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Article

Aboveground Tree Biomass for *Pinus ponderosa* in Northeastern California

Martin W. Ritchie [1,*], Jianwei Zhang [1] and Todd A. Hamilton [2]

[1] USDA Forest Service, Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002, USA; E-Mail: jianweizhang@fs.fed.us

[2] USDA Forest Service, Shasta-Trinity National Forest, 3644 Avtech Parkway, Redding, CA 96002, USA; E-Mail: toddhamilton@fs.fed.us

* Author to whom correspondence should be addressed; E-Mail: mritchie@fs.fed.us; Tel.: +1-530-226-2551; Fax: +1-530-226-5091.

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Abstract: Forest managers need accurate biomass equations to plan thinning for fuel reduction or energy production. Estimates of carbon sequestration also rely upon such equations. The current allometric equations for ponderosa pine (*Pinus ponderosa*) commonly employed for California forests were developed elsewhere, and are often applied without consideration potential for spatial or temporal variability. Individual-tree aboveground biomass allometric equations are presented from an analysis of 79 felled trees from four separate management units at Blacks Mountain Experimental Forest: one unthinned and three separate thinned units. A simultaneous set of allometric equations for foliage, branch and bole biomass were developed as well as branch-level equations for wood and foliage. Foliage biomass relationships varied substantially between units while branch and bole biomass estimates were more stable across a range of stand conditions. Trees of a given breast height diameter and crown ratio in thinned stands had more foliage biomass, but slightly less branch biomass than those in an unthinned stand. The observed variability in biomass relationships within Blacks Mountain Experimental Forest suggests that users should consider how well the data used to develop a selected model relate to the conditions in any given application.

Keywords: allometry; foliage; crown biomass; silvicultural thinning, component ratio

1. Introduction

Tree biomass estimates influence our understanding of both carbon sequestration [1,2] and fuels management [3]. As the behavior of wildfire is strongly influenced by biomass pools in the forest [4,5], treatments designed to reduce biomass, have become common in California and throughout the western United States. The United States Forest Service has treated about 10 million hectares over the last 10 years. With the increasing emphasis on fire resilient systems [6–8], foresters need to accurately quantify effects of management on aboveground biomass.

Therefore, not only are the accurate equations needed to quantify the past biomass or carbon storage [1], but we also need to know whether these equations are affected by management activities or other factors that may vary temporally or spatially [9].

Estimates of aboveground biomass often rely on allometric equations for individual trees with coefficients varying by species. These functions may reflect total aboveground biomass, or some component thereof. Bole volume is important because a large proportion of biomass is found in the main stem. Nonetheless, branch and foliage biomass are important from the standpoint of fire behavior [9]. Crown biomass contributes to estimates of canopy bulk density. Through litterfall, tree crowns are a source for small material (<7.62 cm in diameter) on the forest floor. Biomass of the small branches and leaves both distributed in the crowns and on the forest floor, have great influence on rate of spread and the ability for fire to spread into the crown.

Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) is a commercially valuable tree species in North America and is a common species within much of California's 7.7 million ha of coniferous forests [10]. Yet there is little published information on aboveground biomass for this species [11]. Three published sources for ponderosa pine include a sample of 9 trees from Fort Valley Experimental Forest in the southwest [12], a sample of 23 trees in central Oregon [13], and a sample of 21 trees in the inland northwest [14,15].

These equations are often simple expressions relating tree-level biomass to some expression of tree size [12,16]. Commonly, the independent variable is breast height diameter [16], although some have also used crown dimensions or stand density [13,14,17].

Biomass and carbon may be estimated with equations matched to species and geographic region of interest. If such equations are not available however, any equation for the species may be used [10]. In some instances, species may be pooled [16]. If models are not properly matched to conditions and species, estimation errors will be generated.

Of particular concern for ponderosa pine is the potential for density management to influence the dynamics of biomass and its distribution. For example, an increase of foliage growth may follow mechanical treatment (thinning) with the duration depending on thinning intensity [18,19]. Reliable estimates of canopy bulk density and litter fall depend on the accurate estimate of crown biomass [7,20]. Including crown dimensions in a biomass model will allow biomass estimation to respond to changes in crown length resulting from density management but it will not account for any differentiation resulting from trees maintaining more years of foliage or by accruing more leaf biomass per branch per year. If ponderosa pine trees can effectively increase foliage biomass quickly in response to density management, one would expect to find variation in foliage biomass relationships and perhaps branch biomass among stands with different treatment histories.

As an example of thinning effects on surface fuel accumulation through needle fall in California pine forests, trees thinned to 15 m^2 ha^{-1} produced 2000 kg ha^{-1} while stands at 38 m^2 ha^{-1} produced 3650 kg ha^{-1} after four years [21]. Thus the rate per unit of basal area was actually greater (133 *vs.* 96 kg m^{-2}) among thinned stands of ponderosa pine.

The purpose of this study is to develop allometric relationships for trees across an array of conditions in ponderosa pine stands in northeastern California to ascertain if stand variability within the forest is a contributing factor in aboveground biomass estimation. In addition we graphically compared published equations to those fitted to evaluate the site-specific applicability of published equations.

2. Methods

The study was conducted at Blacks Mountain Experimental Forest (BMEF) in northeast California. The Experimental Forest (40°40' N, 121°10' W) is located approximately 35 km northeast of Mount Lassen and elevation ranges from 1700 to 2100 m. Soils are classed as Typic Argixerolls with mesic soil temperatures at lower elevations. Annual precipitation averages 460 mm falling primarily as snow between October and May. Stands at Blacks Mountain are dominated by ponderosa pine with occasional white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) and incense-cedar (*Calocedrus decurrens* (Torr.) Florin) at higher elevations in the forest. At lower elevations, Jeffrey pine (*Pinus jeffreyi* Balf.) may occasionally be found. The 3715 ha forest has a wide range of stand densities resulting from past research and management activities, as well as some recent disturbance events [22]. Yet, about 1000 ha remain of dense even-aged stands with an age of about 100 years. Productivity on the forest is relatively uniform, with site index [23] ranging from 20 to 27 m at a base age of 100 [24].

We sampled stands from three separate thinning treatments within Blacks Mountain. These stands thinned from below two (T_2), eight (T_8), and ten (T_{10}) years prior to sampling for biomass. In addition, trees were sampled from five different unthinned (U) areas of Blacks Mountain. A total of 82 trees with targeted ages 120 years or younger were initially sampled, and of these, three were subsequently discarded due to exhibition of characteristics of old-growth trees, and ages exceeding 135 years. All stands are similar in respect to species composition and primary age cohort (approximately 100 years). All the thinnings at BMEF were designed to remove trees from smaller diameter classes, while also favoring the retention of pine and minimizing ladder fuels and creating a uniform open canopy condition.

Trees were selected to give an approximately equal representation across a range of diameters from 12 to 52 cm. The means of sampled trees varied from 30.1 to 33.3 cm (Table 1). Heights of sampled trees from thinned stands tended to be shorter for a given diameter, a trait that typically reflects the increased taper associated with lower stand densities. Because of potential conflicts with an existing experiment, sample size was restricted in T_{10}.

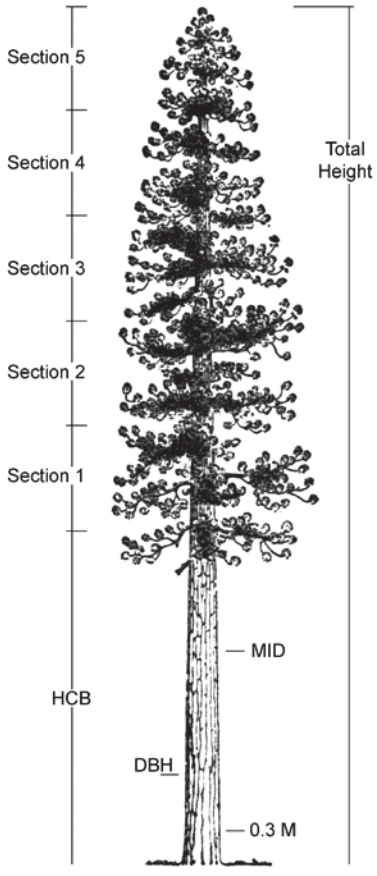
Sampled trees were felled and sectioned in 2007 during late spring and summer. Disks were removed from the bole at the stump (0.3 m), breast height (1.37 m), half way to the base of the live crown, and then at five equally spaced points within the crown, beginning with the base of the live crown. The dimensions (diameter of two axes inside and outside bark and disk thickness at the end of each axis) of each sampled disk and length of each section were recorded in the field.

Table 1. Mean breast height (1.37 m) diameter (*dbh*), height (*h*), crown ratio (*cr*), pre-treatment basal area (BA_p) and current basal area (BA_c) for sampled biomass trees in four different stands (U, T_2, T_8, T_{10}) at Blacks Mountain Experimental Forest.

Treatment	Sample Size	*dbh* (cm)	*Height* (m)	*cr*	BA_p (m^2 ha^{-1})	BA_c (m^2 ha^{-1})
U	21	32.8	17.3	0.54	–	66
T_2	29	33.3	15.2	0.59	66	16
T_8	21	33.3	14.8	0.62	64	17
T_{10}	8	30.1	14.8	0.61	42	18

The crown was divided into five equal sections for branch sampling and diameter measurement (Figure 1). Basal diameter of all live branches was measured within each of the five sections. Branches were selected for weight from each section in the following manner: one representative branch with average basal diameter from Sections 1, 4 and 5 (numbering from the base of the crown) and two from Sections 2 and 3. The top of the main stem, as far as needles were retained (3 to 9 years of growth), was removed. For each selected branch and the top of the main stem, foliage was stripped and weighed separately from the wood.

Figure 1. Trees crowns were broken into five sections and portions of the bole were also removed at the stump (0.3 m), breast height and mid-crown.



The samples for bole wood, branches and foliage were all weighed separately after being oven-dried at 80 °C for two weeks to ensure a stable weight. Total bole biomass was estimated for each tree section from the average of density at either end of each section and the dimensions of that section.

Equations for branch wood biomass (*bw*) and branch foliage biomass (*fw*) were developed as a function of branch basal diameter, section and years after thinning. Current year's foliage was separated to obtain start-of-growing-season foliage biomass. In addition, for each sampled branch, the terminal foliage (starting at the tip of the branch and working back as far as green needles are retained) was separated for each year of production and recorded as weights indexed by years 0 through 9. Year 0 weight was recorded as zero for samples obtained after the end of the growing season. Year 1 biomass was always recorded as the most recent complete year's foliage.

The number of years of foliage retained per branch was evaluated for each section of the tree and each of the four thinning treatments. We evaluated years of foliage retention in a linear model as a function of section identifier.

Branch and bole weights in this analysis all include bark. The foliage weight analyzed excluded the current growing season's needle production and thus represented weight at the start of the growing season. Branch diameters ranged from 7 to 83 mm, oven-dry foliage weight ranged from 5 to 3322 g (Table 2).

Table 2. Minimum, mean and maximum for branch diameter (mm) and weight (g) by crown position for weight-sampled branches.

Section	Branch Diameter			Wood Weight			Foliage Weight		
	min.	*mean*	*max.*	*min.*	*mean*	*max.*	*min.*	*mean*	*max.*
1	13	41	70	33	1122	4241	16	403	1425
2	8	36	83	4	1186	7477	5	437	3322
3	7	34	80	3	891	6379	5	388	2507
4	11	32	53	21	417	1536	18	281	964
5	9	23	39	6	116	489	11	135	412

Wood biomass (g) divided by volume (cm^3), was obtained for each weighed bole section and then averaged over the volume between the sections. Multiplying this value by the volume of each bole section yielded biomass per section. Total oven-dry bole biomass was derived by summation over all sections.

Initial graphical analysis of trends among the trees from untreated areas of the forest indicated no trends across different untreated stands at Blacks Mountain. This was consistent with our observation of fairly uniform conditions within these areas across the entire Experimental Forest. For this reason, in all subsequent analyses we aggregated the untreated trees together into one treatment group (U).

2.1. Branch Wood and Foliage Biomass

The individual branch foliage biomass was fit to data pooled within a stand using weighted nonlinear regression:

$$fw = k_{1t} bdob^{k_{2t}} + \varepsilon_{fw}, \quad (1)$$

where *fw* is foliage biomass (g), k_{it} is model parameter *i* at treatment *t*, *bdob* is branch basal diameter outside bark (mm), and ε_{fw} is a random branch-level error with assumed variance structure $V(\varepsilon_{fw}) = \sigma^2 \widehat{fw}^{1.5}$.

The individual branch woody biomass was fit using weighted nonlinear regression:

$$bw = [q_{1t} + q_{2t}cp^2]bdob^{q_{3t}} + \varepsilon_{bw}, \quad (2)$$

where bw is branch woody biomass (g), q_{it} is model parameter i at treatment t, cp is branch crown position (ranging from 0.1 to 0.9) using the center point of the section's position within the crown and ε_{bw} is random branch-level error with $V(\varepsilon_{bw}) = \sigma^2 \widehat{bw}^{1.5}$.

These fitted regressions were then applied to each branch to obtain wood and foliage biomass for each branch and, through branch summation [15], the entire tree.

2.2. Tree Biomass

Using unconstrained iterative seemingly unrelated regression (SUR) [25–27], we fit a system of equations with three response variables: foliage, branch-wood and bole-wood biomass. The simultaneous fit allowed for improvements in efficiency due to cross-equation correlations in the errors of the system. A full model was specified as:

$$foliage = \exp(a_{00} + a_{01}I_2 + a_{02}I_8 + a_{03}I_{10} + a_{04}cr)\, dbh^{a_1} + e_1 \quad (3.1)$$

$$branch = exp\,(b_{00} + b_{01}I_2 + b_{02}I_8 + b_{03}I_{10} + b_{04}\, cr)dbh^{b_1} + e_2 \quad (3.2)$$

$$bole = exp\,(c_{00} + c_{01}I_2 + c_{02}I_8 + c_{03}I_{10})height^{c_2}dbh^{c_1} + e_3 \quad (3.3)$$

In this model, a, b, and c are unknown parameters, the response variable is tree component biomass (g), I_t is a treatment area indicator (0,1) specified so that, for example, the parameter a_{00} is associated with the unthinned trees and a_{01} is associated with trees in a stand observed two years after thinning, *etc*., cr is observed crown ratio (live crown length divided by total height), dbh is breast height diameter (cm) and height is total tree height (cm).

Heteroskedasticity for the three components of the model was addressed by transformation:

$$et_m = e_m/dbh^{1.5}$$

Various combinations of a reduced form were fit by removing stand-identifier terms (indicator variables) and crown ratio from the model. A final model was selected after fitting the full model and fourteen selected reduced forms of the system. Model selection was guided by an information-criteria approach [28]. Employing an assumption of multivariate normality, Akaike's information criterion (*AIC*) was calculated for each fit [29], with a small sample correction (*AICc*) then applied [30]:

$$AIC\left(\hat{\Sigma}\right) = N\ln\left|\hat{\Sigma}\right| + Np\left(\ln\left(2\pi\right)+1\right) + 2K + p\left(p+1\right),$$

$$AICc\left(\hat{\Sigma}\right) = AIC\left(\hat{\Sigma}\right) + N^{-1}\left(3K\left(p+1\right) + 2K^2p^{-1} + p\left(p+1\right)^2\right),$$

where the matrix: $\hat{\Sigma} = N^{-1}(\hat{\mathrm{e}}\mathrm{t}'\,\hat{\mathrm{e}}\mathrm{t})$, N is sample size, p is number of models in the system, and K is the number of system parameters estimated (including covariance terms).

2.3. Foliage Production

We estimated the annual allocation of foliage by proportioning annual foliage for the terminal in each sampled branch. We then fit the current full year's foliage as a function of the estimated total for the terminal. This gives a proportional estimator that was used to estimate the amount of current year's foliage in any given tree. We tried models with slope adjustments for thinning, for section, for both section and thinning, and with no adjustments. We employed a nonlinear, mixed-model with a random tree-level effect (ε_s) for the slope term to obtain the following predictive model for current annual branch foliage (*af*):

$$af = [r_{1t}i_{1t} + r_{2t}i_{2t} + r_{3t}i_{3t} + \varepsilon_s]\widehat{fw} + \varepsilon_{af}, \quad (4)$$

where r_{it} are parameter estimates for treatment areas t = 1, 2, 3, 4, *af* is the last full year's branch foliage biomass (g) and $\widehat{fw}$ is the predicted branch total from model 1. Indicator variables were used for sections and treatment: i_{1t} = 1 for Sections 1–3, 0 otherwise; i_{2t} = 1 for Section 4, 0 otherwise; i_{3t} = 1 for Section 5, 0 otherwise. The branch-level error term assumed to have variance proportional to prediction, $\widehat{fw}$. This model was then used to estimate the amount of current annual foliage production for each tree by summation over all branches.

We graphically evaluated the number of years of needle retention for branches by treatment area and position in the tree. We then fit a tree level (linear) response for annual foliage biomass for individual trees to evaluate changes in litter fall within the Experimental Forest.

2.4. Application

To evaluate the stand level impact of thinning on total foliage biomass and production rates, we applied the fitted model to a thinned stand sampled in this study (T_2) at Blacks Mountain Experimental Forest. The selected stand for this application was thinned in 2005 and then sampled five years post-thinning. Biomass was estimated pre- and post-thin from a sample of 45 variable radius points with a basal area factor of 5.6 m^2 ha^{-1}. Prior to thinning, this was a dense second growth stand with approximately 781 trees ha^{-1} and a basal area of 53.5 m^2 ha^{-1} (S.E. = 3.0), the quadratic mean diameter was 18.8 cm. After thinning from below (*i.e.*, removal of trees from lower crown classes to favor trees in the larger crown classes), density was approximately 112 trees ha^{-1} and basal area was reduced to 10.6 m^2 ha^{-1} (S.E. = 1.0). This thinning from below elevated quadratic mean diameter to 34.9 cm. Five years post-thinning, basal area had increased to 11.9 m^2 ha^{-1} (S.E. = 1.0). We obtained pre-thin and five-year post-thin estimates of both the branch, foliage biomass and the annual foliage production. We also estimated five-year post-thin biomass using the unthinned model to evaluate the stand-level error generated by mis-application of the model.

At the tree-level, we graphically evaluated predictions from three published biomass models [12–14] for foliage, branches and boles with the models fitted for BMEF, to ascertain differences across the range of observed diameters.

3. Results and Discussion

3.1. Branch Wood and Foliage Biomass

Fits for branch-level foliage biomass (Table 3) show that branch biomass differed by treatment ($p < 0.001$) and was greater for any given branch basal diameter among trees in treated areas across the entire range of branch diameters. The increase in foliage biomass ranged from 8% to 112%, depending on branch size. Inclusion of treatment in the branch model was also significant ($p < 0.001$), however the differences between treated and untreated areas were inconsistent across the range of branch diameters.

Table 3. Parameter estimates with standard errors for the branch foliage biomass model (1) and for the branch wood biomass model (2) by treatment, with weighted mean squared error.

Stand	***U***	***T_2***	***T_8***	***T_{10}***
Foliage				
k_1	0.1658 (0.033)	0.2048 (0.033)	0.1383 (0.030)	0.1654 (0.044)
k_2	2.0136 (0.054)	2.0170 (0.044)	2.2260 (0.056)	2.0614 (0.075)
$\hat{\sigma}^2$	1.61	1.32	1.91	1.14
n	136	187	134	56
Wood				
q_1	0.0319 (0.0043)	0.0221 (0.0029)	0.0161 (0.0029)	0.0209 (0.0043)
q_2	−0.0181 (0.0033)	−0.0120 (0.0021)	−0.0075 (0.0019)	−0.0112 (0.0032)
q_3	2.7674 (0.034)	2.8448 (0.034)	2.9366 (0.045)	2.8861 (0.053)
$\hat{\sigma}^2$	0.741	0.813	1.151	0.654
n	136	187	134	56

3.2. Tree Biomass

Among the 15 models considered based on model 3, most could be eliminated from consideration due to high values (>10) of *ΔAICc*. Of the three with *ΔAICc* less than 10, model 5 (below) had the lowest value. The only difference between these three candidates was the inclusion of terms for treatment area in the branch model. Although foliage and branch biomass were related to thinning, this was more evident with foliage than with branch biomass. Bole biomass was not related to stand structure/history in this model. Model 5 was a reduction to a 12 parameter system (Table 4):

$$foliage = \exp(a_{00} + a_{01}I_2 + a_{02}I_8 + a_{03}I_{10} + a_{04}cr)\, dbh^{a_1} + e_1 \quad (5.1)$$

$$branch = \exp(b_{00} + b_{01}(I_2 + I_8 + I_{10}) + b_{04}cr)\, dbh^{b_1} + e_2 \quad (5.2)$$

$$bole = \exp(c_{00})\, height^{c_2} dbh^{c_1} + e_3 \quad (5.3)$$

The transformed root mean squared error estimates for model 5 were 30.3 for foliage, 85.6 for branches and 114.7 for bole. To obtain root mean squared error in grams, these values must be multiplied by $dbh^{1.5}$. The estimated error correlation matrix from the SUR fit was:

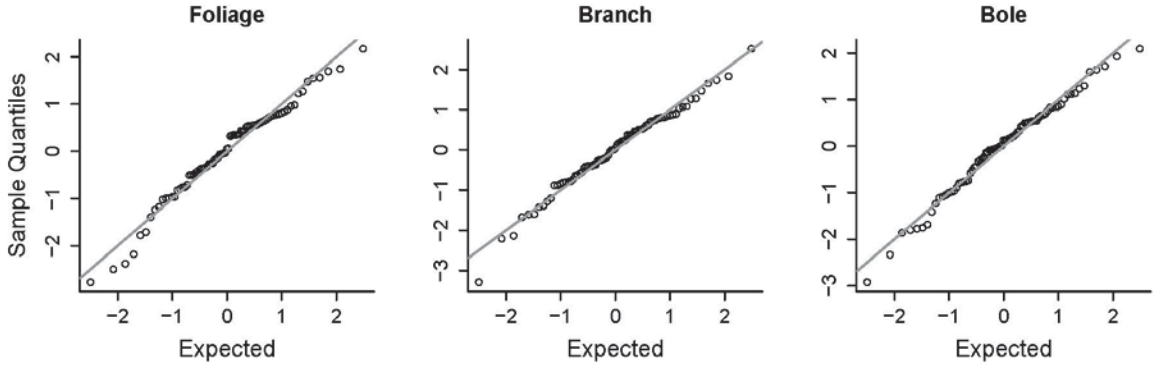
$$\hat{\rho}(\mathbf{et}) = \begin{bmatrix} 1 & 0.91 & 0.63 \\ & 1 & 0.63 \\ & & 1 \end{bmatrix}.$$

Table 4. Parameter estimates for tree foliage biomass, branch biomass, and bole biomass from selected models based on models 5 and 6.

Model	Parameter	Model 5	S.E.	Model 6	S.E.
foliage	a_{00}	1.66802	0.230	2.29770	0.237
	a_{01}	0.20355	0.055	0.29450	0.065
	a_{02}	0.55652	0.054	0.65466	0.062
	a_{03}	0.10737	0.063	0.18726	0.074
	a_{04}	1.68907	0.232	–	–
	a_1	2.08727	0.055	2.17566	0.063
branch	b_{00}	−0.15537	0.419	0.69671	0.429
	b_{01}	−0.16062	0.054	−0.03770	0.061
	b_{04}	2.20682	0.332	–	–
	b_1	2.81810	0.101	2.92409	0.114
bole	c_{00}	−2.73498	0.316	−2.97351	0.344
	c_1	1.47812	0.062	1.44091	0.066
	c_2	1.34334	0.065	1.39323	0.069

The greatest degree of correlation was between foliage and branch biomass (r = 0.91). The assumption of normality required for *AICc* calculation appears to be reasonably well supported by the individual normal-probability plots from the selected model (Figure 2).

Figure 2. Normal probability plots using transformed residuals for the selected system (5) of equations.



Since crown ratio may be problematic for applications where crowns are not observed, we also present a restricted (a_{04} and b_{04} = 0) model 6, without crown ratio:

$$foliage = \exp(aa_{00} + a_{01}I_2 + a_{02}I_8 + a_{03}I_{10})\, dbh^{a_1} + e_1 \quad (6.1)$$

$$branch = \exp(b_{00} + b_{01}(I_2 + I_8 + I_{10}))\, dbh^{b_1} + e_2 \quad (6.2)$$

$$bole = \exp(c_{00})\, height^{c_2} dbh^{c_1} + e_3 \quad (6.3)$$

The transformed root mean squared error estimates for model 6 were 34.1 for foliage, 94.7 for branches and 114.9 for bole. As with model 5, these must be multiplied by $dbh^{1.5}$ to obtain unweighted root means squared error in grams. The estimated error correlation matrix from this SUR fit was:

$$\hat{\rho}(\mathbf{et}) = \begin{bmatrix} 1 & 0.91 & 0.54 \\ & 1 & 0.56 \\ & & 1 \end{bmatrix}.$$

The tree-level foliage weight model, indicates a greater amount of foliage among thinned areas for trees of a given size and crown ratio (Table 4). Given the estimated parameters a_{01}, a_{02}, and a_{03} in model 5, an increase per tree from 11% to 74% is implied for the trees in treated stands. This assumes no change in crown ratio due to thinning. If crown ratio increases due to thinning then the net effect implied from parameter estimates in model 6 is from 21% to 94% per tree. The net effect implied over time for foliage on a per unit area basis, will actually be even larger than this as diameter increment will also increase among individual trees in thinned stands.

In contrast, branch biomass model was marginally lower among thinned stands ($b_{01} < 0$). It is important to note that since crown ratio is in the model already, this does not suggest that trees necessarily lose branch biomass. Since crowns ratio will tend to increase post-thinning, any reduction in branch biomass is at least partially offset by crown dynamics. An indication of this is the result of removing crown ratio from the model on parameter b_{01}, which moves toward zero and is not statistically significant in model 6 ($p = 0.540$).

We do not have a good explanation about this difference. However, the observed increase in foliage production may be influenced by site-to-site differences in site productivity. If this were so, care should be taken in application of any particular foliage biomass model to sites not within the productivity range reflected in the original modeling data.

3.3. Foliage Production

Foliage retention for the sampled branches ranged from one to nine years and tended to increase slightly in the lower portions of the crown in thinned stands (Figure 3). Among trees in the unthinned areas, needle retention was similar at around four years. Duration of needle retention appeared to be shorter, slightly so, near the top of the tree.

Annual foliage production expressed as a proportion of total foliage appears to be slightly lower for trees eight and ten years post thinning (Figure 4). The proportion of the total crown found in the most current year's leaf production (*i.e.*, the slope of regression line) is around 33% for unthinned and only slightly higher (35%) two years after thinning. Whereas the trees eight and ten years after thinning have about 27% allocated to the current year. These proportions may be considered an approximate value for annual needle cast. So while overall foliage per tree was greater for the thinned trees (Table 4), the contribution of this increase in foliage to annual litter fall is offset somewhat by the changes in the proportion of that foliage that is turned over each year.

Figure 3. Box and whisker plots showing median, quartiles and the minimum and maximum years of needle retention by crown position, for branches sampled in unthinned and thinned areas by years since treatment.

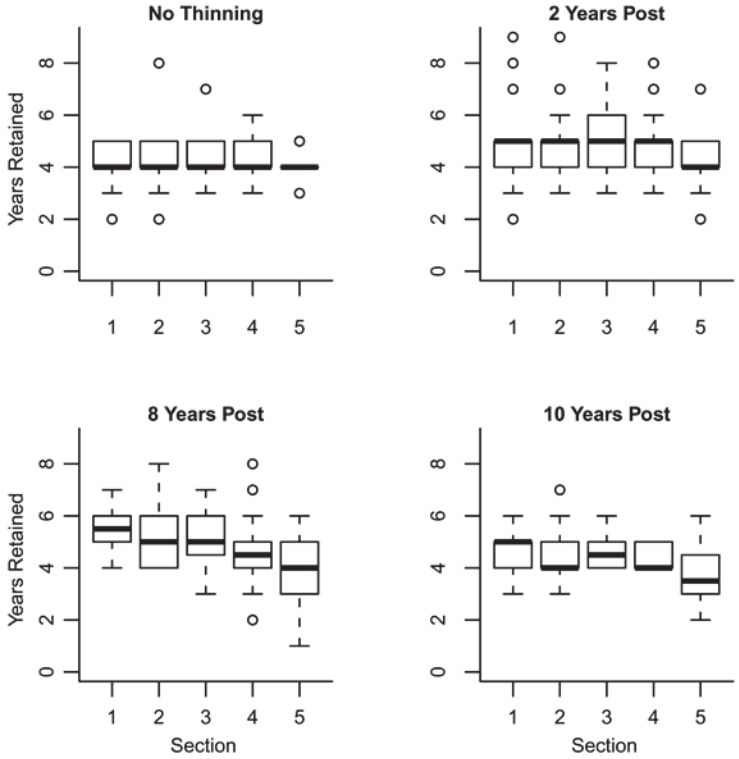
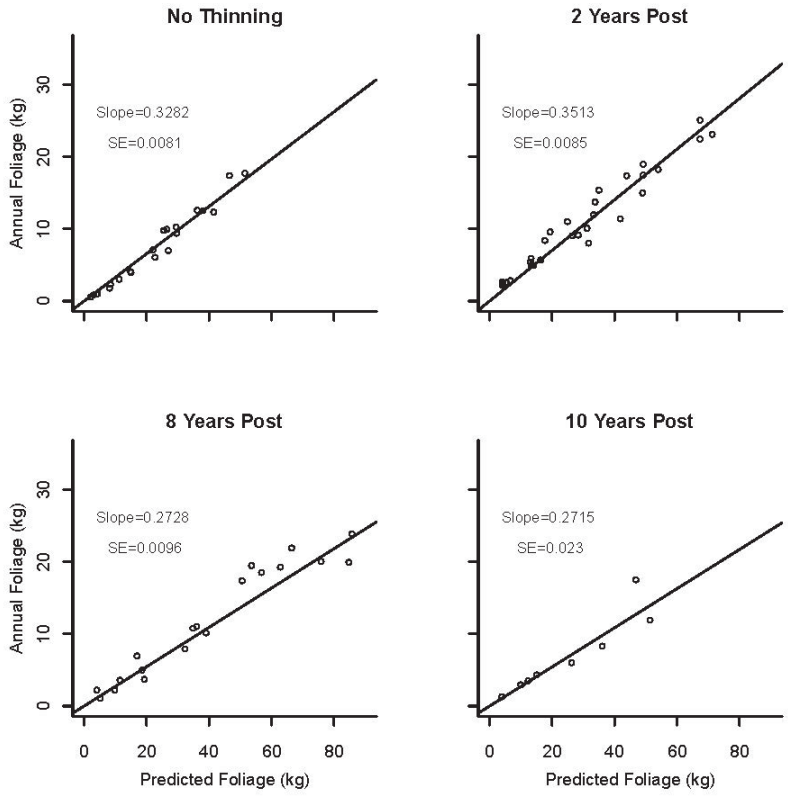


Figure 4. Tree-level annual foliage biomass production (kg) as a function of total foliage estimate (kg) across treatments.



3.4. Application

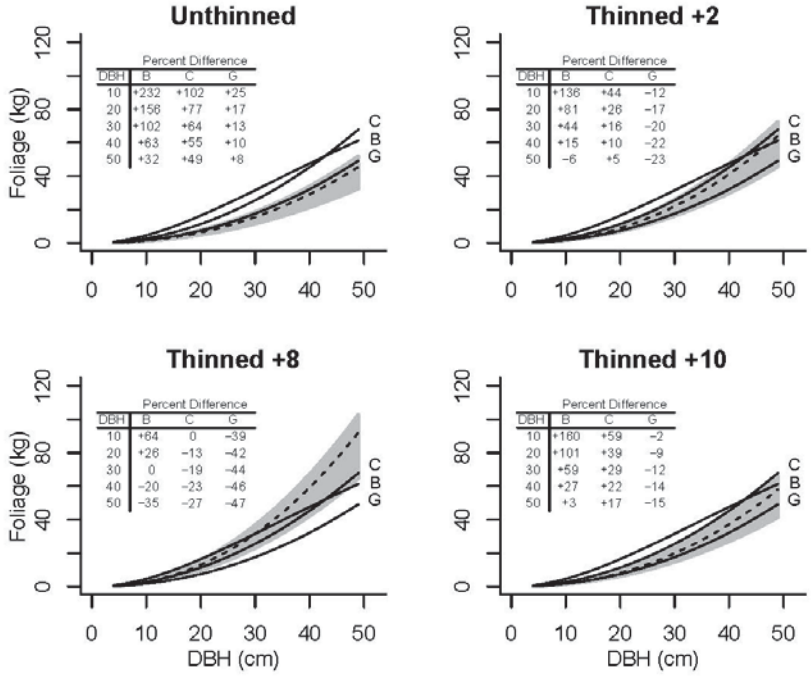
The application of the fitted models to an example stand at Blacks Mountain resulted in a pre-treatment foliage estimate of 12.0 Mg ha^{-1} at 781 trees ha^{-1}, thinning reduced foliage weight (applying the indicator $I_2 = 1$) to 21% post-thin and 33% after five years (Table 5). Reduction in branch biomass was similar, the 29.4 Mg ha^{-1} was reduced to 28% by thinning but only recovered to 31% of pre-treatment after 5 years. Application of the unthinned model ($I_{\cdot} = 0$) resulted in an apparent underestimate of stand foliage weight of 26% and an overestimate of branch biomass of 4%. The net effect was an underestimate of crown biomass by about 0.6 Mg ha^{-1}, or about 5%. The estimate of annual litter fall (from needles only) is still well below the pre-treatment estimate of 4 Mg ha^{-1}, and at this rate will take many years to recover to pre-treatment levels. We cannot be sure about future accumulations, but a linear extrapolation of these rates of recovery suggests that foliage biomass will recover to pre-treatment levels in about 30 years, while the branch biomass recovery to pre-treatment levels will take much longer, closer to 100 years.

Table 5. Estimates of foliage weight (*FW*), branch weight (*BW*) and annual litter fall estimate (Annual) using $I_2 = 1$ in model 6 for post-thin estimates, including error from application of unthinned model ($I_{\cdot} = 0$) five years post thinning.

Condition	*BA* (m^2 ha^{-1})	*QMD* (cm)	*FW* (Mg ha^{-1})	*BW* (Mg ha^{-1})	Annual (Mg ha^{-1})
Pre-Thin ($I_{\cdot} = 0$)	53.5	18.8	12.0	29.4	4.0
Post-Thin ($I_2 = 1$)	10.6	34.9	2.5	8.1	0.8
Thin + 5 year ($I_2 = 1$)	11.9	37.1	3.9	9.1	1.0
Thin + 5 year ($I_{\cdot} = 0$)			2.9	9.5	0.8

A graphical analysis of the foliage biomass models illustrated the degree to which the ponderosa pine foliage biomass to diameter relationship varied within the Experimental Forest (Figure 5). Correspondence with published biomass equations by [12] was best among trees in the untreated stand, yet this was consistently low for the other (treated) stands (Figure 5). The shape of the function from [14] showed a consistent lack of fit across diameter and did not seem to correspond well to our data anywhere at BMEF. The predictions from [13] were high for the unthinned trees, as may be expected because the sample came from thinned stands. Site index represented in [13] was also a little higher (33 m, [23]) than most of Blacks Mountain and is closest to the results we found in the stand sampled eight years after thinning (where site index is maximized for Blacks Mountain, at approximately 26 m). This may be an indication of the influence of variation in site productivity [31], however we cannot confirm this with these limited data; a sample across a greater range of productivity would be necessary.

Figure 5. Foliage biomass at Blacks Mountain Experimental Forest (BMEF) with crown ratio (shaded from 0.45 to 0.85) and without crown ratio (dashed line) compared to three published functions (solid lines B, C, G) from [14], [13], and [12]; percent differences from fitted are tabulated by diameter.



Branch biomass in model 5 did vary across the experimental forest as well and crown ratio contributed to the model (Figure 6). Using AIC for model selection indicated that a term should be included distinguishing between treated and untreated stands but it is worth noting that this term is of marginal statistical significance in the classic sense ($p = 0.055$), and drops to near zero if crown ratio is removed from the branch model. The net effect on total crown biomass was mixed because of the positive impact of thinning on foliage and apparent negative impact on branch biomass. The difference between the thinned and unthinned estimate of crown biomass (the sum of foliage and branches) ranged from −11% to +25% depending on tree size and crown ratio. Where large positive differences, >10%, were observed (thinned exceeding unthinned crown biomass) it was among trees less than 20 cm in diameter.

The presence of crown ratio in the branch and foliage models suggests a weakness in estimation methods that do not include this variable. Inclusion of crown ratio in the foliage model reduced the transformed mean squared error by 21% and in the branch model the crown ratio term reduced the transformed mean squared error by 18%.

Comparison of our fitted branch model to other published equations produced mixed results. For larger trees both [12,13] were very similar to our model, while [14] consistently over estimated branch biomass by as much as 218% (Figure 6).

Not surprisingly, we found little difference between published and fitted values for bole biomass (Figure 7) and we found no evidence of differences between treated and untreated stands for this relationship.

Figure 6. Estimated unthinned branch biomass (**a**) and thinned branch biomass (**b**) at BMEF with crown ratio (shaded, crown ratio from 0.40 to 0.70) and without crown ratio (dashed line) compared to three published estimates (solid lines B, C, G) from [14], [13], and [12] respectively; percent differences are tabulated by diameter.

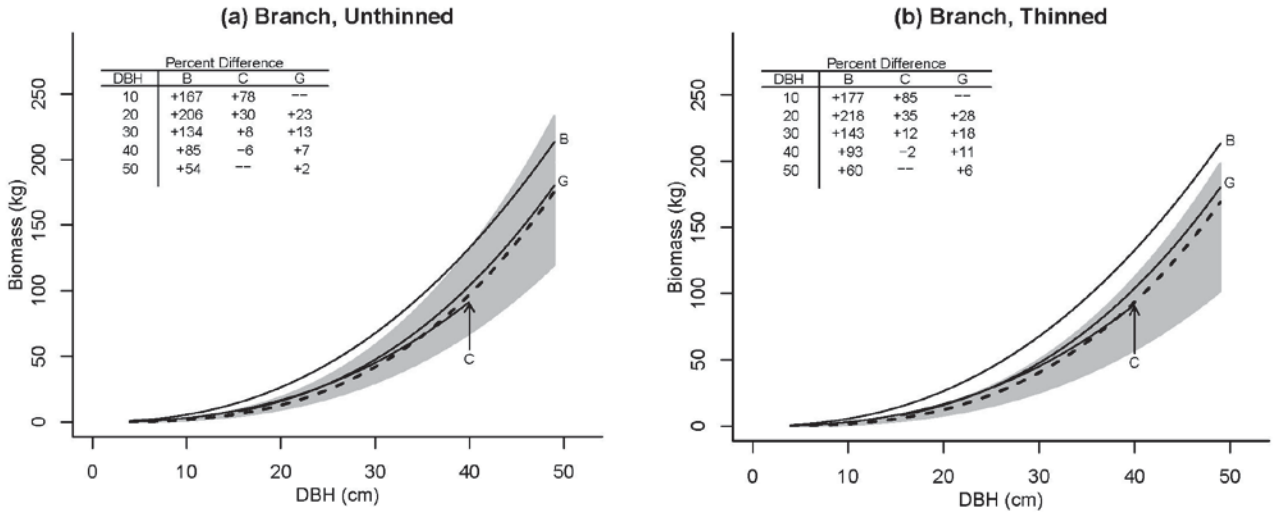
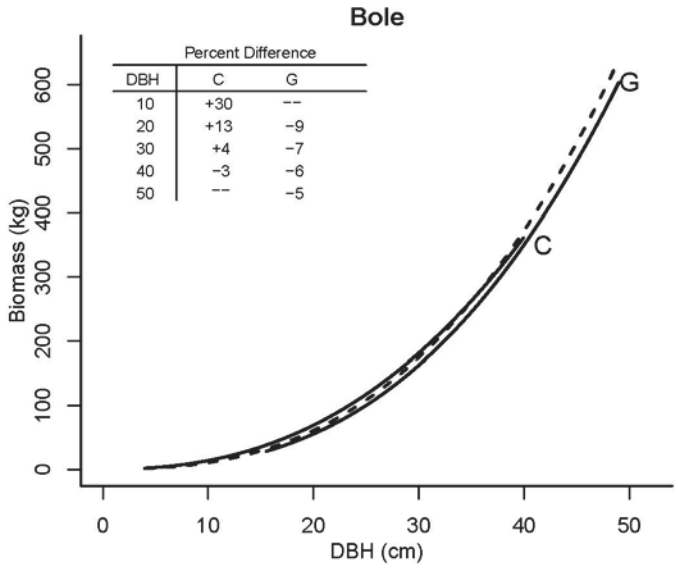


Figure 7. Estimated bole biomass over diameter, at BMEF (dashed line) compared to two published estimates (solid lines C, G) from [13] and [12]; percent differences are tabulated by diameter.



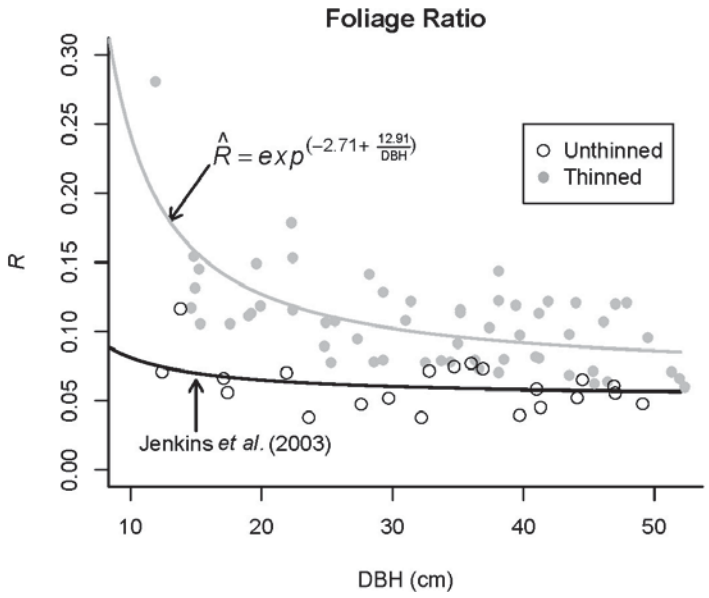
We also considered the impact of foliage biomass with regard to the more recent applications of the component ratio method for biomass estimation [32]. The component ratio method (CRM) is a technique used to develop estimates of biomass for large areas, but has more recently also been suggested for use at smaller project-level scales [33]. In the CRM a simple exponential function of diameter is used to obtain a ratio relating the weight of foliage to the total aboveground biomass [34] for softwoods:

$$\hat{R} = \exp\left(-2.9584 + \frac{4.4766}{dbh}\right). \quad (7)$$

We applied this function and graphically compared this application with our own observed component ratio (Figure 8) and found that the published equation [32] for all softwoods related remarkably well with our observed data for untreated stands. In fact, in fitting our own equation for untreated stands our model did not offer any statistical improvement over the published equation for softwoods ($F = 0.53$; $p = 0.598$). However for trees in treated stands a nonlinear regression of the same form (Figure 8) provided a significant improvement ($F = 103.70$; $p < 0.001$). This is also consistent with the finding that trees from treated stands carrying more foliage. Thus, the published generic ratio [32] appeared to underestimate the foliage proportion in our thinned stands only.

The SUR fit presented for tree biomass is unconstrained for the estimation of total aboveground biomass [26]. The total is thus implied as the sum of the biomass components. Some efficiency can be gained for the total with a constrained fit [27,35] if total aboveground biomass estimates are desired.

Figure 8. Foliage component ratio (R) values plotted over DBH for treated (grey) and untreated (open circles) with published model [16,32] (black line) and fitted for thinned values (grey line).



4. Conclusions

A simultaneous set of allometric equations for foliage, branch and bole biomass were developed from trees in different stand conditions. The bole biomass appeared to be robust across the range of stand conditions sampled. Foliage biomass, on both branch-level as a function of branch diameter and tree-level as a function of tree DBH and crown ratio, was greater among trees in thinned areas than those in untreated areas. However, trees of a given DBH in the thinned areas had slightly less branch biomass than those in thinned area. The net effect of this was an apparent increase in crown biomass for trees in thinned stands when compared with models from unthinned areas of the forest.

The allometric shift could have an impact on planning for forest restoration and fuels treatments. At the stand level we found the recovery in foliage biomass to be accelerated toward pre-treatment levels at a greater rate than that implied for branch biomass. Because foliage is an important source of litter

accumulation, managers should consider possible impacts of thinning on the dynamics of crown and surface fuel accumulation.

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Conflict of Interest

The authors declare no conflict of interest.

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