Comparing Algorithms for Estimating Foliar Biomass of Conifers in the Pacific Northwest

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Abstract

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Accurate estimates of foliar biomass (FB) are important for quantifying carbon storage in forest ecosystems, but FB is not always reported in regional or national inventories. Foliar biomass also drives key ecological processes in ecosystem models. Published algorithms for estimating FB in conifer species of the Pacific Northwest can yield significantly different results, but have not been rigorously compared for species other than Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). We compared five algorithms for estimating FB for seven common coniferous species in the Pacific Northwest. Algorithms based on diameter at breast height (DBH), or on DBH and height, consistently yield higher estimates of FB than algorithms based on sapwood area. At the tree level, differences between algorithms increased with increasing DBH for all species, but their order and magnitude differed by species. At the stand level, differences among algorithms were muted by the mix of species and diameter classes that contributed to total FB of stands of different seral stages and species composition. Significant differences among estimates of FB from different algorithms show the need for consistent methods for estimating FB for carbon accounting, tests of the sensitivity of ecosystem models to these differences, and more field observations to compare algorithms.

Keywords: foliar biomass, carbon, Pacific Northwest, allometry.

Summary

Accurate estimates of foliar biomass (FB) are important for quantifying carbon storage in forest ecosystems, but FB is not always reported in regional or national inventories. In the Pacific Northwest (PNW), inventory data for Washington, Oregon, and California do not include estimates of carbon in tree canopies; although FB represents a small proportion of total stand biomass, it is important for estimating productivity and proportional changes in biomass. Foliar biomass also drives key ecological processes in ecosystem models. Published algorithms for estimating FB in conifer species of the PNW can yield significantly different results, but have not been compared rigorously for species other than Douglas-fir (*Pseudotsuga menziesii (*Mirb.) Franco). We compared five algorithms for estimating FB for seven common coniferous species in the PNW: two that used only diameter and height; two that used sapwood area and leaf area, respectively; and one that calculated foliar biomass from alternate estimates of crown dimensions. Algorithms based on diameter at breast height (DBH), or on DBH and height, consistently yield higher estimates of FB than algorithms based on sapwood area. At the tree level, differences between algorithms increased with increasing DBH for all species, but their order and magnitude differed by species. For example, in coastal Douglas-fir, estimates for large-diameter trees based on diameter alone were higher by a factor of five than those that incorporated crown dimensions. In contrast, for lodgepole pine (*Pinus contorta* Douglas ex Loudon), estimates from the different algorithms were barely distinguishable. At the stand level, differences among algorithms were muted by the mix of species and diameter classes that contributed to total FB of stands of different seral stages and species composition. Significant differences among estimates of FB from different algorithms demonstrate the need for consistent methods for estimating FB for carbon accounting and further documentation of the uncertainties associated with each method. Tests of the sensitivity of forest-succession models to these differences are also needed, as projections of future carbon dynamics depend on carbon accounting within the models, which is sensitive in turn to species-specific allometries. More field observations are also needed to compare algorithms and inform and validate theoretical models, such as pipe-model theory, that could improve our understanding of carbon dynamics within forests.

Introduction

Accurate inventories of carbon in forest ecosystems require accounting for carbon in many ecosystem pools. The foliar biomass (FB) pool is particularly difficult to estimate and is not always reported as a stand attribute in regional inventories. For example, the Pacific Northwest Integrated Database (PNW-IDB) (Waddell and Hiserote 2005), which includes federal forest inventory data for Washington, Oregon, and northern California, does not include an estimate of carbon or biomass in the foliage of trees, leaving users to estimate it themselves. Although FB is a small proportion of total stand biomass, it is important for calculating annual productivity or proportional changes in biomass stocks in forest ecosystems. Accounting for carbon in FB is also important for quantifying the effects of disturbances, such as fire and defoliators, on forest carbon stocks. Disturbances can affect foliage carbon pools greatly, and accurate estimates of FB before and after disturbance are necessary for quantifying this change in carbon pools.

Estimating FB, leaf area (LA) of an individual tree, or leaf area index (LAI) of a stand are also key steps in modeling forest succession and carbon dynamics. Ecosystem process models often use these variables to calculate productivity, and some forest gap and succession models depend on estimates of LA for calculating growth, recruitment, stress, and mortality (e.g., Urban 1993). Fire models may use FB to calculate fuel mass and fire hazard (Reinhardt and Crookston 2003), and hydrology models often require LAI or FB to simulate evapotranspiration and snowpack dynamics (Tague and Band 2004).

Inventories of FB and LAI for large forested areas can be done by either ground-based measurements or remotely sensed data. Light detection and ranging (LiDAR) and satellite imagery are commonly used to estimate FB (Lefsky et al. 2002, Means et al. 1999) and LAI (Lefsky et al. 1999) over large geographic areas, and if temporal sequences of remotely sensed data are available, changes in canopy attributes over time can be detected (Turner et al. 2004). Remotely sensed data should be verified with field measurements, however, and are often not feasible to collect for fine-scale carbon accounting. Thus, there continues to be a need for accurate estimates of LAI and FB from ground-based measurements.

Foliar biomass of individual crowns is difficult to measure directly without destructive sampling, so it must be estimated from other more easily measured tree dimensions with species-specific allometric equations (Gholz et al. 1979, Grier and Logan 1977, Jenkins et al. 2004, Standish et al. 1985). Independent variables for these equations include diameter at breast height (DBH), tree height (HT), and crown dimensions. Foliar biomass can then be converted to LA by using a species-specific value of specific leaf area (SLA), which has units of mass per unit area.

Simulation models also use these allometric equations to estimate canopy attributes from other tree or stand attributes that are predicted by the models or input variables.

An alternative method for estimating FB for individual trees relies on the cross-sectional area of sapwood (SA) at a specific height on the tree, usually breast height (1.37 m) or crown base height (Grier and Waring 1974, Marshall and Waring 1986, Smithwick et al. 2002, Snell and Brown 1978). For this method of estimating FB from SA, SA was measured in several ways, including destructive sampling with staining techniques (Snell and Brown 1978), destructive sampling with a visual estimate of SA based on color (Grier and Waring 1974), with increment cores (Marshall and Waring 1986), or by estimating SA based on species and DBH (Smithwick et al. 2002). With this method, LA of individual crowns is estimated from SA first, and then converted to FB with SLA (the reverse of what is described above). The SA-based method has its origin in the "pipe model" theory, which states that a given unit of foliage is maintained by a corresponding unit of water-conducting sapwood tissue (Shinozaki et al. 1964, Waring et al. 1982), i.e., LA above a specific height on a tree is a linear function of SA at that height.

Methods that use different tree dimensions to estimate FB can yield widely different estimates (Marshall and Waring 1986, Turner et al. 2000, Van Pelt and Sillett 2008). Previous studies have been limited in one of four ways: (1) mainly qualitative comparisons, (2) comparisons for only small DBH trees, (3) comparisons for only a few species, and (4) comparisons of LA only and not FB. For example, Grier and Waring (1974) developed regression equations to estimate FB as a function of SA at breast height for four common PNW conifers with a large range of DBH values (4 to 112 cm). They suggested that SA predicted FB more accurately than DBH alone, particularly for larger and older trees that typically have less uniform crowns, but they offered little quantitative analysis to support this conclusion.

In coastal Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*) and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) forests of the western PNW, DBH-based equations consistently yield higher estimates of LA in large trees and LAI of old-growth forests than SA-based algorithms and other field-based methods of measuring LAI (Marshall and Waring 1986, Turner et al. 2000, Van Pelt and Sillett 2008). These studies focused on LA rather than FB, however, and compared algorithms for only Douglas-fir, western hemlock, and western redcedar (*Thuja plicata* Donn ex D. Don).

Marshall and Waring (1986) compared four methods for estimating LAI of old-growth Douglas-fir forests: (1) litterfall measurements, (2) light interception under the canopy, (3) regression on SA, and (4) regression on DBH. They found that

the first three methods gave similar estimates of LAI, but these estimates were half that of the estimate from regression on DBH. Similarly to Grier and Waring (1974), Marshall and Waring (1986) suggested that DBH-based regressions overestimate LA of large trees, and therefore LAI of mature stands, because (1) most DBH-based equations were derived from small-DBH trees, and (2) large-DBH trees tend to have more variable crowns because of competition, disturbance, and breakage. Smithwick et al. (2002) presented an approach, derived from the methods of Gholz et al. (1976), for estimating FB from SA that does not require sampling SA directly but uses regressions of sapwood width (SW) on DBH.

Allometry based on DBH is frequently used to estimate LA and FB, despite evidence that these equations overestimate foliar characteristics for both Douglas-fir and western hemlock and that SA is a better predictor. This may be because (1) the equations are readily available in comprehensive syntheses and databases of biomass equations (Means et al. 1994, Standish et al. 1985), (2) more variables need to be measured or estimated to use SA-based algorithms, and (3) SA is often not measured in forest inventories, being eschewed for the more easily measured DBH, HT, and crown dimensions.

In this study, we expand on previous research by comparing five allometric methods (table 1) for estimating FB for seven common PNW conifers over a large range of DBH. We also compare the aggregate effects of these methods at the stand level for early-, mid-, and late-seral stands in the western and eastern Cascade Range of Washington state. We discuss potential biases associated with each method, but do not extend the analysis to field-based methods of measuring FB, which are subject to their own sources of error. We also demonstrate the sensitivity of SA-based algorithms to two intermediate variables: (1) the ratio of the leaf area to sapwood area (LA:SA) and (2) specific leaf area (SLA). We seek to enable researchers, modelers, and forest managers to make informed decisions about which methods to use when estimating FB of different species and stands of different seral stages.

We compile and document variables necessary to apply SA-based algorithms to the seven PNW conifers. These variables are available in the literature but have not been synthesized in one publication. We also rebuild regression equations for estimating SA from DBH for these seven conifer species, using the summary data of Lassen and Okkonen (1969). These equations are embedded in some forest gap models (e.g., Urban 1993), but not published independently. This study complements other regional (Means et al. 1994) and national (Jenkins et al. 2003) syntheses of allometric equations for estimating FB that do not include alternative methods based on SA.

Table 1—Summary of algorithms used to calculate foliar biomass (FB)

Algorithm	Description	Equation form	Source
FB_{dbh}	FB is estimated with regression equations based on diameter (D).	$ln(FB) = a + b\ ln(D)$	Jenkins et al. 2004, Means et al. 1994
FB_{dbh+ht}	FB is estimated with equations based on diameter (D) and height (H).	$FB = a + b\ (D/100)^2\ H$	Standish et al. 1985
FB_{sa}	FB is estimated with equations based on sapwood cross-sectional area (SA).	$FB = a\ (SA) + b$ or	Grier and Waring 1974, Snell and Brown 197)
	SA is estimated from diameter (D) and bark thickness.	$ln\ (FB) = a + b\ ln(SA)$	
FB_{la}	Leaf area (LA) is estimated as a ratio of SA.	$FB = LA{:}SA\ (SA)/SLA\ (0.1)$	Gholz et al. 1976, Smithwick et al. 2002
	SA is estimated from diameter and bark thickness.		
	LA is then converted to FB using specific leaf area (SLA).		
FB_{crown}	FB is estimated with regression equations based on diameter (D) or SA and crown dimensions (crown depth, *CD*, and crown width, CW). SA is estimated from DBH and bark thickness.	$FB = a\ (CD^{b)} + c(D^d) + e(CW^f)$ or $FB = a(SA^b) + c(CD^d)$	Van Pelt and Sillett 2008

Note: Coefficients *a* through *f* are species-specific (Van Pelt and Sillet 2008) (table 4). Diameter is diameter at 1.37 m. Not all algorithms were used for all species. FB_{sa} was not used to estimate FB for western hemlock, Engelmann spruce, or lodgepole pine. FB_{crown} was only used to estimate FB for coastal Douglas-fir.

Methods

Inventory Data

We used data from the Pacific Northwest Integrated Database (PNW-IDB) (Waddell and Hiserote 2005) to determine characteristic ranges of independent variables for each species for use in the algorithms. The PNW-IDB combines forest inventory data from the federal inventories on private and public lands. We used measured (DBH and HT) inventory data from the PNW-IDB to obtain characteristic ranges of DBH and total HT for the seven species growing in the PNW. For total HT, we used the mean HT of all trees in each 1-cm DBH class, for each species. For

crown dimensions, each tree in the PNW-IDB has a value for crown width (CW) and crown ratio. Crown ratio is estimated ocularly in the field as the percentage of the tree bole supporting healthy foliage. Crown width was either measured in the field or estimated with equations from the Forest Vegetation Simulator. The equations used in this analysis require crown depth (CD) rather than crown ratio, so we multiplied the crown ratio (percentage, to the nearest 10 percent, of total HT that supports living crown) by total HT to calculate CD.

For the stand-level analysis, we selected 30 stands from the PNW-IDB that were primarily composed of two to four of the seven species. We selected 15 stands from the western Cascade Range region that were dominated by Douglas-fir, western redcedar, and western hemlock (table 2). Some of these stands also included low densities of Pacific silver fir (*Abies amabilis* [Dougl. ex Loud.] Dougl. ex J. Forbes). We selected 15 stands from the eastern Cascade Range region that were dominated by Douglas-fir, western larch (*Larix occidentalis* Nutt.), or Engelmann spruce (*Picea engelmannii* Parry ex Engelm.1) (table 2). These stands also included low densities of ponderosa pine (*Pinus ponderosa* P.&C. Lawson), lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), or grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.). Of the 15 stands in each region, we selected 5 stands from each of three seral stages: young (0 to 80 years), mid (80 to 200 years), and late (>200 years).

Estimating Sapwood Area (SA)

The forest inventories in the PNW-IDB did not measure sapwood width (SW) or SA, so we used data from Lassen and Okkonen (1969) to estimate SA. They reported the number of samples (n_i), mean, and standard deviation (s_i) of SW by DBH-class (2.5-cm classes for DBH <76 cm and 12.7-cm classes for DBH >76 cm) for each species, from which we developed species-specific regression equations of SW on DBH. Ideally, we would have used direct measurements of SW or SA, but they are not available in the PNW-IDB and are often not included in standard forest

Table 2—Stand characteristics by region and seral stage for the 30 stands used in the stand-level analysis

Region	Seral stage	Mean density	Mean basal area	Max DBH	Mean DBH
		Stems/ha^{-1}	*m^2/ha^{-1}*	- - - - *Centimeters* - - - -	
Western Cascade Range	Early	2,316	23.0	35.6	8.9
	Middle	1,109	59.9	96.6	21.6
	Late	1,539	78.4	155.4	25.4
Eastern Cascade Range	Early	856	13.0	32.3	10.7
	Middle	849	6.3	72.4	17.0
	Late	1,538	41.3	88.5	12.5

DBH = diameter at breast height.

inventories for carbon because of time and expense. Regressions of SW on DBH provide an alternative.

We estimated SW by using species-specific bark-thickness coefficients and species-specific regressions of SW on DBH. Nonlinear regression models assume that the errors are independent, normally distributed, with constant variance. Residual diagnostics indicated increasing variance in SW with increasing DBH (heteroscedasticity). Furthermore, the data had large differences in sample size for different levels of DBH. For these two reasons, we used a weighted nonlinear regression model. For each species, we regressed mean SW of the DBH class on the midpoint of that DBH class using the equation.

$$SW = b_1(1 - exp(b_2 \times D)) \tag{1}$$

where D is diameter (cm) outside of the bark at 1.37 m, b_1 is the asymptotic maximum SW (cm) reached in large trees, and b_2 (dimensionless) controls the curve shape. We estimated all species-specific equations with weighted nonlinear regression by using the *nls* function in R (Bates and Watts 1988, R Development Core Team 2008). We assigned weights (wi) as

$$wi = (si^2/ni)^{-1} \tag{2}$$

where n_i is the sample size and s_i is the standard deviation (cm) of each DBH class (i). The weights are proportional to both the sample size and the variance, so this weighted regression corrects for both the large differences in n_i and the heteroscedasticity of the data (Neter et al. 1996).

We calculated SA (cm^2) from SW and species-specific coefficients for bark thickness.

$$SA = (\pi(D(1 - b_3)/2)^2) - (\pi((D(1 - b_3)/2) - SW)^2) \tag{3}$$

where b_3 is the bark thickness coefficient (dimensionless), D is diameter (centimeters) outside the bark at 1.37 m, and SW is the predicted sapwood width (centimeters). We used bark thickness coefficients from Lassen and Okkonen (1969), which were the mean ratio of diameter inside bark to diameter outside bark.

Algorithms for Estimating Tree-Level Foliar Biomass

We selected equations that fit the following three criteria: the equations (1) are available in syntheses of allometric equations (Jenkins et al. 2004, Means et al. 1994), (2) are specific to the PNW, and (3) were developed based on a large range of DBH values. The first algorithm (FB$_{dbh}$) estimates FB based on DBH alone (table 1). The second algorithm (FB$_{dbh+ht}$) predicts FB based on DBH and total HT (Standish et al. 1985) (table 1). These are general equations intended to represent a species over a broad geographic range in the PNW.

The third (FB_{sa}) and fourth algorithms (FB_{la}) were based on SA rather than DBH (table 1). The FB_{sa} algorithm, which was not available for all species, estimates FB directly as a function of SA. These equations were originally developed from regressing FB on SA values that were measured directly (Grier and Waring 1974, Snell and Brown 1978). The FB_{la} algorithm also predicts FB as a function of SA, but it includes two intermediate steps (Smithwick et al. 2002). First, we used SA (square centimeters) to predict LA (square meters) of an individual tree using species- and region-specific values for LA:SA ratios (square meters:square centimeters) (table 3). Then we converted LA to FB using species- and region-specific

Table 3—Ratios of projected leaf area (LA) to sapwood cross-sectional area (SA) for seven common Pacific Northwest conifers

Species	LA:SA at 1.37 m	State (region)	Source	LA:SA crown base	State (region)	Source
	$m^2\ cm^{-2}$			$m^2\ cm^{-2}$		
Western larch	0.29	Washington (east)	Gower et al. 1987			
Engelmann spruce	.34	Oregon (west)	Waring et al. 1982	0.35	Oregon (west)	Waring et al. 1982
	.29[a]	Colorado	Kaufmann and Troendle 1981			
Lodgepole pine	.18[a]	Colorado	Kaufmann and Troendle 1981	0.15	Oregon (west)	Waring et al. 1982
	.14	Washington (east)	Gower et al. 1987			
	.11–0.3		Margolis et al. 1995			
Ponderosa pine	.19	Oregon (west)	Waring et al. 1982	0.25	Oregon (west)	Waring et al. 1982
	.17	Oregon (east)	Kimmins 2004	0.1–0.2	Nevada	Callaway et al. 1994
	.47	Oregon (west)	Waring et al. 1982	0.54	Oregon (west)	Waring et al. 1982
	.35	Washington (east)	Gower et al. 1987			
	.34	Oregon (east)	Waring et al. 1982			
	.25–0.7	Montana	Callaway et al. 2000			
Western redcedar	.50	Oregon (west)	Callaway et al. 2000, Turner et al. 2000			
Western hemlock	.41	Oregon (west)	Waring et al. 1982	0.46	Oregon (west)	(Waring et al. 1982)

[a] Original ratios in Kaufmann and Troendle (1981) were converted from all-sided leaf area to projected leaf area in Waring et al. (1982) by dividing by 2.5.
Note: Oregon (west) and Washington (west) indicate the western Cascade Range region in those states, respectively. Oregon (east) and Washington (east) indicate the eastern Cascade Range region in those states, respectively.

Table 4—Published values of specific leaf area (SLA) for common conifers in the Pacific Northwest

Species	SLA	Region	Source
	$cm^2\ g^{-1}$		
Western larch	83.7	Washington (east)	Gower et al. 1987
	76.0	Washington (east)	Gower and Richards 1990
Engelmann spruce	43.5[a]	Colorado	Kaufmann and Troendle 1981
Lodgepole pine	41.4[a]	Colorado	Kaufmann and Troendle 1981
	39.5	Washington (east)	Gower et al. 1987
	38.0	Washington (east)	Gower and Richards 1990
Ponderosa pine	36.3	Oregon (east)	Bond et al. 1999
	48.9	General	Cregg 1994
	25.8	Idaho	Cregg 1994, Marshall and Monserud 2003
Coastal Douglas-fir	82.4[a]	Oregon (coast)	Gholz et al. 1976
	73.9[a]	Oregon (west)	Gholz et al. 1976
	70.8[a]	Oregon (central)	Gholz et al. 1976
	74.0[a]	Oregon (east)	Gholz et al. 1976
	44.7	Washington (east)	Gower et al. 1987
Rocky Mountain Douglas-fir	34.3	Idaho	Marshall and Monserud 2003
Western redcedar	82.6	Oregon (west)	Gholz et al. 1976
Western hemlock	81.2[a]	Oregon (coast)	Gholz et al. 1976
	91.3[a]	Oregon (west)	Gholz et al. 1976

[a] Converted from all-sided leaf area to projected leaf area. SLA values in the literature for all-sided leaf area can be converted to SLA for projected leaf area by dividing by two times a species-specific needle cross-section correction factor to account for curved, rather than planar, needle surfaces (Gholz et al. 1976).
Note: Oregon (west) and Washington (west) indicate the western Cascade Range region in those states, respectively. Oregon (east) and Washington (east) indicate the eastern Cascade Range region in those states, respectively.

values for SLA ($cm^2\ g^{-1}$) (table 4). SLA is the ratio of LA (square cemtimeters) to leaf dry mass (grams) (Gholz et al. 1976). FB kilograms per tree) was calculated as

$$FB = (LA{:}SA \times SA) / (0.1 \times SLA) \qquad (4)$$

whereby SLA in square centimeters per gram (the units with which it is typically reported in the literature) is converted to square meters per kilogram.

The fifth algorithm (FB_{crown}) uses two equations that estimate FB from DBH or SA and additional variables for crown dimensions (Van Pelt and Sillett 2008). These equations were available for only coastal Douglas-fir. Van Pelt and Sillett (2008) developed the FB_{crown} equations based on an extensive data set of Douglas-fir trees (n = 70) with a wide range of DBH (19 to 237 cm) and age, detailed crown measurements, and destructive samples of FB. One equation predicts FB as a function of SA and crown depth (m). For this equation, we used the same estimates of SA that were used for the FB_{sa} and FB_{la} algorithms. The second equation provides an alternative if SA estimates are not available. This equation estimates FB as a function of DBH, crown depth (m), and crown width (m).

Sensitivity Analysis of the FB_{la} Algorithm

We tested the sensitivity of the FB_{la} algorithm to variation in the values of LA:SA ratios and SLA by comparing predicted FB with a wide range of LA:SA ratios and SLA values reported in the literature for two species (ponderosa pine and coastal Douglas-fir). The FB_{la} algorithm makes two assumptions about the LA:SA ratio and SLA: the values (1) are reasonably consistent within a species and (2) remain constant with succession. Intraspecific variation has been observed, however, for both variables and could introduce uncertainty in results of the FB_{la} algorithm. LA:SA ratios vary by species, with late-seral shade-tolerant species in light-limited environments having higher LA:SA ratios than early-seral species in moisture-limited environments (Kaufmann and Troendle 1981, Waring et al. 1982). A three-fold difference in the LA:SA ratio has been observed between genera and a fivefold difference across all genera (table 3).

Similarly, intraspecific variation in SLA has been attributed to variations in seral stage, site or region, and stand density (Pearson et al. 1984, Whitehead et al. 1984). The SLA is generally higher for shade-tolerant and late-seral species and lower in regions with moisture limitations. The SLA also varies within a species by tree age (Gholz et al. 1976), and within crowns of individual trees, decreasing with increasing branch height within the crown (Marshall and Monserud 2003).

Stand-Level Analysis

We tested differences in stand-level estimates of FB for stands of different successional stages and species composition. We calculated FB for all trees in the stand by using the four algorithms (minus the algorithm for only coastal Douglas-fir). Within-genus substitutions were made for species that did not have published equations for all four algorithms. We used analysis of variance (ANOVA) to compare the differences in FB estimates among algorithms within regions and seral stages. Thus we conducted six ANOVA tests, one for each of the two regions (western and eastern Cascade Range, respectively) and three seral stages (early, middle, and late). We used a Tukey HSD test for a post hoc analysis to determine which pairs of algorithms were different when significant differences between algorithms were found in ANOVA. We used an alpha level of 0.10 because we could thereby control for Type II error better, with Type I error not being the concern it would be, for example, in a biomedical study or a field experiment.

Results

Estimation of Sapwood Area

The nonlinear regressions of SW on DBH explained a high proportion of the variance of mean SW for coastal Douglas-fir, Rocky Mountain Douglas-fir (*Pseudotsuga*

Table 5—Coefficients of regression equations for sapwood width (SW) as a function of diameter at breast height (DBH) for common conifer species in the Pacific Northwest

Species	DBH Min	DBH Max	b_1	b^2	b_3	adj. R^2
	- - *Centimeters* - -					
Coastal Douglas-fir	15	213	5.51	-0.043	0.11	0.95
Rocky Mountain Douglas-fir	16	129	4.57	-.037	.11	.97
Ponderosa pine	16	138	16.55	-.026	.11	.97
Lodgepole pine	14	70	7.08	-.045	.03	.96
Engelmann spruce	15	97	5.56	-.039	.04	.85
Western larch	16	85	2.19	-.111	.13	.19
Western redcedar	15	175	2.43	-.097	.05	.19
Western hemlock			16.30	-.018	.04	

Note: All coefficients except western hemlock were estimated from nonlinear models fit to the data published in Lassen and Okkonen (1969). Coefficients for western hemlock are cited in Turner et al. (2000) and originally from Urban (1993). Sapwood width (SW) (cm) is calculated as: $SW = b_1 \times (1 - \exp(b_2 \times DBH))$. Sapwood area (SA) (cm^2) is calculated from SW: $SA = (\pi \times (DBH \times (1 - b_3)/2)^2) - (\pi \times ((DBH \times (1 - b_3)/2) - SW)^2)$.

menziesii [Mirb.] Franco var. *glauca* [Beissn] Franco), ponderosa pine, lodgepole pine, and Engelmann spruce (table 5) (fig. 1). In contrast, they explained a low proportion of the variance of mean SW for western larch and western redcedar (table 5) (fig. 1). Asymptotic values of SW ranged from a low of 2.2 cm for western larch to a high of 16.6 cm for ponderosa pine (table 5).

Algorithms for Estimating Tree-Level Foliar Biomass

The FB_{dbh} and FB_{dbh+ht} algorithms yield consistently higher estimates of tree-level FB than the SA-based algorithms (FB_{sa} and FB_{la}) for all species (fig. 2), although the order of differences between the FB_{dbh} and FB_{dbh+ht} algorithms was not the same for all species. Of the four algorithms, FB_{dbh} gave the highest estimates of FB for western hemlock, western larch, and Engelmann spruce and FB_{dbh+ht} gave intermediate estimates. In contrast, FB_{dbh+ht} gave the highest estimates of all four algorithms for both varieties of Douglas-fir. The FB_{dbh+ht} and FB_{dbh} algorithms gave similar estimates for western redcedar, ponderosa pine, and lodgepole pine. The two SA-based algorithms gave the lowest estimates of FB for all species, and were similar for all species for which both were available, except for Rocky Mountain Douglas-fir.

Differences between FB estimates from different algorithms increased with increasing DBH for all species, but the DBH at which the algorithms diverged differed between species. For all species, the four algorithms gave similar estimates of FB at small DBH (< ca 40 cm) (fig. 2). The algorithms diverged at a DBH of about 40 cm for Rocky Mountain Douglas-fir, western redcedar, western larch, and Engelmann spruce, but about 70 cm for coastal Douglas-fir and ponderosa pine
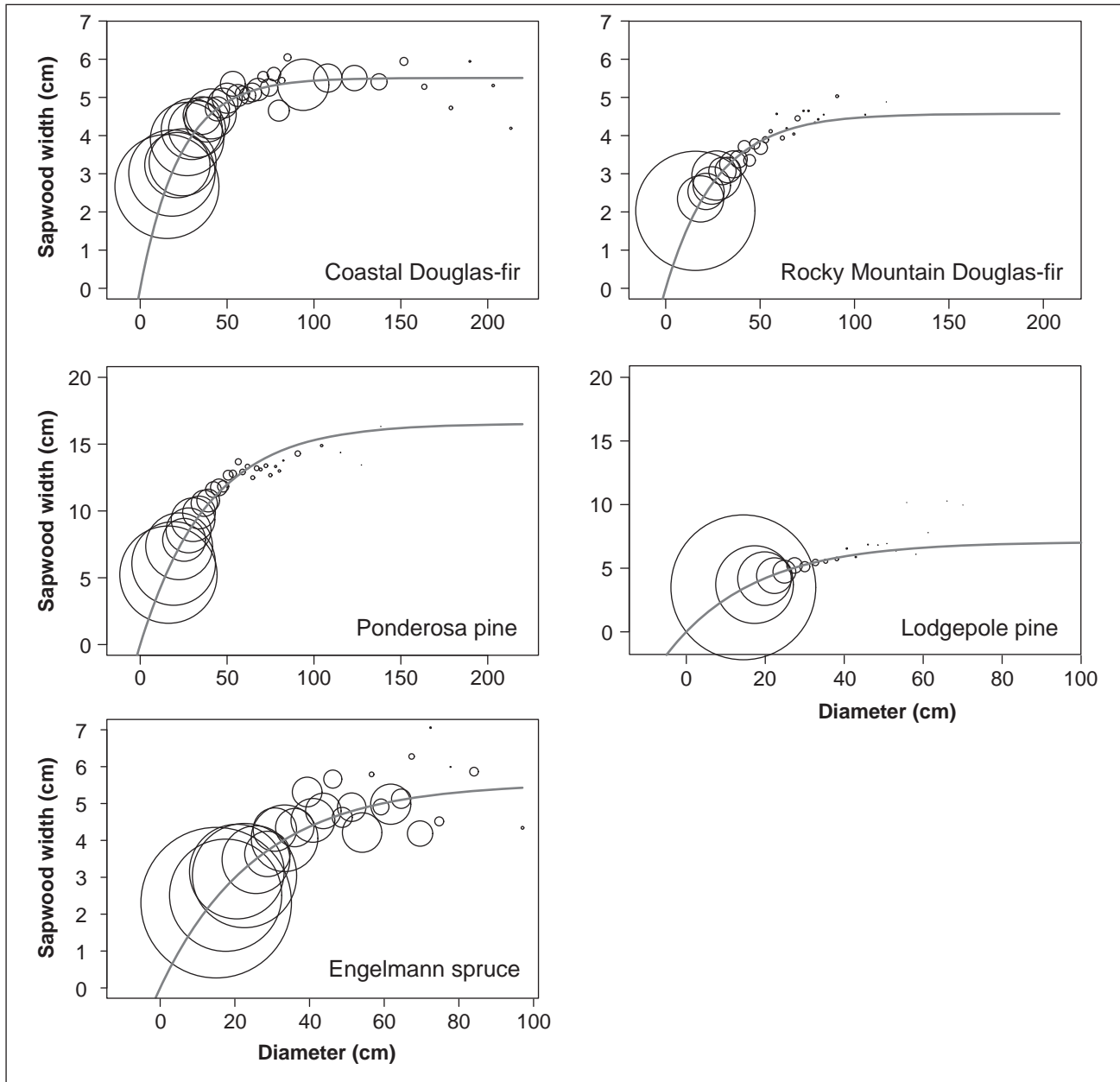
Figure 1—Regression models of sapwood width as a function of diameter at breast height (DBH) class for seven conifer species in the Pacific Northwest. Models are fit to the mean values for each DBH class as reported in Lassen and Okkonen (1969). DBH-classes are 2.5-cm classes for DBH <76 cm and 12.7-cm classes for DBH >76 cm. The sizes of the circles are proportional to the weights used in the nonlinear regression models.

(fig. 2). The FB_{dbh+ht} and FB_{la} algorithms gave similar estimates over a wide range of DBH for lodgepole pine, Engelmann spruce, and western hemlock, diverging only above 80 to 100 cm (fig. 2).

For large DBHs, range width of estimates of FB also varied by species, with western larch and Rocky Mountain Douglas-fir having the largest differences. For western larch the highest estimate of FB was 24 times that of the smallest estimate;
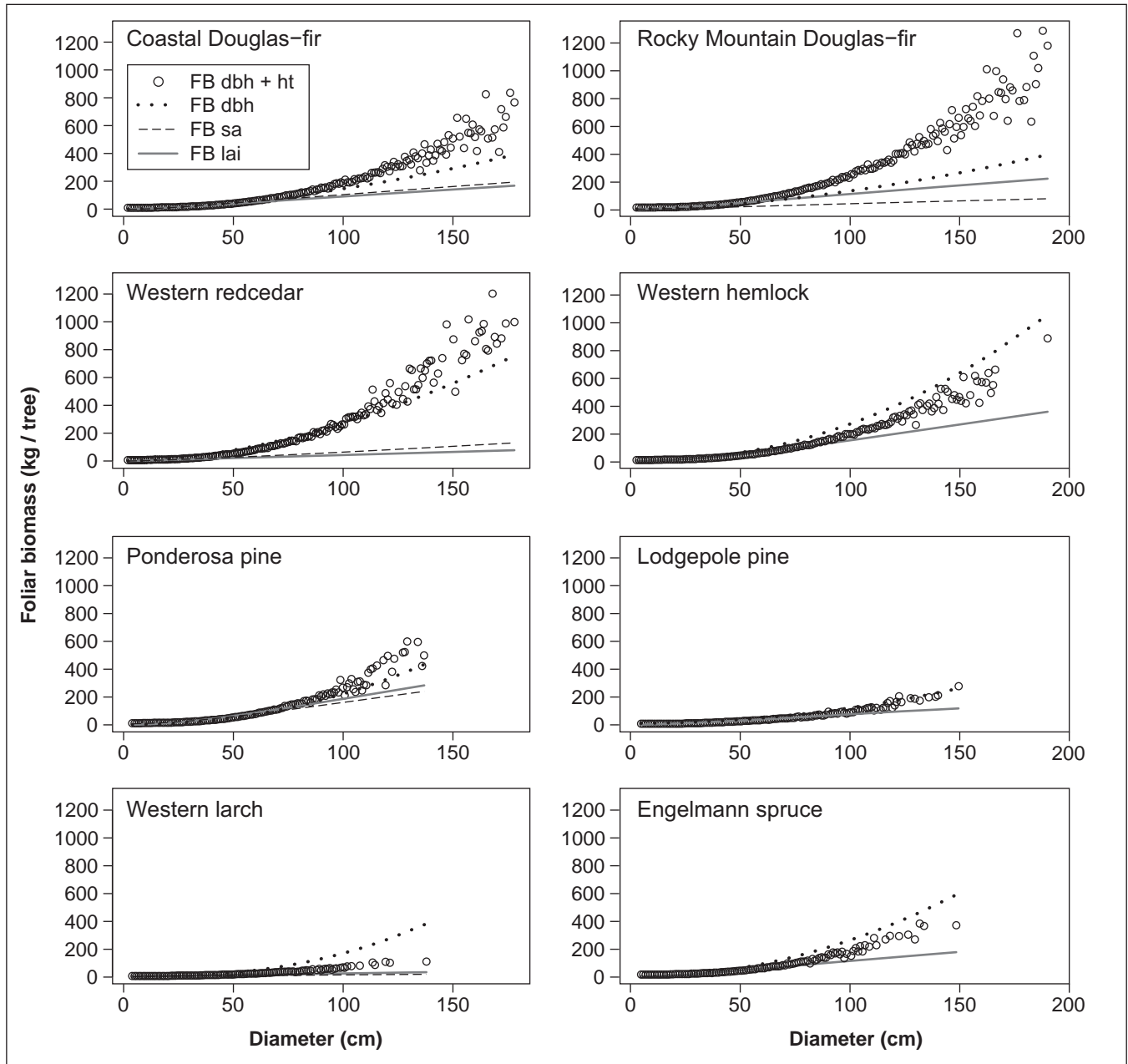
Figure 2—Estimates of foliar biomass (FB) made with four algorithms for eight conifer species common in the Pacific Northwest. The dotted line is FB_{dbh}, the dashed line is FB_{sa}, the solid line is FB_{la}, and the circles are FB_{dbh+ht}, which was calculated for the mean model term (HT) of each 1-cm DBH class. The scatter of points for FB_{dbh+ht} is due to the HT not shown.

a difference of 365 kg for a 140-cm-DBH tree. For Rocky Mountain Douglas-fir, the highest estimate of FB was 16 times that of the lowest estimate; a difference of 1100 kg for a 180-cm-DBH tree. These differences were smaller for ponderosa pine, lodgepole pine, and Engelmann spruce, with the highest being only two to three times the lowest, a difference of 150 to 300 kg for a 140-cm-DBH tree.

Generally, both FB_{crown} equations for coastal Douglas-fir agreed well with the FB_{la} and FB_{sa} algorithms (fig. 3). The FB_{la} and FB_{sa} algorithms gave slightly higher estimates of FB than the FB_{crown} algorithm for trees with DBH greater than about 200 cm.
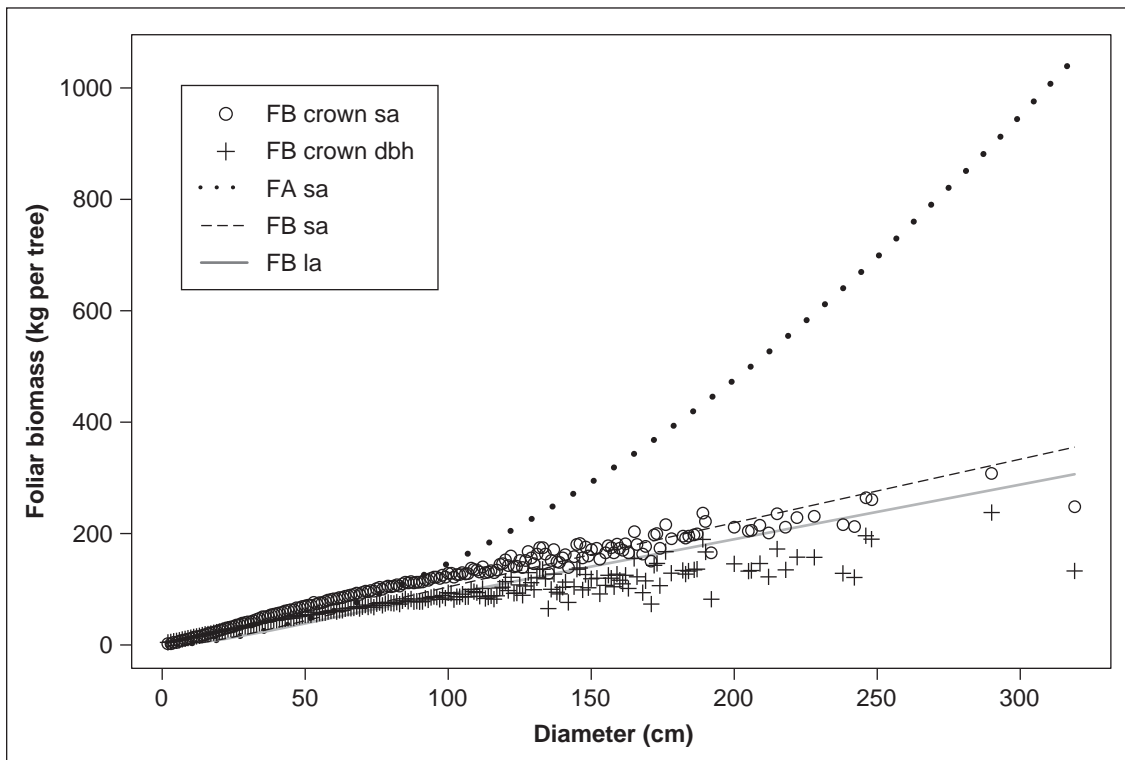

Figure 3—Estimates of foliar biomass (FB) made with five algorithms for coastal Douglas-fir. The two FB_{crown} algorithms use mean crown dimensions (crown width or crown height) for each 1-cm diameter at breast height (DBH) class. The scatter of points is due to the model terms not shown (crown width and crown height).

Sensitivity Analysis of the FB_{la} Algorithm

The selection of LA:SA ratios and SLA values affected the magnitude of differences between the FB_{la} algorithm and the FB_{dbh} algorithm (fig. 4). Ranges of estimates were considerably higher for ponderosa pine than for Douglas-fir. For ponderosa pine FB_{la} estimates using a higher LA:SA ratio and a higher SLA were greater than the estimates with the FB_{dbh} algorithm up to a DBH of about 175 cm, whereas for coastal Douglas-fir, the FB_{dbh} algorithm gave higher estimates than the FB_{la} algorithm, regardless of LA:SA or SLA values, for DBH greater than about 125 cm.

Stand-Level Analysis

We rejected the null hypothesis ($p < 0.10$) of no differences between estimates of FB by using different algorithms for all six ANOVAs (two regions and three seral
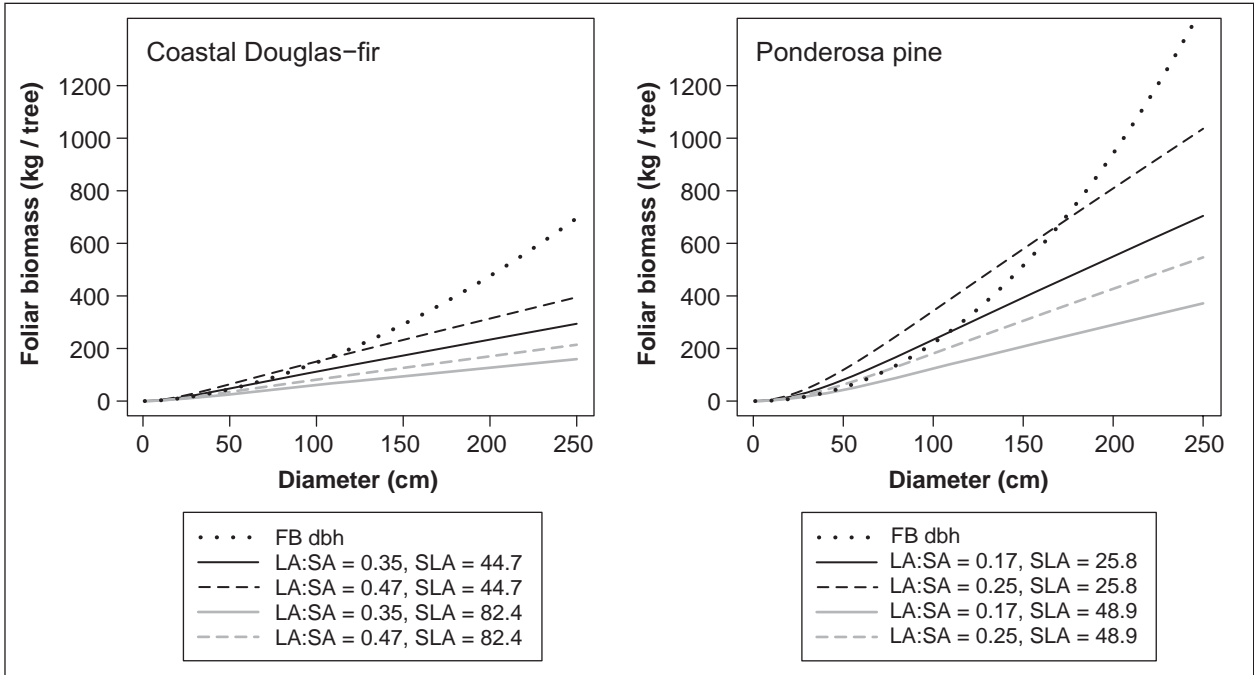
Figure 4—Sensitivity of FB_{lai} algorithm to sapwood area ratios (LA:SA) and specific leaf area (SLA) for (a) coastal Douglas-fir and (b) ponderosa pine. The FB_{dbh} algorithm is shown for comparison. FB = foliar biomass, DBH = diameter at breast height.

stages). The FB_{dbh+ht} algorithm yields significantly higher values of total FB for stands of both regions and all three seral stages than the other three algorithms (table 6). The Tukey HSD test for post hoc pair-wise comparisons indicated that the FB_{dbh+ht} algorithm's estimates of stand-level FB were greater ($p < 0.10$) (as much as three times) than the estimates of the FB_{la} algorithm. The FB_{dbh} algorithm also gave significantly higher ($p < 0.10$) estimates of FB than the FB_{la} algorithm in the mid- and late-seral stands of the western Cascades. The FB_{la} and FB_{sa} algorithms gave similar estimates of stand-level FB for stands of both regions and all seral stages, except the mid-seral stands of the western Cascades.

Table 6—Estimates of mean stand foliar biomass (FB) by region and seral stage for four algorithms

Region	Seral stage	Foliar biomass			
		FB_{dbh}	FB_{dbh+ht}	FB_{sa}	FB_{la}
		Mg/ha_{-1}			
Western Cascades	Early	7.5a	19.1[b]	6.1[a]	6.1[a]
	Middle	16.9[a]	19.6[b]	16.0[a]	12.8[c]
	Late	21.9[a]	32.7[b]	16.6[a,c]	14.5[c]
Eastern Cascades	Early	5.3[a]	10.6[b]	6.0[a,b]	4.5[a]
	Middle	6.6[a]	10.4[b]	5.7[a]	4.5[a]
	Late	10.5[a]	21.4[b]	8.3[a]	7.7[a]

[a b c] Estimates across a single row are not significantly different from one another ($\alpha = 0.10$) if they share a superscript letter. The analysis of variance tested for differences in algorithms only. We did not compare differences in FB between regions or seral stages.

Discussion

Estimating Sapwood Area

The regression models of SW as a function of DBH provide an alternative for estimating SA when it cannot be measured directly, but there are three reasons to be cautious when using them. First, the data we used to develop the models did not include trees with DBH less than 15 cm (Lassen and Okkonen 1969), so they are less appropriate for use with small-DBH trees. Second, the sample sizes of the large DBH trees were small, so outliers with large DBH could be much more influential than the many trees in the mid-range of DBH (fig. 1). Third, direct measurements of SW or SA, if available, should yield more accurate estimates of FB than regressions on DBH. Turner et al. (2000) found that using SW from regression models overestimated LA compared to field-measured SW. The applicability of the FB_{la} and FB_{sa} algorithms is limited when SA is estimated from regression models rather than measured directly. The use of predicted values of SW to estimate FB eliminates tree-level variability that might be observed if SW or SA were measured directly. The ability of SA-based algorithms to capture this variability is one reason that these algorithms estimate FB better than DBH (Grier and Waring 1974).

Diameter was a good predictor of SW for all species except western larch and western redcedar, introducing considerable uncertainty in the end calculation of FB for these two species. For both species, there is a clear tradeoff between the probable bias associated with estimating FB directly from DBH and the low explanatory power and associated uncertainty with the intermediate step via SW and SA. Furthermore, regression models of SW as a function of DBH are available for only a few species in the PNW (notably absent is any species of *Abies*), so species substitutions are required to use this method to calculate SA for other species, introducing even more uncertainty.

Algorithms for Estimating Tree-Level Foliar Biomass

Algorithms based on DBH or DBH and HT gave higher estimates of FB for all species than the algorithms based on SA, although the magnitudes of divergence and the DBH at which the equations diverged differed among species. Divergence between algorithms increases with DBH for two reasons: (1) the exponential form of the DBH- and HT-based equations, and (2) because most of the equations were developed based on only trees with small DBH. Small trees can experience large increases in FB with relatively small increases in DBH, which suggests an exponential response, but that relationship will not hold for large DBH trees because FB growth becomes limited by other factors (Van Pelt and Sillett 2008). Therefore, there is a physiological reason to believe that DBH-based equations may be biased for large trees. More variability in the crowns of large trees is explained

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by the FB_{dbh+ht} algorithm, which gave intermediate estimates between the FB_{dbh} and the SA-based algorithms for some species. For Douglas-fir and western redcedar, however, the FB_{dbh+ht} algorithm gave even higher estimates of FB than FB_{dbh}.

In contrast to DBH- or HT-based allometry, SA-based algorithms for estimating FB invoke a direct physiological mechanism because they are based on the pipe model theory (Shinozaki et al. 1964). The pipe model theory does, however, assume that LA and FB are limited only by water availability.

The FB_{crown} algorithms for Douglas-fir that included both crown dimensions and DBH gave similar estimates to those of the SA-based algorithms for diameters up to about 200 cm. Intuitively, models with explicit crown dimensions should be closest to "truth," given their direct geometric translation to crown volume and reasonable estimates of crown density. The similarity between estimates of the FB_{crown} algorithm and those of the FB_{la} and FB_{sa} algorithms suggests that the SA-based algorithms may be more robust than those based solely on DBH and HT. The FB_{crown} algorithms did, however, give even lower estimates of FB than SA-based algorithms for the largest DBH trees (DBH greater than about 200 cm). The SA-based algorithms may overestimate FB in the oldest and largest trees because they do not capture loss of crown biomass from disturbance and crown breakage, which can be captured with measurements of CW and CD.

The FB_{crown} algorithms are a promising alternative to SA-based algorithms because CD and CW are easier to measure than SA and estimating FB using measured crown variables likely introduces less error than the two-step process of estimating SA from DBH. Definitive answers will require more field observations and destructive sampling, which are currently available for only coastal Douglas-fir, but field-based observations and destructive sampling of tree crowns are also subject to error, because large crowns often must be subsampled, with ratios then used to calculate full crown weight.

In their comparison of DBH and SA as predictors of FB for several coniferous species in the Rocky Mountains, Snell and Brown (1978) found that SA was a better predictor of FB for some species, but SA and DBH were not significantly different predictors of FB for other species. They concluded that the marginal increase in predictive power achieved when using SA was not worth the additional effort required to measure SA. A key limitation of their study, however, was that it included only trees with DBH less than 20 cm. Foliar biomass in mature trees can be much more complicated to estimate or measure, particularly in species like Douglas-fir that have epicormic branching (Ishii et al. 2002).

Despite their apparent bias, simple allometric equations based on HT and DBH have three advantages over SA-based algorithms. First, they exist for more tree

species in the PNW than do SA-based equations, so they may require fewer species substitutions. Second, they are readily available in syntheses and databases of equations commonly used to calculate FB. Third, they require only tree measurements that are commonly collected in the most basic forest inventories. The similarity between DBH-based equations and other algorithms for small DBH trees suggests that DBH-based algorithms are appropriate for estimating FB for smaller trees (less than about 50 cm DBH) and early seral stands in the PNW, whereas FB of larger-DBH trees and mature stands in the PNW calls for SA-based algorithms.

Sensitivity Analysis of the FB_{la} Algorithm

Algorithms based on SA are sensitive to user-selected values of LA:SA ratios and SLA. When they were initially developed, LA:SA ratios and SLA values were assumed to be constant for a species, but as these values were measured over a wider range of environments, more variability was observed (Margolis et al. 1995 and citations therein). Ideally, site-specific values would be measured when applying SA-based algorithms to specific stands. Alternatively, care should be taken to select variables from the literature that are from environments similar to a given study area.

The pipe model theory, the justification for SA-based algorithms, applies strictly only when SA and LA:SA ratios are measured at the base of the crown. We did not account for differences in LA:SA ratios between breast height and crown base height in our use of SA-based algorithms; such accounting would likely improve the accuracy of estimates of FB, because LA:SA ratios depend on how far from the crown base stem SA is measured (Whitehead et al. 1984). The SA-based algorithms can also be improved if the predicted SA contains an adjustment for taper between breast height and the crown base (Waring et al. 1982), via species-specific taper equations (Maguire and Hann 1987, Urban 1993). Alternatively, Dean and Long (1986) accounted for stand- and tree-level differences in LA:SA ratios with a nonlinear model of LA as a function of SA rather than a constant LA:SA ratio.

Stand-Level Analysis of Foliar Biomass Estimates

Some differences among the algorithms for FB at the stand level were large, up to threefold (table 6), especially for stands with high densities of large-DBH (>20 cm) trees and composed primarily of Douglas-fir (either variety), western redcedar, or western larch. For most regions and seral stages, however, estimates of FB at the stand level were not significantly different between the FB_{la} and FB_{dbh} algorithms. At the stand level, the differences between these two algorithms are neutralized

because the FB_{dbh} algorithm predicts lower FB for trees with the smallest DBH (less than about 15 to 20 cm) for some species than the SA-based algorithms. Therefore the differences in FB for small DBH trees compensate for the large differences between the large DBH trees. The late-seral stands used in this analysis had a high density of small DBH trees, as well as large DBH trees, which accounts for the lack of significant differences between the FB_{la} and FB_{dbh}. Differences in the estimates of stand-level FB also depend on species composition. This stand-level analysis should be considered preliminary and can inform future studies that go into greater detail and account for differences in species composition. More detailed work at the stand level is needed to understand the effects of varying species composition and stand structure.

Implications for Ecological Modeling and Carbon Accounting

Foliar biomass is a relatively small component of total ecosystem carbon in late-seral forests of the western PNW (Grier and Logan 1977, Smithwick et al. 2002), but it is a larger proportion of total ecosystem carbon in early-seral forests. The proportion of aboveground biomass estimated to be FB depends on species composition and seral stage of the stand, but also on how it is estimated, as we have shown. The DBH-based algorithms estimate FB to be a larger portion of total biomass than do SA-based algorithms. In this study, FB calculated with SA-based algorithms was about 10 percent of aboveground biomass in early-seral stands of the western Cascades, 6 percent in early-seral stands in the eastern Cascades, and 3 percent to 5 percent in the mid- and late-seral stands of both regions. In contrast, FB calculated with the FB_{dbh+ht} algorithm was 28 percent in early-seral stands of the western Cascades and 15 percent in early-seral stands of the eastern Cascades.

More research is needed on the sensitivity of ecological models to the algorithms they use to calculate FB and LAI. For example, when forest gap and succession models calculate FB, LA, or LAI with algorithms based on DBH, the modeled understory light environment is likely to be too dark, especially when overstory trees are large. This could lead to unrealistic stand structure because of the effect of light on recruitment and growth stress, thereby overestimating the proportion of late-seral species. Similarly, succession models that include fire may overestimate crown fuels (and therefore crown bulk density) if using DBH-based algorithms to predict FB. More fine fuels increase fire severity, altering carbon stocks, forest demography, and age and stand structure. The SA-based algorithms may improve model results, but then species substitutions may introduce new uncertainties if a model simulates species not in the limited database for SA-based models. Fine-scale (30-m) hydrological models, such as the regional hydro-ecological simulation

system (RHESSys) (Tague and Band 2004) and the distributed hydrology-soil-vegetation model (DHSVM) (Wigmosta et al. 1994), use LAI to calculate evapotranspiration, interception, and snowpack energy dynamics, and will be similarly affected. Modelers should be aware of the origins of the LA and FB data and of their sensitivity to three sources of uncertainty: (1) choice of FB-estimation algorithms, (2) parameters used in SA-based algorithms, and (3) species substitutions.

Forests are being proposed as carbon storage offsets, thus accurate and reliable methods are needed to account for carbon in all FB pools. We have documented differences among algorithms that estimate FB for seven species in the PNW. These methods actualize the FB component in forest carbon accounting, but the significant differences between stand-level estimates of FB for different algorithms show the need for their informed use. Consistent methods are needed for estimating FB when comparing different stands, monitoring the same stand over time, or comparing stands with established baselines above which additional carbon storage is measured. Which of these methods is generally more accurate is not known because independent measures of FB (e.g., destructive sampling or litter fall) are not available except for Douglas-fir, for which SA-based algorithms are more accurate (Marshall and Waring 1986, Turner et al. 2000). Direct measurements of FB on other species are needed to confirm if a more mechanistic approach, based on pipe-model theory, proves indeed to be superior.

Acknowledgments

English Equivalents

When you know:	Multiply by:	To find:
Millimeters (mm)	0.0394	Inches
Centimeters (cm)	.394	Inches
Grams (g)	.0352	Ounces
Kilograms (kg)	2.205	Pounds
Hectares (ha)	2.47	Acres
Megagrams per hectare	.446	Tons per acre

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