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NEW DIMENSION ANALYSES WITH ERROR ANALYSIS FOR QUAKING ASPEN AND BLACK SPRUCE.

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ABSTRACT

Woods, K. D., D. B. Botkin, and A. Feiveson. New dimension analyses with error analysis for quaking aspen and black spruce.

Dimension analyses for black spruce (<u>Picea</u> <u>mariana</u> (Mill.) B.S.P.) in wetland stands and trembling aspen (<u>Populus</u> <u>tremuloides</u> Michx.) are reported, including new approaches in error analysis. Biomass estimates for sacrificed trees have standard errors of 1 to 3%; standard errors for leaf area are 10 to 20%. Bole biomass estimation accounts for most of the error for biomass, while estimation of branch characteristics and area/weight ratios accounts for error for leaf area. Error analysis provides insight for cost-effective design of future analyses. Predictive equations for biomass and leaf area, with empirically derived estimators of prediction error, are given. Systematic prediction errors for small aspen trees and for leaf area of spruce from different site-types suggest a need for different predictive models within species. Predictive equations are compared with published equations; significant differences may be due to species responses to regional or site differences. Results yield biological insight. Proportional contributions of component biomass in aspen change in ways related to tree size and stand development. Spruce maintains comparatively constant proportions with size, but shows changes corresponding to site. This suggests greater morphological plasticity of aspen (consistent with differences in predictive models), and significance for spruce of nutrient conditions.

NEW DIMENSION ANALYSES WITH ERROR ANALYSES FOR QUAKING ASPEN AND BLACK SPRUCE

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INTRODUCTION

Estimates of forest biomass and production are often necessary for ecological studies of communities and ecosystems and for good forest management. Biomass, leaf area, and production are most frequently estimated by dimension analysis. In this approach predictive relationships, derived from analysis of sacrificed trees, allow non-destructive estimates of biomass for standing trees. These relationships are typically fit by least-squares regression, using simply-measured dimensions as independent variables (Whittaker and Marks 1975; Tables 1 and 2).

Estimates of tree or stand characteristics obtained by dimension analysis are of limited scientific use, however, unless they include a valid variance. We required estimates of biomass and leaf area, with variances, for a cooperative study between NASA and UCSB examining the sensitivity of satellite-borne spectral sensors to forest leaf area index (LAI) and biomass density (LAI can be an important intermediate variable in estimating biomass or production by remote sensing). Calibrations of spectral data against ground-based estimates of biomass density and LAI can only be evaluated if the precision of these estimates is known, but valid statistical variances are rarely obtained.

Our study area is in the Superior National Forest, near Ely, MN, USA, in the transition between northern hardwood-pine and boreal forests. We chose study sites in pure stands of trembling aspen (*Populus tremuloides*) and lowland black spruce (*Picea mariana*). These species represent ecological contrasts; aspen is an early-successional angiosperm of upland sites, while black spruce is a conifer which, in the bog sites studied, can be regarded as mid- to late-successional. Both are widespread in North American boreal forests. An extensive literature presents many dimension analysis relationships for these species (summarized in Tables 1 and 2), but these, for several reasons, did not meet our needs.

First, existing studies do not provide satisfactory variances for leaf area or biomass estimates for sacrificed trees, or of estimates of stand LAI and biomass density. Estimators for the variance of predicted biomass or leaf area for standing trees are sometimes given, but generally involve untested assumptions about error distributions (most are related to the "error of estimate" of Whittaker and Marks (1975), which is a function of the standard error of the dimension analysis regression).

Second, dimensional relationships have been shown to be locality-specific due to genetic variation and morphological plasticity (Alban and Laidly 1982; Green and Grigal 1978; Pastor, et al. 1983; Johnston and Bartos 1977). Although several studies were done in Minnesota and adjoining states and provinces, these generally did not provide estimators for leaf area or applied only to a limited range of tree sizes.

Finally, most studies are based on relationships between logarithmically transformed variables. Biases inherent in predictions from these models can be corrected only if stringent distributional assumptions are met, and estimation of variance for predictions is very difficult. We wished to work with more statistically tractable models and to test particular independent variables which might have geometric or allometric relationships with leaf area and biomass.

Our results are of both methodological and biological significance. We found coefficients of variation in biomass estimation to be 1-3%, but frequently as high as 20% for leaf area. In both cases, estimates tended to be less accurate for small trees. We present new equations for the estimation of leaf area and biomass, with variances, for aspen and black spruce trees, with empirically-derived variance estimators. Separate evaluation of variances associated with each stage of our analysis offers new insight into the most effective ways for improving procedures and estimators; for example, improvement of biomass estimates requires more accurate estimates of bole biomass, while leaf area estimates may be improved by more accurate estimation of green weight:area ratios or by more intensive within-tree sampling. We discuss practical tradeoffs in achieving improved estimates. Predictions using our dimension analysis equations are compared to those using other published equations.

Differences between the two species in variance distributions and in dimensions proving to be the best predictors may be associated with ecological and morphological differences. Our results suggest that aspen trees are more morphologically plastic than spruce trees. Variability in dimensional relationships appears to be largely a function of age and perhaps stand density for aspen, while spruce also respond to physical site characteristics.

METHODS

Figure 1 presents a schematic outline of our data set and analytic procedures. For each sacrificed tree, green weights of sub-components (leaves, current extension growth, woody portions) were measured for a sample of branches and related to branch dimensions. Oven-dry weights (105° drying temperature) were obtained for samples of each component. This allowed estimates of dry weights for all branches. Total branch biomass and bole biomass were summed to give total tree biomass. Leaf area estimation followed similar procedures. Variances were calculated at each stage of estimation.

Estimates of biomass and leaf area for whole trees were used to fit and compare various regression models using tree dimensions as independent variables, and formulas for variance of predictions of leaf area and biomass of standing trees developed. A detailed statistical treatment of our approach is given for the particular case of aspen leaf area in Feiveson and Chhikara (1986). We present a simplified digest of statistical methods, generalized to treat both biomass and leaf area for both species.

Field and Laboratory Procedures

Selecting and Felling Trees: Sample size and diameter (at breast height) distribution for the sample were set in advance to take into account 1) the greater effect of large trees on the regression equations and 2) the much greater time required for processing large trees. Diameter classes were established by dividing the range of diameters encountered into five equal intervals. The distribution of sampled trees for each species was initially set at 5,6,6,7, and 6 trees in the smallest through largest classes for a total of 30.

Ten pure stands of > 0.5 ha each of lowland black spruce and trembling aspen were selected to cover the range of age and density seen in the study area. In each stand eight live trees were arbitrarily selected without regard to condition. Selection was constrained to include only trees falling in unfilled diameter classes. Three of the eight trees were randomly selected for sacrifice. The distribution over diameter classes of sampled aspen trees was 9,5,7,7,4 for 32 trees (additional trees in the smallest class were sampled to check seemingly anomalous results). The distribution of sampled spruce trees was 6,7,7,7,4 for 31 trees.

Tree-level measurements (independent variables for dimension analysis) included diameter at breast height (dbh), height to first live branch, and total height (the difference between the last two measurements gives crown depth). The felling cut was made as close as possible to the ground. Detached branches were collected and reassembled as fully as possible.

Crown Measurements: Crowns were stratified by dividing the crown (from tree top to lowest live branch) vertically into three equal sections. All branches were numbered and detached and the following were recorded: branch height of attachment; diameter at base (above any basal swell); total length; length to first live secondary branch; and diameter at first live secondary branch. Lengths were measured in a straight line from point of attachment, not following the curve of the branch. Three to seven branches from each stratum were sampled randomly for additional measurements.

For sampled aspen branches all leaves, with petioles, were plucked and weighed in the field. Plucked leaves were pooled by stratum and a grab sample of around 200 leaves was taken for each stratum, weighed, and carried in plastic bags to the laboratory where total leaf area was measured with a Licor leaf area meter. This work was completed within several hours of felling; tests showed changes in weight and area were minimal over the time involved. Leaf samples were then dried for 24 h and weighed again. (Drying times for all components were determined by repeated weighing; drying was continued until weight loss stopped). All current-year extension growth (current twigs) was clipped from sampled branches, weighed by branch, pooled by stratum, dried for 24 h, and weighed again. Woody parts of each branch were weighed green in the field.

Removal of spruce needles from branches in the field proved impractical, so needle-bearing portions of sampled branches were separated and taken to the laboratory. Remaining woody portions were weighed in the field and a 10-cm long section was taken from near the base and weighed, dried for 48 h, and weighed again. Needle-bearing branches were separated into current year's growth and older sections and dried for 24 h. Needles fell of during drying and needles and twigs were separated and weighed for both age classes.

Projected leaf area for spruce was determined photographically. From each crown stratum a grab sample of seven twigs, bearing both old and current year's growth, was taken from unsampled branches in the field. These were wrapped in wet paper towels, sealed in plastic bags and shipped to Johnson Space Center in Houston where 21 needles each of new and older growth were photographed. The photographs were digitized and projected area determined. The accuracy of this technique was tested using segments of wire of known dimensions; for wires of size comparable to the needles, measurements were very accurate. Green and dry weights were also measured for each set of 21 needles. We found that needles packed in this way lost no weight and showed no detectable change in shape for at least two weeks.

For 10 aspen and all spruce trees all woody parts of one sampled branch from each stratum were dried for 48 h and weighed.

Bole Measurements: Boles were cut into sections small enough to be handled and sections were weighed in the field. Height above ground of bottom and top cut were recorded for each section. Four "disc" sections, 5-20 cm long, were cut from 1) the base of the bole; 2) half-way between the base and the first live branch; 3) just below the first live branch; and 4) half-way between the first live branch and the top of the tree. For each disc, diameter was measured with and without bark and bark and wood were weighed separately, dried 48 hrs, and weighed again.

Analytic Procedures: Estimating Biomass for Sacrificed Trees

Total above-ground biomass of a sacrificed tree, B, may be written

$$B = Bo + \sum_{i}(Br_i + Tw_i + Fo_i) \qquad [1]$$

where Bo is bole biomass, and Bw_i is biomass of wood, Tw_i biomass of twigs, and Fo_i biomass of foliage for branch i; all terms represent dry biomass. Thus, tree biomass is considered as the sum of two components -- total branch biomass and total bole biomass -- which were estimated separately for sacrificed trees. None of the variables in equation 1 was measured directly. Entire boles were weighed green, but these weights had to be converted to dry weights.

Other components were weighed only for sampled branches, and these were also green weights. For unsampled branches weights were estimated from regression equations. Procedures for estimation of total tree biomass were essentially the same for aspen and black spruce. Unless otherwise specified, measurement errors are assumed to be negligible in this and subsequent analyses.

Branch biomass: Branch biomass, the sum of foliage, twig (current year's growth), and wood biomass, was estimated by: 1) deriving dry weight:green weight ratios for components of sampled branches; 2) converting green to dry weights and summing these for entire sampled branches; 3) developing regression equations relating branch biomass to branch dimensions; 4) applying the regression equations to estimate biomass of unsampled branches; 5) summing estimated biomass for sampled and unsampled branches for total branch biomass for the tree; and 6) estimating mean squared prediction error (MSPE) for total branch biomass.

Ratio estimation: Single dry weight:green weight ratios were used for each species for woody portions of branches. Measured ratios varied little among branches and trees, and small sample sample size dictated this approach.

Measured green weight:dry weight ratios for aspen leaves and twigs were sometimes subject to significant measurement error due to small sample size. We attempted to reduce these errors by using "smoothed" ratios. These were estimated as sums of a least-squares approximations of tree and stratum (and, in the case of spruce needles, age) effects. The procedure is the same as that used by Feiveson and Chhikara (1986) for estimating aspen leaf area:weight ratios. For spruce, dry weights of needles by age class and twigs were measured directly for sampled branches, so no ratio conversion was required.

Developing branch regressions: Total dry biomass estimates for sampled branches were regressed on branch dimensions. Independent regressions were done for each tree. Of several regression models tested, that which proved generally most effective, as judged by variance explained and examination of residuals, was

$$y = aV + b(DC) + c(DC)2 + e \qquad [2]$$

where y is branch biomass (in grams), DC is branch "length of crown" or straight-line distance from base of first secondary branch to tip of branch, V is "volume" or basal diameter squared times branch length, a, b, and c are coefficients to be fitted, and e is an error term (which incorporates errors due to ratio estimation). The error term was judged, by of inspection of plots of branch biomass and dimensions, to have variance proportional to V, so regressions of y on DC and DC^2 were weighted by reciprocals of V's.

To improve predictive capabilities, all coefficients were constrained to be positive; negative coefficients entail a possibility of negative predicted branch biomass.

Consequently not all terms were included in predictive equations for particular trees. Seven sets of regression coefficients, in which all combinations of none, one, or two coefficients were set to 0, were estimated for each tree, and that with the lowest residual mean square and no negative coefficients was selected.

Estimation of total branch biomass: Total branch biomass for a tree (denoted by Br) was estimated as the sum of the biomass of all sampled branches plus the sum of the estimated biomass of all unsampled branches obtained by application of branch regression equations. The MSPE (Mean Square Prediction Error) for total branch biomass is estimated by

$$\widehat{\mathrm{MSPE}}(Br) = s^2\ [tr(W^{-1}) + x^T(X^TWX)^{-1}x] \qquad [3]$$

where s2 is the residual mean square from the branch biomass regression for the tree, W is the n x n weighting matrix (diag $(1/V_1 \ldots, 1/V_n)$, where n is the number of sampled branches), x is a column vector with elements equal to the sums of the three independent variables (V, DC, and DC^2) over unsampled branches, and X is the n x d matrix containing the values of d (1-3) chosen independent regression variables for the sampled branches.

Estimation of bole biomass: Bole biomass estimates were based on measurements of green weight and bole location measured for all bole sections and dry weights and diameters measured only for "disc" sections. Dry weight:green weight ratios for other sections were estimated as a function of diameter using the model

$$r_{ij} = a_i + b(z_{ij}-\bar{z}_{i.}) + e_{ij} \qquad [4]$$

where r_{ij} is the estimated ratio for section j of tree i, a (a tree-specific mean ratio) and b (common to all trees) are parameters estimated by least squares analysis, z_{ij} is diameter of section j (estimated from an assumption of constant taper between measured diameters), $z_{i.}$ is the mean of disc diameters for tree i, and e_j is an error term. The parameter b was taken as constant because initial inspection of data indicated that the slope of the relationship between diameter and ratio (presumably determined by proportions of bark, sapwood, and heartwood) was common to all trees. The estimator of a_i is the mean ratio for disc sections for tree i. For b, the estimator obtained by standard least squares was

$$\hat{b} = \sum_i\sum_j r_{ij}(z_{ij}-\bar{z}_{i.})/\sum\sum(z_{ij}-\bar{z}_{i.})^2 \qquad [5]$$

Thus, total bole biomass of the i'th tree is estimated as

$$B_o = \sum y_{ij} + \sum{}' x_{ij}[\hat{a}_i + \hat{b}(z_{ij}-\bar{z}_{i.})] \qquad [6]$$

where x's are section green weights, y's are dry weights for disc sections, the first summation is over disc sections only, and $\sum'$ indicates summation over non-disc sections only. The associated MSPE is estimated by

$$\widehat{\text{MSPE}}(\text{Bo}) = \widehat{\text{sig}}^2\sum{}' x_{ij}^2[1+1/N_i + (z_{ij}-\bar{z}_{i.})^2/\sum\sum(z_{ij}-\bar{z}_{i.}) \qquad [7]$$

where N_i is the total number of sections in tree i and $\widehat{\text{sig}}^2$ is estimated by the normalized sum of squares of residuals after fitting Equation 4.

Now, the total biomass estimate for the tree is given as

$$B = Br + Bo \qquad [8]$$

and its MSPE is estimated by

$$\widehat{\text{MSPE}}(B) = \widehat{\text{MSPE}}(Br) + \widehat{\text{MSPE}}(Bo). \qquad [9]$$

Analytic Procedures: Estimation of Leaf Area

The total leaf area of a tree may be written

$$A_{..} = \sum\sum A_{ij} \qquad [10]$$

where A_{ij} is the total area of the leaves on branch j in stratum i. A_{ij}'s were not measured directly; foliage weight for sampled branches was converted by ratios to area, and areas were estimated for unsampled branches using a regression model.

Statistical methods for estimating aspen leaf area and associated variance were, presented in detail for aspen by Feiveson and Chhikara (1986), were parallel to those for estimation of branch biomass. We present a brief overview and adaptations for black spruce.

Leaf weights for sampled branches were regressed, for each tree, against branch dimensions. Experimentation with various linear models showed depth of branch crown and depth of crown squared were the variables best explaining variation in branch leaf weight; addition of other variables did not significantly improve the regression. Weighted regressions were carried out separately for each tree using the model

$$y_i = b_0 + b_1 DC_i + b_2 DC_i^2 + e_i \qquad [11]$$

where y_i is foliage weight (green weight for aspen, dry weight for spruce) for branch i, b's are coefficients to be estimated, DC_i is depth of crown for branch i, and e is an error term. As in branch biomass estimation, the best subset of regression coefficients with no negative values was chosen for each tree. Reciprocals of branch depth of crown squared were used as weights (this weighting factor was chosen because scatter plots suggested that e, in equation 14, was proportional to DC^2). For spruce separate regressions were used for current year and older needles.

Measured and estimated foliage weights were summed within trees, strata, and, for spruce, age class and converted to leaf areas using ratios. As for foliage dry weight:green weight ratios, a least-squares based "smoothing" procedure was used to correct for measurement errors in area:weight ratios. For aspen tree and stratum effects were estimated. For spruce, the effect of needle age was also significant.

The estimator of MSPE for the tree-level leaf area estimate is complex, taking into account errors from estimation of area:weight ratios and in the fitting of branch-level regression models. The estimator and its derivation are given in full for aspen in Feiveson & Chhikara (1986).

Analytic Procedures: Selecting and Fitting Tree-Level Regression Models

Predictive equations to be applied to standing trees -- the final product of dimension analysis -- are obtained by using data for sacrificed trees to fit models relating dependent variables such as biomass or leaf area to simple dimensions. Models are generally fit by standard least-squares regression. Regression models used, including independent variables (dimensions), are however, quite variable and choices are critical. Many studies assume a particular model from the outset. Studies which examine alternative models usually select among them on the basis of the squared correlation coefficient (r2), but this is only appropriate if sampling is random from an underlying multivariate normal distribution -- an unwarranted assumption in this case. A few studies (Schreuder and Swank 1971; Crow and Laidly 1980) have compared this approach with a likelihood technique; the two approaches may produce different results.

The most frequently used model, often simply referred to as the "allometric" (not to be confused with the more general definition of "allometric" as referring to any dimensional relationship) relates dependent variables to some power of the independent variables. The allometric model is usually fit, by linear regression, in its logarithmic transformation (see Tables 1 and 2):

$$\ln Y = a + b \ln X \qquad [12]$$

where Y is the variable to be predicted (say biomass), X the tree dimension chosen as predictor, and a and b coefficients to be estimated. Additional independent variables may be incorporated, in this form, with additional linear terms. The logarithmic transformation reduces heteroscedasticity in dimensional relationships, but introduces a bias in the estimator which can only be corrected if a particular distribution (usually normal) of error terms is assumed (Baskerville 1972; Mountford and Bunce 1973; Beauchamp and Olson 1973). Madgwick and Satoo (1975) show that regression estimates thus corrected can retain a bias. The only other model used with any frequency is a simple linear model, incorporating one or more independent variables.

The independent variable most frequently used is diameter at breast height (dbh). Height is occasionally used, as are complex variables -- height times diameter squared, for instance. Models and independent variables used in published dimension analyses of trembling aspen and black spruce are summarized in Tables 1 and 2.

We chose to use linear models without logarithmic transformation to avoid assumptions about error distributions and to facilitate estimation of variance. We selected independent variables which we believed would be well-related to biomass and leaf area as a consequence of tree geometry and growth patterns. Diameter, or dbh, has been shown to be well-correlated with bole length or tree height (Berlyn 1962; Ek 1974), so diameter alone can be used to accurately describe bole volume and biomass. Since boles contain a large proportion of total, above-ground biomass many workers -- especially those interested in marketable timber -- have found dbh sufficient to estimate total biomass. In some studies, inclusion of tree height has improved estimation of total biomass (Tables 1,2). We also used an index of crown volume to more accurately estimate branch biomass and leaf area. Actual crown volume is the product of the square of crown width, crown depth, and some species-specific coefficient determined by crown shape. We did not measure crown width directly, but it is closely related to dbh (Ek 1974) which we used as a surrogate; thus our index is D^2C, where D is dbh C is crown depth. Only a few studies have used crown dimensions as independent variables for aspen; none are reported for spruce (Tables 1 and 2). Our list of potential independent variables, then, included dbh (D), height (H), bole volume index (D^2H), crown volume index (D^2C, where C is crown depth), and the squares and square roots of these variables.

We chose from among linear models using one, two, or three of these variables, with and without constant (y-intercept) terms (although models for very small trees should, presumably, pass through the origin, forcing through the origin may lead to poorer fit for larger trees). Choices of initial variables were made by inspection of data plots. Variables, including a y-intercept, were added to the predictive equations only if they caused a significant increase in the proportion of total variance explained -- that is, significantly improved fit to data from the sacrificed trees. Negative y-intercepts or coefficients were not permitted.

Models were fit to data from sacrificed trees using standard, unweighted least squares procedures. Since variances in biomass and leaf area were not constant over the size range of sampled trees -- both increased with tree size -- weighted least squares estimation would be preferred. However, the variance function is unknown and, with 32 data points, estimating weights from the data could seriously bias estimates of coefficients. Furthermore, in this data set, a weighted regression would give to small trees a very large effect on estimation of coefficients, and we wanted to retain accuracy for larger trees. Therefore, we used the unweighted estimates which remain unbiased.

Functions for evaluating uncertainty of biomass or leaf area predictions for standing trees were also developed. Rather than relying on error terms from the unweighted regression, as in most previous studies, these took the form of a power function of the the predicted value of the dependent variable, allowing heterogeneity of variance to be accounted for. Thus,

$$\widehat{\mathrm{Var}}(Y|X) = a\ E(Y|X)^b \qquad [13]$$

where E(Y|X) is a particular estimate of Y and a and b are parameters that were fitted by iterative analysis of empirical distributions of observed and estimated values. This procedure is described in detail in Feiveson and Chhikara (1986).

RESULTS

Tables 3 and 4 give summary statistics for the 32 aspen and 31 spruce trees sacrificed for this study. Leaf area and biomass are estimates obtained by the procedures described in Section 2. Biomass estimates and standard errors (estimated as square root of MSPE) are given for total and bole biomass; values for branches may be obtained by subtraction. Most of the tree-level variance is due to bole biomass estimation. However, since bole biomass is much larger than branch biomass, coefficients of variation (standard error/estimate) are much lower for bole than branch estimates. Figures 2a and 2b show proportional contributions to biomass of foliage, branch wood, and bole components as a function of diameter. Coefficients of variation for biomass estimates (Figures 3a and 3b) for both species were highest for small trees (up to 15%), declining rapidly with size and stabilizing at 1-3% .

Variance trends were similar for leaf area estimates, but values for the coefficients of variance were higher, ranging from 20% for some small trees, and declining to around 10% for large trees (Figures 3a and 3b). Variances of leaf area estimates were partitioned into portions due to estimation of area:weight ratios and due to regression estimation of leaf weights for unsampled branches (see Feiveson and Chhikara 1986). For aspen trees (excluding six trees for which all branches were sampled), of all sizes, the majority of variance, on average, is due to the estimation of leaf weights for unsampled branches. For spruce trees estimation of unsampled branch weights accounts for > 85% of total variance in leaf area estimates (>95% for most trees).

Ratios of green to dry biomass by component, leaf area to dry biomass (spruce), and leaf area to green biomass (aspen) are shown in Table 5. Extreme values for area to weight ratios tend to be those obtained for small quantities of leaves, where measurement and sampling error are both likely to be more important.

Dimension analysis equations for biomass and leaf area, with equations for associated variance estimates, are in Table 6. Different regression models produced the best estimators (i.e., explained the greatest proportion of mean square error) for the two species as well as for estimation of different components within species. Table 6 also gives coefficients of determination (r^2) and F-ratios, with degrees of freedom, for comparison of explained and residual mean squares. Figures 4a-4d show distributions of biomass and leaf area with respect to primary independent variables.

DISCUSSION

Our results provide both procedural and ecological insights. Our segregation of estimation error according to tree components and procedural source is unique and suggests the most effective ways for improvement of estimates and, consequently, of dimension analysis equations. Differences in results for the two species, and for different size classes within each species, appear related to biological differences.

Error Analysis and Procedural Implications

In general, standard errors for tree biomass estimates (Tables 3 and 4) were quite low (1-2.5% of biomass). Typically, most of the error in estimating tree biomass was due to estimation of bole biomass, even though coefficients of variation for bole biomass estimates were low. Standard errors for bole biomass for both species were functions of tree size, ranging from about 2.5% of bole biomass for the smallest trees to about 1% for the largest (Figure 3). This error is due predominantly to error in estimating dry weight:green weight ratios (Equation 4).

Errors in estimating branch biomass were a function of the accuracy of regression of branch biomass on dimensions for sampled branches (Equation 3). Low accuracy may be a consequence of poor estimation of coefficients (e.g., due to a small branch sample) or to inappropriateness of the regression model for some trees. Also, since branches were sampled randomly, the largest branches were sometimes not sampled, requiring extrapolation of regression relationships beyond the size range of sampled branches. Coefficients of variation for total branch biomass estimates were higher than those for bole biomass, ranging from <5% to about 15% for most aspen trees (c.v.s were higher for small trees) and from 5% - 20% for spruce (Figures 5a and 5b). Typically higher values for spruce are probably a consequence of much larger numbers of branches. Bole biomass c.v.'s are also slightly higher for spruce.

Standard errors for biomass estimates could be reduced by sampling more branches and by a sampling scheme that always includes the largest branches of the tree. However, decreasing coefficients of variation for branch biomass would have little consequence for error of the total tree biomass estimate since bole biomass accounts for most of the biomass of the tree. Biomass estimates could be more effectively improved by reducing variance of bole biomass estimates. Bole biomass estimates could be improved by improving the model by which bole section diameters are estimated and by increasing the number of bole "disc" sections for which both dry biomass is measured (in particular, a disc near the top of the bole would be valuable).

Standard errors for tree-level estimates of leaf area were much larger than those for biomass -- up to 20% total leaf area for both species (Tables 3 and 4). The main determinants of this error were (1) accuracy of estimation of leaf area to weight ratios and (2) accuracy of branch-level regressions for prediction of leaf weight (Feiveson and Chhikara 1986).

For aspen, error in leaf area estimation was about equally partitioned between these two sources, so reduction of either component could improve the tree-level estimate significantly. Ratios could most effectively be improved by increasing the number of leaves per stratum for area measurement. The largest coefficients of variation for leaf area were for small trees, probably primarily due to smaller leaf samples. Improvement of branch regressions could be obtained through changes in branch sampling scheme discussed above, and possibly by increasing number of branches sampled, but the increased effort would be greater than that for improving ratio estimation.

For spruce, on the other hand, nearly all of the error in leaf area estimation stems from the branch regression. Spruce trees bear many more branches than aspen (up to 400 on sampled trees, as opposed to a maximum of 60 for aspen), so the difference between species may be a consequence of a much smaller proportion of branches having been sampled. Because of this difference, improvement of ratio estimates for spruce would serve little purpose. Larger branch samples, however, would increase effort greatly, since branch sampling is more expensive in field time and effort than is leaf area measurement. Therefore, something like the observed apportionment of error may result from the most cost-efficient approach to spruce leaf area estimation, unless improved branch regression models could be developed.

Evaluation of Tree-Level Biomass and Leaf Area Predictors

In Figures 6a-6b, values of biomass and leaf area derived from our field measurements of sacrificed trees are plotted against values predicted by our dimension analysis equations. "Measured" and predicted biomasses for both species are nearly equal; the scatter for leaf area is much greater. Patterns of residuals (Table 7) suggest inadequacies of our models which may be rooted in ecological patterns.

Biomass appears to be consistently underestimated by our predictive equations for very small aspen trees, possibly due to forcing the regressions through the origin. Leaf area, on the other hand, is overestimated for small aspen trees. Systematic errors are not apparent, though, for larger aspen trees. These results suggest that separate models might be profitably used for small and large aspen trees. Although our sample size is too small for development of two regressions, the same effect is accomplished, to some extent, in our equation for leaf area; the first term is predominant for small trees because of the large coefficient, while the larger exponent of the second term causes it to dominate the estimate of leaf area for larger trees. Other studies have developed biomass estimators (but not leaf area) specifically for small aspen trees (2, 16, and 19 in Table 1), but it is unclear at what size a division should be made.

Predicted leaf areas for four spruce trees with the greatest measured leaf area were very low; all four are from unusually rich bog stands. Leaf areas tended to be overestimated for spruce trees of intermediate "true" leaf area, probably due to the leverage on the regression by the four high leaf area trees. Biomass, for small spruce trees, was overestimated; these trees were from stands growing on extremely poor sites. These results suggest dependence on site-quality of dimensional relationships in spruce. Moore and Verspoor (1973) and Parker et al. (1983) point out changes in morphology between types of upland sites and between upland and bog sites; our results suggest differences among types of bogs. Habitat-specific models might be appropriate, but it is not clear how the cut-off point between models should be determined. Our data set was too small to adequately fit separate models.

Of the many dimension analyses published for aspen and black spruce (Tables 1 and 2), the results of only a few can be directly compared to ours; most are for different regions or size ranges or estimate different variables. Four studies of aspen (6, 8, 10, and 22 in Table 1) in the upper midwestern United States and adjacent Ontario cover a size range comparable to that of our study and give estimators of total dry biomass; two of these offer leaf area estimators. For spruce only two studies are available for our study region (Schlaegel 1975b; Roussopoulos and Loomis 1979), size range is not given for the first and the second addresses only small trees, pools black spruce and white spruce (*P. glauca*), and incorporates trees from upland stands. Only one study, from Quebec, estimates spruce leaf area (Weetman and Harland (1964)l; we have not attempted comparison with our results, as areas estimated by Weetman and Harland are all-sided rather than projected. None of the studies examined offer detailed information on variance associated with estimates of leaf area or biomass for sacrificed trees. Estimators for variance of biomass or leaf area predictions for standing trees are sometimes given, but involve untested assumptions about error distributions.

Figures 6a-6c compare predictions of biomass and leaf area for our sacrificed trees, using predictors from our study and selected published studies, with our field-measured values. For aspen biomass, all predictors but that of Pastor and Bockheim (1981) significantly underestimate biomass for small trees (not visible in Figure). Predictions from Schlaegel (1975b) are significantly below measured values throughout. Other predictors give similar, and not notably biased, results for mid-size and large trees. Biomass estimators for spruce give more divergent results. Those of Ker (1984) and Ouellet (1983a) give good predictions for small trees while those from this study and Schlaegel (1975b) give underestimates. Predictions for larger trees are significantly below measured values for Schlaegel; Ker and Ouellet both tend to overestimate biomass for large trees. Aspen leaf area estimates show a broader scatter. Both predictors from the literature underestimate leaf area for small trees, but show no clear bias for larger trees. No leaf area predictors for spruce were comparable with ours.

Bias of a predictor for our data set does not necessarily imply that the predictor is inaccurate in the situation for which it was derived. Some divergence may be due to statistically inappropriate application of equations (i.e., for trees beyond the size range for which predictors were developed). In most of the cases in Figure 6, however, it is more likely that divergence is due to local variations in allometry or in different responses to habitat. Predictors for spruce biomass, in particular, were derived using trees from upland and bog stands and from different geographical regions. Again, the general implication is that predictors should be used only in circumstances similar to those for which they were derived.

Biological Meanings in Dimensional Relationships

The form of dimensional relationships (Table 6) and patterns of biomass allocation (Figure 2) show differences between species. In aspen trees the proportion of biomass in boles is greatest at intermediate sizes, while branch biomass proportion increases towards both extremes of size. Among spruce trees branch biomass remains a relatively constant proportion of the total over size after a decrease from the smallest sizes. (Foliage biomass proportion for both shows fairly constant trends and is, except for the smallest trees, a very small proportion of the total.) The high branch biomass proportion in small trees and its subsequent decrease in both species is probably a necessary consequence of supporting a sufficient canopy of foliage on a small bole. The differences between species may be due to greater plasticity of growth form of aspen and its early successional role. The proportional increase in branch biomass in large aspen may be a successional pattern. During early and mid succession aspen trees are generally in closed stands and crown expansion is limited by competiton with surrounding trees. The largest aspen trees sacrificed in this study were from later successional stands where the canopy had become more open due to senescence and death of some trees. Consequently, crowns were proportionally wider and more hemispherical than those in closed stands. Although spruce trees were selected from a wide range of stand densities and closure, crown shape apparently remained relatively constant, perhaps due to the more determinant growth form of conifers.

This reasoning is consistent with the differences between models which proved most successful in the two species for prediction of biomass and leaf area. Directly measured crown dimensions proved the best predictors of leaf area for aspen, and these variables also significantly increased accuracy in prediction of tree biomass. For spruce, however, crown dimensions did not significantly improve predictive power of equations based on whole-tree dimensions (diameter and height). Relations among dimensions of spruce trees are apparently sufficiently determinant that crown dimensions can be accurately predicted from diameter and height. Greater variability in aspen makes incorporation of crown dimensions desirable.

Patterns of residuals (Table 7), and dimension analysis equations suggest morphological differences among size classes within species. For aspen these differences are presumably ontogenetic; tree size, in our sample, is determined by age since nearly all trees were from even-aged stands. Other workers have found dimensional relationships for aspen to differ among site-types (Hocker 1982) and clones and/or ecotypes (Johnston and Bartos 1977), but we saw no clear suggestion of such variation. Differences in the allometry of spruce trees, on the other hand, appears to be a function of habitat. Small trees were from mixed-age, open bog stands and ages covered a wide range; large trees were from rich sites where canopies were closed and approximately even-aged. Trees of highest leaf area were from similar stands of tall, well-spaced, mature trees. Parker et al. (1983) suggest ecotypic variation between bog and upland black spruce, but it is unclear whether variation seen here is genetic or due to plastic response to site conditions and stand density.

The ratios in Table 5 show patterns consistent with ecological understanding. Leaf area:weight ratios decrease from higher to lower strata, while dry weight:green weight ratios show the reverse patterns. This pattern, also observed in aspen by Zavitkovski (1971) and Pollard (1972), is consistent with differences between broad, thin shade leaves and thicker, more rigid sun leaves. Spruce needles also showed an increase in density (i.e., a decrease in area:weight ratios) with age; this may be due to increasing concentrations of heavier structural compounds and resins.

SUMMARY AND CONCLUSIONS

Although many dimension analyses have been published, several for the species addressed here, this study offers advances in statistical procedures, including variance estimators that are free of some questionable distributional assumptions and analyses of sources of error which point to cost-effective means for improving estimates. Since our results support those of several other studies (Pastor et al. 1983; James and Smith 1977; Koerper and Richardson 1980; Moore and Verspoor 1973; Parker et al. 1983) showing that dimension analysis relationships are region-and habitat-specific and should be applied only within the size range of trees used to derive them, our estimators will also be applicable in some cases where no others are available.

Our results suggest that, for high estimation accuracy over all size ranges and site-types, single models are probably not appropriate for aspen and spruce. Some of our estimators are least accurate, and may be biased, for small trees. Design of future dimension analyses should take into account the probable need for separate models for young and old aspen. Part of such a study should be determination of the size or age where models should be changed. Separate models for different site conditions (e.g., stand nutrient or water regime as suggested by floristics or tree growth rates) may be appropriate for bog-grown spruce.

Our error evaluation, for each stage of analysis, allows more more objective assessment of the reliability of dimension analysis results. More importantly, we have shown that, by comparing particular sources of error, one may determine the most cost-effective procedural means of improving tree biomass and leaf area estimates and predictive equations. For example, we have suggested changes in branch sampling schemes, bole modeling, etc., which may be weighed against one another in light of their relative contributions to improved accuracy.

Finally, carefully conducted studies of dimensional relationships in trees can provide biological and ecological insight. For example, our results suggest that spruce and aspen differ in morphological plasticity. This difference might have further consequences in determining responses of these two species to competition or physical limiting factors.

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TABLE 1: PUBLISHED DIMENSION ANALYSES OF QUAKING ASPEN

	Study[1]							
	1	2	3	4	5	6	7	8
Location	Maine	N.Br., N.S.	Alb.	Minn.	Ont.	Wisc.	Minn.	Ont.
# Trees	14	20	49	50	26	50	25	132
Size range (dbh in cm)	5.8-9.8	0.2-4.1	4.5-33.0	**	*	2.7-29.1	*	**
Model[2]	AL	AL	A	L,AL	AL	AL	AL	AL
Component[3] Biomass Estimated	Bo,Br Rt,To	Fo,To	Bo,Br Fo,To	Fo+Tw	None	Bo,Ba Br,Fo To	***	Fo,To
Leaf Area	No	No	Yes	No	Yes	Yes	No	Yes
Indep. Variables[4]	D,H	D	D^2H,D H,C C/H	H,W^2 W^2C	D	D^2H DC	D	D
Drying Temp. (°C)	*	70	85	95	80	70	*	*

	Study[1]							
	9	10	11	12	13	14	15	16
Location	Maine	Minn.	Minn.	B.C.	New Br.	Utah, Wyo.	Ont.	Minn.
# Trees	30	491	10	19	15	20	36	28
Size range (dbh in cm)	1.0-16.5	5.0-33.0	*	10.0-60.0	0.0-20.0	3.0-36.0	10.7-24.0	0.5-1.75
Model[2]	AL	AL	AL	L	AL	****	L,AL	A
Component[3] Biomass Estimated	Bo,Br Fo,To	Bo,Ba To	Bo	Bo,Ba Br,To *****	Bo,To	Fo,Tw Br,Bo To	Bo,Br Fo,To	Fo,Tw Bo,To
Leaf Area	No	No	No	No	No	Yes	No	No
Indep. Variables[4]	D	D^2H	D^2H	D^2H	D^2H D,H	D	D^2H,D H,DH	D
Drying Temp. (°C)	*	103	105	*****	70	70	80	70

	Study[1]							
	17	185	19	20	21	22	23	24
Location	N.H.	N.Y.	Minn.	N.S.	Alb., Sask.	Wisc.	Alaska	N.H.
# Trees	128	31	27	46	279	9	144	34-80
Size range (dbh in cm)	0.3-14.7	*	0.5-3.3	1.8-33.3	2.0-31.0	14.7-39.7	0.5-8.2	0.3-15.0
Model[2]	AL	L	A	AL	AL	AL	AL	AL
Component[3] Biomass Estimated	To,Ba	Bo,To	Bo+Br Fo,To	Bo,Br Ba,Fo To	Bo,Ba Br,Fo To	Bo,Br Ba,Fo To	Bo,Br Fo,Tw To	Fo,Br Bo
Leaf Area	No	No	No	No	No	No	Yes	Yes
Indep. Variables[4]	D,H C/H	D,D^2, H,D^2H	D	D,H W,C	D^2H	D	D	D
Drying Temp. (°C)	70	*	105	105	*	60	70	85

	Study[1]			
	25	26	27	28
Location	Man., Alb.	Que.	Alb.	N.S., N.Br.
# Trees	60	133	*	200
Size range (dbh in cm)	<10.0->31.0	1.5-47.2	2.0-22.0	******
Model[2]	L	*****	AL	A
Component[3] Biomass Estimated	Bo,Ba Br,To	Bo,To	Bo,Br Fo,Tw To	Bo,Br, Fo,To
Leaf Area	No	No	Yes	No
Indep. Variables[4]	D,H,D^2 D^3,D^2H	D,H	D	D,H
Drying Temp. (°C)	103	105	90	*

[1] Studies are as follows:

1. Young, et al. (1964); 2. Telfer (1969); 3. Peterson, et al. (1970); 4. Peek (1970); 5. Pollard (1970); 6. Zavitkovski (1971); 7. Sando and Wick (1972); 8. Pollard (1972); 9. Ribe (1972); 10. Schlaegel (1973, 1975a); 11. Schlaegel (1975b); 12. Adamovich (1975); 13. Maclean and Wien (1976); 14. Johnston and Bartos (1977), Bartos and Johnston (1978); 15. James and Smith (1977); 16. Grigal and Ohmann (1977); 17. Goldsmith and Hocker (1978); 18. Monteith (1979); 19. Roussopoulos and Loomis (1979); 20. Ker (1980); 21. Bella and DeFranceschi (1980); 22. Pastor and Bockheim (1981); 23. Van Cleve and Oliver (1982); 24. Hocker (1982); 25. Singh (1982); 26. Ouellet (1983b); 27. Lieffers and Campbell (1984); 28. Ker (1984).

[2] L = linear; A = allometric; AL = allometric, logarithmic form;

[3] Fo=Foliage, Tw=Current Twig, Br=Branch, Bo=Bole, Bk=Bark, To=Total, Rt=Root

[4] D=Diameter (at breast height or, in some cases, 15 cm), H=Height, W=Width of Crown, C=Depth of Crown

[5] Species of *Populus* pooled

* Information not given.

** Only H given: range .79-3.65 m (study 4), 2.0-26.0 m (study 8).

*** "Crown weight" estimated: defined as foliage plus branches less than 2.5 inches in diameter.

**** Uses power function of D.

***** Estimators are for wet or green weight only.

****** Not given; range of D is 35.9 cm.

TABLE 2: PUBLISHED DIMENSION ANALYSES OF BLACK SPRUCE

	Study[1]						
	1	2	3	4	5[5]	6	7
Location	Que.	Que.	Minn.	Alaska	Minn.	Que.	N.Sc.
# Trees	20	22	10	36	25	15	49
Size range (dbh in cm)	6.0-17.0	2.5-15.0	*	1.4-12.9	0.5-3.3	1.0-15.0	1.6-33.8
Model[2]	AL	AL	AL	AL	A	AL	AL
Component[3] Biomass Estimated	Fo,Bo Br,To	To	Bo	Fo,Br Ba,Bo To,Co	Bo+Br, To,Fo	Fo,Co Br,Bo Rt	Fo,Br Bo,Ba To
Leaf Area	Yes	No	No	No	No	No	No
Indep. Variables[4]	D	D	D^2H	D	D W	D D^3,D^2H	D,H H,D
Drying Temp. (°C)	110	85	105	65	105	70	105

	Study[1]		
	8	9	10[6]
Location	Alb., Sask.	Que.	N.S., N.Br.
# Trees	60	734	200
Size range (dbh in cm)	<10.0->31.0	3.1-32.9	***
Model[2]	L	**	A
Component[3] Biomass Estimated	Br,Bo Ba,To	Bo,To	Bo,Br, Fo,To
Leaf Area	No	No	No
Indep. Variables[4]	D^2,	**	D,H
Drying Temp. (°C)	103	105	*

[1] Studies are as follows:

1. Weetman and Harland (1964); 2. Moore and Verspoore (1973); 3. Schlaegel (1975b); 4. Barney, *et al.* (1978); 5. Roussopoulos and Loomis (1979); 6. Rencz and Auclair (1980); 7. Ker (1980); 8. Singh (1982); 9. Ouellet (1983a); 10. Ker (1984).

[2] L = linear; A = allometric; AL = allometric, logarithmic form;

[3] Fo=Foliage, Tw=Current Twig, Br=Branch, Bo=Bole, Bk=Bark, Co=Cones, To=Total, Rt=Root

[4] D=Diameter, H=Height, W=Width of Crown, C=Depth of Crown

[5] Species of *Picea* (*P. mariana* and *P. glauca*) pooled.

[6] *Picea mariana* and *Picea rubens* pooled.

* Information not given.

** Uses power function of D and H, fitting exponents.

*** Not given; range of D is 36.6.

TABLE 3: DESCRIPTIVE STATISTICS FOR SACRIFICED ASPEN TREES.

DBH (cm)	HEIGHT (m)	CROWN DEPTH (m)	DRY BIOMASS (g)	STD. ERROR BIOMASS	BOLE BIOMASS (g)	STD. ERR. BOLE BIOMASS	LEAF AREA (cm2)	STD. ERR. LEAF AREA
0.9	2.2	1.8	132	2	83	2	4315	504
1.2	2.8	1.8	169	24	129	4	1829	282
1.4	3.2	2.0	257	9	197	8	3681	485
1.8	3.8	2.6	598	70	351	11	9093	1681
2.0	4.6	2.4	567	19	419	16	8546	1017
2.2	3.1	1.8	607	17	370	10	11218	2232
3.4	5.7	4.4	1909	38	1453	37	20329	1517
3.4	5.4	4.1	1937	60	1223	36	31875	4223
3.5	5.4	4.2	1532	30	1121	29	14059	1124
7.3	9.2	4.9	14346	621	10832	343	104078	18775
9.1	9.4	4.4	11250	313	9258	294	83114	11473
10.5	11.5	5.3	29413	966	24790	952	143226	14714
13.0	16.1	5.1	54487	1179	48272	1140	110107	12799
13.7	15.9	4.7	60834	1118	55455	1101	109691	12272
15.1	16.7	7.0	67338	1262	62863	1253	87924	8180
15.4	17.4	7.1	80391	1515	70555	1497	139376	10003
15.8	15.6	5.4	71016	1281	64234	1280	193882	15452
17.3	15.5	8.4	73013	1163	61756	1158	214423	16086
19.4	23.0	10.3	171922	2513	155230	2513	314396	22374
19.5	19.4	7.4	107218	1803	97045	1794	174606	15312
21.5	23.1	5.8	177286	2196	166542	2147	183795	22422
22.5	22.5	7.2	238477	3219	215043	2469	499317	55293
22.6	18.1	7.4	191768	2248	166592	2241	287096	20648
22.8	22.4	6.6	233178	2992	208481	2966	416032	39163
23.0	22.5	8.7	237964	3036	219828	3030	386747	24904
25.1	23.8	8.9	274652	3343	253794	3042	272000	28540
25.2	22.5	8.8	270826	3766	243271	3506	237089	48559
27.8	23.5	16.3	448440	6264	396826	5313	722894	79509
30.2	23.5	10.0	437032	5503	359388	3226	742009	83488
32.1	23.8	8.9	456140	4754	402129	4416	524909	80093
32.4	23.5	12.8	533888	5360	442562	4885	1020140	107477
35.4	22.5	11.5	559047	5050	433478	4290	1208025	132880

TABLE 4: DESCRIPTIVE STATISTICS FOR SACRIFICED SPRUCE TREES.

DBH (cm)	HEIGHT (m)	CROWN DEPTH (m)	DRY BIOMASS (g)	STD. ERROR BIOMASS	BOLE BIOMASS (g)	STD. ERR. BOLE BIOMASS	LEAF AREA (cm2)	STD. ERR. LEAF AREA
2.9	2.9	1.7	958	80	648	22	7873	1224
4.1	3.7	3.6	3541	332	1770	114	28206	5495
4.1	4.4	4.2	5252	619	2653	185	41854	18514
4.4	4.2	2.6	3287	227	2276	81	18620	2748
4.9	5.6	2.1	3720	449	3085	138	12195	2154
5.1	4.1	1.9	4389	223	3354	162	18602	1687
5.5	8.6	5.0	6242	448	4488	213	37878	4102
5.7	6.0	3.1	6178	561	4124	200	47458	2854
6.9	6.9	5.1	8869	442	6549	257	43460	6151
8.2	9.3	3.5	14610	796	12943	643	33439	5346
9.1	10.6	4.8	16968	1217	14820	732	55592	7219
9.2	11.7	3.4	19913	845	17722	623	48989	5897
11.0	12.9	5.1	35582	1207	29825	875	115176	12081
11.0	10.9	7.5	31188	1461	23352	956	109665	17454
11.5	12.6	7.6	43376	1767	33397	989	155916	14872
12.1	11.0	4.0	32545	1605	26362	867	94870	14027
12.7	14.7	7.7	45657	2627	40344	1102	72945	15341
14.1	11.9	9.4	53861	4158	40427	1424	152336	25252
14.3	13.9	7.8	60977	2439	46074	1548	324149	28043
14.4	13.1	7.5	52109	2382	43679	1228	116248	20117
15.6	14.4	8.0	59781	1913	53077	1354	63381	6412
15.6	13.1	8.1	62144	2264	53614	1358	115965	20770
16.4	11.8	8.5	70467	3186	45991	1500	441508	73562
18.1	19.9	8.7	133180	4717	117617	2701	206061	34412
18.9	18.8	8.4	128709	3860	113455	2245	234699	32942
19.0	14.2	12.4	114136	5035	78343	2402	426617	64383
19.6	14.7	10.5	114821	5202	92142	2397	290586	42746
20.2	14.6	12.4	128890	5305	96216	2443	245049	27308
20.8	15.3	7.3	104982	4430	91417	2362	144542	23571
22.8	17.5	10.1	137075	4062	117393	2424	234332	34967
23.0	20.0	12.5	204609	9661	163426	3176	459806	55340

TABLE 5A: DRY WEIGHT:GREEN WEIGHT RATIOS BY COMPONENT

	Aspen						Spruce
	FoliagebyStratum						
	Upper	Middle	Lower	New Twigs	Bole	Branch	Bole
Mean	0.462	0.460	0.433	0.518	0.548	0.529	0.540
Minimum	0.377	0.380	0.363	0.447	0.435	0.413	0.357
Maximum	0.689	0.673	0.630	0.710	0.644	0.700	0.672
Std.Dev.	0.078	0.073	0.067	0.045	0.041	0.051	0.060

TABLE 5B: SMOOTHED LEAF AREA:WEIGHT RATIOS BY STRATUM AND AGE CLASS

	Aspen (cm2/g green weight)			Spruce (cm2/g dry weight)		
				Current Year's Needles		
	Upper	Middle	Lower	Upper	Middle	Lower
Mean	49.226	52.039	52.929	40.810	42.458	45.093
Minumum	40.587	43.400	44.290	31.209	32.856	35.491
Maximum	70.729	73.542	74.432	48.689	50.336	52.972
Std.Dev.	8.589	8.589	8.589	4.548	4.548	4.548

	Previous Years' Needles		
Mean	33.952	35.599	38.234
Minumum	24.350	25.998	28.633
Maximum	41.830	43.478	46.113
Std.Dev.	4.548	4.548	4.548

TABLE 6: DIMENSION ANALYSIS EQUATIONS AND REGRESSION STATISTICS*

BIOMASS:

Aspen

$E(B|X) = 13.72\ D^2H + 14.07\ D^2C$

$r^2 = .997$ $F(2,30) = 4337$

$Var(B|X) = 172.08\ E(B|X) 1.15$

Spruce

$E(B|X) = 4609.55 + 18.14\ D_{2H}$

$r_2 = .969$ $F(1,29) = 910$

$Var(B|X) = 129170\ E(B|X)^{0.6}$

LEAF AREA:

Aspen

$E(L|X) = 3959.31\ (D2C)0.5 + .00295\ (D^2C)^2$

$r^2 = .958$ $F(2,30) = 352$

$Var(L|X) = 90.071\ E(L|X) 1.4$

Spruce

$E(L|X) = 4481.363\ D + 469.871\ D_2$

$r_2 = 828$ $F(2,29) = 70$

$Var(L|X) = .18325\ E(L|X)^2$

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* Variables in equations are: B = biomass, L = leaf area, D = diamter, H = height, and C = crown depth. All F-values are significant at $p < .001$.

TABLE 7: TREE-LEVEL PREDICTION RESIDUALS

Aspen:

Biomass (g)	Biomass Predicted (g)	Residual (g)	Leaf Area (cm^2)	Predicted Leaf Area (cm^2)	Residual (cm^2)
132	45	-87	4315	4751	436
169	91	-78	1829	6323	4493
257	152	-105	3681	8124	4443
598	288	-311	9093	11537	2444
567	388	-180	8546	12268	3728
607	328	-278	11218	11685	468
1909	1624	-285	20329	28341	8012
1937	1507	-429	31875	27098	-4777
1532	1614	83	14059	28238	14179
14346	10400	-3946	104078	64180	-39898
11250	15830	4579	83114	76143	-6971
29413	25617	-3796	143226	96715	-46511
54487	49339	-5148	110107	117815	7708
60834	53224	-7611	109691	119215	9524
67338	74539	7201	87924	165020	77096
80391	80308	-83	139376	170833	31457
71016	72398	1382	193882	150731	-43151
73013	99020	26007	214423	217166	2743
171922	173307	1384	314396	290844	-23552
107219	140540	33322	174606	233382	58776
177286	183899	6613	183795	224964	41169
238477	207921	-30557	499317	279607	-219709
191768	180017	-11750	287096	285555	-1541
233178	208035	-25143	416032	266639	-149392
237964	228057	-9907	386747	331085	-55662
274652	284170	9518	272000	387348	115348
270826	274665	3839	237089	388107	151018
448440	425879	-22561	722894	908975	186080
437032	423026	-14006	742009	626907	-115101
456140	465497	9357	524909	627255	102346
533888	527521	-6367	1020140	991580	-28560
559047	589618	30571	1208025	1087980	-120044

TABLE 7 (cont.)

Spruce:

Biomass (g)	Biomass Predicted (g)	Residual (g)	Leaf Area (cm^2)	Predicted Leaf Area (cm^2)	Residual (cm^2)
958	5052	4094	7873	16948	9075
3541	5738	2197	28206	26272	-1934
5252	5942	690	41854	26272	-15582
3287	6085	2798	18620	28815	10195
3720	7049	3329	12195	33240	21045
4389	6568	2179	18602	35076	16474
6242	9301	3059	37878	38861	983
6178	8146	1968	47458	40810	-6648
8869	10569	1700	43460	53292	9832
14610	16014	1404	33439	68341	34902
16968	20472	3504	55592	79690	24098
19913	22573	2660	48989	80998	32009
35582	32836	-2746	115177	106149	-9028
31189	28534	-2655	109665	106149	-3516
43376	34837	-8539	155917	113676	-42241
32545	33824	1279	94871	123018	28147
45657	47619	1962	72945	132699	59754
53861	47670	-6191	152336	156602	4266
60977	56171	-4806	324149	160167	-163982
52109	53885	1776	116249	161964	45715
59781	68179	8398	63381	184257	120876
62144	62440	296	115965	184257	68292
70467	62181	-8286	441508	199871	-241637
133180	122872	-10308	206061	235047	28986
128709	126430	-2279	234699	252540	17841
114136	97271	-16865	426617	254769	-171848
114821	107049	-7772	290586	268340	-22246
128890	112676	-16214	245049	282250	37201
104982	124685	19703	144542	296497	151955
137076	169633	32557	234332	346433	112101
204609	196051	-8558	459806	351633	-108173

Figure 1. Flow chart for data analysis. Box at bottom includes field data. Arrows upward show flow of analysis. Predictive equations are underlined. Other terms refer to predictions or estimates.

Figure 2. Proportion of total tree biomass by component. Proportions of total biomass of sacrificed aspen (A) and spruce (B) trees are plotted against diameter at breast height for bole (squares), branch (crosses), and foliage (diamonds) components.

Figure 3. Coefficients of variation for tree biomass (squares) and leaf area (crosses) estimates. C.V.s for sacrificed aspen (A) and spruce (B) trees are plotted against diameter at breast height.

Figure 4. Tree biomass and leaf area versus important dimensions. (A) Aspen biomass vs. tree volume index (D2H). (B) Aspen leaf area vs. crown volume index (C2H). (C) Spruce biomass vs. tree voume index. (D) Spruce leaf area vs. D2.

Figure 5. Coefficients of variation for component biomass. C.V.s for bole biomass (squares) and total branch biomass (crosses) are plotted against diameter at breast height for aspen (A) and spruce (B). Five low values of branch biomass C.V.s for aspen of 15-20 cm dbh are for trees where branches were censused, not sampled.

Figure 6. Biomass and leaf area predicted for sacrificed trees by dimension analysis equations from this and other studies, plotted against measured values. (A) Aspen biomass. (B) Aspen leaf area. (C) Spruce biomass. (D) Spruce leaf area. Values above diagonal are overestimates, those below line are underestimates. Squares always represent predictions by equations from this study. Other symbols are predictions using equations from other studies; numbers in legend refer to Tables 1 (for Figures A and B) and 2 (for Figure C).

FIGURE 1: FLOW CHART FOR DATA ANALYSIS

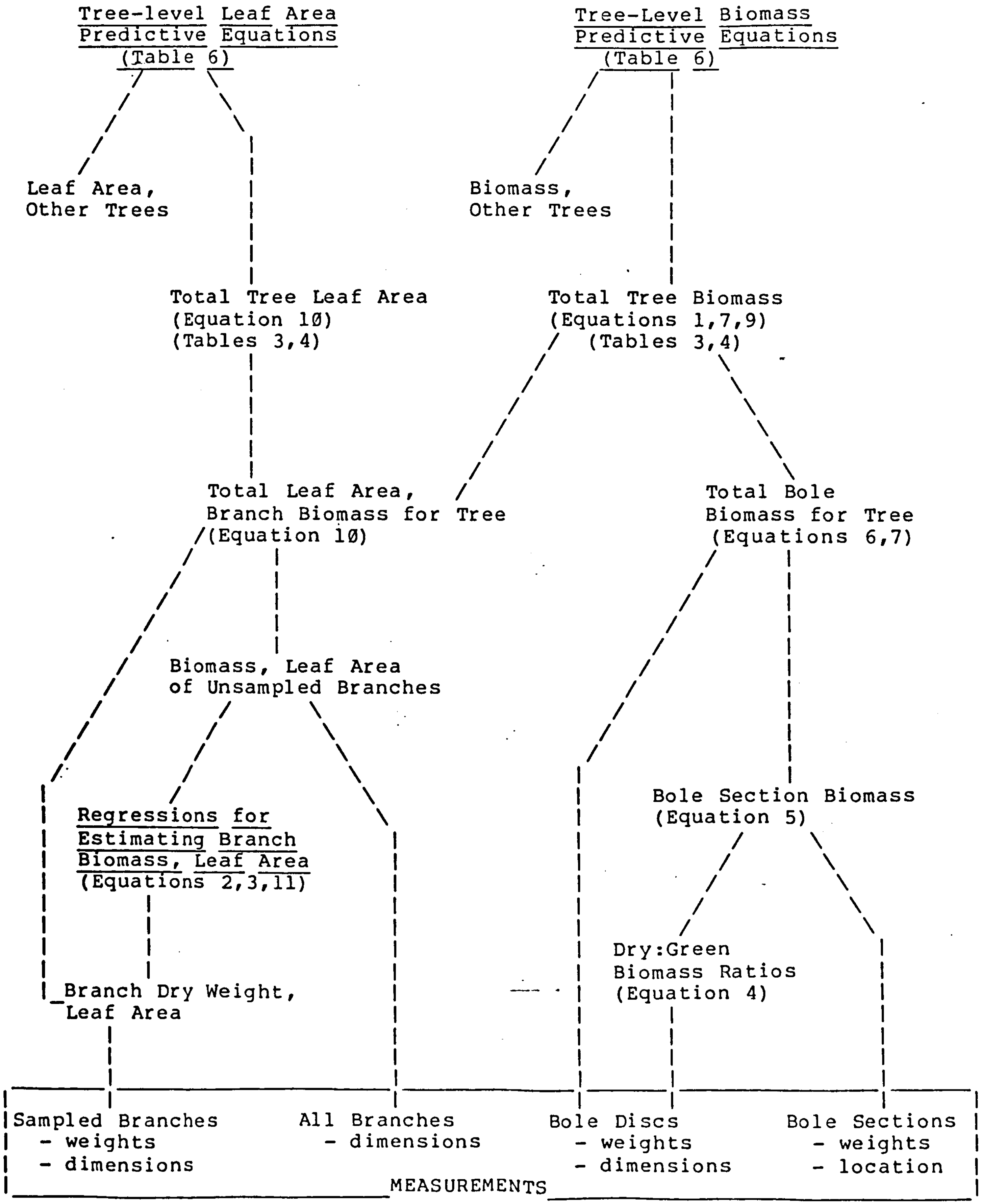


FIGURE 2A.

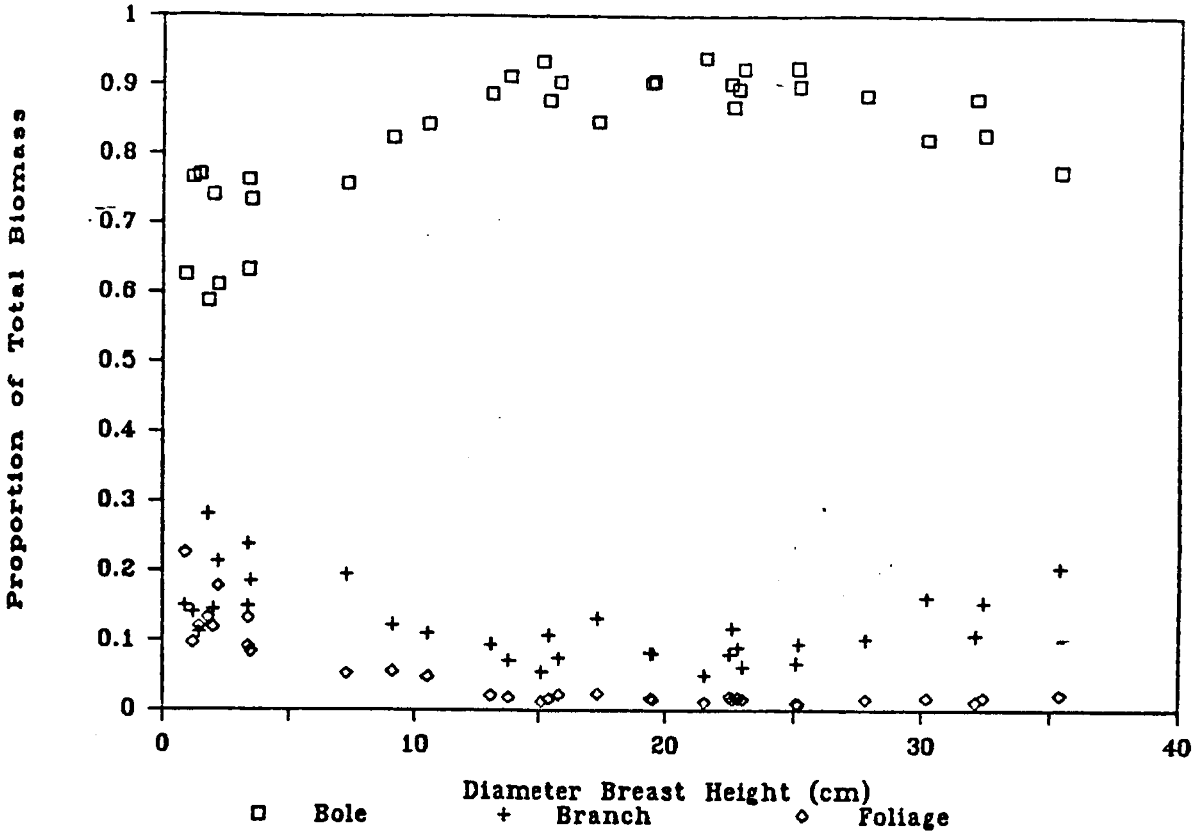


FIGURE 2B.

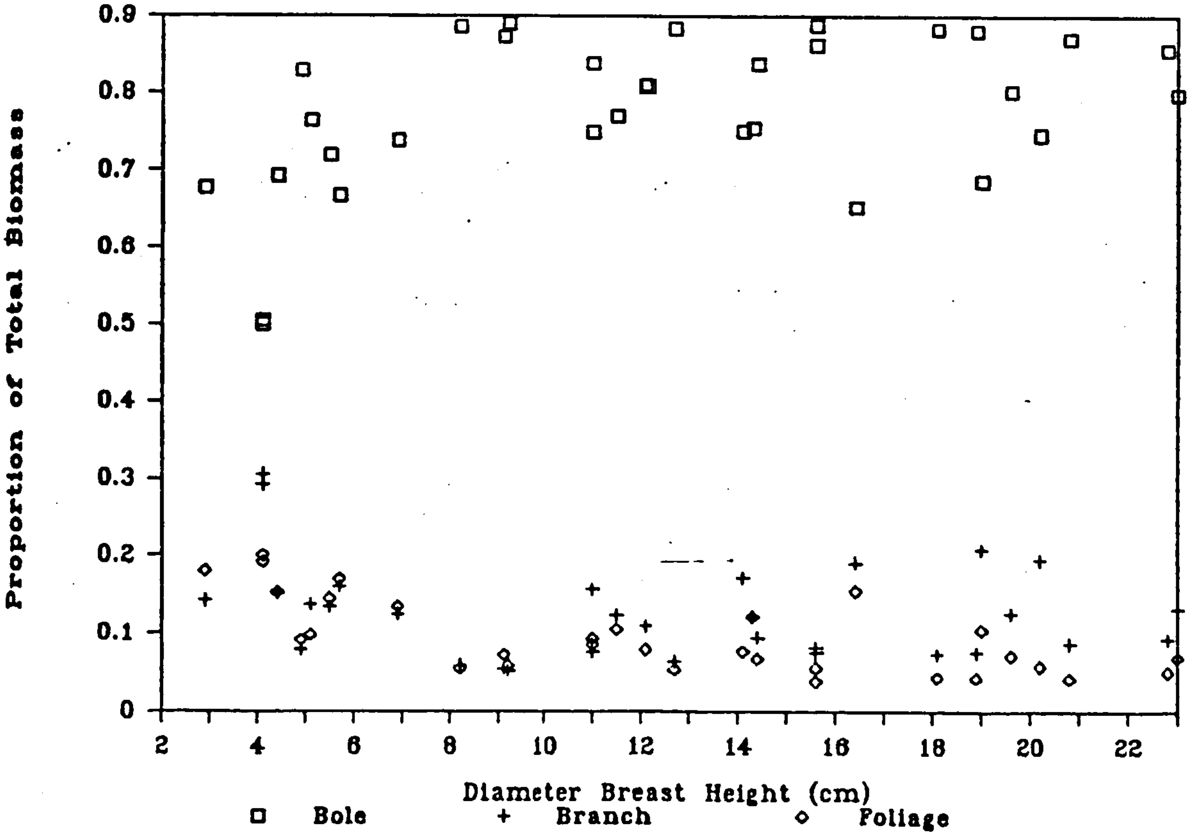


FIGURE 3A

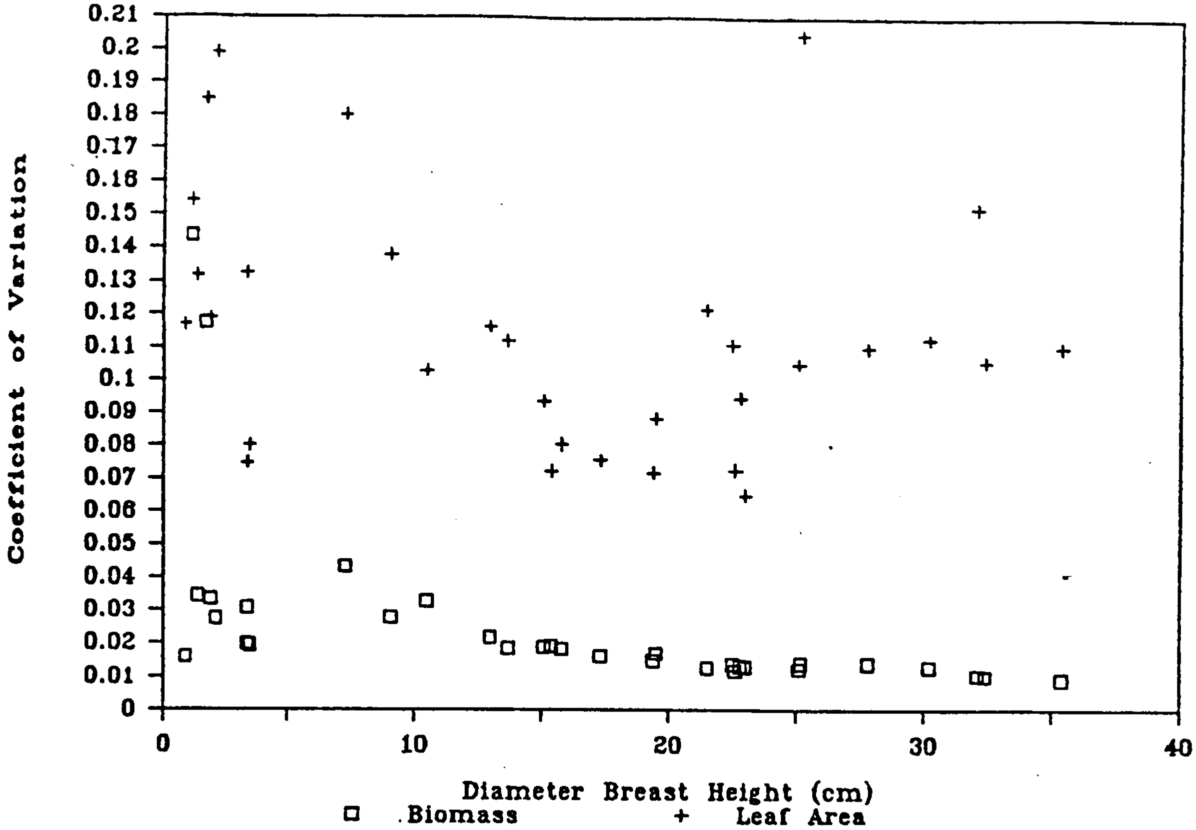


FIGURE 3B.

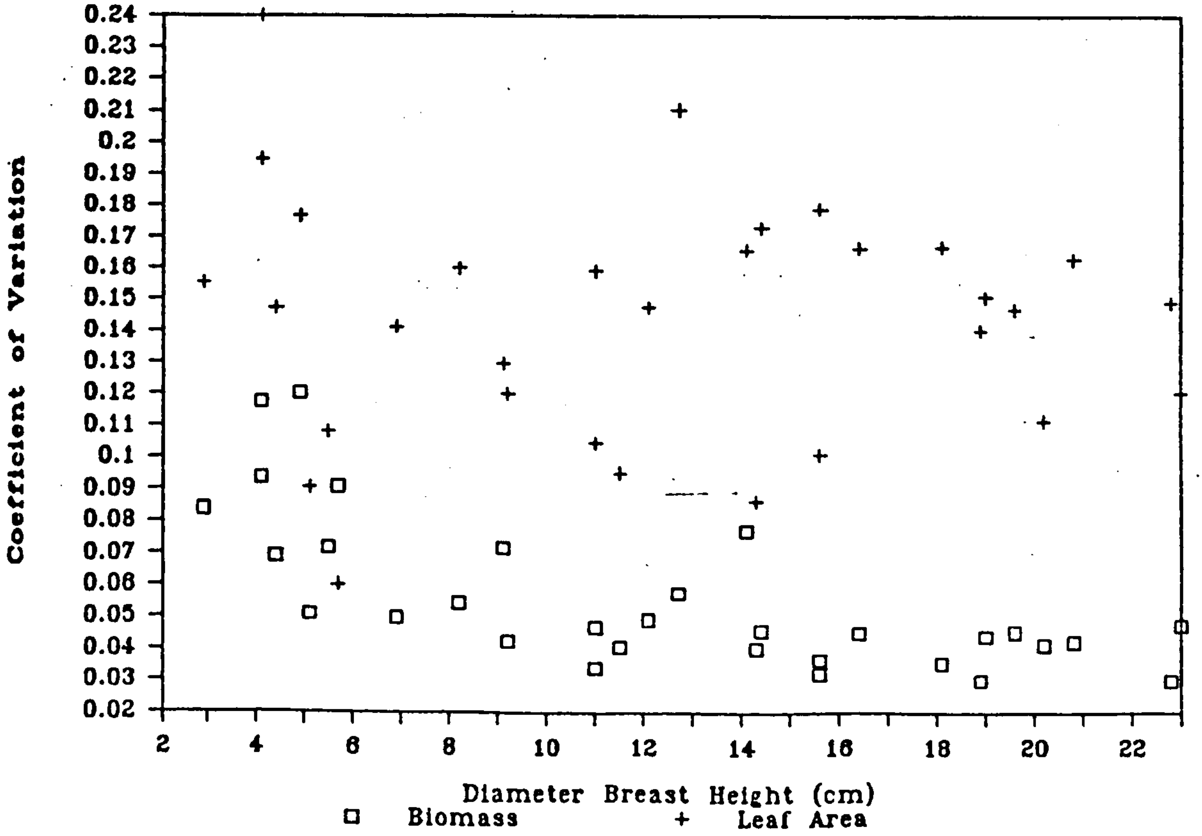


FIGURE 4A.

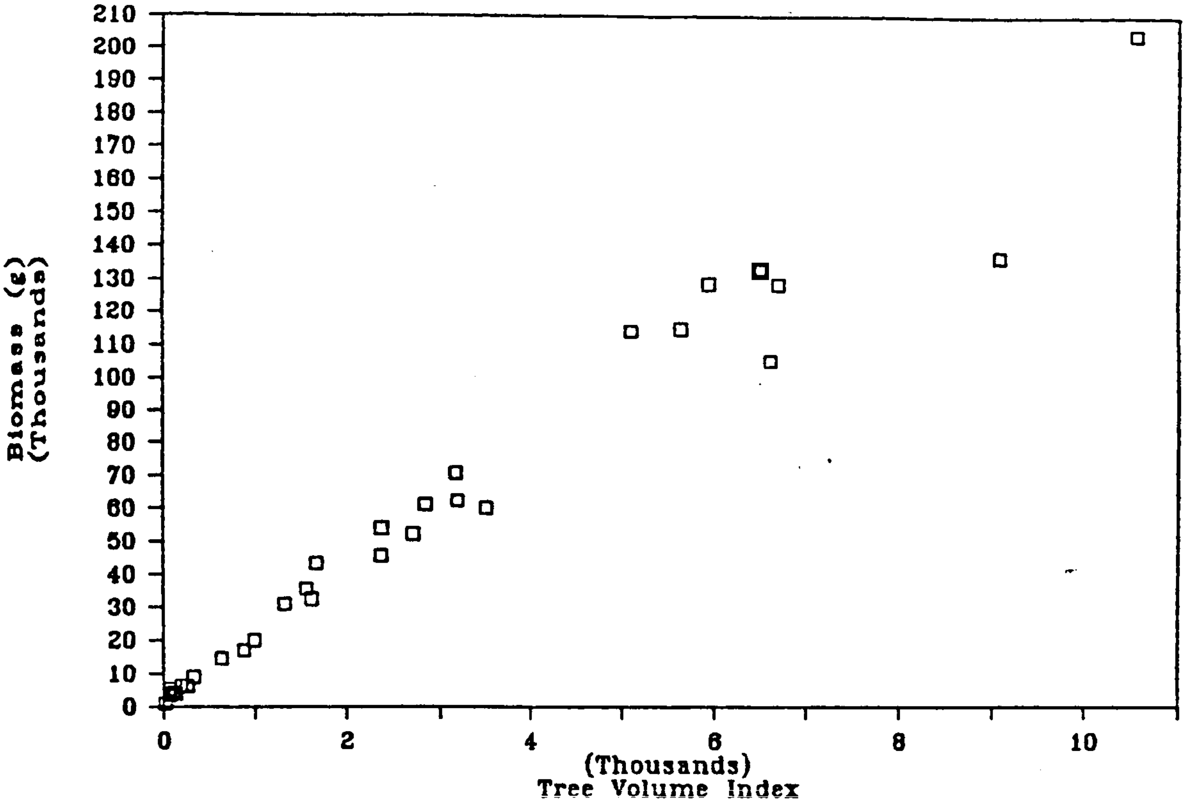


FIGURE 4B.

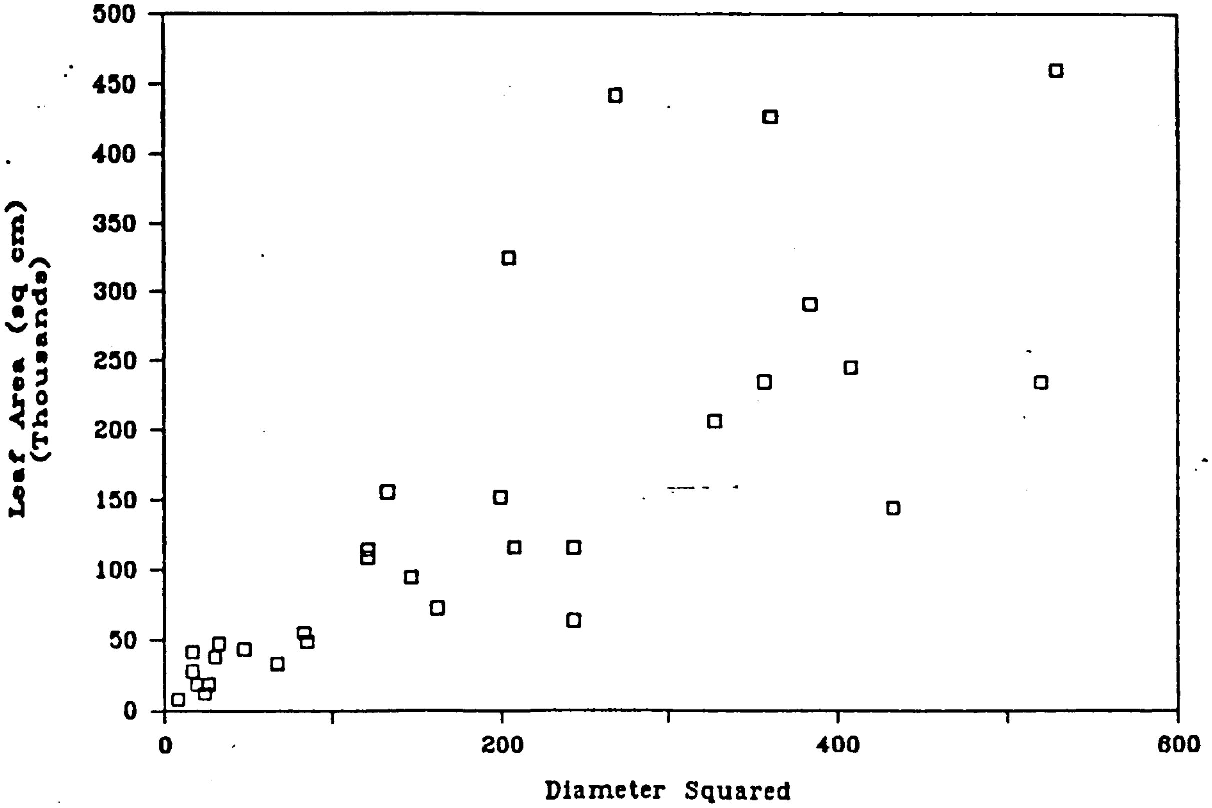


FIGURE 4A.

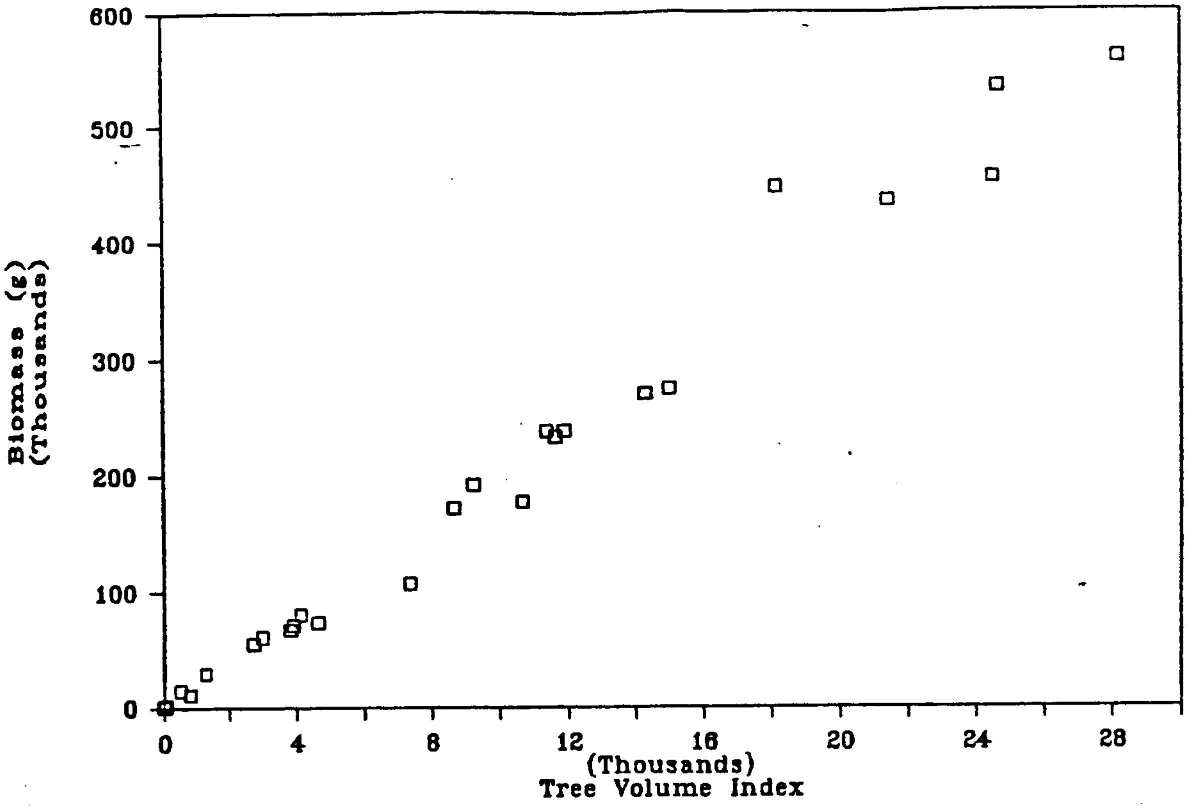


FIGURE 4B.

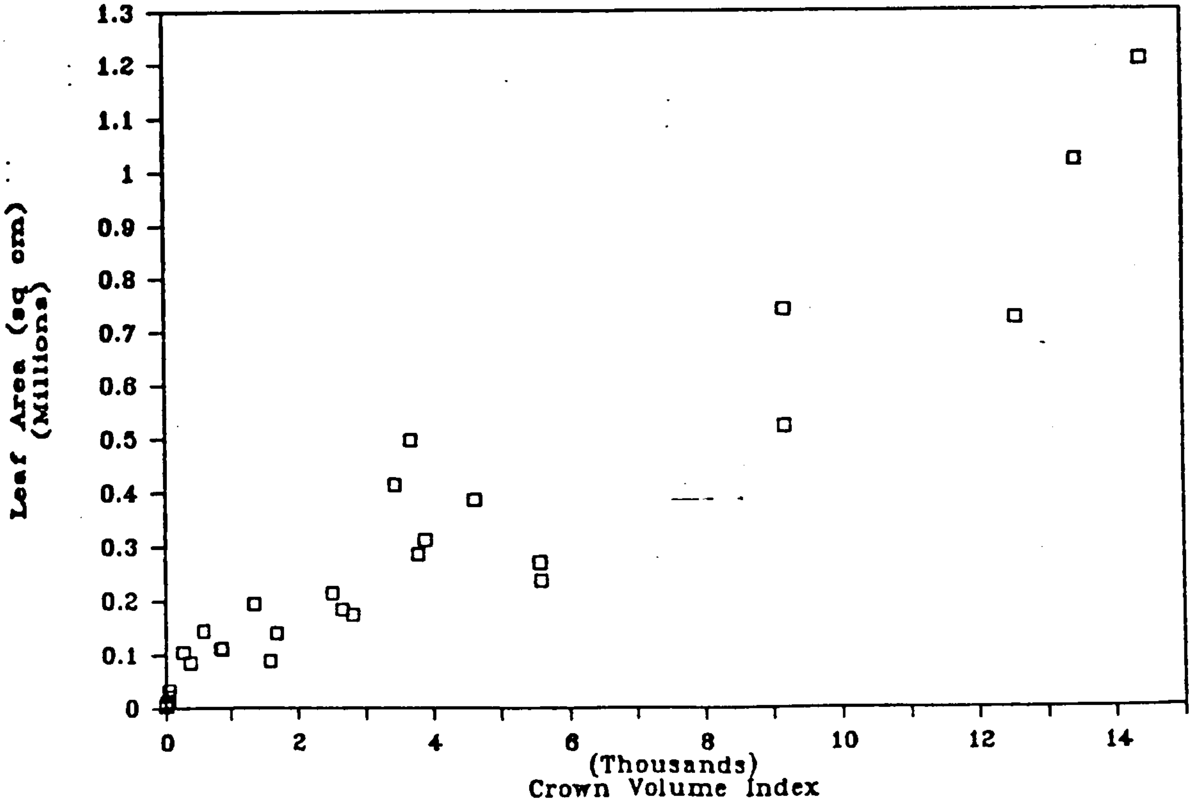


FIGURE 5A

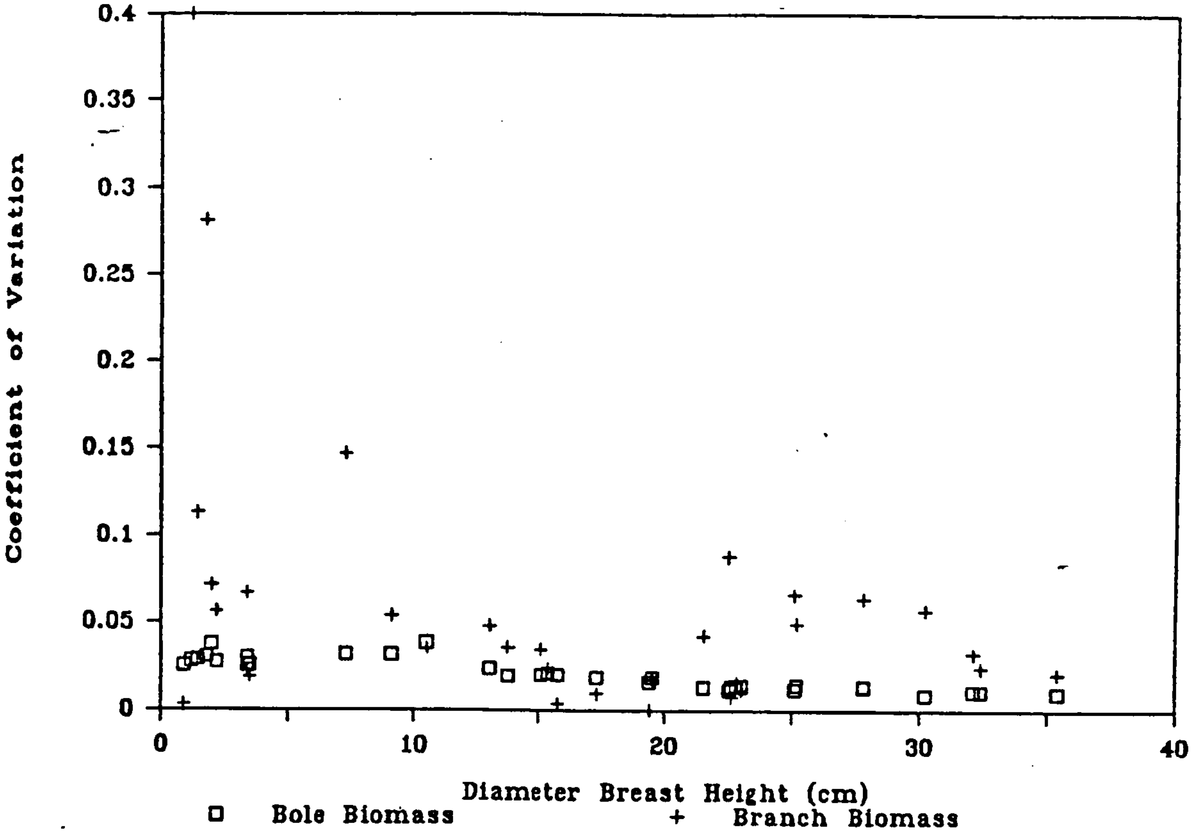


FIGURE 5A.

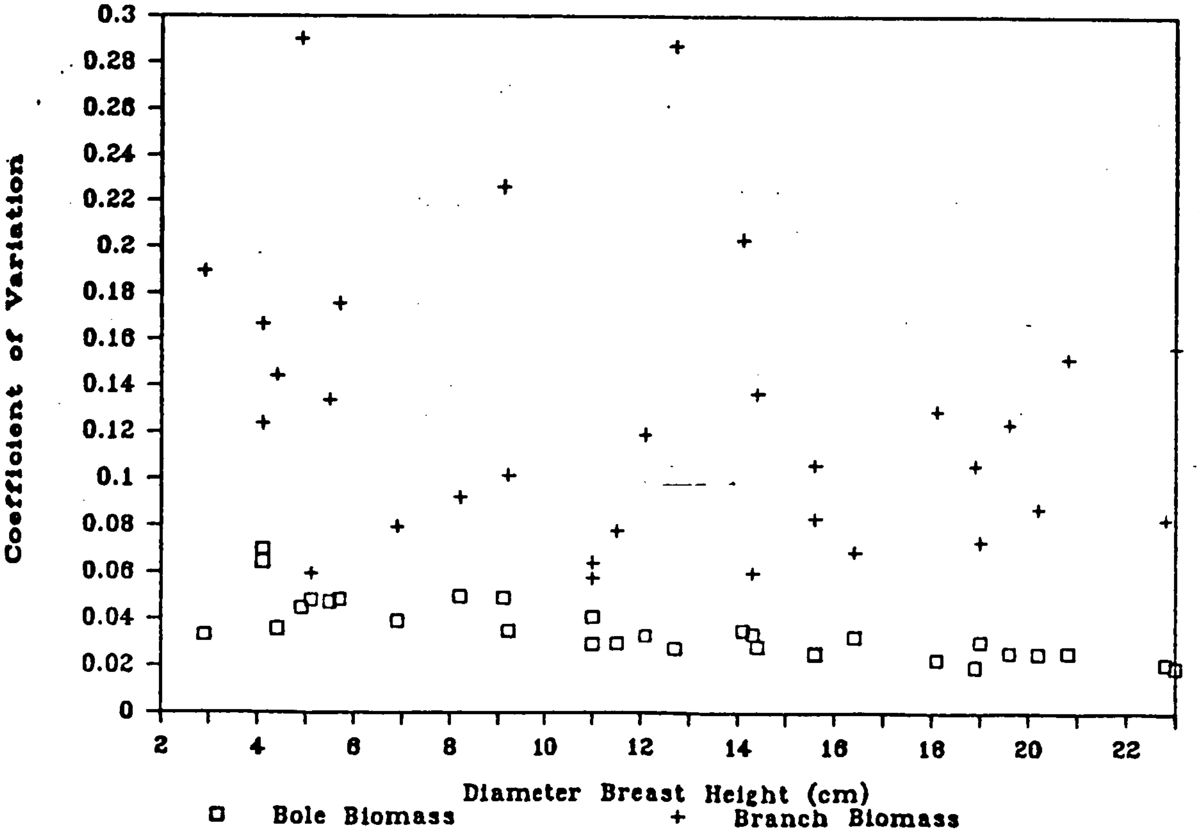


FIGURE 6A.

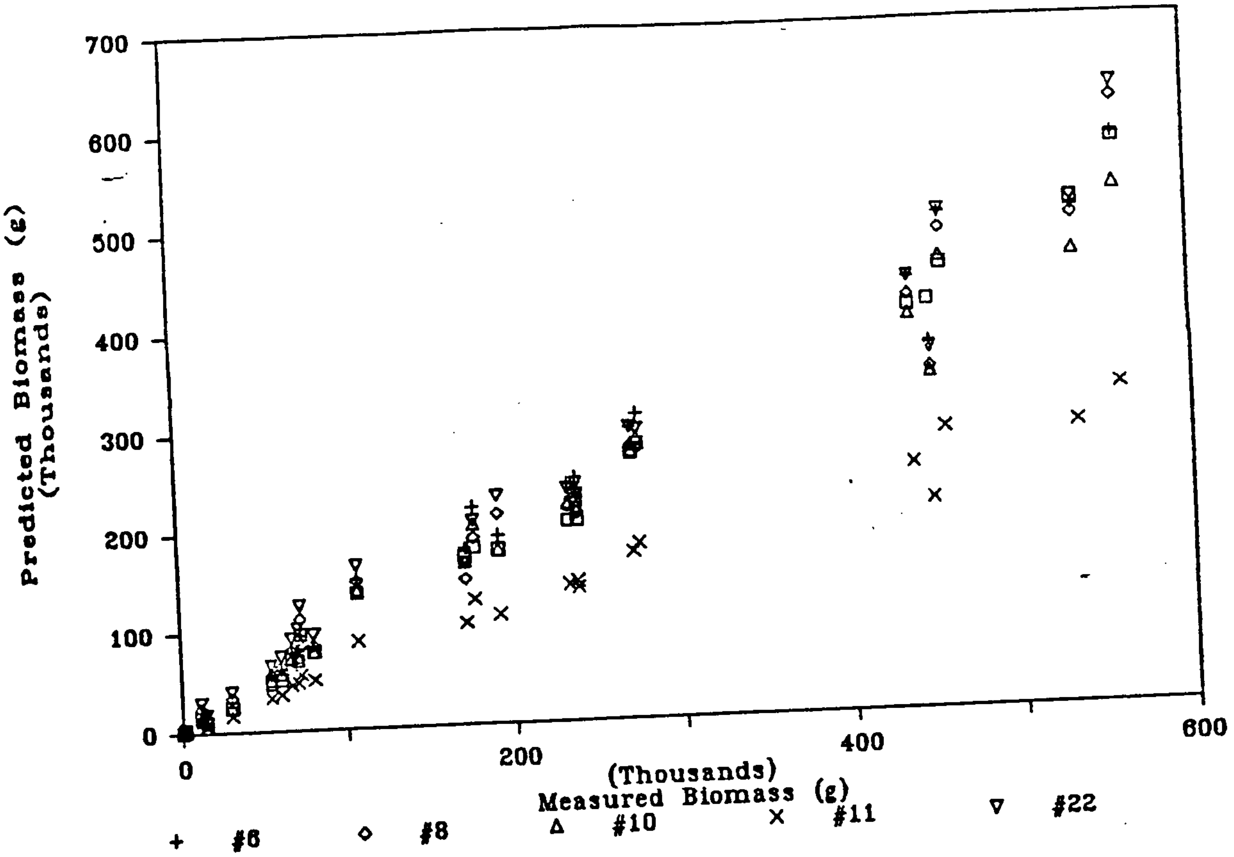
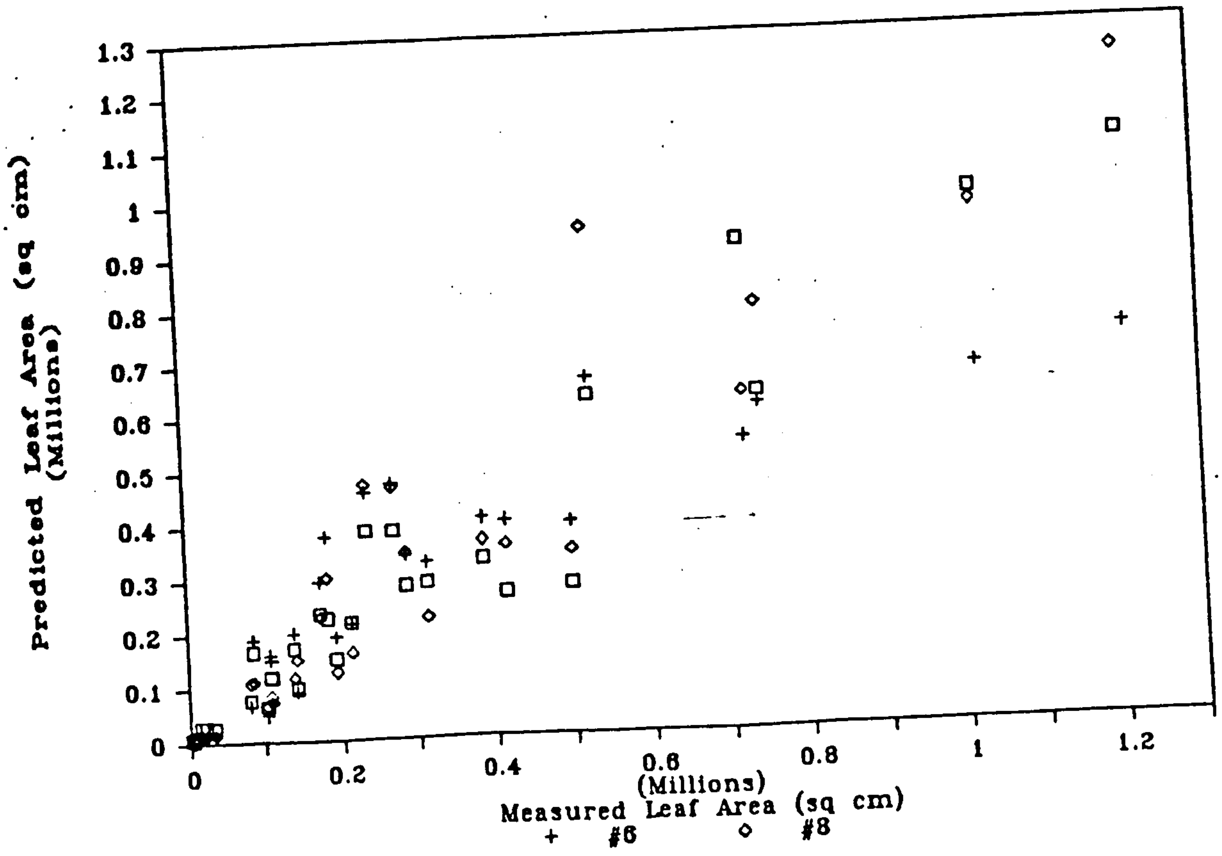


FIGURE 6B.



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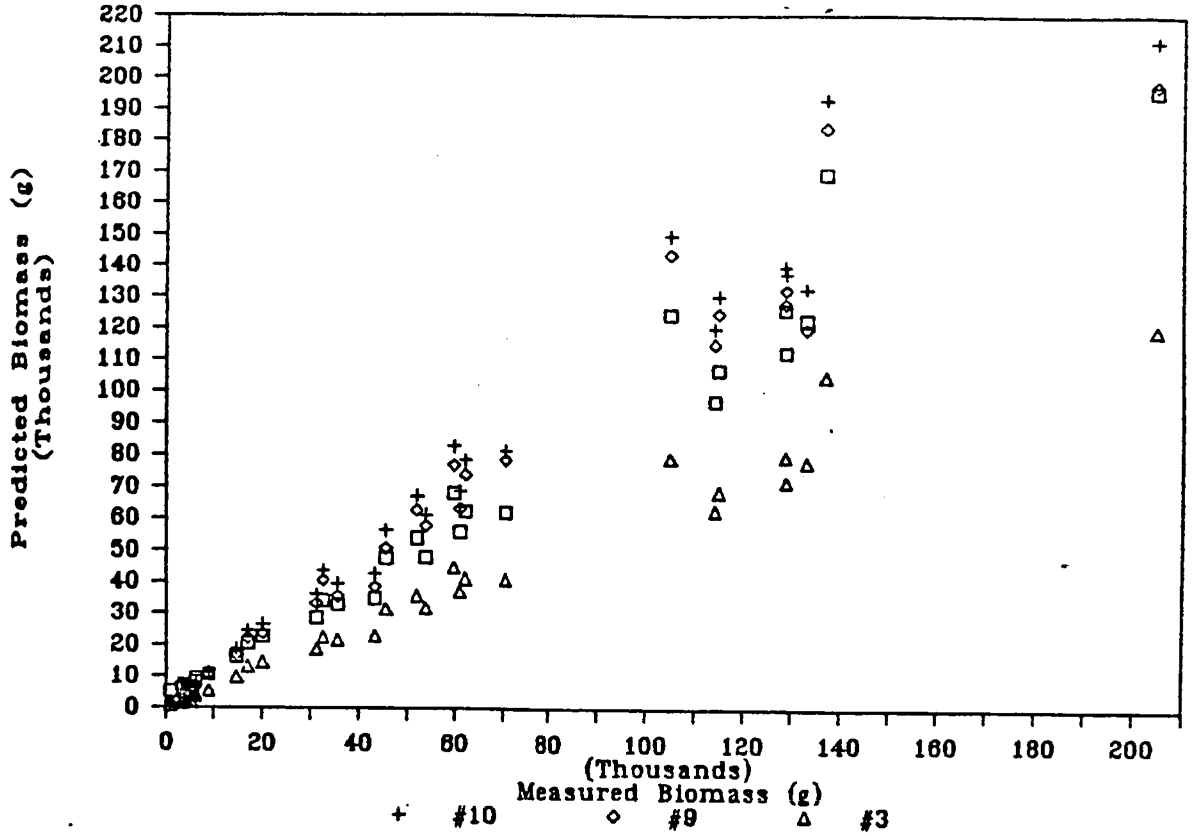

FIGURE 6D.