A Comparison of Regional and Site Specific Biomass Equations for Three North Idaho Conifers

A Dissertation
Presented in Partial Fulfillment of the Requirements for the
Degree of Doctorate of Philosophy
with a
Major in Natural Resources
in the
College of Graduate Studies
University of Idaho
by
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August 2017

Authorization to Submit Dissertation

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Abstract

Predictive equations were developed for both individual branch and total tree branch biomass, branch wood biomass, leaf biomass, and specific leaf area for grand fir (*Abies grandis* Douglas ex D. Don Lindl.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca*), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in northern Idaho, USA based on observations representing a range of variability in mixed species stands. Based on two randomly selected branches from each of four crown quarters, both full and reduced models were generated to predict branch quantities, however the reduced models were able to account for nearly as much variability in the response variables as the full models. The individual-branch equations were scaled to generate whole-tree biomass and leaf area estimates from which both full and reduced models were developed. All models explained a significant amount of variability in crown biomass components, resulting in an improved ability to explain crown biomass in these three species.

A nonlinear mixed effects model was developed to predict branch basal diameter (mm) from the distance from the branch to the top of the tree for grand, Douglas-fir, and western hemlock in northern Idaho, USA. An asymptotic model was used to describe the nonlinear relationship with an autocorrelation term to account for the lack of independence in the residuals. As indicated by both the significance of the parameter estimates and plots of predicted values overlaid onto observed values, these models are sufficiently accurate to predict branch basal diameter in grand fir, Douglas-fir, and western hemlock. These models provide improved estimates of tree biomass for carbon accounting and improved crown biomass estimations for use in empirical modeling efforts.

Douglas-fir crown biomass data from two separate studies were validated and pooled for use in examining whether a regional allometric equation for estimating crown biomass is sufficient or whether site-specific equations are required. Soil parent material was the basis for stratifying the sites in terms of soil nutrition. To account for potential confounding of site effects by climatic regime, a suite of climate variables were selected using hierarchical cluster analysis and were included in the modeling as predictor variables. While diameter at breast height (DBH) accounted for most of the variability in crown biomass ($R^2 = 0.76$), both soil parent material and climate variables added modest yet significant improvements to the model. The results suggest that interactions may be present between soil parent material and climate variables, however the sites from which the trees sampled for the two studies included in this research did not have enough variability in the climate variables to allow for full exploration of the interactions.

Acknowledgements

I would like to extend thanks to my advisor, Dr. Mark Kimsey, and to my committee members Dr. Steve Krone, Dr. Andrew Nelson, and Dr. Deborah-Page Dumroese along with Dr. Randy Brooks. Without their guidance, advice, and support, this work would not have been possible. Andrew Robinson, John Marshall, and Katy Kavanagh provided valuable manuscript advice. Dedicated assistance in the field and laboratory was provided by Colleen McHugh, Wei-Jin Wang, Curtis Kvamme, Ben Baker, and James Donley. This research was funded by McIntyre-Stennis, the Rocky Mountain Research Station (03-JV-11222063-285), and the Intermountain Forestry Cooperative.

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Chapter 1 Crown Biomass Equations for Three Northern Idaho Conifers

Abstract

Predictive equations were developed, influenced by pipe model theory to predict both individual branch and total tree branch biomass, branch wood biomass, leaf biomass, and specific leaf area for grand fir (*Abies grandis* Douglas ex D. Don Lindl.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca*), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in northern Idaho, USA based on observations representing a range of variability in mixed species stands. Based on two randomly selected branches from each of four crown quarters, both full and reduced models were generated to predict branch quantities, however the reduced models were able to account for nearly as much variability in the response variables as the full models. The reduced branch level equations were then scaled to generate whole tree biomass and leaf area estimates from which both full and reduced models were developed. All models explained a significant amount of variability in crown biomass components, resulting in an improved ability to explain crown biomass in these three species.

Introduction

Allometry is the study of relationships between two or more characteristics of an organism, and can be expressed with a scaling exponent based on a major aspect of the organism (Thompson, 1992; Huxley, 1972). Allometric equations are used in forestry to estimate quantitative relationships between characteristic dimensions of trees, often using diameter at breast height as the base characteristic. Obtaining direct measures of branch biomass and leaf area is a difficult and expensive task, resulting in the necessity of allometric equations to predict such quantities from easier and less expensive measured variables. The general form of the allometric equation is $Y = \beta X^{\alpha}$, where α is the scaling factor and β is the integration factor (Parresol 1999). The scaling factor α describes the proportion between the relative growth rates of biomass and stem diameter. In regression analysis, the equation is often transformed to a linear logarithmic form to account for heteroscedasticity using correction factors to account for the bias in back transformation (Baskerville 1972; Sprugel 1983). The United States national-scale equations for estimating aboveground forest biomass for whole-trees (Jenkins et al. 2003) were developed using the logarithmic form as $bm = \mathrm{Exp}\,(\beta_0 + \beta_1 \ln dbh)$ where bm = total aboveground biomass (kg dry weight), dbh = diameter at breast height (cm), Exp = exponential function, and ln = log base e (2.718282). Monserud and Marshall (1999) developed equations to estimate both whole-tree and individual-branch biomass in the general form directly, using nonlinear regression to avoid transformation bias.

Forests are an important renewable natural resource, and have significant impacts on the environment. Forests exchange large fluxes of carbon with the atmosphere through photosynthesis, respiration and decomposition (Waring and Running, 1998) and thus have a prominent role in the global carbon cycle. Wood production, wildlife protection, soil fertility protection, carbon and other gas absorption are among the aspects of environment impacts that forests have (Heri et al. 1999).

As a part of the active carbon pool in the global carbon cycle, standing forest biomass is essential. Estimates of forest biomass are needed for tracking changes in carbon stocks (Ketterings et. al. 2001) and better quantification of branches may help improve estimates of carbon dioxide storage in forest ecosystems (Dewar and Cannell 1992). As more knowledge is gained into forest ecosystem processes, more accurate quantification of individual components, such as branch biomass and branch volume become necessary (MacFarlane 2010). The biomass contained in tree branches is also a factor in debates over efforts to sustainably extract more biologically renewable fuels from forests (Egnell and Valinger 2003).

Bole diameter (dbh) is commonly the most important predictor of whole-tree biomass (Jenkins et al. 2003), and branch basal diameter has been found to be the most important predictor of individual branch biomass (Zhao 2012). Measuring every branch in a tree is difficult, time consuming and expensive, therefore model-based or model-assisted solutions are a reasonable approach to obtaining accurate estimates for branch biomass. While there are a variety of model-based and model-assisted tools to estimate tree bole volume (Ozcelik 2008), models predicting individual branch biomass components are scarce (Flewelling 2007). Individual branches influence tree growth as the amount and display of leaf area are controlled by the branches (Vose et al., 1994). The size and number of branches on a stem affect the value of lumber (e.g. Maguire et al., 1991b), and influence radiation interception (Whitehead et al. 1990; Kucharik et al. 1998) and precipitation interception (Keim, 2004). Several models have been developed to predict crown dynamics (Mitchell, 1975; Ford et al. 1990; Ford and Ford, 1990; Gavrikov and Karlin, 1992, Sorrensen-Cothern et al., 1993; Grace, 2003), however, it is less common for crown dynamics models to predict the dynamics of individual branches. Those models that do predict individual branch dynamics have typically not been incorportated into forest growth models (Weiskittel et al., 1997).

Grand fir (*Abies grandis* Douglas ex D. Don), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca*), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) were selected as study species for this research due to their abundance in the northwest United States and particularly in north Idaho as well as their commercial value. Grand fir can be an indicator of productive forest sites (Graham 1998, Hall 1973). Douglas-fir and western hemlock are important commercial species, used for structural lumber and veneers. Douglas-fir can occupy a variety of site conditions (Graham 1988), yet estimates of needle biomass as well as branch wood biomass may add to knowledge regarding site productivity. Since western hemlock is a commonly used tree for veneer, information about branch biomass and locations improves knowledge about wood quality.

The three species included in this research represent a range of shade tolerance (Minore 1979); western hemlock tends to be the most shade tolerant and Douglas-fir is the least shade tolerant. This research will provide key information on the influence of shade tolerance on branch level biomass predictions both due to the species selected and the sampling of locations with a mix of naturally occurring species.

The objectives of this research were to 1) develop predictive equations for individual branch quantities: individual branch biomass, individual branch wood biomass, individual branch needle biomass and leaf area by determining which branch level quantities are key predictors of biomass components; 2) develop predictive equations for whole tree crown components: whole tree branch biomass, whole tree leaf biomass, whole tree branch wood biomass and whole tree leaf area using tree basal area as the primary tree level predictor and 3) gain knowledge about how detailed the measurements must be from which quality predictions can be made about the crown biomass of grand fir, Douglas-fir and western hemlock. A goal was to sample a range of tree sizes (10 to 50cm), and stand densities.

Materials and Methods

Study Area

Data used in this study were collected in two locations in northern Idaho: Priest River Experimental Forest (PREF) and the University of Idaho Experimental Forest (UI) (Figure 1). PREF is a 2,590 acre area managed by the US Forest Service and is located near the town of Priest River, Idaho. UI covers 3,237 acres and is northeast of Moscow and the University of Idaho. PREF has more variable terrain ranging from 680 – 1,800 m than UI (1,000 – 1,519 m), and has a larger average precipitation (810 mm) than UI (686 mm). The ranges of species are similar within the two locations with the exception of THSE, which is effectively absent from UI.

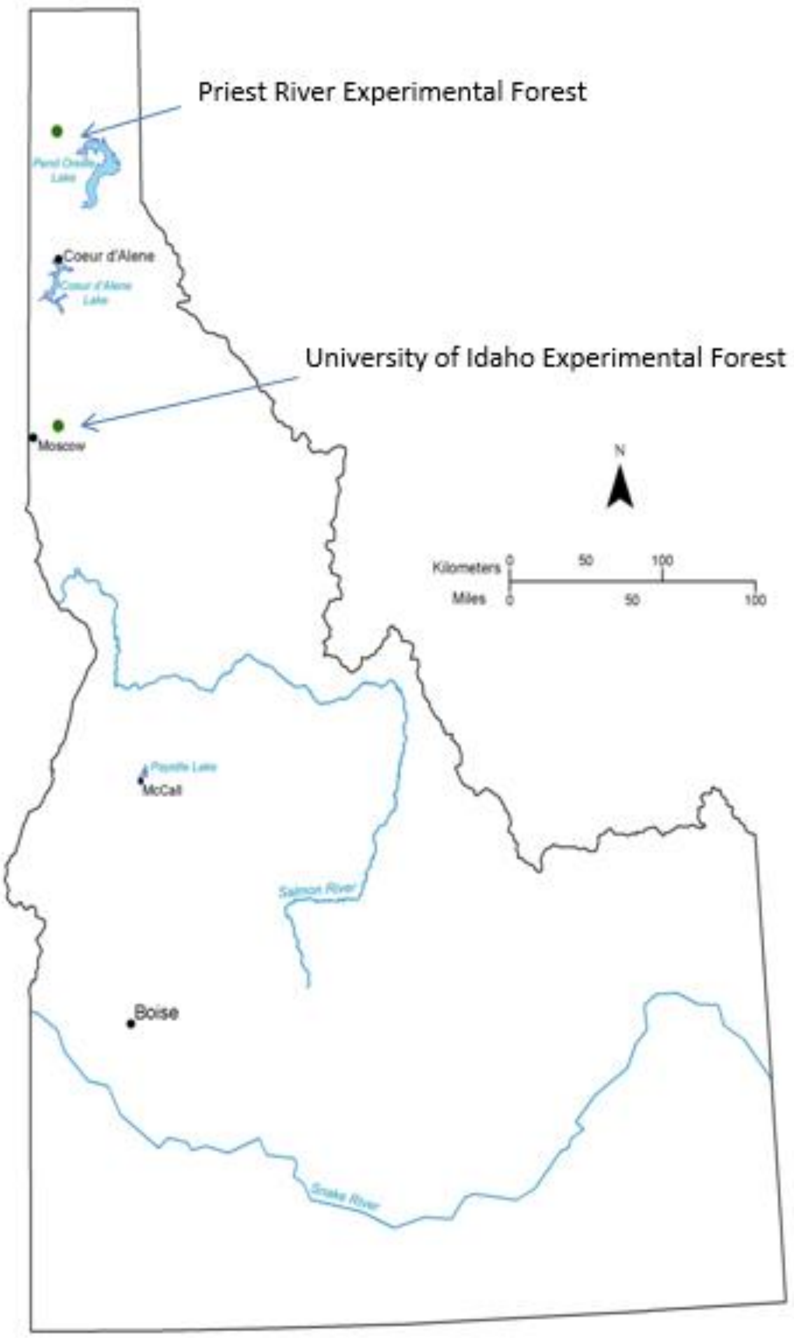

Figure 1-1. Map of Idaho showing the two locations in northern Idaho where the three species in this study were selected for sampling.

Field Data Collection

Data were collected during the 2005 summer sampling season. During these two summers, grand fir, Douglas-fir and western hemlock were chosen for destructive sampling from PREF and UI.

Plots were chosen to represent the broad range of variability that occurs in different age, mixed species stands in north Idaho including variation in plot densities and ages. Ideal plots contained all three of the study species among other species with a minimum of two of the three species.

Stands were purposively chosen to be likely to include the mixture of tree species based on visual observation and personal communication from managers. Within a stand, plots were chosen by randomly selecting a compass bearing, then moving 30 m into the stand from the edge. If the potential plot contained at least two of the three species of interest, we established a plot for destructive sampling. If the plot did not contain at least two of the three species, we moved 30 m along the same bearing and again checked for the species mix. If three plots were checked on the same bearing without finding the necessary species mix, a new starting location was identified and the process was repeated.

Trees were selected for sampling using a variable radius plot, and limited to only those trees with diameter at breast height (DBH) between 10 and 50 cm to develop equations for a range of large trees. A 4 m^2 ha^{-1} BAF basal area factor (BAF) prism was used to tally trees within the plot beginning with the first tree to the right of north and continuing clockwise. DBH was measured and recorded along with species for each tree in the tally. The diameters were ordered and the median diameter was noted for each plot. For each of the species of interest within the plot, the first tree (from north) larger than the median was sampled, and the first tree smaller than the median was sampled. Not all plots had trees both larger and smaller than the median DBH of each of the study species, in which case the tree with the median DBH itself was used as necessary. In plots with an uneven number of trees in the tally, we did not include the tree with median DBH as a sampled tree for consistency.

The selected trees from each site were felled for destructive sampling following the methods of Monserud and Marshall (1999). In summary, whole tree measurements included total height of tree, height to crown base from breast height and crown length. The crown base was defined as the lowest whorl with at least two live branches such that there were no dead whorls above that whorl. The live crown was divided into quarters. Above the crown base, branch diameters were measured with calipers in each crown quarter, and noted whether the branch was dead, live or broken and its height from breast height on the bole. Height to crown base and height of branches along the bole were later converted to total height to crown base and total height to branch insertion by adding 1.37 m to each measurement. All of the branches within each crown quarter were measured to obtain branch basal diameter (mm). Basal diameter was measured 1 cm above the branch collar for accuracy and consistency.

Two branches within each crown quarter were randomly sampled for detailed measurements. Using the number of branches measured in each crown quarter as a sampling frame, a simple random sample of *n* = 2 from each quarter was sampled using a random number table. A total of 58 trees were destructively sampled for analysis with detailed measurements on 428 branches (Table 1-1).

Table 1-1. The number of trees and individual branches for grand fir (ABGR), Douglas-fir (PSME) and western hemlock (TSHE) that were destructively sampled at each location (PREF and UI) during the 2005 sampling season.

Area	ABGR	PSME	TSHE	Total
PREF	3 (18)	15(106)	14(93)	32(217)
UI	11(91)	15(120)	-	26(211)
Total	14(109)	30(226)	14(93)	58(428)

Note: Number of individual branches is in parentheses.

Detailed branch measurements began with green weights taken in the field. The branches were measured for foliated length, length of each annual node, and length of each secondary branch. Total branch length was calculated by summing the lengths of the annual nodes in the primary branch. Branch diameters were measured at the branch collar before sampling, at the point where live foliage begins, and at three equal distances from the foliated edge to the tip of the branch. Needle subsamples were taken from each of the sampled branches, both current and all age classes of the older needles. Needles for the subsamples were selected to represent the entire branch by dividing the foliated length of the primary branch into quarters and randomly selecting two secondary branches per quarter, then removing all needles from each of the selected secondary branches. The needles were frozen until they could be weighed in the lab and scanned to determine projected leaf area. Following being weighed green and measured for area using a flatbed scanner and Image J software (National Institute of Health, Bethesda, MD), the needles were dried at 70° C for at least 24 hours to obtain dry weights. In the lab, all of the needles were removed from each sampled branch by hand, and then the wood and needles were separately dried and weighed at 70° C for at least 24 hours.

Disks were cut from the bole at seven locations: at breast height, at 10% of the total height, at 33% of the total height, at crown base, and at each of the quarter marks within the crown. Disks were measured on two axes for inside bark diameter and age was determined using a digital measuring system (TDI Model 100, Technology Dynamics, Inc., Bergenfield, NJ) on the disk sampled at breast height. The disks were sanded and the two axis lines were smoothed with a router to improve the accuracy of the measurements for age assessment.

Analyses

Predictive equations were developed for biomass components both at the individual-branch level and at the whole-tree level. Mixed-effects models were used to account for the hierarchical aspect of the data, where multiple branches were sampled from individual trees, and multiple trees were sampled from individual plots. At the individual-branch level, equations were constructed to estimate the following branch components: individual-branch biomass, individual-branch wood biomass, individual-branch leaf biomass, and individual-branch leaf area (Table 1-2). At the whole-tree level, equations were constructed for whole-tree branch biomass, whole-tree branch wood biomass, whole-tree leaf biomass, and whole-tree leaf area. At both the individual-branch and the whole-tree levels, two prediction equations were developed for each biomass component and leaf area. “Full” models for branches included predictor variables included in the dataset that are not necessarily easy to obtain, such as branch length, foliated branch length, and the distance between the branch insertion height and the top of the tree as well as branch basal area. The equations for the full models for individual-branches is

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4 \quad [1]$$

where y is the individual-branch quantity (total biomass, wood biomass, needle biomass, or leaf area), β_0 is the y-intercept and $\beta_1 – \beta_4$ are the parameter estimates for the predictor variables branch basal area, distance between tree top and insertion height, branch length, and foliated branch length. “Reduced” branch models only included branch basal area as a predictor and have the form

$$y = \beta_0 + \beta_1 x \quad [2]$$

where β_1 is the parameter estimate for branch basal area. A similar protocol was used for the whole-tree models, where “full” models included stand density with tree basal area at breast height and several other tree and plot level predictors (Table 1-2). The equations for the whole-tree full models are of the form

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4 \quad [3]$$

where y is the whole-tree quantity (total biomass, wood biomass, needle biomass, or leaf area), β_0 is the y-intercept and $\beta_1 – \beta_4$ are the parameter estimates for the potential predictor.The whole-tree “reduced” models only included tree basal area and has the form

$$y = \beta_0 + \beta_1 x \quad [4]$$

where β_1 is the parameter estimate for tree basal area. Two equations were developed for each quantity so that the best possible prediction could be obtained using all available data, so that a prediction equation could be used that only included the least expensive and easiest to obtain predictor, and to assess the necessity of obtaining the additional variables for future work.

Table 1-2. Potential Predictor Variables for the branch biomass and leaf area prediction equations.

Plot	Tree	Branch
BA (m^2/ha)	Total tree height (m)	Branch basal diameter (mm)
Trees per hectare	Crown length (m)	Branch basal area (cm^2)
	Diameter at breast height (cm)	Branch insertion height (m)
	Tree basal area (m^2)	Branch length (cm)
	Diameter inside bark at breast height (cm)	Foliated branch length (cm)
	Diameter inside bark at crown base (cm)	Foliated branch length (%)
	Age	Depth into tree (m)
	Height to diameter ratio	
	Crown ratio	

For the individual-branch equations, specific leaf area (SLA; $cm^2 \cdot g^{-1}$) was calculated as the ratio of the projected leaf area from the leaf subsamples to the dry mass of the subsamples for each branch. The mass of the whole branch was measured green in the field, which included both needles and wood. The dry mass of the wood and needles were measured individually in the laboratory. The ratio of the dry needle mass of the SLA subsample to the green subsample mass was used to estimate the green needle mass for each branch. The ratio of the scanned area (cm^2) of the needle subsamples to the dry weight of the needle subsamples (g) multiplied by the dry weight (g) of the needles for the entire branch. The sum of the dry wood mass and the dry needle mass was used for the total mass of each branch.

Since there is a linear relationship between branch basal area as the primary predictor for the individual-branch models and the branch response variables, and between individual tree basal area and the whole-tree response variables, a linear mixed effects modeling strategy was employed to obtain prediction equations for the crown biomass components. Random effects were included in the models to account for the hierarchical structure of the data in which multiple branches were selected from sample trees, and multiple sample trees were selected from plots. To develop the models, the random effects (individual tree and individual plot respectively for the branch and whole-tree models) were examined first. Likelihood ratio tests were used to determine whether the random effects added predictive value to the models. Once the random effects had been evaluated, the fixed effects were chosen sequentially, by adding variables individually and assessing the models with each additional variable. When all the effects for each model had been identified, the models were evaluated for goodness of fit and to ensure that the assumptions for linear regression were met (Ott and Longnecker, 2001.) Autocorrelation of the residuals often required an addition error term, and in most cases a power weighting function was necessary to correct for heteroscedasticity. Best fitting models were selected by first ensuring that all model assumptions were met. Within each group of models for the four branch quantities, models with the lowest Akaike's information criterion (AIC) with significant parameter estimates and biological interpretability were selected. Models were further selected based on the marginal R^2 (the proportion of variance explained by the fixed factors alone), and the conditional R^2 (the proportion of variance explained by both the fixed and random factors) (Nagakawa and Schielzeth 2013).

To scale the results of the individual-branch equations up to the whole-tree level, the fixed effects parameter estimates from the equations developed from the individual branches were used to predict the branch biomass components and leaf area using the basal area measurements from all of the branches on each tree. Since every branch within the crown was measured for branch basal diameter in order to obtain the random sample of branches for intensive measurement, those measurements allowed biomass and leaf area predictions for every branch on a sample tree. When the predictions had been calculated for all individual-branches on a tree, they were summed for whole-tree quantities.

The models for individual-branch biomass components and leaf area were validated using the observations collected from the intensively sampled branches on trees sampled in 2004.

Results

Natural Variability within Stands

The plots selected for sampling represented a range of variability in species mix. Six of the 45 plots selected contained all three of the species. Average diameter at breast height ranged from 15.6 to 50.2 cm in grand fir, from 16.2 to 50.7 cm in Douglas-fir, and from 10.2 to 35.6 cm in western hemlock, and average tree height ranged from 9.2 to 36.7 m for grand fir, from 9.1 to 36 m for Douglas-fir, and from 10.2 to 35.6 m for western hemlock (Table 1-3). Variation was also observed in the ages of the sample trees, which ranged from 21 to 131yr for grand fir, from 42 to 146yr for Douglas-fir, and from 70 to 140yr for western hemlock.

Table 1-3. Descriptive statistics for grand fir (ABGR), Douglas-fir (PSME), and western hemlock (TSHE) at both sampling locations (PREF and UI.)

Area	Species	DBH (cm)			Tree Height (m)			Age			Plot Basal Area ($m^2 \cdot ha^{-1}$)		
		n	mean	std	n	mean	std	n	mean	std	n	mean	std
PREF	ABGR	3	22.67	6.17	3	16.83	6.63	2	-	-	3	40.00	24.33
PREF	PSME	15	37.19	11.34	15	26.30	6.74	13	115.85	10.17	15	54.13	15.18
PREF	TSHE	14	33.34	9.60	14	26.40	7.03	11	118.73	24.47	14	54.29	10.37
UI	ABGR	11	31.06	10.06	11	25.57	6.55	9	88.44	32.96	11	49.82	13.67
UI	PSME	15	35.78	9.86	15	26.34	6.24	15	90.32	31.63	15	53.3	16.95

Note: Branch biomass is the biomass contained with the branches (wood + needles) for the whole tree, estimated from the individual branch equations.

The range of DBH in the sample trees represented a similar distribution for each species and covered the 10 – 50 cm sizes for which the allometric equations were desired. Although there are TSHE in UI, the number and location of them is severely limited, thus they were excluded from sampling since they were not present in any of the plots sampled. All of the descriptive measures of the trees and plots indicate that a full range of DBH and age variability was sampled throughout the study area; however the range of stand densities was less variable than anticipated. The three locations from which trees were selected for sampling are all relatively productive in terms of tree growth and the denser, higher basal area stands were over-represented in this study, therefore the results may serve as an upper limit for productive areas.

Based on 8 sample branches per tree, a total 428 branches were available for individual-branch observations of total branch biomass: leaf biomass, wood biomass, projected leaf area, and specific leaf area (Table 1-2). Model fit was determined using AIC, the number of significant predictor variables, and ensuring that model assumptions were met for all four branch quantities. When a single “best” model was not obvious based on these criteria, the simplest model that best represented the biological relationship with significant parameter estimates was chosen. The residuals for all of the models showed heterscedasticity, and the final models were weighted by a power variance function of the primary predictor variable. The variance function for this analysis is defined as $s^2(v) = |v|^{2\delta}$ where v is the primary predictor variable, $s^2(v)$ = is the variance function evaluated at v, and δ is the variance function coefficient (Myers 1990.) Autocorrelation plots suggested that the assumption of independence of errors was also violated; therefore an autocorrelation function was added to the standard errors of the parameter estimates (Chi and Reinsel 1989).

Individual Branch Models

Individual-branch total biomass, wood biomass and leaf biomass were well explained by variation in branch basal area, while the variability in individual-branch leaf area was less strongly related to branch basal area (Figure 1-2.) Branch length was a significant effect in all of the full models for the individual-branch components, yet on average, the predictive ability of the fixed effects had a small increase over models using branch basal area alone (Tables 1-4 and 1-5).

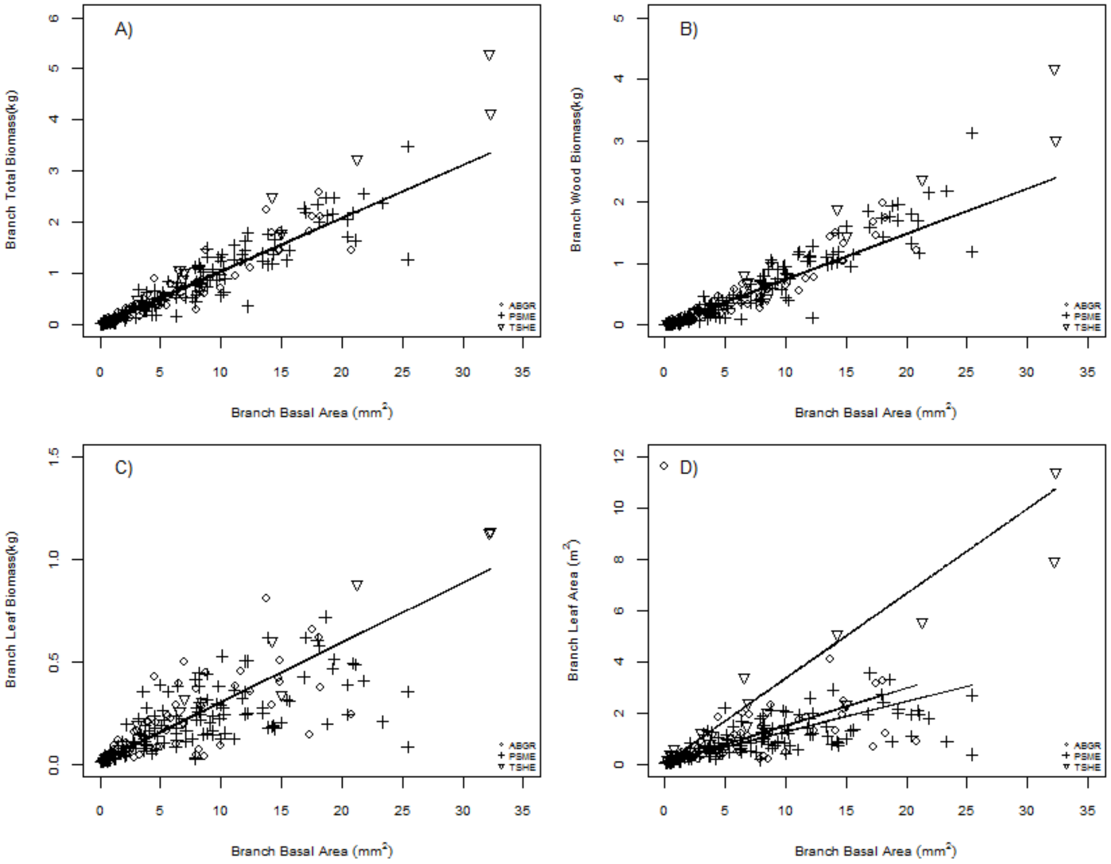

Figure 1-2. Scatterplots of A) Individual-branch total biomass (g), B) Individual-branch wood biomass (g), C) Individual-leaf needle biomass (g), and D) Individual-branch leaf area (cm^2) against branch basal area (mm^2) for grand fir (ABGR), Douglas-fir (PSME) and western hemlock (TSHE), pooled over both sampling locations (PREF and UI). Branch leaf area is one-sided (projected) area.

Table 1-4. The *b* coefficients in the full allometric equation $Y = b_0 + b_1X_1 + b_2X_2$ predicting individual branch dry biomass (g), individual branch dry wood biomass (g), individual branch dry leaf biomass (g), and individual branch leaf area (m^2). Standard errors for the estimates are given in parentheses.

Response Variable	Species	n	b_0	b_1	b_2	φ	δ	AIC	RMSE	R^2_M	R^2_C
Dry Branch Biomass	ABGR	53	-0.1288 (0.0522)	0.0876 (0.0065)	0.00138 (0.0002)	0.17	0.88	39.57	0.2317	0.92	0.93
	PSME	155	-0.1317 (0.0609)	0.0848 (0.0064)							
	TSHE	26	-0.2067 (0.0942)	0.1281 (0.0073)							
Dry Branch Wood Biomass	ABGR	59	-0.0165 (0.0046)	0.0685 (0.0036)	0.00014 (0.0001)	0.51	0.92	-346.82	0.3564	0.64	0.64
	PSME	163	-0.0046 (0.0054)								
	TSHE	28	-0.0204 (0.0077)								
Dry Branch Leaf Biomass	ABGR	39	0.0310 (0.0154)	0.0243 (0.0012)	-	-	-	-293.687	0.5114	0.63	0.71
	PSME	160									
	TSHE	27									
Leaf Area	ABGR	64	0.0273 (0.0174)	0.1482 (0.0170)	-	0.49	0.96	162.91	0.5279	0.89	0.89
	PSME	156	0.0766 (0.0227)	0.1189 (0.0192)							
	TSHE	25	0.0284 (0.0505)	0.3322 (0.0676)							

Note: Dry branch wood mass does not include needles and leaf areas are projected (one-sided). The predictor variables are X_1= branch basal area (mm^2), X_2 = branch length (cm). φ is the parameter estimate for the AR(1) term, and δ is the power term in the variance function. AIC is Akaike's information criterion, R^2_M is the proportion of variance explained by the fixed effects, and R^2_C is the proportion of variance explained by both the fixed and random effects.

Table 1-5. The *b* coefficients in the reduced allometric equation $Y = b_0 + b_1X_1$ predicting individual branch dry biomass (g), individual branch dry wood biomass (g), individual branch dry leaf biomass (g), and individual branch leaf area (m²).

Response Variable	Species	n	b_0	b_1	φ	δ	AIC	RMSE	R^2_{M}	R^2_{C}
Dry Branch Biomass	ABGR	61	-0.0021 (0.0050)	0.1041 (0.0034)	0.40	0.90	-243.696	0.3011	0.84	0.84
	PSME	156	0.0134 (0.0062)							
	TSHE	26	-0.0050 (0.0085)							
Dry Branch Wood Biomass	ABGR	67	-0.0075 (0.0032)	0.0743	0.45	0.85	-356.945	0.5621	0.70	0.70
	PSME	163	0.0031 (0.0041)							
	TSHE	29	-0.0088 (0.0066)							
Dry Branch Leaf Biomass	ABGR	69	0.0310 (0.0154)	0.0243 (0.0012)	-	-	-293.687	0.5114	0.63	0.71
	PSME	160								
	TSHE	27								
Leaf Area	ABGR	64	0.0273 (0.0174)	0.1482 (0.0170)	0.49	0.96	162.91	0.5279	0.89	0.89
	PSME	156	0.0766 (0.0227)	0.1189 (0.0192)						
	TSHE	25	0.0284 (0.0505)	0.3322 (0.0676)						

Note: Dry branch wood mass does not include needles and leaf areas are projected (one-sided). The predictor variable is X_1= branch basal area (mm²). φ is the parameter estimate for the AR(1) term, and δ is the power term in the variance function. AIC is Akaike's information criterion, R^2_{M} is the proportion of variance explained by the fixed effects, and R^2_{C} is the proportion of variance explained by both the fixed and random effects.

Individual branch biomass

The full mixed effects model, where the trees from which branches were sampled was included as a random effect, suggests that grand fir and Douglas-fir branch biomass can be estimated from a single equation, however western hemlock branch biomass increased more with an increase in branch basal diameter than the other two species (Table 1-4). The fixed effects of the full model accounted for 92% of the variability in individual-branch total biomass, and the random effects added another 1% to the amount of variability explained by variation in branch basal area and branch length.

The fixed effects of the reduced model for branch biomass were able to account for nearly as much variability as the full model (84%), and the random effects did not increase the amount of variability explained. When branch length was not included in the model as a covariate, individual-branch biomass for all three species increased similarly with branch basal area for all three species. In the reduced model, grand fir and Douglas-fir had unique intercepts while grand fir and western hemlock were not significantly different (Table 1-5).

Individual-branch wood biomass

The fixed effects and random effects for the full model for individual-branch wood biomass accounted for a similar amount of variability from branch basal area as the model for total branch biomass (64%). Branch length was the only additional predictor variable that improved the model. The distance between the top of the tree and the branch insertion height was strongly correlated with individual-branch wood biomass; however branch length provided a better fit. Western hemlock and grand fir branch wood biomass can be estimated with a single model, while the equation for Douglas-fir had a significantly different intercept than the other two species (Table 1-4). A single slope was sufficient for all three species.

The fixed effects and random effects in the reduced model for individual-branch wood biomass accounted for nearly the same amount of variability from branch basal area as the full model (70%). Again, western hemlock and grand fir branch wood biomass was estimated with a single equation while Douglas-fir had a different intercept (Table 1-5.)

Individual-branch needle biomass

Branch basal area was a significant predictor of dry branch leaf biomass in the full models for all three species as was the distance from the top of the tree. Branch length did not increase the amount of variability in dry needle biomass. The fixed effects and random effects in the reduced model were able to explain 71% of the variability in dry needle biomass from branch basal area. There were no significant differences in the intercept for the three species, therefore a single equation was able to predict needle biomass from branch basal area (Table 1-4).

Individual-branch leaf area

The amount of variability in leaf area for individual-branches that could be explained by the fixed effects for the predictor variables in the full model was intermediate between the amount explained by the model for total branch biomass and wood biomass, and needle biomass. For individual-branch leaf area, no other predictor variables in addition to branch basal area were found to improve over the reduced model, where the fixed and random effects explained 89% of the variability (Table 1-5). Individual equations were required for each species. The rate of increase in needle area was not significantly different between grand fir and Douglas-fir, and the intercepts were not significantly different between grand fir and western hemlock.

Whole-tree Models

Using the reduced equations developed from the individual intensively sampled branches, branch biomass quantities and specific leaf area were estimated using measured diameters from the branches that were not selected for intensive sampling. The individual-branch quantities were summed over each tree for the whole-tree estimates.

The whole-tree models in reduced form were able to predict much of the variability from the fixed effects in the branch biomass and leaf area components based on the basal area of the tree alone, and somewhat more for the full models (Figure 1-3); Additional predictor variables in the full models were not able to increase the explanatory ability by an appreciable amount (Table 1-6).

Table 1-6. The *b* coefficients in the full allometric equation $Y = b_0 + b_1X_1 + b_2X_2$ predicting whole-tree dry biomass (g), whole-tree branch dry wood biomass (g), whole-tree dry leaf biomass (g), and whole-tree leaf area (m^2). X_1 is tree basal area and X_2 is crown ratio.

Response Variable	Species	n	b_0	b_1	b_2	δ	AIC	RMSE	R^2_M	R^2_C
Dry Branch Biomass	ABGR	14	-28.90	835.53	53.36	1.07	464.0138	14.80	0.96	0.99
	PSME	30								
	TSHE	14								
Dry Branch Wood Biomass	ABGR	14	-20.88	593.26	37.47	1.08	426.3582	6.35	0.96	0.99
	PSME	30								
	TSHE	14								
Dry Branch Leaf Biomass	ABGR	14	-7.87	237.92	16.51	1.02	331.08	2.64	0.96	0.99
	PSME	30								
	TSHE	14								
Leaf Area	ABGR	64	-64.68	1334.48	108.33	1.17	486.3584	13.80	0.98	0.99
	PSME	156	-36.43	854.36						
	TSHE	25	-59.69	2590.81						

Note: Dry branch wood mass does not include needles and leaf areas are projected (one-sided). The predictor variables are X_1= tree basal area (cm^2), X_2 = crown ratio. δ is the power term in the variance function. AIC is Akaike's information criterion, R^2_M is the proportion of variance explained by the fixed effects, and R^2_C is the proportion of variance explained by both the fixed and random effects.

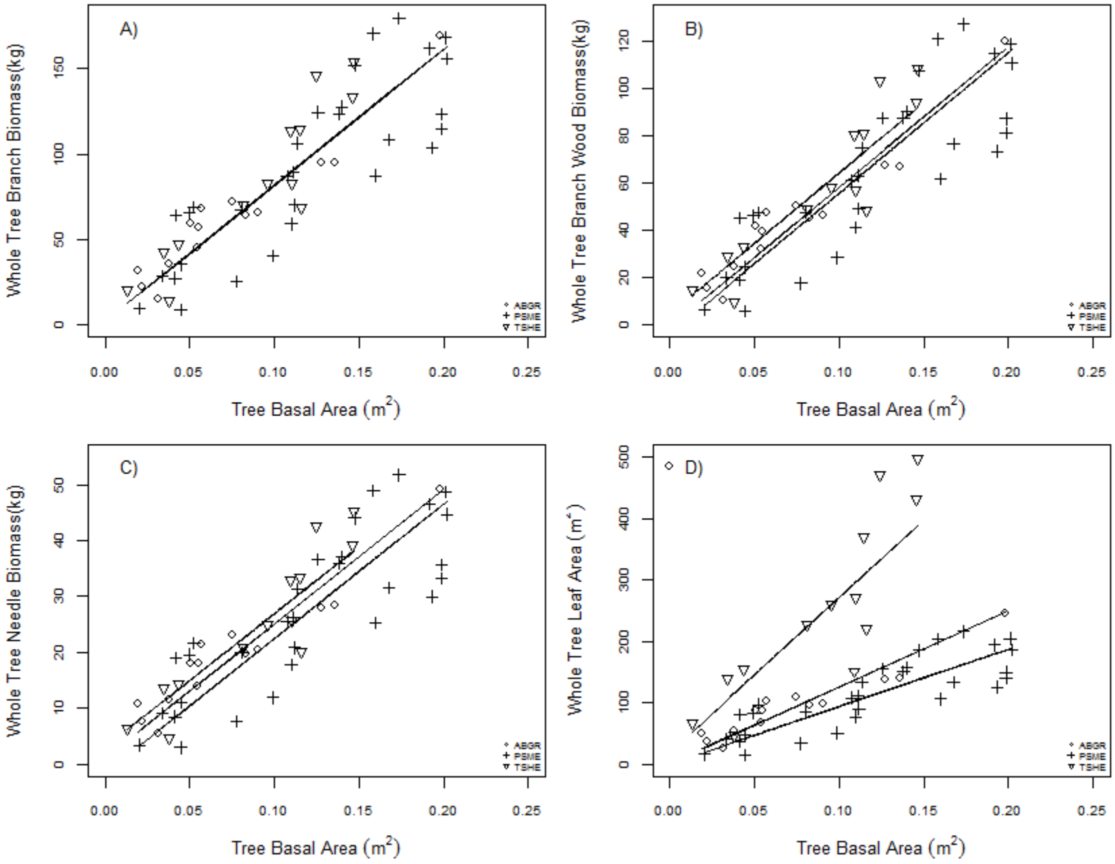

Figure 1-3. Scatterplots of whole-tree branch quantities versus tree basal area (m^2) for grand fir (ABGR), Douglas-fir (PSME) and western hemlock (TSHE) pooled over both locations (PREF and UI). A) is whole-tree branch biomass (kg), B) is whole-tree branch wood biomass (kg), C), is whole-tree leaf biomass (kg) and D) is whole-tree leaf area (m^2). Leaf area is one-sided (projected) area.

Whole-tree total branch biomass

A single slope and a single intercept were sufficient to explain the variability in whole-tree total (wood plus needles) biomass. The fixed effects of the equation accounted for 96% of the variability from the basal area of the tree and crown ratio (Table 1-6), and the random effects were able to explain an additional 3% of the variability in dry branch biomass. When crown ratio was removed from the equation, a reduction in the variability explained of 5% from the fixed effects was observed (91%), but the random effects kept the amount of variability explained in the reduced model equal to the amount explained by the full model (99%). A single equation was again sufficient for all three species, indicating that the increase in total branch biomass for the whole-tree had a similar relationship to branch basal diameter regardless of species (Table 1-7.)

Table 1-7. The *b* coefficients in the reduced allometric equation $Y = b_0 + b_1X_1$ predicting whole-tree dry branch biomass (g), whole-tree dry branch wood biomass (g), whole-tree dry branch leaf biomass (g), and whole-tree leaf area (m^2).

Response Variable	Species	n	b_0	b_1	δ	AIC	RMSE	R^2_M	R^2_C
Dry Branch Biomass	ABGR	14	-0.96	839.11	0.82	485.20	14.80	0.91	0.99
	PSME	30	-7.30						
	TSHE	14	7.28						
Dry Branch Wood Biomass	ABGR	14	-1.24	595.54	0.81	448.36	10.37	0.91	0.99
	PSME	30	-5.65						
	TSHE	14	4.60						
Dry Branch Needle Biomass	ABGR	14	1.05	240.67	0.84	354.7761	4.50	0.90	0.99
	PSME	30	-1.53						
	TSHE	14	2.90						
Leaf Area	ABGR	14	1.09	1242.69	0.97	519.52	22.45	0.94	0.99
	PSME	30	.015	936.30					
	TSHE	14	19.66	2512.21					

Note: Dry branch wood mass does not include needles and leaf areas are projected (one-sided). The predictor variables is X_1= tree basal area (cm^2). δ is the power term in the variance function. AIC is Akaike's information criterion, R^2_M is the proportion of variance explained by the fixed effects, and R^2_C is the proportion of variance explained by both the fixed and random effects.

Whole-tree dry branch wood biomass

In the full model for total dry branch wood biomass, much of the variability was explained with tree basal area (Table 1-6). Adding crown ratio resulted in the fixed effects accounting for the same amount of variability explained for whole-tree branch wood biomass as for whole-tree total branch biomass (96%). When crown ratio is included as a predictor, a single equation was sufficient to estimate whole-tree dry branch wood biomass for Douglas-fir and western hemlock, however a unique intercept is required for grand fir.

The fixed effects in the reduced model for grand fir branch wood biomass explained slightly less variability in dry branch wood biomass than the equation for total branch biomass with tree basal area alone (91%). Similar to the equation for whole-tree total branch biomass, the relationship between tree basal area and dry wood biomass did not significantly differ between the three species; however they did have significantly different intercepts.

Whole-tree needle biomass

Crown ratio was the best additional predictor in the model for whole-tree needle biomass. Tree height and plot basal area individually were able to improve the model over tree basal area alone but they were not significant when crown ratio was also included. Individually, tree height and plot basal area predictive ability was lower than that of crown ratio. The fixed effects of the model accounted for 96% of the variability in whole-tree needle biomass with a single equation with a common intercept and slope (Table 1-6). The random effects improved the amount of variability explained by tree basal area and crown ratio by 3%.

The fixed effects of the reduced model for whole-tree needle biomass accounted for 90% of the variability in needle biomass for the whole-tree. The increase in needle biomass due to an increase in tree basal area was not significantly different among the three species; however the intercept for western hemlock was significantly different than that for grand fir and Douglas-fir (Table 1-7).

Whole-tree leaf area

The fixed effects in the full equation for whole-tree branch leaf area explained 98% of the variability in leaf area from the tree basal area and crown ratio (Table 1-6), and was increased by 1% by the random effects. The increase in whole-tree leaf area related to an increase in tree basal area was significantly different for each species. The intercept for Douglas-fir was significantly different than that for grand fir and western hemlock.

The fixed effects of the reduced equation predicting whole-tree leaf area from tree basal area were able to account for somewhat less of the variability in the response variable than were the full models (94%), however the random effects were able to account for an additional 5% of the variability in leaf area from tree basal area. Both the intercepts and slopes were significantly different for all three species. (Table 1-7).

Discussion

Allometric equations were developed that explained a significant amount of the variability in the response variables for both individual-branch biomass components and whole-tree biomass components, as well as for leaf area both at the individual-branch and the whole-tree level for three species in this study. The form of the equations was generally similar to other equations predicting crown biomass components (Jenkins et al. 2003, Zhao 2012) in that branch basal diameter was used as the primary predictor for individual-branch quantities, and diameter at breast height was used as the primary predictor for the whole-tree models. Previous work on allometric biomass equations most often uses either a natural logarithm transformation to both linearize the data as well as to correct for heteroscedasticity (Brown 1978), or uses nonlinear modeling to directly account for the nonlinear relationship between branch basal diameter and branch biomass as well as that between tree basal diameter and whole-tree biomass (Monserud and Marshall 1999, Weiskittel et al. 2007). By converting branch basal diameter to branch basal area as the primary predictor, we were able to avoid the need to transform the data yet analyze the data with linear modeling which is attractive for the additive rather than multiplicative errors resulting from nonlinear modeling (Myers 1990).

Both Monserud and Marshall (1999) and Kershaw and Maguire (1995) found that branch diameter was the best predictor of branch biomass and that branch locations on the bole were important. Branch basal diameter is proportional to branch basal area; however the assertion of the pipe model that sapwood area is related to leaf area (Shinozaki et al. 1964) may explain why our models were slightly better using basal area for both the individual-branch models and the whole-tree models in terms of amount of variability explained than the models we examined using branch basal diameter. Sapwood area was not measured in this study; instead we assumed that it was proportional to basal area. It is possible that our equations may have been able to account for more variability without this assumption and using direct measurements.

The equations produced in this research explained at least 64% of the variability in response variables for individual-branch quantities depending on the response variable and predictor variables used and also at least 76% of the variability in the whole-tree quantities, again depending on the response variable and predictor variables included in the equations. Individual-branch biomass was strongly related to the basal area of the branch and branch length for predictions for all of the individual-branch quantities that were examined in this study. Branch location measured as the distance between the top of the tree and the insertion height of the branch was also a significant predictor of the biomass and leaf area quantities estimated; however the relationships were less strong than those using branch length. These findings support previous studies of branch allometry, where branch location was also a significant predictor (van Hees and Bartelink 1993; Berninger and Nikinmaa 1994). Branch basal area alone was the best possible predictor of branch level needle biomass for grand fir; no other potential predictor variables within our dataset could be found to improve the model.

Both grand fir and western hemlock are shade tolerant species, retaining long crowns within deep canopies (Graham 1988, Minore 1979). These results follow others (Garber and Maguire 2005, Maguire et al. 1994) who have shown strong relationships between branch basal diameter and tree height, in that branch biomass and wood biomass can be well explained by branch basal area and the location on the bole. The shade tolerance of western hemlock and its propensity to retain branches deep in the crown with little leaf biomass (Minore 1979, Bond 1999) may be related to the better predictive ability of branch length for wood biomass. All three species have the ability to thrive in deep canopies; therefore the change in needle morphology from the top to the bottom of the crown could be related to the predictive ability of the length of the branch, which also varies with location within the crown.

For both the individual-branch and whole-tree models, both individual intercepts and slopes were required for the three species in this study to account for variation in leaf area. The increase in leaf area for western hemlock was highest for an increase in branch basal area in the individual-branch models, and for an increase in tree basal area for the whole-tree models. The increases in leaf area for grand fir with increases in individual branch and tree basal area was intermediate, and the lowest increases in leaf area per unit basal area occurred in Douglas-fir. Using the ability to survive in a low intensity light environment as a definition of shade tolerance (Minore 1979), our results suggest that the rate of increase in leaf area per unit basal area follows the shade tolerance of the species.

On average, the branch basal area alone was able to account for most of the variability in dry branch biomass and leaf area for the individual-branch models, while the addition of branch length, distance from the top of the tree and information about branch foliage only accounted for a slight addition to the variation explained. With such a small amount of increased explanatory ability realized from the additional measurements, branch basal area alone should be sufficient to estimate biomass and leaf area estimates for these three species in most cases, and the costs of obtaining insertion heights, branch lengths or foliated branch lengths did not offset the model improvements in this study.

The equations to predict whole-tree branch biomass, branch wood biomass, and leaf area were able to predict similar amounts of variability from the predictor variables to what others have shown (Jenkins et al. 2003, Monserud and Marshall 1999). In addition to tree basal area, crown ratio was the only other potential predictor variable that was a significant predictor in addition to tree basal area. Sapwood area was not measured in this study either at crown base or breast height. It is likely that the models would explain more of the variability in leaf biomass and leaf area had sapwood area been included in the model since it has closer relationships to crown characteristics than diameter at breast height (Monserud and Marshall 1999, McDowell et al. 2002).

Based on the results of this research in which the differences in the amount of variation explained between the full and reduced models for individual branch biomass is small, it does not appear that the additional time and expense necessary to measure branch length and foliated length is critical in obtaining prediction equations for any of the branch characteristics that were included in this study. Obtaining observations of branch basal diameter alone will allow for much simpler parameter estimates. Predictions for whole-tree branch biomass and leaf area components, however, were greatly improved by inclusion of crown ratio with basal diameter of the tree. In the past these requirements would have been difficult to achieve but with advances in forest measurement technologies such as the availability to inexpensively measure a large number of tree heights with Lidar, these equations can provide improved estimates of crown biomass for these three species than has been available in the past and potentially at larger scales.

The equations produced in this study are important in that they provide biomass equations for a range of stand densities and species mixes that naturally occur within north Idaho forests, for species with a range in shade tolerance. They are constructed from variables that are relatively quick and inexpensive to measure, so the parameters can be adapted for process models, as well as being inserted into existing growth and yield models with their empirical origins. For more robust biological relationships, branch basal area and tree basal area rather than branch basal diameter and diameter at breast height were used as the primary predictors in the resulting in a set of simple but effective predictive equations.

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Chapter 2 A Nonlinear Mixed Effects Model Predicting Branch Basal Diameter for *Abies grandis*, *Pseudotsuga menzeseii*, and *Tsuga heterophylla* in Northern Idaho, USA.

Abstract

Branch diameter is an important tree characteristic because it is strongly related to branch biomass, it has a large effect on wood quality, and it can be a critical factor in modeling crown dimensions for both process and empirical models. A nonlinear mixed effects model was developed to predict branch basal diameter (mm) from the distance from the branch to the top of the tree for grand fir (*Abies* grandis (Douglas ex D. Don) Lindl), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca*), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in northern Idaho, USA based on observations representing range of variability in mixed species stands. An asymptotic model was used to describe the nonlinear relationship with an autocorrelation term to account for the lack of independence in the residuals. As indicated by both the significance of the parameter estimates and plots of predicted values overlaid onto observed values, these models are sufficiently accurate to predict branch basal diameter in grand fir, Douglas-fir, and western hemlock. These models provide improved estimates of tree biomass for carbon accounting and improved crown biomass estimations for use in empirical modeling efforts.

Introduction

There is an ever increasing interest in quantifying whole-tree value, of which biomass is an important component (Field et. al. 2008). Estimates of forest biomass are also needed for tracking changes in carbon stocks (Ketterings et. al. 2001) and better quantification of branch biomass may help improve estimates of carbon storage in forest ecosystems (Dewar and Cannell 1992). As more knowledge is gained about forest ecosystem processes, more accurate quantification of individual components, such as branch biomass and branch volume become necessary (MacFarlane 2010). The biomass contained in tree branches is a factor in debates over efforts to sustainably extract more biologically renewable fuels from forests (Egnell and Valinger 2003). Branch diameter estimates are important for estimating wood quality as knot size is considered a defect in structural lumber (Samson 1993) and veneer (DeBell et al. 1994).

Quantifying branch biomass by measuring every branch in a tree is difficult, time consuming and expensive, therefore model-based or model-assisted solutions are a reasonable approach to obtaining accurate estimates for branch biomass. A good alternative to making detailed branch level biomass measurements is to use a model that first estimates branch diameter from the location of branch insertion. Then, since the relationship between branch diameter and branch biomass is strong (Monserud and Marshall 1999, Jenkins et al. 2003, Abbott et al. *in review*), an equation yielding branch diameter from a simple tree level predictor such as the location of branch insertion could further result in accurate crown biomass estimates.

Constructing models to obtain branch diameter estimates are not new. Maguire et al. (1999) estimated branch diameter using an allometric equation relating branch diameter to depth in crown and relative density (Curtis 1982) estimated by plot basal area/quadratic mean diameter, finding a monotonic increase in branch diameter with increasing depth into the crown for second growth Douglas-fir *(Pseudotsuga menziesii var menziesii)*. Colin and Houllier (1991) used segmented polynomial models for maximum branch diameter in Norway spruce related to depth into crown, and found that when the widest part of the crown was above the base of the live crown, maximum branch diameter exhibits a peaking behavior. Maguire et al. (1994) and Roeh and Maguire (1997) also used segmented polynomial models for maximum branch diameter in Douglas-fir. While branch diameter prediction equations based on insertion height have been developed for Douglas-fir in other studies (Maguire et al. 1999, Garber and Maguire 2005, Weiskittel et al. 2007), predictions are more limited for grand fir and western hemlock, and for all three species in the mixed conifer stands of varying ages and densities.

Diameter at breast height (DBH) has been suggested to be adequate for whole tree biomass estimates at either local or regional levels, however others have shown that height must be included for larger scale estimations (Honer, 1971, Crow 1978). Since there are established equations predicting tree height from DBH (Curtis 1982, Flewelling 1994, Jayaraman and Lappi 2001), subsequent equations that directly estimate branch diameters from height and then branch biomass from diameter can be combined for a potentially more accurate estimation of whole tree biomass.

Although bias can be introduced when measuring tree heights using LiDAR, (Anderson et al. 2006, Sterenczak and Zasada 2011), the bias can be estimated and thus used to estimate tree height and crown depth. Using the established relationships between height and diameter, it may be possible to predict DBH from height, and aboveground biomass from LiDAR based measurements of tree height and canopy depth when coupled with predictions of branch diameter from insertion point and thus branch biomass. Therefore it is important to establish and test models that predict branch diameter from crown position for several tree species under a variety of conditions.

Grand fir (*Abies grandis* Douglas ex D.Don) Lindl.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca*), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) were selected as study species for this research due to their abundance in the northwest United States and particularly in north Idaho as well as their commercial value. Grand fir can be an indicator of productive forest sites (Graham 1998, Hall 1973). All three of these species are important commercial species, used for structural lumber and veneers. Douglas-fir can occupy a variety of site conditions (Graham 1988), yet estimates of needle biomass as well as branch wood biomass may add to knowledge regarding site productivity. Since western hemlock is a commonly used tree for veneer, information about branch biomass and locations improves knowledge about wood quality. Since knot size is an important component of wood quality for both lumber and veneer grades, the ability to attain realistic estimates of both branch diameter and the location of insertion from trees grown under a variety of naturally occurring conditions is useful for timber production planning. Branch diameter equations can also be incorporated into programs that include wood quality into economic analyses such as DEPRUNE (Fight et al. 1987) and TREEVAL (Briggs 1989).

The three species included in this research represent a range of shade tolerance (Minore 1979); western hemlock tends to be the most shade tolerant and Douglas-fir is the least shade tolerant. This research will provide key information on the influence of shade tolerance on branch diameter predictions both due to the species selected and the sampling of locations with a mix of naturally occurring species.

The objective of this study was to develop a simple yet robust prediction model for each of the three species that will estimate the basal diameter of branches based on the insertion height along the bole using a nonlinear mixed effects model. Nonlinear models have an advantage over log transformed linear models in that they are fit directly to the observations, so there is no bias to account for when using the model for predictions (Baskerville 1972). To increase the broader applicability of the models, they were developed using a range of tree species with varying shade tolerance, tree sizes, and stand densities.

Materials and Methods

Study Area

Data used in this study were collected in two locations in northern Idaho: the Priest River Experimental Forest (PREF) and the University of Idaho Experimental Forest (UI) (Figure 2-1). PREF is a 2,590 acre area managed by the US Forest Service and is located near the town of Priest River, Idaho. UI covers 3,237 acres and is northeast of Moscow and the University of Idaho. PREF has more variable terrain ranging from 680 – 1,800 m than UI (1,000 – 1,519 m), and has a higher average annual precipitation (810 mm) than UI (686 mm). The tree species are similar within the two locations with the exception of THSE, which is effectively absent from UI.

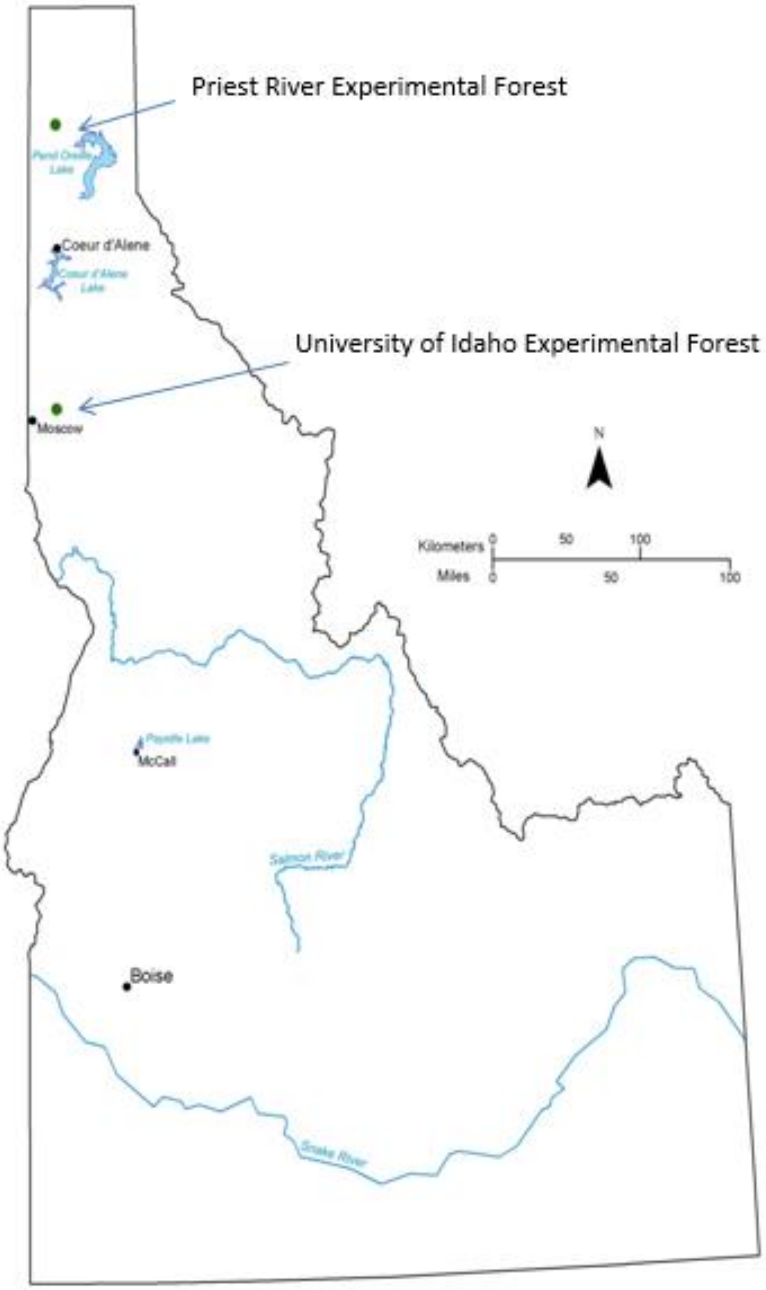

Figure 2-1. Map of Idaho showing the two locations in northern Idaho where the three species were selected for sampling.

Field Data Collection

Data were collected during the 2005 summer sampling season. Grand fir, Douglas-fir and western hemlock were chosen for destructive sampling from PREF and UI.

Plots were chosen to represent the broad range of variability that occurs in mixed species stands with varying ages in north Idaho. Ideal plots contained all three of the study species among other species with a minimum of two of the three species.

Stands were purposively chosen to be likely to include the mixture of species based on visual observation and personal communication from managers. Within a stand, plots were chosen by randomly selecting a compass bearing, then moving 30 m into the stand from the edge. If the potential plot contained at least two of the three species of interest, we established a plot for destructive sampling. If the plot did not contain at least two of the three species, we moved 30 m along the same bearing and again checked for the species mix. If three plots were checked on the same bearing without finding the necessary species mix, a new starting location was identified and the process was repeated.

Trees were selected for sampling using a variable radius plot, and limited to only those trees with DBH between 10 and 50 cm to develop equations for a range of larger trees. A 4 m^2 ha^{-1} BAF prism was used to tally trees within the plot beginning with the first tree to the right of north and continuing clockwise. DBH was measured along with species for each tree in the tally. The diameters were ordered and the median diameter was noted for each plot. For each of the species of interest within the plot, the first tree (from north) larger than the median was sampled, and the first tree smaller than the median was sampled. Not all plots had trees both larger and smaller than the median DBH of each of the study species, in which case the tree with the median DBH itself was selected for sampling. In plots with an uneven number of trees in the tally, we did not include the tree with median DBH as a sampled tree for consistency.

The selected trees from each site were felled for destructive sampling following the methods of Monserud and Marshall (1999). In summary, whole tree measurements included total height of tree, height to crown base from breast height and crown length.

The crown base was defined as the lowest whorl with at least two live branches such that there were no dead whorls above that whorl. Above the crown base, branch diameters were measured with calipers in each crown quarter, and noted whether the branch was dead, live or broken and its height from breast height on the bole. Height to crown base and height of branches along the bole were later converted to total height to crown base and total height to branch insertion by adding 1.37 m to each measurement. All of the branches within each crown quarter were measured to obtain branch basal diameter (mm). Basal diameter was measured 1 cm above the branch collar for accuracy and consistency. A total of 58 trees were destructively sampled for analysis with 7,945 branch basal diameters (Table 2-1).

Table 2-1. The number of trees and individual branches for grand fir (ABGR), Douglas-fir (PSME) and western hemlock (TSHE) selected for destructive sampling at each location (PREF and UI).

Area	ABGR	PSME	TSHE	Total
PREF	3 (440)	15 (2178)	14 (1533)	32 (4151)
UI	11 (1567)	15 (2227)	-	26 (3794)
Total	14 (2007)	30 (4405)	14 (1533)	58 (7945)

Note: Number of branches selected is in parentheses.

Analysis

Due to the nonlinear form of the relationship between branch basal diameter and the distance to branch insertion on the bole from the top of the tree, a locally weighted scatterplot smoothing (LOESS) curve (Cleveland 1979; Cleveland and Devlin 1988) was used to suggest a nonlinear form for estimation. The mixed effects aspect of the model chosen has the ability to account for the correlations within individual trees and was also used to investigate the potential additional correlation between trees sampled within the same plot versus trees sampled from other plots. Likelihood ratio tests were used to determine whether one model could adequately represent all the trees for each species or separate models for each area sampled was necessary.

Whether the parameters of the selected curve should be included in the models as random effects was assessed by examining the correlations between parameters in the full model, using a diagonal variance-covariance structure to avoid over parameterization. Once the important random effects were determined, we used likelihood ratio tests to choose the variance-covariance structure that best fit the data. Continuous first order autoregressive terms were tested and when likelihood ratio tests indicated that the models were improved, they were included. When heteroscedasticity was detected based on residual plots, the equations were weighted by a power variance function of the relative distance from branch insertion to the top of the tree. The variance function for this analysis is defined as $s^2(v) = |v|^{2\delta}$ where v is the primary predictor variable, $s^2(v)$ = is the variance function evaluated at v, and δ is the variance function coefficient (Myers 1990.)

The best models to explain branch basal diameters from insertion height on the tree were chosen based on overall fit, significant effects in the model, and having the assumptions for nonlinear modeling met (normally distributed and independent residuals).

Results

Based on the LOESS curves for each of the tree species at both sampling locations, an asymptotic nonlinear curve represented the curvilinear relationship and was selected to predict branch diameters from location on the bole (Figure 2-2). A random effects asymptotic model is used to model a response that approaches a horizontal asymptote as values of the predictor variable increase, and can be written as

$$Y = \Phi_1 + (\Phi_2 - \Phi_1) \exp[-\exp(\Phi_3)x] + \varepsilon \qquad [1]$$

where Φ_1 is the random component of the asymptote (asym), Φ_2 is the random component of the intercept ($y(0)$), and (Φ_3) is the random component of the logarithm of the rate constant (lrc). The logarithm is used to ensure positivity of the rate constant so that the model does approach an asymptote. Although the shorter trees did not always show a clear asymptote, we assumed that the relationship was still reasonable and that the data for the younger trees simply represented the lower sections of the curves.

Based on likelihood ratio tests used to determine whether sampling location was a significant factor in the models, all the trees for both grand fir and Douglas-fir were pooled over the areas and analyzed as a single dataset for each species.

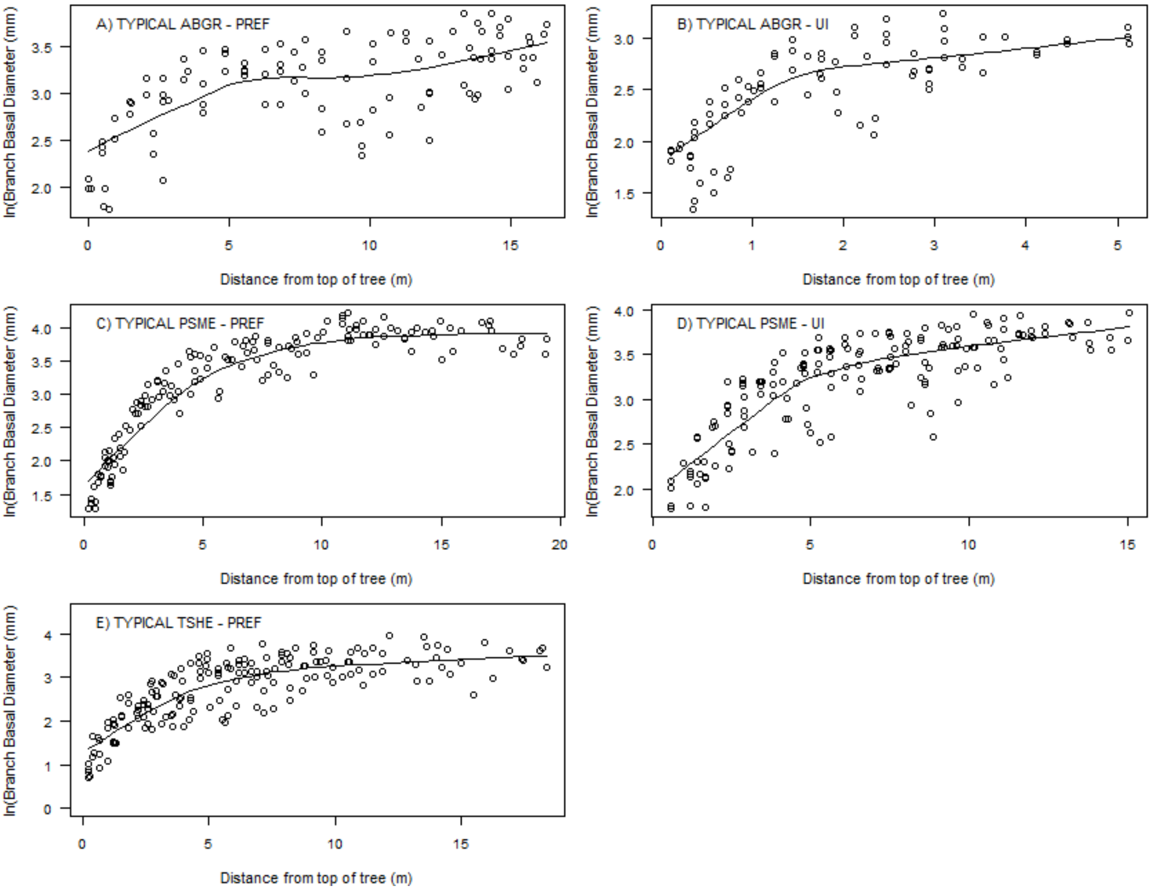

Figure 2-2. Scatterplot of ln(branch basal diameter (mm)) against the distance from the top of the tree for A) a typical grand fir (ABGR) at the Priest River Experimental Forest (PREF), B) a typical grand fir (ABGR) at the University of Idaho Experimental Forest (UI), C) a typical Douglas-fir (PSME) at PREF, D) a typical PSME at UI and E) a typical western hemlock (TSHE) at PREF. Predicted ln (branch basal diameters (mm)) based on the LOESS curve are indicated by the line through the data.

The model for grand fir did not have a significant random intercept; however both the asymptote and lrc were significant for the random effects ($p < 0.0001$). Both Douglas-fir and western hemlock had significant random effects for all three parameters ($p < 0.0001$) (Table 2-2). A general positive definite matrix was sufficient to account for the variance-covariance structure for all three species when only the significant random effects parameters for the asymptotic curve are included in the model and the data are pooled over both areas.

Autocorrelation of the data was investigated since the branches on individual trees lack independence when the autocorrelation plots for grand fir and Douglas-fir suggested significance at lag 1 indicating the branch diameters were related to the diameter of the previous branch as well as to the height of the tree. Adding the autocorrelation term improved the model for these two species, and the autocorrelation plots for the adjusted models did not indicate its presence; therefore the equations for grand fir and Douglas-fir include an additional parameter estimate to account for it (Table 2-2).

The final models for both Douglas-fir and western hemlock required that the one additional parameter estimate be included; an exponent for a power variance term to correct for heteroscedasticity in the data. The model for grand fir was not improved by the weighted variance function (Table 2-2). All three fixed effects parameters for the asymptotic model were highly significant for all three species.

Table 2-2. Parameter estimates and p-values in the asymptotic model $Y = \Phi_1 + (\Phi_2 - \Phi_1) \exp[-\exp(\Phi_3)x] + \varepsilon + \Psi$ for grand fir (ABGR), Douglas-fir (PSME), and western hemlock (TSHE), pooled over both the PREF and UI sampling locations.

Species	Φ_1	Asym	Φ_2	*y(0)*	Φ_3	*lrc*	Ψ	δ
ABGR	3.39**	3.38**	1.65**	1.64**	-0.96**	-0.96**	0.39**	ns
PSME	3.60**	3.58**	1.41**	1.39**	-0.86**	-0.85**	0.23**	-0.41**
TSHE	3.63**	3.58**	1.03**	0.99**	-1.06**	-0.97**	ns	0.28

Note: Φ_1, Φ_2, and Φ_3 are the random effects parameter estimates for the asymptote, intercept, and log(rate constant) in the asymptotic model. Asym, *y(0)* and *lrc* are the estimates for fixed effects in the asymptotic model. Ψ are the parameter estimates for the autocorrelation term, and δ are the parameter estimates for the weighting exponent in the variance function.
** indicate significance at $p < 0.001$.

By overlaying the scatterplots of the observed ln(branch basal diameters) plotted against the distance between branch insertion height and the top of the tree with a line indicating the predicted values (Figure 3), there is evidence that the models were able to capture the form of the relationship.

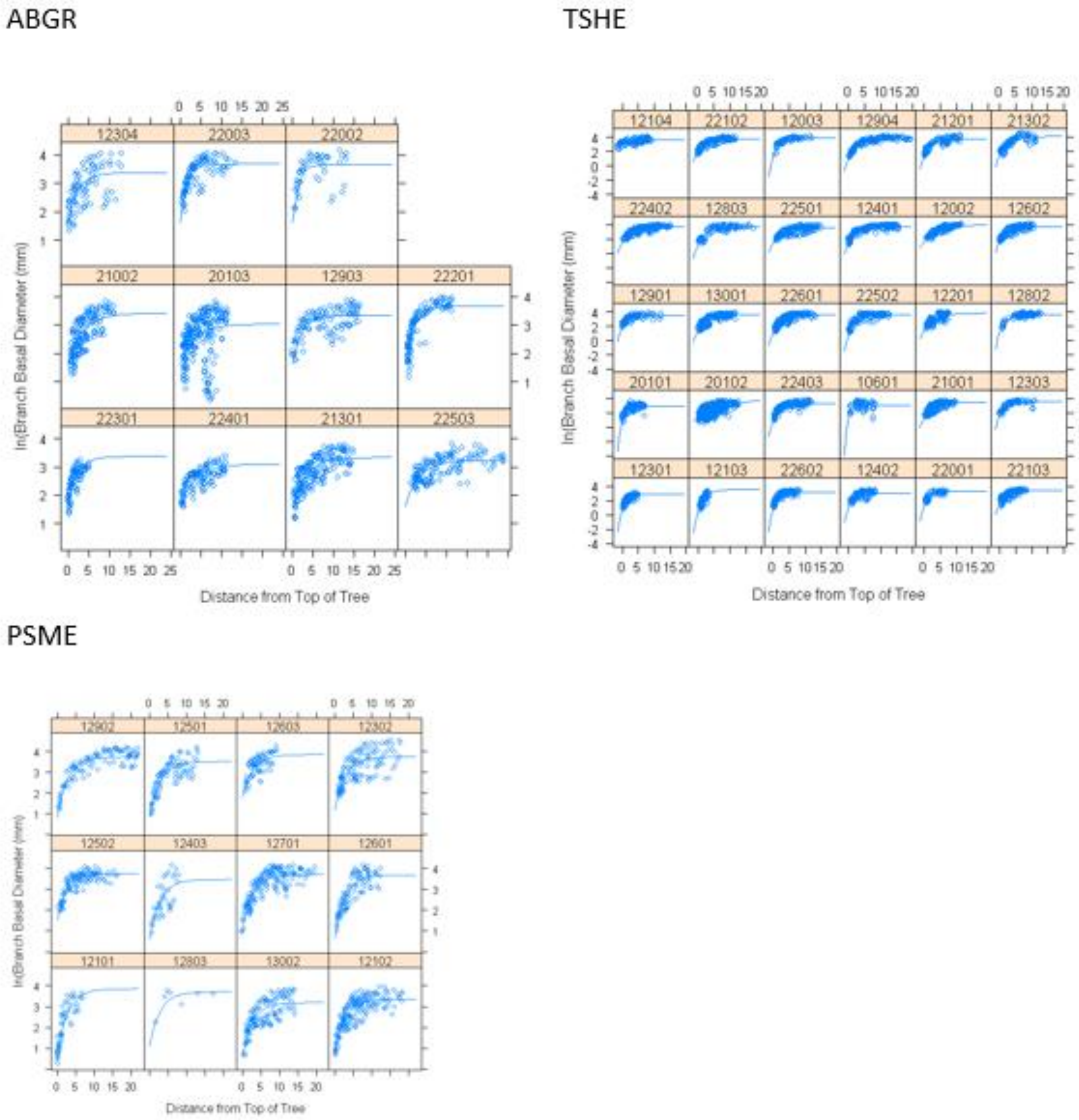

Figure 2-3. Scatterplots for the individual trees in the dataset overlaid with the predicted values for ln (branch basal diameter (mm) against distance between insertion height and the top of the tree. Panel A) are the plots for the individual grand fir (ABGR), panel B) are the plots for the individual Douglas-fir (PSME), and panel C) are the plots for the individual western hemlock (TSHE).

Discussion

A nonlinear model was developed for grand fir, Douglas-fir, and western hemlock that represents the relationship between branch basal diameter and insertion height on the tree. The model accounted for most of the variability in branch basal diameter with random effects due to the individual trees but was also strongly significant for the fixed parameters, resulting in a robust model that can be used for stands with mixed species, varying ages, and varying densities.

The form of the equations developed in this research were similar those found in previous work (Maguire et al. 1999, Garber and Maguire 2005, Weiskittel et al. 2007) in that they all account for the nonlinear relationship between branch diameter and insertion height, however the previous work relied on logarithmic transformations and allometric scaling rather than the nonlinear approach used here. Our equations resulted in biologically realistic estimates of branch diameter (Figure 3).

The additional structure needed to predict the branch basal diameters for Douglas-fir may be necessary due to an incomplete understanding of branch diameter growth (Weiskittel et al. 2007). Kozlowski and Pallardy (1997) suggest that branch diameter growth is likely due to a combination of site conditions such as water potential and light interception, and Makinen (2002) has reported that light availability may be the primary factor influencing diameter growth and in certain conditions wind may also be a factor (Watt et al. 2005). Both Douglas-fir and western hemlock are more variable in their crown shape and condition than grand fir (Kershaw and Maguire 1995), which may also explain why the autocorrelation term was not significant for western hemlock. Their propensity to hold living branches for long periods of time with little foliage is shown in the increased variance in branch diameter as the branches occur lower in the crown (Figure 2-3) by the significance of the weighting exponent in the models for Douglas-fir and grand fir (Table 2-3).

Sloughing of dead branches is extremely slow in grand fir, in second-growth Douglas-fir, and in western hemlock (Kershaw 1995). Fahey (1991) found that wood quality was affected in nearly all stands less than 80 years of age due to the persistence of the dead branches. With the ability to estimate branch diameter at the base of the live crown, estimates of branch size indices can be made for logs containing the lowest live whorl. The branch size indices would result in improved estimates of quality of the logs based on the crown length of the tree.

Since the relationships between branch diameter and branch biomass are strong (Monserud and Marshall 1999, Jenkins et al. 2003, Abbott et al. *in review*) the equations for branch diameter resulting from this research combined with existing branch biomass equations have the ability to produce improved estimations of crown biomass and leaf area for the three species studied in this research. Improved estimates for forest biomass can be obtained using LiDAR to estimate a large number of tree heights and crown depth (McCombs et al. 2003, Popescu and Wynne 2004) relatively inexpensively, which can then be used with the equations for branch diameter here along with current biomass equations for landscape level biomass estimations.

Various geometric shapes have been used to describe the form of tree crowns although they are stochastic in nature (Biging and Gill 1997), however when viewed from above, the crown can be approximated by a circle. Doruska and Burkhart (1994), in their investigations of the circular distributions of branches within loblolly pine crowns found that in most cases a circular uniform distribution was appropriate to approximate branch distributions within crowns for trees that have been measured with Lidar. Coupled with more detailed models of branch distributions and dimensions such as our equations can provide, it may be possible to improve large scale biomass estimates that use a geometric form rather than a representation of the natural form of the crown.

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Chapter 3 Analysis of Site Type on Douglas-fir Allometrics

Abstract

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) biomass data from two separate studies were validated and pooled for use in examining whether a regional allometric equation for estimating crown biomass is sufficient or whether site-specific equations are required. Soil parent material was the basis for stratifying the sites in terms of soil nutrition. To account for potential confounding of site effects by climatic regime, a suite of climate variables were selected using hierarchical cluster analysis and were included in the modeling as predictor variables. While diameter at breast height (DBH) accounted for most of the variability in crown biomass (R^2 = 0.76), both soil parent material and climate variables added modest yet significant improvements to the model. The results suggest that interactions may be present between soil parent material and climate variables, however the sites from which the trees sampled for the two studies included in this research did not have enough variability in the climate variables to allow for full exploration of the interactions.

Introduction

Knowledge about tree crowns is central to predicting tree- and stand-level growth and structural dynamics. Crowns absorb both carbon dioxide and light, providing two key components for photosynthesis, which is the driving process for carbon accretion (Caspersen et al. 2002; Schmiel et al. 2000). Thus, the quantity of crown that a tree supports is strongly related to its annual growth potential. Dimensions of tree crowns are also central to predicting stand-level processes such as fire effects (Cruz et al. 2012), precipitation interception (Veliz-Chavez et al., 2014), radiation transfer (Widlowski, J.-L. et al. 2014), solar radiation reaching the soil surface (Arx et al. 2013) and snowmelt dynamics (Ershov et al. 2016). Forest biomass is a component of climate and environmental modeling, and standing forest biomass is a critical component of the global carbon cycle.

In the Northern Idaho variant of the Forest Vegetation Simulator (FVS), the crown dynamics model predicts change in the proportion of the bole that supports the live crown. The crown model is based on an empirical equation that was constructed using inventory data, and it predicts crown ratio as a function of site, tree size, competitive status and stand density (Hatch 1980). Periodic crown change is estimated by differencing crown ratio predictions that are made at the start and at the end of a time period, and adjusting the actual initial crown ratio accordingly.

Detailed crown descriptions are produced within the Fuels and Fire Effects (FFE) extension of FVS, including crown biomass, branch size and other attributes related to fire behavior. Crown width is predicted using empirical equations (Crookston, in prep), and other crown attributes are largely derived from tree size, stand density, and predicted crown ratio. Spatial canopy structure is not predicted. Better models of crown processes would improve several submodels within the structure of FVS, by making them more realistic.

The quality of wood in the tree bole, in terms of number, location, and size of knots, is influenced by crown structure dynamics such as the number of branches, size of branches, crown recession timing and rate, and related ecophysiological processes (Brazier 1977). An improved crown model would therefore improve predictions for product valuation and economics. Submodels areas such as defoliation effects of pest attacks, leaf area index estimates, improved mortality predictions, and pruning would also benefit from improved estimates of crown biomass.

Estimates of forest carbon sequestration are required for participation in both international and domestic carbon trading programs. With increasing focus on carbon sequestration, meathods used to estimate aboveground biomass are being carefully examined since the estimates are critical components of greenhouse gas dynamics (de Jong, 2001), are required to predict potential carbon stocks (Coomes et al. 2002), and are used to predict the amount of carbon sequestered in tree biomass (Specht and West, 2003). Biomass equations are necessary to convert forest inventory measurements into regional scale carbon sequestration estimates, and site-specific equations are limited as to the range of appropriate extrapolation into regional estimates. Model development at the site-specific scale is expensive and time consuming, however the increased accuracy may be necessary for finer scale biomass analysis (Zhou and Hemstrom, 2010), and the selection of a regional versus a site-specific model may further result in a biased understanding of aboveground biomass estimates (Zhao et al. 2012).

However, a limitation of site-specific biomass equations is that the variance of the parameters may not be included, and internal consistency may not be present (Ung et. al. 2008). The wider range of observations used to develop regionally based models can increase the predictive ability of the biomass equations. Regional models that rely primarily on diameter measurements may be more accurate than site-specific equations that depend on more difficult to measure predictor variables that could have a higher measurement error associated (Zhao et al. 2012). Effective regional models avoid the time-consuming and costly process of the destructive sampling necessary for site-specific equations when the regional models are developed from a broad range of locations with the the region of interest.

The ability of terrestrial ecoystems to sequester carbon is constrained by resource availability, and soil nutrients are a key resource. Soil parent material has been shown to have an impact on nutrient limitations. Augusto et al. (2017), using global data on soil fertility and plant growth, found that P limitation was driven by soil parent material, and that the connection between the actual P pools in soils and the acidity and P richness of the parent materials. Parent materials also influence soil acidity, particularly pH, fractions of aluminum and hydrogen, and their effects on soil organic matter. Increased acidification in soils has been shown to have a positive influence on the accumulation and stabilization of organic material in soils (Gruba and Socha 2016). Plant-induced weather and complexation of metals increases total acidity in soil and may affect the stability of soil organic material (Mueller et al. 2012). In Douglas-fir, competitive relationships have been shown to be related to rock type quantified by tree size and stand density (Shen et al. 2000).

The specific objectives in this research are to test the hypotheses that 1) there is a significant difference in predictive ability between generalized biomass models for Douglas-fir (*Psuedotsuga menziesii* (Mirb.) Franco*)* and site-specific tree biomass models; and 2) that site-specific biomass models for Douglas-fir can significantly improve the biomass estimates over existing regional biomass models. An additional objective is to develop protocols for creating multi-species, site-specific biomass models across the Intermountain West.

Methods

Douglas-fir trees were destructively sampled in seven different locations in the Inland Northwest (Figure 1) as part of two different studies. Five of the sampling sites were selected from a set of research sites that had been established by the Intermountain Forestry Cooperative (IFC) for a long-term soil-site nutrient management study (IFC Study). Forests in the Intermountain West had been stratified by soil temperature and moisture regimes and geologic formations that had been derived using digital surveys of the Natural Resource Conservation Service and the United States Geological Survey. All of the IFC sites were located within the Xeric moisture and frigid temperature regime. The sampling sites were located in areas with one of three soil parent materials: granite, basalt, or metasedimentary to examine variation in biomass related to parent material.

Two additional sampling areas were located on the US Forest Service Priest River Experimental Forest and the University of Idaho Experimental Forest in northern Idaho for a study (USFS Study) with the objective of developing biomass equations in mixed species stands to include the broad range of variability that occurs in mixed species stands with varying ages in northern Idaho (USFS). Ideal plots contained all three of the study species (grand fir (*Abies grandis* Douglas ex D. Don Lindl.), Douglas-fir, and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)) among other species with a minimum of two of the three study species. The location of the sites for both studies varied between United

States Forest Service (USFS), Idaho Department of Lands (IDL) and Bennett Lumber Products (Figure 3-1).

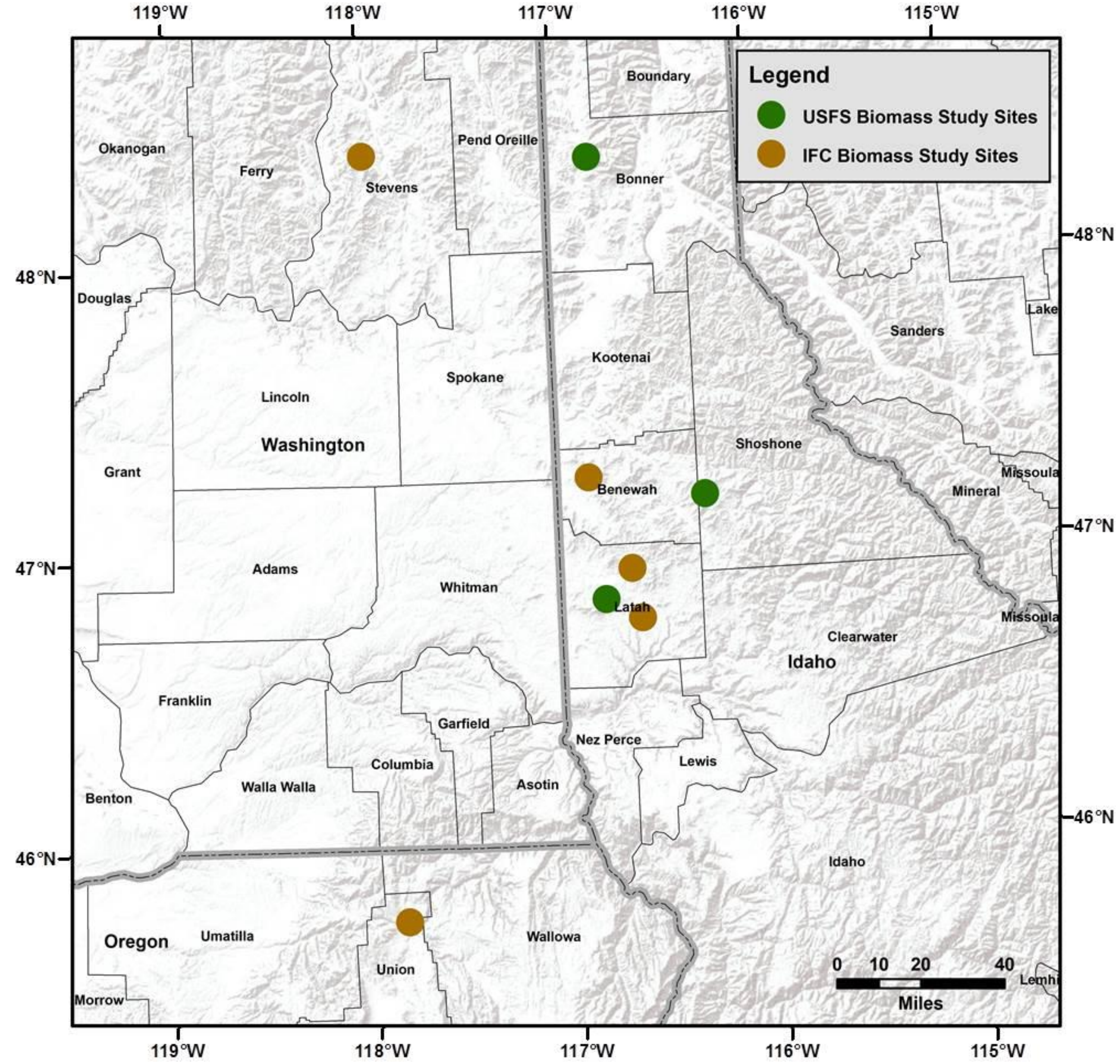

Figure 3-1. Map showing the site locations for Intermountain Forestry Cooperative (IFC) Biomass Study Sites and USFS Biomass Study Sites.

Prior to sampling for the IFC study, a pre-harvest forest inventory was conducted on each site to record stand density index, stem diameter distribution, and bole and crown measurements. Those indices were used to determine sample sizes and to develop biomass model parameter selection (Avery and Burkhart 2002; Brown 1978; Monserud and Marshall 1999). Each inventory was used to develop size categories based diameter at breast height (DBH) into 3 - 5 size classes. Up to three trees were selected from each size category for detailed measurements. The selected trees were felled, de-limbed, and then cut into mechantable length bole sections. Biomass measurements were taken in the field for five categories: 1) foliage, 2) live branches, 3) dead branches, 4) stemwood, and 5) bark. Green weights were measured in the field for each of these categories, and subsamples from each category were returned to the laboratory for detailed analysis of dry weights and wood density. For this analysis, we will focus strictly on crown biomass measurements.

Stands for the USFS study were purposively chosen to be likely to include the mixture of species based on visual observation and personal communication from managers. Within a stand, plots were chosen by randomly selecting a compass bearing, then moving 30 m into the stand from the edge. If the potential plot contained at least two of the three species of interest, we established a variable radius plot for destructive sampling. If the plot did not contain at least two of the three species, the next potential plot was located 30 m along the same bearing and checked for the requisite species mix. If three plots were checked on the same bearing without finding the necessary species mix, a new starting location was identified and the process was repeated.

Trees were selected for sampling using a variable radius plot, and limited to only those trees with DBH between 10 and 50 cm to develop equations for a range of larger trees. A 4 $m^2 \cdot ha^{-1}$ BAF prism was used to tally trees within the plot beginning with the first tree to the right of north and continuing clockwise. DBH was measured along with species for each tree in the tally. The diameters were ordered and the median diameter was noted for each plot. For each of the species of interest within the plot, the first tree (from north) larger than the median was sampled, and the first tree smaller than the median was sampled. Not all plots had trees both larger and smaller than the median DBH of each of the study species, in which case the tree with the median DBH itself was selected for sampling. In plots with an uneven number of trees in the tally, we did not include the tree with median DBH as a sampled tree for consistency.

The selected trees from each site in the USFS study were felled for destructive sampling following the methods of Monserud and Marshall (1999). In summary, whole tree measurements included total height of tree, height to crown base from breast height and crown length. The crown base was defined as the lowest whorl with at least two live branches such that there were no dead whorls above that whorl. Above the crown base, all branch diameters were measured with calipers in each crown quarter, and noted whether the branch was dead, live or broken and its height from breast height on the bole. Insertion height was recorded for all branches along the bole. All of the branches within each crown quarter were measured to obtain branch basal diameter (mm). Basal diameter was measured 1 cm above the branch collar for accuracy and consistency.

Analysis

Observations for the IFC study included the total green crown biomass for each of the selected trees and equations were developed for whole-tree crown biomass directly.

Before the crown biomass observations from USFS study were pooled with those from Study 1, several validations were performed. For the USFS study, allometric equations were first developed for individual branches to relate the biomass of each branch to its basal area measured 1 cm from the insertion point on the bole. The sample trees collected during the Summer 2005 sampling season were used for the initial branch-level equations. The equations were validated using observations collected for the same study but in the Summer 2004 sampling season.

The individual-branch biomass equations were used to predict branch biomass for each of the selected trees in the USFS study using the observed branch diameters, converted to branch basal area, from the selected trees in the 2005 sampling season. Whole-tree crown biomass models were then developed from the tree- and stand-level variables, using the predicted branch biomass from the individual-branch equations. The whole-tree equations developed with the 2005 trees were validated with the trees selected in the 2004 sampling season.

As a final stage of validation prior to pooling the two datasets, the crown biomass equations resulting from the USFS study were used to predict crown biomass for the sample trees collected in the IFC study.

Whole-tree allometric equations were developed for crown biomass using the pooled dataset. Transformations were applied to both biomass and tree-level predictor variables to ensure that the homogeneity of variance condition necessary for using a linear model was met. To evaluate whether site-specific allometric equations or single regional equation would perform better, subsurface soil parent material was included in the modeling process, as were several variables to represent climatic differences.

Cluster analysis was used to reduce the number of climate variables examined in the allometric equations using hierarchical clustering. To account for varying distances between annual, seasonal, and monthly measures of variables (Nocke et al. 2004), the single variable within each cluster with the highest correlation to the centroid of the cluster was retained as a potential predictor variable in the crown biomass equations. To develop the crown biomass models, diameter at breast height was included as a predictor variable in each of the candidate models. Soil parent material (SPM) was considered as a predictor variable and included in the models as an indicator variable, and five climate variables were identified through the cluster analyses. The cluster analysis used to reduce the number of climate variables examined in the allometric equations suggested that five clusters were able to account for a large amount of the correlation among variables. The goal of the cluster analysis was to reduce the dimensionality of the climate variable dataset into a small number of individual variables with high correlations with the cluster centroids while retaining biological reasonability. A total of five variables were retained for use in the modeling process: Hargreave's moisture deficit (CMD), mean annual radiation (MAR), mean annual precipitation (MAP), effective frost free period (eFFP), and degree days above 5° C (DD5). The r^2 values between these five variables and the centroids of the identified clusters were 0.9791, 0.9933, 0.9847, 0.9299, and 0.9845 respectively. These five potential predictors were used so that a simple and straightforward prediction model could be developed. Two-way interactions between the climate variables were also were considered during the model development.

The climate variables for the sites included in this research did not contain a large amount of variability between sites, which may be a factor in the unexplained variability in the models resulting from the analysis (Figure 3-2).

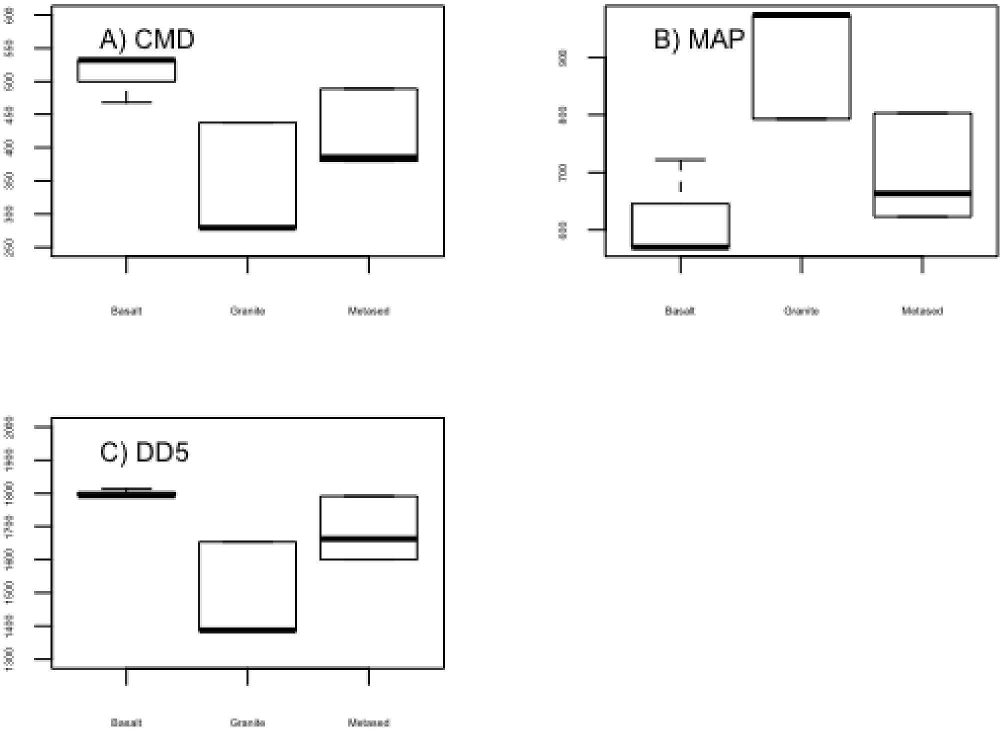

Figure 3-2. Boxplots showing the range of the climate variables within each of the three soil parent materials. A) is Hargreave's moisture deficit (CMD), B) is mean annual precipitation (MAP), and C) is the number of degree days above 5°C (DD5).

Models were initially evaluated using Akaike's Information Criterion (AIC), coefficient of determination (R^2), and root mean squared error (RMSE). Within the set of potential models with low AIC and RMSE coupled with high R^2, additional criteria used in the model selection process included those with fewer parameters if possible, those with all of the parameters significant in explaining biomass variability, and those with parameter estimates reflecting reasonable biological processes. Likelihood ratio tests were used to compare the suite of candidate models and evaluate the significance of additional parameter estimates within the models.

Results

To capture the variability present in the sample sites, a range of tree sizes were sampled. A total of 83 trees were selected for destructive sampling from the seven sampling sites included in both studies (Table 3-1). Diameters measured at 1.37 m above the ground (DBH) ranged from 10.2 to 78.7 cm, and tree heights ranged from 8.5 to 36.33 m. Mean DBH at the Pleasant Hill site was significantly smaller than for the other four sites included in Study 1 (Figure 3-1), and while the mean tree height was also lower at Pleasant Hill than for the other sites, the difference was smaller than for DBH. Fewer larger trees at Pleasant Hill was due to an absence of data, not due to site resource limitations or management differences.

Table 3-1. Mean diameter at breast height (DBH) and tree height for the sample trees.

Site	*n*	Soil Parent Material	DBH (cm)		Height (m)	
			Mean	Standard Deviation	Mean	Standard Deviation
Canus	12	Basalt	41.6	17.0	22.0	6.5
Lovell Valley	12	Metasedimentary	44.6	22.7	23.3	8.4
Pleasant Hill	4	Basalt	21.0	6.9	17.2	6.9
Ruby Bug	13	Metasedimentary	53.3	20.8	26.0	7.8
Slice Above	11	Metasedimentary	40.7	16.6	21.2	7.8
Priest River	15	Metasedimentary/ Granite	37.2	11.3	26.3	6.7
Moscow Mountain	15	Granite	35.8	9.9	26.3	6.7

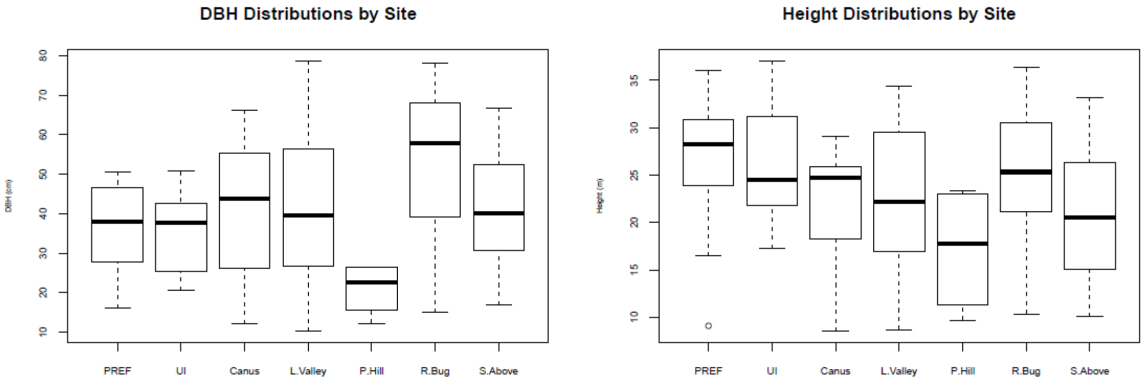

Figure 3-3. Diameter at breast height (DBH) distributions of the sample trees for each sampling site and total tree height distributions for each sampling site.

Whole-tree Crown Biomass for USFS Study

Allometric equations were developed in the USFS study for whole-tree crown biomass. In developing the biomass prediction equation, forest (PREF or UI) was considered as an indicator variable. The model including forest as in indicator variable was compared to a single equation for both of the sites included in the USFS study to evaluate whether location was able to account for a significantly larger amount of variability than the regional equation. Both models were able to predict a large amount of the variability in whole-tree crown biomass ($r^2 = 0.99$ and $r^2 = 0.96$) using DBH as the only additional predictor variable. While increase in the amount of variability in biomass that can be explained by adding forest into the model, forest did have a significant effect ($p = 0.0121$). Adding tree height to the model resulted in no change in R^2 although the effect was significant ($p = 0.0457$).

Validation Results for USFS Study

After the equations developed for individual-branch biomass in the USFS study were validated with the selected trees from the 2004 sampling season for that study, the results were also validated using the branch biomass equations developed by Monserud and Marshall (1999) (Figure 3-3). The whole-tree branch biomass equations from

Monserud and Marshall were used with the tree-level predictors used in the USFS study to validate that the estimates resulting from these equations were within the range in the previous work. In comparing the crown biomass estimates resulting from the equations developed in the USFS study with the those resulting from the Monserud and Marshall (1999) equations, a significant difference in the biomass estimates was not observed ($p > 0.05$). In a comparison of predicted crown biomass from the USFS study equations using the predictor variables associated with the selected trees for the IFC study, there was not a significant difference between the predicted crown biomass and the measured crown biomass for the the USFS study trees.

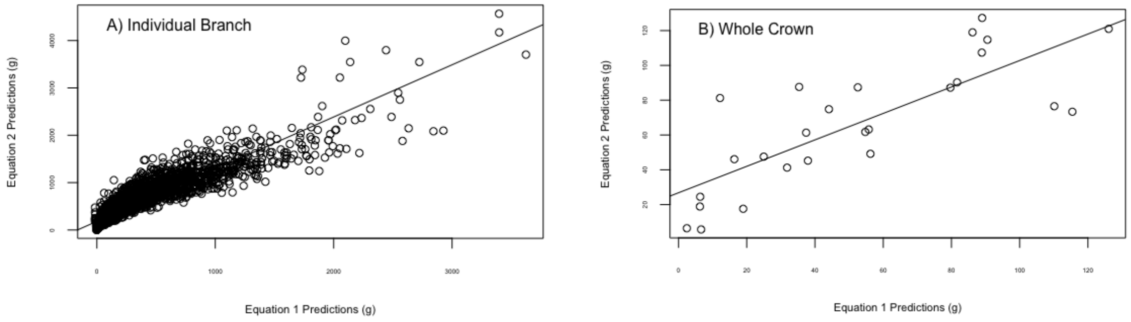

Figure 3-4. Comparison of predicted dry wood biomass predictions. A) compares predictions of individual branch dry wood biomass from branch diameter (mm) and branch length (cm) (Equation 2) to predictions from branch basal area (mm^2) and branch length (cm) (Equation 1). B) compares predictions of crown dry wood biomass from diameter at breast height (m) and stand basal area ($m^2 \cdot ha^{-1}$) (Equation 1) to predictions from tree basal area (m^2) and crown ratio (Equation 2).

Allometric equations were subsequently developed for crown biomass using the pooled dataset. Both crown biomass (kg) and diameter at breast height (cm) were transformed with a natural logarithm to ensure that the homogeneity of variance condition necessary for using a linear model was met. To evaluate whether site-specific allometric equations or single regional equation would perform better, subsurface soil parent material was included in the modeling process, as were five climatic variables.

Crown Biomass Model Development

A forward selection process was used to develop the model. To develop the model for crown biomass, DBH was used as a predictor in all of the candidate models (Table 3-2), and as a single predictor was able to account for 76% of the variability in crown biomass (Figure 3-3, Table 3-3). Adding tree height (Ht_m) to the model increased R^2 to 0.77. Although a likelood ratio tests suggests that Ht_m did have a significant effect on the model, the small increase in R^2 was insufficient for it to be included as an additional parameter, therefore it was not included in the subsequent model search. To explore the utility of site specific equations as compared to a single regional predictive equation for crown biomass, soil parent material (SPM) was included in the models, as were climate variables identified either through the cluster analysis results or by their correlations with crown biomass. The sites from which the trees were selected for both studies were on three different parent materials: granite, metasediments, and basalt. When SPM was included in the model, it and DBH were able to account for 84% of the variability in crown biomass. The effects of granitic and metasedimentary SPM were not significantly different in this model, but when the biomass of the trees from these two groups were pooled (SPM2), the R^2 dropped and AIC increased from 105.863 to 130.0463.

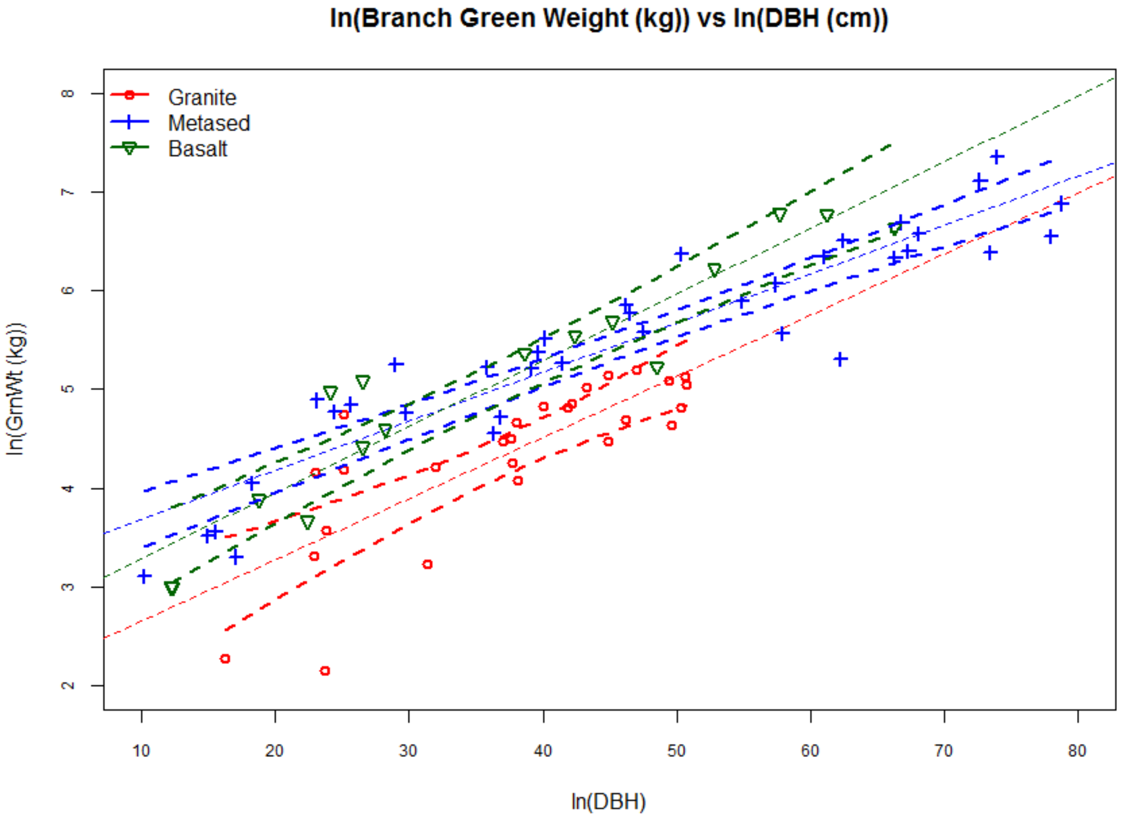

Figure 3-5. Crown biomass (green weight, kg) related to diameter at breast height (cm), plotted on the natural logarithm scale. Heavy dashed lines are 95% confidence bands.

Each of the climate variables identified by the cluster analysis was added individually to the model with DBH and SPM. Of the models with a single climate variable, MAP resulted in the highest increase in R^2 over DBH alone (0.8151), followed by DD5 and CMD. When MAR was added to the model with DBH, it did not show a significant effect on crown biomass estimation. When climate variables were added to the model with SPM, the resulting R^2 values were all approximately 0.84, but only MAP was a significant predictor in the model. Starting with the two climate variables that were individually the most significant predictors when added to DBH, a series of models were considered that included two-way interactions between the climate predictors, but no combination of climate variables was able to measurably increase the R^2 of the model (Table 3-2).

Table 3-2. Summary of candidate models to estimate crown biomass.

Model	Predictor Variables	R^2	RMSE	AIC
1	ln(DBH)	0.7616	0.5558	135.3629
2	ln(DBH) + ln(Ht)	0.7746	0.5404	131.8862
3	ln(DBH) + Subsurface SPM	0.8398	0.4556	105.863
4	ln(DBH) + SPM2	0.7798	0.5341	130.0463
5	ln(DBH) + Subsurface SPM + CMD*	0.8388	0.4571	107.33
6	ln(DBH) + Subsurface SPM + MAR*	0.8427	0.4515	105.3637
7	ln(DBH) + Subsurface SPM + NFFD*	0.8379	0.4583	107.7655
8	ln(DBH) + Subsurface SPM + MAP	0.8380	0.4582	107.7144
9	ln(DBH) + Subsurface SPM + eFFP*	0.839	0.4567	107.2116
10	ln(DBH) + Subsurface SPM + DD5*	0.8382	0.4582	107.604
11	ln(DBH) + Subsurface SPM + MWMT	0.8384	0.4576	105.3637
12	ln(DBH) + CMD	0.7951	0.5152	124.3546
13	ln(DBH) + MAR	0.7917	0.5195	125.6761
14	ln(DBH) + MAP	0.8151	0.4895	116.2757
15	ln(DBH) + eFFP	0.7706	0.5452	133.2952
16	ln(DBH) + DD5	0.8072	0.4999	119.5786
17	ln(DBH) + MAP* + DD5* + MAPDD5*	0.8122	0.4934	119.3977
18	ln(DBH) + CMD* + MAP* + CMDMAP*	0.8109	0.495	119.937
19	ln(DBH) + CMD + MAP	0.8127	0.4927	118.2318
20	ln(DBH) + CMD + MAP + DD5 + CMDDD5 + MAPDD5	0.8380	0.4581	109.5147
21	ln(DBH) + CMD + MAP* + DD5 + MAPDD5	0.8383	0.4578	109.4109
22	ln(DBH) + CMD + eFFP + MAP* + DD5 + MAPDD5	0.8383	0.4578	109.4106

Variables noted with an (*) did not have a significant parameter estimate in the model ($p > 0.05$)

Two potential models from the list of candidate models have good predictive ability using the criteria of high R^2, low RMSE, low AIC, and parameter estimates that were both significantly related to crown biomass and the estimates were biologically reasonable; one model that included SPM (Model 8) and one model that included a combination of climate variables without SPM (Model 20).

For Model 8, the change in crown biomass related to increasing DBH was not significantly different for the three SPM, however the overall crown biomass was different (Table 3-3).

Table 3-3. Parameter estimates for the model predicting $\ln(Y) = b_{0,i} + b_1X_1$ for Douglas-fir. Standard errors are included in parentheses.

SPM	$b_{0,i}$	Pr(> |t|)	b_1	Pr(> |t|)
Granite	3.049 (0.160171)	< 2e-16**	0.056 (0.003087)	< 2e-16**
Basalt	2.293 (0.143761)	1.31E-06**		
Metasedimentary	2.939 (0.140226)	0.437		

** indicates significance at $\alpha = 0.05$. Y is crown biomass, $b_{0,1}$ is the intercept for granite soil parent material, $b_{0,2}$ is the intercept for basalt soil parent material, $b_{0,3}$ is the intercept for metasedimentary soil parent material, and X_1 is the natural logarithm of diameter at breast height (lnDBH).

Biomass estimates on granite parent material were significantly different than the estimates from basalt and metasedimentary parent material, however there was not a significant difference observed between basalt and metasedimentary soil parent material. When the biomass estimates for basalt and metasedimentary parent material were combined and compared to those from granite parent material, the amount of variability in biomass that the model could account for with variability in DBH and SPM was reduced to 77% and the AIC increased to 135.31.

The best model without SPM included CMD, MAP, DD5, and interactions between MAP and DD5 as well as between CMD and DD5 (Model 20, Table 3-4). This model was able to account for 84% of the variability in crown biomass with a low AIC and low RMSE, with all of the parameter estimates being biologically reasonable.

Table 3-4. Parameter estimates for the model $\ln(Y) = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_3X_4 + b_6X_1X_4$ predicting crown biomass for Douglas-fir including climate predictor variables. Standard errors are included in parentheses.

Predictor	Estimate	SE (Estimate)	Pr (> |t|)	
b_0	52.17	14.46	0.000613	**
b_1	0.05594	0.003025	< 2e-16	**
b_2	0.07975	0.02251	0.000698	**
b_3	-0.07245	0.01972	0.000456	**
b_4	-0.04947	0.01421	0.00085	**
b_5	-0.0001244	0.00003411	0.0005	**
b_6	0.00007455	0.00002035	0.000472	**

** indicates significance at $\alpha = 0.05$. Y is the natural logarithm of crown biomass, X_1 is the natural logarithm of diameter at breast height (lnDBH), X_2 is Hargreave's moisture deficit (CMD), X_3 is mean annual precipitation (MAP), and X_4 is degree days above 5°C (DD5).

Discussion

In all of the models considered for crown biomass estimation, DBH was the primary predictor variable. Although inclusion of tree height has been suggested to allow for the presence of site factors in previous research (Crow 1978; Ketterings et al., 2001), height did not increase the amount of variability in crown biomass for the data included in this research either when SPM was included in the model or when it was not, nor when surficial deposits were included in the models. Tree height has little predictive ability in biomass estimation equations in other research (Ung et al. 2005, Lambert et al. 2005) suggesting that DBH is the most critical predictor of biomass.

Soil parent material, when included in the biomass estimation equation, had a modest but significant relationship, increasing the amount of variability the model could account for by 8% (, suggesting that a site effect is present when SPM is used as the stratification factor. The effects of granitic and metasedimentary parent material were not significantly different from each other but they were both separate from basalt. When SPM was collapsed to only two categories (basalt and granite/metasedimentary), however, R^2 was 0.7746 resulting in less than 2% increase in variability explained.

Augusto et al. (2017) observed interactions between soil parent material and climate in nutrient limitations in their examination of 27 terrestrial sites in Europe, supplemented by 90 more sites in both Europe and North America. The authors observed that N limitation was not linked to soil parent material for their sites but rather to climate, and in contrast that P limitation was explained by a combination of both climate and soil parent material.

The best fitting model does suggest that site-specific equations based on parent material perform better in crown biomass estimation than those based on tree-level predictors alone, however the low between site variability in the climate factors for these data has a potential of masking interactions that may be better seen when more between site climate variability is present. The sampling sites located on metasedimentary soil parent material had both higher density stands as well as more moist soil conditions compared to the other locations. A wider range of stand densities and soil moisture regimes across the different soil parent materials will be necessary to illuminate the relative contributions to crown biomass that are from soil parent material versus climate.

The effect of soil parent material and climate variables on crown biomass examined in this research limits the focus of the study to only component of the total tree biomass and specifically excludes relationships between these predictor variables and stem biomass as well as root biomass. There is evidence suggesting that the hypothesis that under cold temperatures, biomass accumulation into roots as opposed to aboveground biomass (Poorter et al. 2012, Vogel et al. 2008, Oleksyn et al. 1999). Reich et al. (2014) hypothesized that the proportion of biomass allocated to roots should increase while the proportion allocated to foliage should decrease when belowground resources are limited based on optimal portioning theory (McCarthy and Enquist 2008).

Individual tree competitive relationships have been shown to vary between moisture levels (habitat types) and mineral (parent material) environments (Shen et al. 2000), where large, dominant trees on moist sites showed the largest absolute growth over 10 years in a fertilization experiment. Within-stand fertilizer response is better demonstrated by relative growth, however, when rock types vary. Augmenting the data used in the current research with Douglas-fir crown biomass measured on sites with a wider variety of climate regimes and soil moisture profiles will be necessary to better illuminate the climate and parent material relationships that are evident.

The variability in crown biomass is better explained by models where either soil parent material or certain climate variables are incorporated into the model, although a single (regional) model using only tree diameter performed nearly as well. These results are similar to other findings that suggest that while site-specific equations are able to account for more of the biomass variability than regional equations, that the regional equations include the range of estimates seen in the site-specific equations (Weiskittel et al. 2007, King 2005, Augusto et al. 2017). Regional biomass equations are appealing since it is time consuming and costly to obtain data for use in model developments, and a more generalized regional equation does not require measured observations on all sites for which estimates may be made. Equations that have a lower number of parameter estimates can also be more stable when based heavily on diameter measurements as measurement errors are less commonly made, resulting in more stable equations. To fully assess whether site-specific or a regional equation will best represent the data included in this research, however, biomass observations from sites that have more climate variability must be included.

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