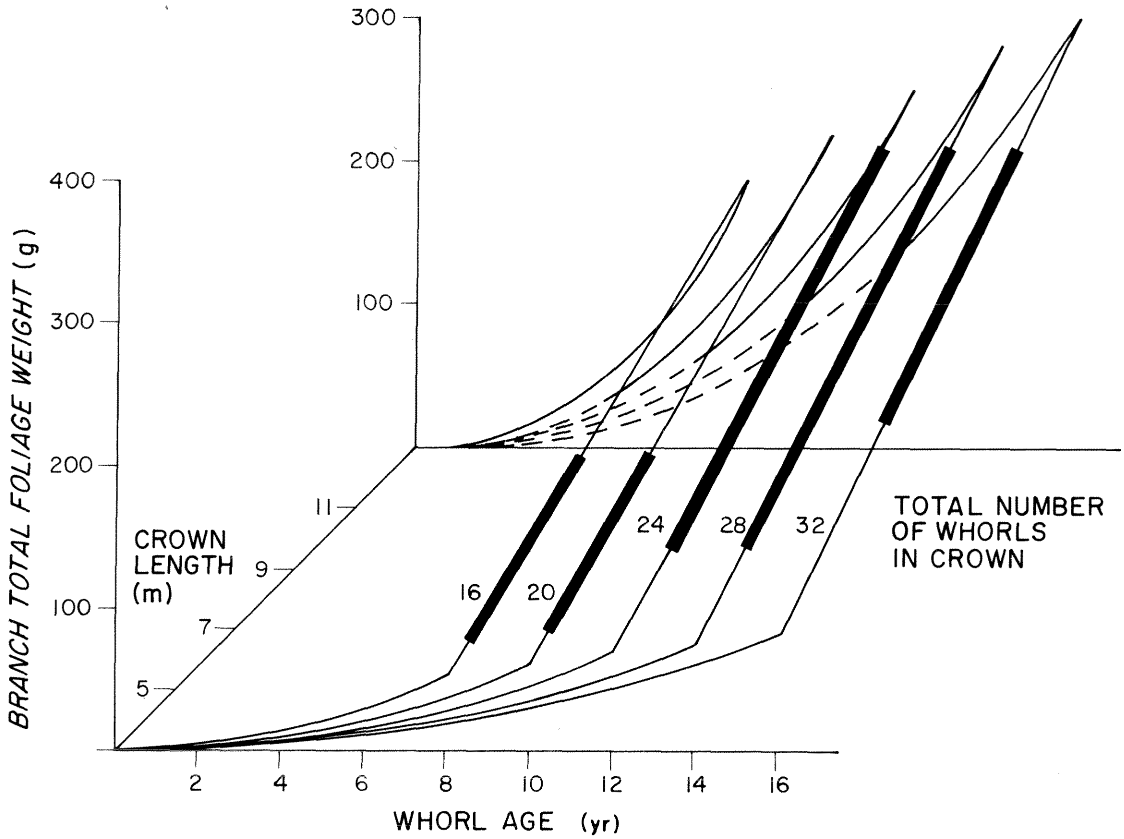
I_{2j} = previous 5-year radial increment at breast height on tree j.

The mean of the β coefficient (0.96) was not significantly different from 1.0. Therefore, the normal growth and hence normal dbh can be estimated from the radial growth increment prior to defoliation and the previous dbh.

Foliage age-class ratio

In order to create an index for estimating a 5-year annual defoliation history, the

Figure 1.—The weight of foliage on a branch by whorl age for the top half of various size crowns on a 45-year-old, 14-cm dbh balsam fir. The heavy lines indicate the range of crown lengths sampled.



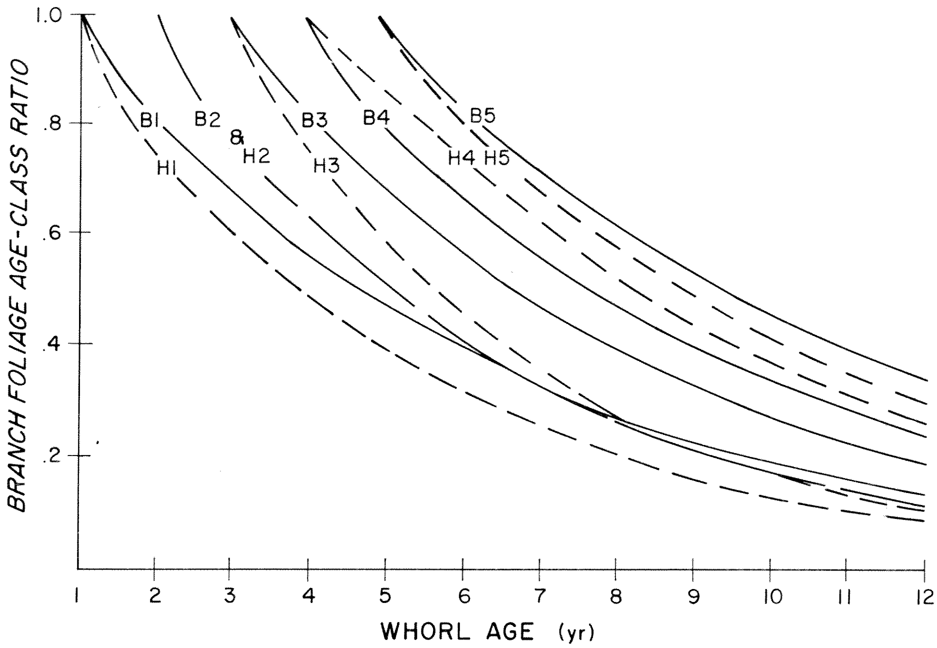
branch foliage weight must be separated into age classes. To predict the distribution of foliage by age, the weight of an age class of foliage was recoded as the ratio to the weight of foliage the same age and older. In this manner the foliage in each age class was predicted and then was not considered in the estimation of the older age classes. By definition, this foliage age-class ratio is equal to 1.0 when whorl age is equal to foliage age.

When the foliage ratio for each age class was plotted against the branch variables, a negative exponential relationship was evident. Whorl age proved to be the best branch variable predictor of the foliage age-class ratio for each age of foliage from the New Hampshire and New Brunswick trees (Fig. 2).

Differences in the relative position of the foliage ratio curves were evident between the two areas over the age classes and were found to be attributable to the periodic flowering of balsam fir. Every 2 or possibly 3 years, balsam fir produces a generous supply of cones which results in a decrease of foliage production (Morris 1951). Flowering records and the presence of cone scales indicated that the New Brunswick trees flowered concurrent with 2- and 4-year-old foliage production, while the New Hampshire trees flowered with 1-, 3-, and 5-year-old foliage production. The alternating pattern of age-class curves for New Brunswick and New Hampshire repeats this pattern of flowering (Fig. 2).

The foliage ratio data from both locations were combined and a single equation model, using whorl age, needle age, and a dummy variable to describe the effect of flowering, was developed. Flowering effect was added in

Figure 2.—Regression curves for the ratio of the weight of an age class of foliage to the weight of foliage the same age and older on a branch by foliage age and whorl age. The letter labels for each curve indicate the sampling location (H = New Hampshire, B = New Brunswick) while the number labels indicate foliage age.



the model both as an exponential and a linear term. The flowering effect term in the exponent reduced the sum of squares only slightly, and was dropped from the model. The linear term reduced the sum of squares by 8 percent over the model using whorl number and needle age. Needle age was also added to adjust the asymptote in the model and improved the fit by 14 percent. The remaining branch and tree variables only marginally reduced the residual sum of squares. Thus, the foliage age-class ratio model is:

$$P_{ia} = b + 0.858e^{(-0.265(N_{ij}) + 0.236(a))} + 0.075e^{(0.220(a))} \text{ for } a < N_{ij} \quad (5)$$

$$= 1.0 \text{ for } a = N_{ij}$$

where

P_{ia} = ratio of foliage weight in age class (a) to weight of foliage the same age and older on a branch from i^{th} whorl

N_{ij} = age of the i^{th} whorl on the j^{th} tree

b = 0.038 for nonflowering years and

= -0.012 for flowering years.

The model had an R^2 of 0.91 for the 968 sets of measurements.

Foliage weight by age

The branch total foliage weight and the foliage age-class ratio estimates can be used to predict foliage weight by age class on a given whorl. The predicted 1-year-old foliage ratio from equation (5) is multiplied by the predicted branch total foliage weight from equation (4) to estimate the weight of 1-year-old foliage on a branch. The remaining foliage weight is calculated by subtracting the predicted 1-year-old foliage from the predicted total foliage weight. Similarly the 2-year-old foliage ratio is estimated from equation (5) and multiplied by the remaining branch foliage weight to predict the weight of 2-year-old foliage. This process is continued until the weight of foliage in five age classes is estimated for a branch on a given whorl.

The procedure for predicting the weight of age (a) foliage on a branch from whorl (i) can be written as:

$$W_{ia} = P_{ia} \left[\prod_{k=1}^{a-1} \left(1 - P_{ik} \right) \right] W_i \qquad (6)$$

where

W_i = the total weight of foliage on a branch from the i^{th} whorl

and

$\prod_{k=1}^{a-1}$ symbolizes the product of the (a–1) variables within the parenthesis.

Total foliage weight per branch and the remaining foliage weight after calculating W_{ia} for each whorl and foliage age is depicted for a typical balsam fir in Figure 3.

DISCUSSION

A series of equations was developed to estimate (a) the normal weight of foliage on

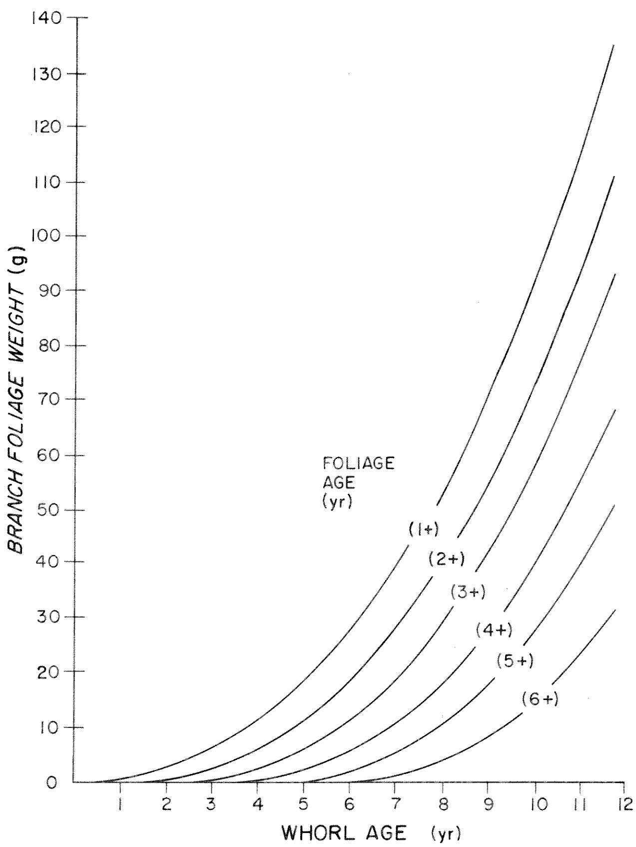


Figure 3.—The predicted weight of foliage for a given age and older on a branch from each whorl for the top half of a 45-year-old balsam fir (DBH = 14 cm; crown length = 7.0 m; 24 whorls in the crown; flowering with foliage aged 2 and 4).

whorl branches from the top half of balsam fir crowns and (b) the proportion of each age class of foliage on these branches. By combining these two estimates, the normal weight of foliage by age class on a branch can be compared to the weight of foliage remaining after budworm attack to estimate annual, historic defoliation for an individual tree. To use the normal foliage models as a standard in a defoliation index, it was necessary to relate branch foliage weight to tree variables that are minimally affected by the loss of foliage. However, when a portion of a tree's photosynthetic base is destroyed, the entire tree can be affected. Thus, to predict the normal total foliage weight on a branch for trees under budworm attack, models were developed to estimate branch diameter, bole height, and radial growth from predefoliation performance (equation 4). On the other hand, the proportion of each age class of foliage on a branch was readily estimated in a single equation by variables that are little affected by defoliation (equation 5).

The models developed between total branch foliage weight and tree variables indicate that dbh and release age are linearly related to branch diameter but exponentially related to branch foliage weight. This agrees with the exponential relationship between dbh and tree foliage weight noted by Kittredge (1944). Similarly, there is a negative, exponential relationship between release age and total foliage weight which has also been observed by Baskerville (unpublished data) in fir trees ranging in age from 30 to 85 years.

The models can be used as a standard for estimating historic defoliation and should be applied primarily to trees from good, upland sites. Nodal branches should be sampled through the upper crown of a defoliated tree, the foliage separated by age, ovendried, and weighed. Normal weights for each age of foliage are then predicted by equation (6) for each branch sampled. Predicted and actual foliage weights are summed for each age of foliage over all branches sampled on a tree and then compared. The difference between predicted and measured foliage for each of the five age classes is defined as the weight of needles destroyed by the budworm in the year when that age class was current foliage. The weight of foliage destroyed divided by the predicted foliage weight in each age class is the annual index of defoliation over each of the past 5 years.

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