Diameter-based biomass regression models ignore large sapwood-related variation in Sitka spruce

B. T. Bormann

Volume 20 • Number 7 • 1990

Pages 1098–1104
Diameter-based biomass regression models ignore large sapwood-related variation in Sitka spruce

B. T. BORMANN

USDA Forest Service, Pacific Northwest Research Station, 3200 Jefferson Way, Corvallis, OR 97331, U.S.A.

Received September 13, 1989
Accepted February 2, 1990


Precise estimates of biomass are needed in productivity and nutrient cycling studies, and for improved estimates of potential productivity. Improvements in prediction of foliage and branch biomass were sought by comparing multiple regression models using stem diameter, sapwood radial thickness, and tree height as independent variables in stands of Sitka spruce (Picea sitchensis (Bong.) Carr.) in southeast Alaska. Five sites were sampled by stratifying trees into four diameter and three sapwood-thickness classes. Within stands, sample trees with thick sapwood consistently had 2–3 times more foliage and branch biomass than paired trees with thin sapwood but nearly equal diameter. Inclusion of both diameter and sapwood thickness in equations increased precision of foliage and branch biomass, leaf area, and net primary productivity by 15–31% and reduced standard error by 35–48% when compared with equations containing only diameter as an independent variable. Height growth over the last 30 years of intermediate and codominant trees with thick sapwood was 12–27% greater than that of paired trees with thin sapwood but nearly equal diameter at breast height. The addition of total tree height to multiple regression models, however, had little effect on their precision. Stem biomass equations were not improved by including tree height or sapwood thickness. The use of a diameter–sapwood thickness sampling matrix for construction of biomass equations may reduce the sample size needed and result in equations with wider application.

Introduction

Concepts of forest production, productivity, and potential productivity are changing as more concern is shown for long-term site productivity, forest decline, climate change, forest insect–disease interactions, and nontimber resources. As a result, there is a greater need to quantify forest end products other than currently merchantable timber volume alone. Nonmerchantable biomass may be an important resource by itself or may directly or indirectly influence future timber, wildlife, or water resources. Better measures of potential forest productivity are needed to assess how natural processes, management actions, air pollution, or climate fluctuations can affect the sustainable production of multiple resources and ecological values over the near and long term.

Precise prediction of nonstem biomass and net primary productivity may only be achieved when we develop predictor variables that relate well to physiological function. Prediction of leaf area and weight can be based on a simple pipe-model theory that states that transpiration, hence the area of leaves, is related to the area of water-conducting sapwood (Shinozaki et al. 1964; Waring et al. 1982). Precise models based on this idea have been constructed for western United States conifers (Grier and Waring 1974; Kaufmann and Troendle 1981), Scot's pine (Whitehead 1978; Albrektson 1984), red spruce and balsam fir (Marchand 1984), and oak (Rogers and Hinckley 1979). Few attempts have been made to relate sapwood to tree parts other than leaves (Snell and Brown 1978; Makela 1986).

Traditional biomass equations that use only diameter at breast height (DBH) have been constructed for many species to predict biomass components in forest stands (e.g., Whittaker and Woodwell 1968; Koerper and Richardson 1980; Grigal and Kernik 1984). Although many DBH models predict stem biomass precisely, relative lack of precision is observed with foliage and branch components (e.g., Gholz et al. 1979; Grigal and Kernik 1984; Marshall and Waring 1985). Many attempts have been made to improve predic-
BORMANN

Table 1. Characteristics of stands used to develop biomass equations

<table>
<thead>
<tr>
<th>Stand description and history</th>
<th>Mendenhall chronosequence</th>
<th>Vank Island</th>
<th>Pavlof</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M1</td>
<td>M2</td>
<td>M3</td>
</tr>
<tr>
<td>Avg. spruce $DBH$ (cm)</td>
<td>9.5</td>
<td>11.7</td>
<td>37.4</td>
</tr>
<tr>
<td>Min. spruce $DBH$ (cm)</td>
<td>3.0</td>
<td>3.0</td>
<td>10.1</td>
</tr>
<tr>
<td>Max. spruce $DBH$ (cm)</td>
<td>26.1</td>
<td>42.1</td>
<td>68.0</td>
</tr>
<tr>
<td>Avg. spruce SAP (mm)$^a$</td>
<td>22.7</td>
<td>13.9</td>
<td>15.5</td>
</tr>
<tr>
<td>Avg. spruce age (years)</td>
<td>46</td>
<td>90</td>
<td>178</td>
</tr>
<tr>
<td>No. of spruce per hectare</td>
<td>3980</td>
<td>3640</td>
<td>1400</td>
</tr>
<tr>
<td>Avg. spruce height (m)</td>
<td>10.2</td>
<td>12.0</td>
<td>31.4</td>
</tr>
<tr>
<td>Spruce basal area (m$^2$.ha$^{-1}$)</td>
<td>15.6</td>
<td>10.6</td>
<td>22.2</td>
</tr>
<tr>
<td>Hemlock basal area (m$^2$.ha$^{-1}$)</td>
<td>26.9</td>
<td>46.9</td>
<td>61.1</td>
</tr>
<tr>
<td>Alder basal area (m$^2$.ha$^{-1}$)$^b$</td>
<td>0.0</td>
<td>3.0</td>
<td>20.5</td>
</tr>
<tr>
<td>Cottonwood basal area (m$^2$.ha$^{-1}$)</td>
<td>0.7</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Total tree basal area (m$^2$.ha$^{-1}$)</td>
<td>35.3</td>
<td>50.9</td>
<td>81.6</td>
</tr>
</tbody>
</table>

$^a$ Sapwood radial thickness at breast height.
$^c$ Alnus sinuata in M1; A. rubra in Vank Island and Pavlof sites.

The Pavlof site is near Freshwater Bay on the eastern side of Chichagof Island about 16 km northeast of Tenakee, Alaska (57°53'N, 135°10'W). The stand originated following a major windthrow event in about 1888 on alluvially reworked mixed glacial till (Bowers 1987).

The Vank Island site is on small island that lies about 16 km east of Wrangell, Alaska (56°27'N, 132°41'W). This site was logged in 1922 using track skidders that greatly disturbed soil horizons. This was followed by a post-logging fire. These factors probably account for the presence of red alder (Harris and Farr 1974). The importance of alder is declining in this 60-year-old stand as alder is overtopped by spruce.

Methods

Stand description and history

Five Sitka spruce stands were selected to represent an array of age and site conditions in the northern half of the Tongass National Forest (Table I). A variety of stand types were represented including young, unproductive stands of Sitka spruce (Picea sitchensis (Bong.) Carr.) mixed with Sitka alder (Alnus sinuata (Reg.) Rydb.) and black cottonwood (Populus trichocarpa Torr. & Gray) on young glacial soils; older moderately productive spruce mixed with western hemlock (Tsuga heterophylla (Raf.) Sarg.); and a highly productive stand with spruce and red alder (Alnus rubra Bong.) developed after logging. All stands were naturally regenerated and situated near sea level.

Three sites, M1, M2, and M3, were established in the Mendenhall Valley, about 16 km north of Juneau, Alaska (58°16'N, 134°30'W). These forest stands developed on glacial till deposited about 70, 110, and 200 years ago, respectively, during the retreat of the Mendenhall Glacier (Chandler 1942; Crocker and Dickson 1957).

The Vank Island site is on small island that lies about 16 km east of Wrangell, Alaska (56°27'N, 132°41'W). This site was logged in 1922 using track skidders that greatly disturbed soil horizons. This was followed by a post-logging fire. These factors probably account for the presence of red alder (Harris and Farr 1974). The importance of alder is declining in this 60-year-old stand as alder is overtopped by spruce.

Tree selection

Sample quadrats were 0.05 to 0.20 ha with a minimum of 50 spruce trees per quadrat. Sample trees were selected from within these quadrats to represent a wide range in both $DBH$ and sapwood radial thickness at breast height (SAP). From measurements of $DBH$ on all trees in a quadrat, a mean ($\bar{X}$), standard deviation (SD), and four diameters, specifically targeted for sampling, were calculated. Target diameters, roughly corresponding to the crown classes suppressed (SUP), intermediate (INT), codominant (CODOM), and dominant (DOM), were calculated as follows: $X + 1$ SD; $X + 2$ SD, respectively. The SAP was measured on the six trees with $DBH$'s closest to each of these $DBH$ targets. Because most biomass in the stand was thought to be contained in trees with $DBH$'s close to INT and CODOM diameters, two from each of these groups of six trees, with the thickest and thinnest SAP, were selected. Trees were stratified in this manner to compare biomass on trees having nearly equal diameters but different SAP. In the SUP and DOM classes, a single tree was selected closest to the mean SAP of the group of six closest to the $DBH$ target. Thus, six trees in all were sampled from each stand, two INT and CODOM and one SUP and DOM.

Sapwood is easily identifiable in Sitka spruce by its greater translucency and moisture content relative to heartwood. Iodine dyes verified visual identification procedures. Two to three short
FIG. 1. Foliage and branch biomass on sample trees with nearly identical DBH but different sapwood radial thickness (SAP). Numbers above the thick-SAP class bars are the ratio of the thick-to-thin-SAP class pair. The first two characters below each bar are the site abbreviations (Mendenhall sites are M1–M3, VI is Vank Island, and PAV is Pavlof); the third letter represents either an intermediate (I) or codominant (C) DBH class.

Increment cores were extracted at breast height from trees at 120° angles and averaged. Sapwood radii were generally quite constant around the stem in these trees.

Sample collection and processing

The six sample trees selected in each quadrat were felled, and the live crowns were divided into five equal parts. All branches in a tree were measured for their basal diameter and distance from the terminal and were classified as whorl or internode branches. A single branch not damaged during felling was randomly selected from the middle of each crown fifth. Branches were divided into six components; current year foliage and branches (woody portion); last year foliage and branches; and older foliage and branches. Components were dried in the laboratory at 70°C to a constant mass and weighed. For each sample branch, foliage and branch biomass were calculated as the sum of all foliage and branch biomass components, respectively. Sample branch data were used with a multiple regression model to predict total weight of branch components per tree. Crown biomass was defined as the sum of foliage and branch biomass in the tree. Aboveground net primary productivity of spruce was estimated by adding weight of current year foliage and branch segments to weight of annual growth of stems and branches. Annual growth of stems and branches was calculated by multiplying current year stem volume increment (volume of current annual ring divided by volume of stem wood) by stem and noncurrent year branch dry weights (Whittaker and Woodwell 1968). Because many of these trees had not stopped radial growth at the time of sampling, radial growth on the year preceding the current year was used with section lengths to calculate volume increment.

Stems were also divided into five equal length sections and weighed in the field. A stem disk was taken from the base of each of the five stem sections and at DBH. Disks were also weighed in the field, returned to the laboratory, and oven-dried (70°C) to calculate stem moisture content and total stem dry weight. Height growth was reconstructed by identifying annual whorls and their position along the stem. Ring counts on sample disks were used to verify whorl ages and to determine ages of positions along the stem below identifiable whorls. One-sided leaf area was determined on fresh needle subsamples from each foliage age-class on each subsampled branch using a Li-Cor area meter (model LI-3000). Samples were oven-dried (70°C) to determine leaf dry weight. Green leaf area : oven dry weight ratios were multiplied by total foliage dry weight per branch to estimate total green leaf area.

No data on stem weight were collected on INT, CODOM, and DOM trees on the Pavlof site and the one DOM tree on the M3 site because trees were not felled. A modified rock climbing approach (Denison 1973) was used to collect branch data on these trees. Sapwood thickness was inadvertently not measured on two trees less than 6 cm DBH (SAP trees in M1 and M2), resulting in a sample size of 21 for stem and net primary productivity equations and 28 for the remaining equations.

Model development

Because it was unfeasible to disassemble and measure all biomass components of all branches within each sample tree, common branch equations were developed to predict foliage and branch weights of all branches in sample trees. Independent variables representing branches (diameter; position; and type, whorl or

---

1 The use of trade names in this publication is for the information of the reader. Such use does not constitute an official endorsement or approval by the USDA of any product to the exclusion of others that may be suitable.
TABLE 2. Comparison of the biomass model based on DBH alone (\(\log_e(Y) = \beta_0 + \beta_1\log_e(DBH)\)) with the multiple regression models \(\log_e(Y) = \beta_0 + \beta_1\log_e(DBH) + \beta_2\log_e(THT)\) and \(\log_e(Y) = \beta_0 + \beta_1\log_e(DBH) + \beta_2\log_e(SAP)\).

<table>
<thead>
<tr>
<th>Biomass component</th>
<th>DBH</th>
<th>DBH + THT</th>
<th>DBH + SAP</th>
<th>% change for DBH to DBH + SAP</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(R^2)</td>
<td>(S_{xy})</td>
<td>(R^2)</td>
<td>(S_{xy})</td>
</tr>
<tr>
<td>Current-year foliage</td>
<td>0.71</td>
<td>0.14</td>
<td>0.72</td>
<td>0.14</td>
</tr>
<tr>
<td>Last-year foliage</td>
<td>0.67</td>
<td>0.12</td>
<td>0.70</td>
<td>0.13</td>
</tr>
<tr>
<td>Older foliage</td>
<td>0.82</td>
<td>0.13</td>
<td>0.83</td>
<td>0.13</td>
</tr>
<tr>
<td>Current-year branches</td>
<td>0.71</td>
<td>0.13</td>
<td>0.71</td>
<td>0.14</td>
</tr>
<tr>
<td>Last-year branches</td>
<td>0.77</td>
<td>0.12</td>
<td>0.77</td>
<td>0.12</td>
</tr>
<tr>
<td>Older branches</td>
<td>0.80</td>
<td>0.13</td>
<td>0.81</td>
<td>0.13</td>
</tr>
<tr>
<td>Stem biomass</td>
<td>0.97</td>
<td>0.05</td>
<td>0.99</td>
<td>0.04</td>
</tr>
<tr>
<td>Net primary productivity</td>
<td>0.67</td>
<td>0.17</td>
<td>0.67</td>
<td>0.17</td>
</tr>
<tr>
<td>Leaf area</td>
<td>0.79</td>
<td>0.15</td>
<td>0.80</td>
<td>0.15</td>
</tr>
<tr>
<td>Foliage biomass</td>
<td>0.81</td>
<td>0.13</td>
<td>0.82</td>
<td>0.13</td>
</tr>
<tr>
<td>Branch biomass</td>
<td>0.80</td>
<td>0.13</td>
<td>0.81</td>
<td>0.13</td>
</tr>
<tr>
<td>Crown biomass</td>
<td>0.81</td>
<td>0.13</td>
<td>0.82</td>
<td>0.13</td>
</tr>
</tbody>
</table>

Model equations:

- DBH alone: \(LCYF = -7.752 + 2.323 \times LDBH\)
- DBH + SAP: \(LCYF = -2.225 + DBH \times 0.056 + LSAP \times 0.725\)

Note: \(R^2\) and \(S_{xy}\) are in logarithmic scale for both models and hence are directly comparable. Biomass units are kilograms, DBH and sapwood thickness units are centimetres, tree height units are metres, and leaf area units are square metres.

Epimorphic, trees (DBH; tree height (THT); and SAP), and stands (site index) were allowed to enter multiple regression equations using a stepwise procedure with an inclusion and exclusion \(p\)-value of 0.15. \(R^2\) for these equations ranged from 0.75 for current-year foliage to 0.96 for older branches (unpublished data and equations on file, Forestry Sciences Lab, 3200 SW Jefferson Way, Corvallis, OR 97331). Data from every branch in sample trees were used with these equations to estimate total dry weight of branch biomass components per tree.

A series of multiple regression models were constructed for entire trees to compare biomass equations containing DBH, DBH and THT, and DBH and SAP. Appropriateness of assumptions necessary for regression analysis was evaluated graphically. A log transformation was always required for the dependent variables to linearize models and equalize the variance, making it possible to compare \(R^2\) and standard errors of all equations (Payandeh 1981). The dependent variables were selected in either their transformed or untransformed state with a stepwise multiple regression procedure using an inclusion and exclusion \(p\)-value of 0.15.

Results and discussion

Paired Sitka spruce trees growing in the same stand with nearly identical DBH's but with variable sapwood thickness had remarkable differences in foliage and branch biomass (Fig. 1). Foliage and branch biomass of sample trees with thick sapwood averaged 2.6 and 2.5 times greater, respectively, than their paired thin sapwood sample tree of nearly equal DBH (\(p < 0.01\); paired t-test). Alternatively, stem biomass was little affected by sapwood thickness. With differences of this magnitude, it is easy to understand (i) the difficulty in constructing precise equations to predict foliage and branch biomass from DBH alone and (ii) the potential for bias in constructing equations using DBH alone based on trees selected nonrandomly.

It is also therefore not surprising that SAP is a useful additional independent variable in foliage and branch biomass equations. The \(R^2\) of equations using the DBH-alone model, excluding that for stem biomass, ranged from 0.67 to 0.82 (Table 2). This increased dramatically in DBH + SAP equations to 0.88 to 0.95, a 15 to 31% increase. Net primary production and single-year growth components were most improved by the addition of SAP followed by foliage, leaf area, and older multiple-year foliage and branch components. The effect of SAP on the regression surface for foliage, for example, is considerable, especially as DBH and SAP get larger (Fig. 2). Sapwood thickness did not improve the DBH-based equation for stem biomass (\(p > 0.15\)), suggesting that vigor of individual trees did not greatly influence stem form.
FIG. 3. Patterns of height growth in paired thick and thin sapwood radial thickness (SAP) class sample trees. Paired trees have nearly identical DBH and are from intermediate (II) and codominant (III) diameter classes. Mendenhall sites are M1–M3 and VI is Vank Island.

FIG. 4. Average paired difference in height growth (thick minus thin sapwood thickness class trees) over the past five 10-year periods. Bars are 95% confidence intervals. Paired trees have nearly identical DBH and are from intermediate and codominant diameter classes.

Inclusion of tree height in the model had little or no effect on the precision of biomass equations (Table 2). Tree height appears to be a less sensitive indicator of current nonstem biomass than SAP because it is more of a cumulative measure that does not always reflect current conditions. This is also revealed in the complex and variable relationship between SAP and tree height growth (Fig. 3). Differences in total height and patterns of height growth development between paired thick and thin sapwood trees appeared to be less consistent than differences in foliage and branch biomass (Fig. 1). Trees with thick sapwood were taller in six of eight pairs of trees. In five of eight pairs, trees with thick sapwood had slower early growth that was maintained or increased recently. Thick sapwood trees, however, did grow 3–8 cm·year^{-1} (12–27%) more than their thin sapwood pair during the last 30 years (Fig. 4). Beyond 30 years, pairs had similar rates of height growth, which suggests that current sapwood thickness, and perhaps nonstem biomass, is related to how fast the tree has grown over the past 30 years. Age of trees appears independent of current sapwood radial thickness. Four of the eight pairs of trees with similar DBH had similar ages; in two pairs, the thick sapwood tree was older and in the other two pairs, the thick sapwood tree was younger (Fig. 3).

Combined use of DBH and sapwood radial thickness has several key advantages over the use of sapwood cross-sectional area. Measurement of sapwood thickness requires one or more short increment cores where sapwood is directly measured. To nondestructively measure sapwood cross-sectional area, it is necessary to measure sapwood thickness and either inside-bark radius with an increment core to the pith, or outside-bark radius from a circumference measurement minus bark thickness. Either way, some additional error due to an off-center pith or measurement of bark thickness should be expected. Also, sapwood cross-sectional area can mask important differences because a larger tree with a small sapwood thickness can have the same sapwood cross-sectional area as a smaller more vigorous tree. The most important advantage of separating sapwood area into sapwood thickness and DBH is the increased information on possible age and site effects that allows for better model application.

Individual sample trees were well dispersed in the DBH, SAP sampling matrix (Fig. 5), suggesting the possible need for unique biomass equations for various combinations of site and age if the equations are a function of DBH alone. This dispersal reflects a wide range in site, age, and structure among-selected stands (Table 1). Because SAP explains a considerable amount of variation in foliage and branch biomass, information on the dispersal of trees within a DBH, SAP matrix could help to reduce misapplication of equations by defining the two-dimensional limits beyond which extrapolation will occur.
Fig. 5. Distribution of sample trees in the DBH - sapwood thickness sampling matrix. Trees from a common site are encircled (Mendenhall sites are M1-M3, VI is Vank Island, and PAV is Pavlof).

**Conclusions**

We should expect increased precision and applicability of biomass models when predictive variables are included that relate in some causal way, dimensional or functional, to the biomass of tree components. The DBH that represents two of the three dimensions of stem volume adequately describes stem biomass, at least in trees that do not greatly differ in wood density or stem taper. Inclusion of THT, the third dimension of stem volume, in addition to DBH did not appear to have any significant effect on the precision of biomass equations. Foliage, leaf area, branches, and current-year growth are less well represented by DBH alone or DBH + THT. Sapwood thickness, a structural variable more closely related to physiological processes, should be considered when constructing equations to predict these dependent variables.

Traditional models that predict nonstem biomass should be questioned in light of the large variation in SAP and nonstem biomass not explained by DBH or DBH + THT. Studies where traditional models have achieved high precision for nonstem biomass may indicate less of a sapwood effect in that species, cultural practices that have reduced within-stand variation, a more limited range in climatic or edaphic conditions, or nonrandom sampling. The net primary productivity estimation procedures using change in nonstem biomass based on radial increment (Newbould 1967) are dependent on the quality of the DBH-alone models and should also be questioned. While single-year estimates of net primary productivity suffer from year to year climatic and other factors, they represent the only useful method of establishing ground truth in remote sensing trials or tests of other single-year measurement indices. New approaches are needed to incorporate sapwood thickness into multiyear net primary productivity estimation procedures that perhaps involve the relation of sapwood thickness to ring pattern or height growth.

Sapwood is easy to measure in many species with relatively low measurement error. Sapwood, however, is not a useful predictor variable for some species, like western hemlock where it is difficult to identify. It should also be recognized that because sapwood performs many important functions, including transport of water and nutrients, storage of carbohydrates, nutrients and water, and defense from insects and disease, it may not relate closely to biomass in all situations. Sapwood-heartwood ratios may adjust to wind conditions to provide necessary support (Long et al. 1981), and sapwood permeability can also vary (Whitehead et al. 1984; Bancalari et al. 1987).

Additional understanding of tree to tree variation through measurement of sapwood thickness could help reduce needed sample size, better identify mean trees, and better evaluate the applicability of equations for a site not included in the sample used to construct the equation. This knowledge could also be incorporated into new intensive thinning strategies that use diameter and sapwood thickness to identify trees that are changing diameter, crown class, or rate of height growth.

**Acknowledgements**

This work was carried out under sometimes difficult logistical and weather conditions with adept field assistance from Robert Deal, Kirk Vail, Robert Haberman, and Dave Bassett. Thanks are also due to W.A. Farr, P. Alaback, R.H. Waring, and the Associate Editor for their insightful review comments.


