National-Scale Biomass Estimators for United States Tree Species

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ABSTRACT. Estimates of national-scale forest carbon (C) stocks and fluxes are typically based on allometric regression equations developed using dimensional analysis techniques. However, the literature is inconsistent and incomplete with respect to large-scale forest C estimation. We compiled all available diameter-based allometric regression equations for estimating total aboveground and component biomass, defined in dry weight terms, for trees in the United States. We then implemented a modified meta-analysis based on the published equations to develop a set of consistent, national-scale aboveground biomass regression equations for U.S. species. Equations for predicting biomass of tree components were developed as proportions of total aboveground biomass for hardwood and softwood groups. A comparison with recent equations used to develop large-scale biomass estimates from U.S. forest inventory data for eastern U.S. species suggests general agreement (±30%) between biomass estimates. The comparison also shows that differences in equation forms and species groupings may cause differences at small scales depending on tree size and forest species composition. This analysis represents the first major effort to compile and analyze all available biomass literature in a consistent national-scale framework. The equations developed here are used to compute the biomass estimates used by the model FORCARB to develop the U.S. C budget. For. Sci. 49(1):12–35.

Key Words: Allometric equations, forest biomass, forest inventory, global carbon cycle.

Researchers in various countries have developed national-scale forest carbon (C) budgets to increase understanding of forest-atmosphere C exchange at large scales and to support policy analysis regarding greenhouse gas reductions (Birdsey and Heath 1995, Turner et al. 1995, Kauppi et al. 1997, Nabuurs et al. 1997, Kurz and Apps 1999, Nilsson et al. 2000). These C budgets have been based primarily on regional forest inventory data, which provide a good representation of forest conditions and trends when the data are based on extensive networks of sample plots that are remeasured periodically. In the United States, the USDA Forest Service's Forest Inventory and Analysis (FIA) sampling design includes a network of plots chosen to represent conditions across the landscape. In the past, the plots were periodically measured; however, an annualized design was recently adopted. In either design, plot-level information is computed directly from individual tree characteristics, such as diameter at breast height (dbh) and species, which are measured during the inventory. Plot statistics may then be aggregated to provide information about forest populations of interest, provided those populations are adequately sampled by the inventory.

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Biomass Estimation

In this article, we define biomass in dry weight terms. "Aboveground tree biomass," for example, refers to the weight of that portion of the tree found above the ground surface, when oven-dried until a constant weight is reached. Plot-level biomass estimates are typically expressed on a per-unit-area basis (for example, Mg ha^{-1} or kg m^{-2}), and are made by summing the biomass values for the individual trees on a plot, then standardizing for the land area covered by that plot.

"Dimensional analysis," as described by Whittaker and Woodwell (1968), is the method most often used by foresters and ecologists to predict individual tree biomass. This method relies on the consistency of an allometric relationship between plant dimensions (usually dbh and/or height) and biomass for a given species, group of species, or growth form. In the biological sciences, the study of size-correlated variations in organic form and process is traditionally called "allometry" (Greek *allos,* "other" and *metron,* "measure") (Niklas 1994). Using the dimensional analysis approach, a researcher samples many stems spanning the diameter and/or height range of interest, then uses a regression model to estimate the relationship between one or more tree dimensions (as independent variables) and tree component weights (as dependent variables). "Tree components," as defined here, refer to the different portions of a tree such as foliage, merchantable stem, roots, or branches.

Most published biomass equations were developed using trees sampled from isolated study sites or from very small regions. As a result, it is difficult to use existing biomass equations with forest inventory datasets at large spatial scales because the literature is site-specific, often disorganized, and sometimes inconsistent. Existing compilations of equations (Tritton and Hornbeck 1982, Ter-Mikaelian and Korzukhin 1997), for example, are incomplete or ignore differences in tree component definitions. Furthermore, unless an equation was developed exclusively for the species and study region of interest, and in conditions typical of the study site, it is impossible to know which of several potentially applicable equations to choose for a particular species and site.

For biomass estimation at large scales, one would use a set of biomass equations that applies equally well to every stem across the region of interest. These equations would be "generalizable," in that they would be applicable, for the purposes of broad-scale biomass estimation, to trees growing anywhere in the region. They would also be consistent in terms of component definitions, equation forms, and input data requirements. Because these consistent and generalizable equations have not been available for biomass estimation in the United States to date, regional FIA program units have applied published equations to each region on a species-specific basis, using equations that appear to be most appropriate for that geographic area [e.g., Wharton et al. (1997), Wharton and Griffith (1998)]. This method can be cumbersome and difficult to comprehend. In addition, because the approach has been implemented independently in different regions of the United States, it has resulted in some inconsistency in methodology and probable inconsistency in results (Birdsey and Schreuder 1992).

Objective

In this analysis, we sought to develop consistent and generalizable biomass regression equations for use in large-scale inventory-based forest C budgets. Forest C budgets include C in several ecosystem components: live biomass, detritus, and soil. Of these, C in live biomass is most directly tied to inventory measurements and is most affected by human activities and natural disturbances. The equations presented here should provide a consistent basis for evaluating forest biomass across regional boundaries, thereby helping to reduce uncertainty in analysis of forest-atmosphere C exchange.

The equations developed for this study are also used by the USDA Forest Service to develop the U.S. C budget using the model FORCARB (Heath and Birdsey 1993, Plantinga and Birdsey 1993, Birdsey and Heath 1995, Heath et al. 1996). For use with FORCARB, biomass estimates developed from diameter for individual trees are incorporated into forest-type-specific volume: biomass ratios using FIA data—which are then used to estimate forest biomass based on volume projections. The biomass estimates for individual trees are thus the foundation for the volume-based biomass projections in the model.

Sources of Uncertainty in Large-Scale Biomass Estimation

Ideally, to develop consistent national-scale biomass equations, one would sample hundreds, if not thousands, of trees of different sizes from a representative sample of species, regions, and sites across the nation. This would ensure an unbiased sample of trees, but it would be very expensive and time-consuming. Alternatively, one could attempt to collect sample data for reanalysis from all available sources of tree mensurational data in as many species and regions as possible. This approach is also prohibitively difficult: most scientists have not published the raw data from which their biomass equations were developed, and even if the raw data were available, many scientists do not keep adequate metadata from studies completed decades before. Even if this approach were adopted, however, it would still be impossible to be certain that the accumulated biomass data from mensurational studies represent all conditions across the United States in proportion to occurrence. Instead, to accomplish our goal of consistent and generalizable biomass equations for U.S. tree species, we undertook a comprehensive analysis and synthesis of the existing dimensional analysis literature.

Though applying equations developed via dimensional analysis is the only reasonable method to estimate tree biomass without destructive sampling, some potential errors are inherent in estimating forest biomass at large scales using published biomass equations (Wharton and Cunia 1986). These include: (1) application of coefficients developed for one species (or group of species) to another species (or group of species); (2) sample trees and wood density samples not representative of the target population because of factors such as size range of sample trees and stand conditions; (3) statistical error associated with estimated coefficients and form of selected equation; (4) inconsistent standards, definitions, and methodology; (5) use of indirect estimation methods that compound errors; and (6) measurement and data processing errors. It may be nearly impossible to quantify all of these errors in a practical application (Phillips et al. 2000). Indeed, inconsistencies in methods, analyses, and reporting among the numerous published biomass studies were substantial obstacles in this analysis.

Despite these inconsistencies, or perhaps because of them, the need is clear for a consistent method for forest biomass estimation for application in large-scale studies. To accomplish this goal with our synthesis of the existing literature, we incorporated data from published studies into new biomass estimation equations. Variations on this technique have been applied successfully in the past by other researchers wishing to combine measured or modeled data points into new, more general, equations (Schmitt and Grigal 1981, Pastor et al. 1984, Schroeder et al. 1997).

Methods

Overview

The formal statistical method for compiling information from many studies is meta-analysis (Hedges and Olkin 1985). This method was devised to summarize studies on the same topic by different investigators, generally to obtain a combined significance level for an overall mean among studies. Simply stated, meta-analysis is: (1) identification of a problem; (2) retrieval of relevant studies; (3) extraction of appropriate data; and (4) formulation of a statistical model for combining data (Iyengar 1991).

Unfortunately, an accepted statistical model for combining diverse regression equations has not yet been developed. For example, a recent paper by Peña (1997) describes an approach for combining regression estimates from independent samples, but formal meta-analytic approaches like this one do not apply to the current situation because: (1) formal meta-analysis requires an estimate of regression errors, which are rarely published in an appropriate format for existing biomass equations; (2) all equations used in such a meta-analysis must have identical forms and identical variable transformations; and (3) there is no clear method for combining estimates from three or more regression equations. Application of formal meta-analytic techniques for combining regression coefficients would not work in our study, with its goal of developing generalizable biomass equations based on all available published literature. Application of published formal meta-analytic techniques would have limited the number of available equations (by requiring identical model forms and variable transformations, as well as specific information on regression errors) to the point where the resulting biomass equations would have been internally consistent, but not at all generalizable.

Therefore, we chose for our analysis a modified version of a type of meta-analysis used by Pastor et al. (1984). Pastor followed the first three steps in Iyengar's definition of meta-analysis, but refitting of regression predictions was used in place of a formal statistical model for combining the regression results. Because development of new statistical methods is beyond the scope of this study, we based our approach on Pastor's "modified meta-analysis" to develop new diameter-based regression equations from predictions by equations in the literature.

We grouped species across taxonomic and geographic bounds. We did this because all species were not represented by published biomass equations, and because equations were not always available throughout the entire range for a species. For each species group, we sought a pool of regression equations that adequately captured trends in the diameter-to-biomass relationship. Using systematic graphing of published species-specific equations for total aboveground biomass, we found that within-species variation (i.e., variation among biomass regressions published by different authors for the same species) often exceeded variation between different species. Regional differences might account for this phenomenon, but we found no apparent regional pattern in the published data. Most likely, noise in biomass measurements due to differences in methodology, together with some site-level variability in biomass values and the relatively small sample size, are the main contributors to this within-species variability.

Theoretical literature on plant allometry (West et al. 1997, Enquist et al. 2000) groups the diameter-to-total aboveground biomass correlation in a family of allometric scaling relationships that view plants as fractal-like networks, which can be described by the same model regardless of species or size. Whether a single allometric equation can adequately describe all tree species needs to be rigorously tested, but the apparent similarity in the diameter-to-total aboveground biomass relationship across species in our data encourages such investigation. For this study, species were grouped into six softwood and four hardwood categories based on a combination of taxonomic relationships, wood specific gravity, and diameter-to-aboveground biomass relationships. The woodland "softwood" group includes some hardwood mesquite, acacia, and oak species; these woodland species are all from dryland forests and are measured for diameter at ground line (see below for procedure used to transform diameters from ground line to breast height). In addition to the ten species-group equations for predicting total aboveground biomass, we also developed equations to predict the relative biomass of tree components for hardwood and softwood types.

Literature Search

The first step in this analysis was to compile all available published biomass equations for U.S. tree species from the literature. Because many tree species common in the United States have also been studied intensively by Canadian researchers, we included all applicable information from studies conducted in Canada. In some cases, we also included biomass information for U.S. genera growing on other continents.

While many researchers have reported that dbh is adequate for local or regional biomass estimation, others have suggested that both dbh and height must be included for larger scale application (Honer 1971, Crow 1978). We excluded biomass equations that required tree height as an independent variable because tree height is more difficult to measure accurately in closed-canopy stands than dbh and because we wished to make our equations as accessible to all researchers as possible. Furthermore, currently the publicly accessible version of the USDA Forest Service FIA Data Base includes height data only for western states (Hansen et al. 1992, Woudenberg and Farrenkopf 1995), and even for those states the height data are a mixture of true measurements and values estimated ocularly or predicted from dbh. Given that the FIA Data Base is the major source of large-scale forest inventory data for the United States, it is most appropriate to use dbh only as the basis for equations meant to develop large-scale biomass and C estimates for the entire country. Finally, there is evidence that including height as an additional dependent variable adds only a marginal amount to the predictive capacity of a diameter-based regression (Madgwick and Satoo 1975, Wiant et al. 1979).

Because site level measurements other than dbh may be defined differently from site to site and from study to study, we also excluded from our compilation any equation that required additional site-level variables (such as site index or soil texture). In this first phase of the analysis, we compiled 2,456 equations for 64 eastern U.S. species and 40 western U.S. species. An additional 170 equations for western species were obtained from the "BIOPAK" compilation of Means et al. (1994). All of these equations use diameter as the single independent variable, with biomass (of any tree component or combination, for example "total aboveground biomass," "stem," "foliage," or another as defined by the author) as the single dependent variable. The full compilation of diameter-based equations from the literature, together with metadata describing methods used by the original authors, geographic origin, component definitions, and other information relevant for potential users of the equations, will be published by these authors as a USDA Forest Service General Technical Report. For this analysis, we assembled 318 total biomass equations (Tables 1, 2, and 3), and selected 389 component equations (Table 7) for over 100 species from 104 sources. The remaining equations were excluded primarily because component definitions did not correspond with the components identified as critical for this analysis, as described below.

Identifying Equations for Inclusion

To standardize component definitions for our consistent national-scale equations, and to provide the most flexible set of components for researchers wishing to estimate the biomass of portions of the tree, we developed estimation methods for the following five tree components: total aboveground (above the root collar), foliage, merchantable stem wood [from 12 in. (30.48 cm) stump height to 4 in. (10.16 cm) top diameter outside bark (dob)], merchantable stem bark, and coarse roots. We did not develop separate branch biomass equations because this component can be obtained by subtraction. Equations that were not consistent (with some transformations as described below) with these component definitions were excluded from the analysis.

When an author presented equations based on independent tree samples from different sites, we included all of the published equations in this analysis. However, if the same author also presented one equation based on "pooled" data from all sites sampled, we used the pooled equation only. Where a researcher presented a group of equations for different components that added together to total aboveground biomass, we used the additive equations for this analysis. However, if the same author also presented one equation for total aboveground biomass, we used that equation only.

If merchantable stem biomass was presented along with a description of limiting top diameter close to 4 in. (8 to 12 cm), then we used that equation directly in this analysis, with modifications to account for stump height as necessary (see section on stump calculations). No modifications were made for top diameter: if an author did not report the limiting top diameter for a stem biomass equation, that equation was excluded from this analysis. For some woodland species, the only equations available were based on diameter at the root collar (drc), rather than dbh. For these species, dbh was predicted from drc using algorithms as published in Chojnacky and Rogers (1999), and biomass was related to dbh as for all other species.

Stump Calculations

Many authors describe their equations as representing aboveground totals, when in fact the sampled trees were felled leaving a stump some height above ground level. Stump biomass can be an important source of error, especially if each measured tree represents tens or hundreds of trees per unit area. For example, in an analysis of forest biomass and productivity based on the USDA Forest Inventory and Analysis data for the mid-Atlantic region of the United States, stumps 6 in. (15.24 cm) tall comprised approximately 2.5% of aboveground biomass (Jenkins et al. 2001). To develop equations representing total aboveground biomass for this analysis, we added stump biomass to the aboveground totals presented by individual authors where appropriate. To develop merchantable stem equations for this analysis, it was more common to subtract the biomass of that portion of the stump between stump height and 12 in. (30.48 cm).

If the original authors reported stump height, it was used in the analysis. If no stump height was given, we assumed that the stump was 6 in. (15.24 cm) tall. Stump height was assumed to be zero if any one of the following were true: (1) the methods of Whittaker and Woodwell (1968) or Whittaker and Marks (1975) were used for sampling (these authors were very explicit about felling the trees at groundline); (2) the authors state that trees were "felled at groundline"; (3) the stump is described as "as short as possible"; (4) the same authors also report an equation for root biomass only (as opposed to stump plus root biomass); or (5) the authors discuss that they estimated (using their own method) that portion of the stump not included when the trees were felled.

To find stump biomass, tree diameters inside and outside bark were estimated from dbh at a height corresponding to the

Table 1. Hardwood species groups for the diameter-based aboveground biomass equations.

Species group	No. of eqs.	Genus	Species	Wood-specific gravity*	Literature reference†
Aspen/alder/ cottonwood/ willow	36	*Alnus*	*rubra*	0.37	7,8,44,55
			sinuata		7
			spp.	0.37	71,83,101
		Populus	*balsamifera*	0.31	90
			deltoides	0.37	2,3,19,59
			grandidentata	0.36	32,54,100
			spp.	0.37	45,65,101
			tremuloides	0.35	16,32,47,51,58,61,72,74,76,78,83,85,90,96
		Salix	spp.	0.36	83,101
Soft maple/ birch	47	*Acer*	*macrophyllum*	0.44	33
			pensylvanicum	0.44	101
			rubrum	0.49	12,22,23,25,26,32,45,51,53,61,63,65,77,81,83,100,101
			spicatum	0.44	14,60,79,101
		Betula	*alleghaniensis*	0.55	32,65,67,81,83,89,101
			lenta	0.60	15,45,63
			papyrifera	0.48	6,25,45,48,51,61,81,83,101
			populifolia	0.45	32,45,51,83,101
Mixed hardwood	40	*Aesculus*	*octandra*	0.33	15
		Castanopsis	*chrysophylla*	0.42	33
		Cornus	*florida*	0.64	10,63,77
		Fraxinus	*americana*	0.55	65,100,101
			nigra	0.45	71,81,101
			pennsylvanica	0.53	22
		Liquidambar	*styraciflua*	0.46	22,23,77
		Liriodendron	*tulipifera*	0.40	15,22,23,63,77,100
		Nyssa	*aquatica*	0.46	22
			sylvatica	0.46	22,77,100
		Oxydendrum	*arboreum*	0.50	63,77
		Platanus	*occidentalis*	0.46	23
		Prunus	*pensylvanica*	0.36	15,61,83,101
			serotina	0.47	100
			virginiana	0.36	83,101
		Sassafras	*albidum*	0.42	100
		Tilia	*americana*	0.32	45,101
			heterophylla	0.32	15
		Ulmus	*americana*	0.46	81
			spp.	0.50	23
Hard maple/ oak/hickory beech	49	*Acer*	*saccharum*	0.56	15,20,25,32,45,65,67,72,83,89,100,101
		Carya	spp.	0.62	22,23,63,77
		Fagus	*grandifolia*	0.56	15,45,65,83,89,101
		Quercus	*alba*	0.60	22,23,63,77,81,98
			coccinea	0.60	23,63,98
			ellipsoidalis	0.56	81
			falcata	0.52	23,77
			laurifolia	0.56	22
			nigra	0.56	22
			prinus	0.57	23,63,77
			rubra	0.56	15,20,36,45,53,63,65,101
			stellata	0.60	23,77
			velutina	0.56	100

* US Forest Products Laboratory. 1974. Wood handbook: Wood as an engineering material. USDA Agric. Handb. 72, rev.

† Reference numbers are matched to authors in Table 2. Reference number 32 for Freedman's combined species equation is also included in each species group.

midpoint of the stump portion to be analyzed, using species-specific equations as described by Raile (1982). From these diameters, we computed total stump volume (outside bark) and stump wood volume (inside bark) assuming the stump was cylindrical. Stump bark volume was found by difference. Stump wood and bark volume were multiplied by specific gravity values appropriate for each species and component, and added together to find total stump biomass.

Aboveground Biomass

"Pseudodata" from published equations.—The first step in the Pastor et al. (1984) method was generation of "pseudodata" from published equations. Biomass values were calculated for each of five diameters equally spaced within the diameter range of the trees used to develop each published equation. The diameter and biomass values were log-transformed to linearize the dbh/biomass rela-

Table 2. Key to reference numbers in Tables 1 and 3.

Ref. no.	Author reference	Ref. no.	Author reference
1	Acker and Easter (1994)	52	Ker and van Raalte (1981)
2	Anurag et al. (1989)	53	Kinerson and Bartholomew (1977)
3	Bajrang et al. (1996)	54	Koerper and Richardson (1980)
4	Barclay et al. (1986)	55	Koerper (1994)
5	Barney et al. (1978)	56	Krumlik (1974)
6	Baskerville (1965)	57	Landis (1975)
7	Binkley (1983)	58	Lieffers and Campbell (1984)
8	Binkley and Graham (1981)	59	Lodhiyal et al. (1995)
9	Bockheim and Lee (1984)	60	Lovenstein and Berliner (1993)
10	Boerner and Kost (1986)	61	MacLean and Wein (1976)
11	Bormann (1990)	62	Marshall and Wang (1995)
12	Briggs et al. (1989)	63	Martin et al. (1998)
13	Brown (1978)	64	Miller et al. (1981)
14	Bunyavejchewin and Kiratiprayoon (1989)	65	Monteith (1979)
15	Busing et al. (1993)	66	Moore and Verspoor (1973)
16	Campbell et al. (1985)	67	Morrison (1990)
17	Carlyle and Malcolm (1986)	68	Naidu et al. (1998)
18	Carpenter (1983)	69	Nelson and Switzer (1975)
19	Carter and White (1971)	70	Ouellet (1983)
20	Chapman and Gower (1991)	71	Parker and Schneider (1975)
21	Chojnacky (1984)	72	Pastor and Bockheim (1981)
22	Clark et al. (1985)	73	Pearson et al. (1984)
23	Clark et al. (1986)	74	Perala and Alban (1982)
24	Clary and Tiedemann (1987)	75	Perala and Alban (1994)
25	Crow (1976)	76	Peterson et al. (1970)
26	Crow (1983)	77	Phillips (1981)
27	Darling (1967)	78	Pollard (1972)
28	Dudley and Fownes (1992)	79	Rajeev (1998)
29	Felker et al. (1982)	80	Ralston (1973)
30	Feller (1992)	81	Reiners (1972)
31	Freedman (1984)	82	Rencz and Auclair (1980)
32	Freedman et al. (1982)	83	Ribe (1973)
33	Gholz et al. (1979)	84	Ross and Walstad (1986)
34	Gower et al. (1987)	85	Ruark and Bockheim (1988)
35	Gower et al. (1992)	86	Sachs (1984)
36	Gower et al. (1993)	87	Schnell (1976)
37	Green and Grigal (1978)	88	Schubert et al. (1988)
38	Grier et al. (1984)	89	Siccama et al. (1994)
39	Grier et al. (1992)	90	Singh (1984)
40	Grigal and Kernik (1984)	91	St. Clair (1993)
41	Harding and Grigal (1985)	92	Swank and Schreuder (1974)
42	Harmon (1994)	93	Teller (1988)
43	Hegyi (1972)	94	Van Lear et al. (1984)
44	Helgerson et al. (1988)	95	Vertanen et al. (1993)
45	Hocker and Earley (1978)	96	Wang et al. (1995)
46	Honer (1971)	97	Westman (1987)
47	Johnston and Bartos (1977)	98	Whittaker and Woodwell (1968)
48	Jokela et al. (1981)	99	Whittaker and Niering (1975)
49	Jokela et al. (1986)	100	Williams and McClenahen (1984)
50	Ker (1980a)	101	Young et al. (1980)
51	Ker (1980b)		

tionship, so that it could be fitted with simple linear regression rather than a more complicated nonlinear model. Finally, a new linear equation was fitted from the pseudodata. In this way, the new regression was a synthesis of the original published regressions.

We modified this approach slightly. In our analysis, if the range between the minimum and maximum diameters of the original equations was wider than 25 cm, the diameter range was divided by 5 to obtain (to the nearest integer) the number of diameter values included for that equation, spaced at 5 cm intervals. If the upper diameter limit for a given equation was larger than 100 cm, we spaced the diameter values larger than 100 cm at 10 cm intervals to moderate the influence of the these few large-tree equations. The median number of pseudodata points per equation was 8, but 10% of the equations spanned diameter ranges that exceeded 100 cm; these large-tree equations were all developed for softwood species and represented between 20 and 50 pseudodata predictions each.

Generalized regression for total aboveground biomass.—The pseudodata developed from the published equations were used to predict the relationships between tree dbh

Table 3. Softwood and woodland species groups for the diameter-based aboveground biomass equations.

Species group	No. of eqs	Genus	Species	Wood-specific gravity	Literature reference*
Cedar/larch	21	*Calocedrus*	*decurrens*	0.37	42
		Chamaecyparis	*nootkatensis*	0.42	42,56
		Chamaecyparis/ Thuja	spp.		33
		Juniperus	*virginiana*	0.44	87
		Larix	*laricina*	0.49	18,51,90,101
			occidentalis	0.48	13,34
			spp.	0.44	36
		Sequoiadendron	*giganteum*	0.34	42
		Thuja	*occidentalis*	0.29	50,75,81,101
			plicata	0.31	1,13,30,42
Douglas-fir	11	*Pseudotsuga*	*menziesii*	0.45	4,13,30,33,34,35,38,42,44,62,91
True fir/ hemlock	32	*Abies*	*amabilis*	0.40	33,42,56
			balsamea	0.34	6,32,46,51,61,101
			concolor	0.37	42,97
			grandis	0.35	13
			lasiocarpa	0.31	13,42
			magnifica	0.36	42,97
			procera	0.37	33,42
			spp.	0.34	33
		Tsuga	*canadensis*	0.38	15,45,65,101
			heterophylla	0.42	1,13,33,42,56,86
			mertensiana	0.42	33,42,56
Pine	43	*Pinus*	*albicaulis*	0.37	13
			banksiana	0.40	37,43,51,61,90
			contorta	0.38	13,17,33,34,42,73,84
			discolor	0.50	99
			edulis	0.50	27,39
			jeffreyi	0.37	42
			lambertiana	0.34	33,42
			monophylla	0.50	64
			monticola	0.35	13
			ponderosa	0.38	13,33,36,42,84
			resinosa	0.41	9,36,51,101
			rigida	0.47	98
			strobus	0.34	36,45,53,61,65,92,101
			taeda	0.47	68,69,80,94
Spruce	28	*Picea*	*abies*	0.38	36,49,93
			engelmannii	0.33	13,42,57
			glauca	0.37	6,32,41,51,52,90
			mariana	0.38	5,32,40,51,66,70,82,90
			rubens	0.38	32,61,89
			sitchensis	0.37	11,42
			spp.	0.38	65,101
Woodland	11	*Acacia*	spp.	0.60	28,60,88
		Cercocarpus	*ledifolius*	0.81	21
		Juniperus	*monosperma*	0.45	39
			osteosperma	0.44	27,64
		Prosopis	spp.	0.58	29,95
		Quercus	*gambelii*	0.64	24
			hypoleucoides	0.70	99

* Reference numbers are matched to authors in Table 2.

(as the independent variable) and aboveground biomass for each species group. The logarithmic model form, common in biomass studies, was used:

$$bm = Exp(\beta_0 + \beta_1 \ln dbh) \qquad (1)$$

where

bm = total aboveground biomass (kg dry weight) for trees 2.5 cm dbh and larger
dbh = diameter at breast height (cm)
Exp = exponential function
ln = log base e (2.718282)

Species groups.—Species were assigned to 10 groups (Tables 1 and 3) for developing the generalized total aboveground biomass regressions. Specific factors considered in assigning groups were (in approximate order of importance): (1) phylogenetic relationships; (2) similarity of pseudodata; (3) adequate numbers of equations per species group; (4) ease of applying the equations for species not represented in the published literature; (5) adequate diameter range of pseudodata; and (6) similarity of wood specific gravity. Though we recognize that wood specific gravity is an important determinant of tree biomass, we chose not to emphasize this parameter as a primary means of assigning species to groups because specific gravity was rarely reported with the published equations, and when reported it often varied among different portions of an individual tree. Instead, we grouped species primarily according to similarities in tree morphology, which are reflected in taxonomic affiliations. Where very few equations existed for species in a particular taxonomic group, pseudodata were examined and species were assigned to groups with similar dbh/biomass relationships.

Large trees.—In addition to ensuring that the species group equations were developed from adequate numbers of pseudodata, came from populations with reasonably similar dbh/biomass relationships and were appropriate for use with species not represented by a biomass equation, we ensured that each of the equations will be applicable for the entire dbh range of stems growing in the United States. Inclusion of large-tree equations for each group was especially critical because logistic regression equations may not extrapolate well beyond the range of data. Based on the full set of Eastwide and Westwide FIA data (Hansen et al. 1992, Woudenberg et al. 1995), the largest softwood and hardwood trees measured in the most recent inventory sample in the United States were 250 and 230 cm, respectively. Ample softwood pseudodata included trees as large as 250 cm dbh, such that we were able to include one equation with a dbh limit close to 250 cm in each of the softwood species groups.

However, published hardwood equations have upper dbh limits ranging only from 56 to 73 cm. To ensure that our generalized hardwood equations would be applicable at diameters substantially larger than this, the generalized hardwood equation published by Freedman (1984) was used to predict biomass values for diameters between 100 and 230 cm for each hardwood species group. This equation's stated upper limit is 31.3 cm, so we were concerned that it might bias biomass estimates at large dbh values. We plotted the generalized Freedman (1984) hardwood equation together with the pseudodata from the softwood equations based on measured data to 250 cm that were used to develop the generalized regressions in this analysis. The Freedman (1984) equation matched the large-tree softwood equations closely at all values of dbh, suggesting that this equation does not contribute to substantial bias at large dbh values.

While this solution is clearly not ideal, we re-emphasize that there are no published hardwood regression equations available for use in this analysis that were developed using hardwood trees as large as the largest trees in the inventory sample. Furthermore, we assert that: (1) it is important for our equations to be applicable at the large dbh values observed in nature; (2) equations developed without this correction were quite clearly biased upward at large diameters; (3) available mensurational datasets (e.g., Baker 1971, Sollins and Anderson 1971, Crow 1976, Briggs et al. 1989) do not include trees at diameters approaching 230 cm; and (4) the only other approach to estimate biomass for hardwood trees with very large diameters would have been to use pseudodata from equations developed for softwoods.

Correction factors.—Logarithmic regressions are reported to result in a slight downward bias when data are back-transformed to arithmetic units (Baskerville 1972, Beauchamp and Olson 1973, Sprugel 1983). To remedy this problem, it has been proposed that the back-transformed results (from natural logarithmic units) be multiplied by a correction factor (CF), defined as $exp(MSE/2)$ (Sprugel 1983), where MSE refers to the mean squared error of a line fit by least-squares regression. Because MSE varies inversely with sample size, however, the CF also varies with sample size. This does not necessarily result in more accurate estimates, and the correction itself might be biased for small sample sizes (Flewelling and Pienaar 1981). To avoid the bias potentially introduced by using such CFs, we uncorrected any equation coefficients that were presented by the original authors as having been corrected, and we did not use CFs when they were presented separately. In addition, though our regressions are presented in logarithmic form, we do not include CFs for the reader to use after back-transformation. The root mean squared error (RMSE) for each regression is included in Table 4, however, for the reader who wishes to calculate CF values.

Goodness-of-fit.—Because our generalized regressions were refit from published equations without using a technique that included a measure of the variability of the equations, it was difficult to calculate confidence intervals or other standard regression statistics to assess prediction error. However, we examined regression residuals in terms of percentage of predicted value. The residuals (pseudodata minus predicted value) from the generalized regressions were first expressed in terms of "percent of the predicted value," and these percentage values were ranked. Table 5 lists the 10th and 90th percentiles of the residual distribution (expressed as percent of predicted value) for each species group, which is an upper and lower bound for 80% of the pseudodata. These results indicated that 80% of the pseudodata fell within about 20 to 35% of our generalized regression equations.

Comparison with other datasets.—As stated above, there is no available, representative, and complete set of tree mensurational data against which to compare our generalized biomass equations at the national scale. As a test of our equations, then, we compared our equations against other equations that were developed to be reasonably generalizable, and which have also been used to develop large-scale biomass estimates. While this comparison cannot determine unequivocally whether any of these equations truly represent the conditions observed in nature, it can point out areas of disagreement and suggest topics for further study.

We predicted biomass for dbh values between 5 and 80 cm using our equations and equations for northeastern species, which have also been applied to the USDA Forest Service FIA dataset for large-scale biomass estimation, published by Schroeder et al. (1997) and Brown et al. (1999). For this comparison, our four hardwood species group equations were compared with the general hardwood equation published by Schroeder et al. (1997); our spruce and true fir/hemlock equations were compared with the spruce/fir equation published by Brown and Schroeder (1999); and our pine equation was compared directly with the equation for pine published by Brown and Schroeder (1999). Three of our species groups—Douglas-fir, woodland, and cedar/larch—were excluded from this analysis because trees in these groups were not represented in the dataset used by Schroeder et al. (1997) and Brown and Schroeder (1999) to develop their equations.

Table 4. Parameters and equations* for estimating total aboveground biomass for all hardwood and softwood species in the United States.

	Species group	Parameters β_0	β_1	Data points[†]	Max[††]dbh cm	RMSE[§] log units	R^2
Hardwood	Aspen/alder/cottonwood/willow	−2.2094	2.3867	230	70	0.507441	0.953
	Soft maple/birch	−1.9123	2.3651	316	66	0.491685	0.958
	Mixed hardwood	−2.4800	2.4835	289	56	0.360458	0.980
	Hard maple/oak/hickory/beech	−2.0127	2.4342	485	73	0.236483	0.988
Softwood	Cedar/larch	−2.0336	2.2592	196	250	0.294574	0.981
	Douglas-fir	−2.2304	2.4435	165	210	0.218712	0.992
	True fir/hemlock	−2.5384	2.4814	395	230	0.182329	0.992
	Pine	−2.5356	2.4349	331	180	0.253781	0.987
	Spruce	−2.0773	2.3323	212	250	0.250424	0.988
Woodland[‖]	Juniper/oak/mesquite	−0.7152	1.7029	61	78	0.384331	0.938

* Biomass equation:

$bm = \mathrm{Exp}(\beta_0 + \beta_1 \ln dbh)$

where

bm = total aboveground biomass (kg) for trees 2.5cm dbh and larger

dbh = diameter at breast height (cm)

Exp = exponential function

ln = natural log base "e" (2.718282)

[†] Number of data points generated from published equations (generally at 5 cm dbh intervals) for parameter estimation.

[††] Maximum dbh of trees measured in published equations.

[§] Root mean squared error or estimate of the standard deviation of the regression error term in natural log units.

[‖] Woodland group includes both hardwood and softwood species from dryland forests.

Component Biomass

We could not determine if the species groups used for total aboveground biomass were appropriate for grouping components because adequate numbers of equations were not available to predict the biomass of each component in each of the species groups. Attempts to devise new species groupings raised suspicions that dbh-based allometric relationships for tree components are much more complex than for total aboveground biomass. As a result, equations were pooled into hardwood and softwood groups for component biomass estimation.

Merchantable stem and bark were defined from a 12 in. (30.48 cm) stump height to a 4 in. (10.16 cm) top (dob). Foliage estimates exclude twigs and include the current year's foliage and petioles plus any previous year's foliage still on the tree. Due to the scarcity of root biomass equations, we included all equations describing root biomass, regardless of the author's definition of roots. While some authors did not specify a root definition, most equations limited roots to a minimum diameter ranging from 0.15 to 5 cm. Where an author specified that an equation referred to stump plus roots, the biomass of the stump portion was calculated as described above and then subtracted to find root biomass only.

Where allometric equations were available for each component of interest [coarse roots, merchantable stem (wood and bark computed separately), and foliage], biomass estimates of component biomass were made and expressed as proportions of aboveground total biomass. The logarithms of these proportions were modeled as functions of inverse diameter so that the ratios reach an asymptote for large trees:

$$ratio = \mathrm{Exp}\left(\beta_0 + \frac{\beta_1}{dbh}\right) \qquad (2)$$

Table 5. Distribution percentiles of regression residuals—expressed as a percentage of predicted value—for aboveground biomass equations (Table 4) for all hardwood and softwood species in United States.

	Species group	Data points*	Percent of predicted biomass 10th percentile	90th percentile
Hardwood	Aspen/alder/cottonwood/willow	230	−35.2	31.4
	Soft maple/birch	316	−23.8	28.5
	Mixed hardwood	289	−24.7	34.8
	Hard maple/oak/hickory/beech	485	−19.2	22.3
Softwood	Cedar/larch	196	−33.7	35.7
	Douglas-fir	165	−23.0	27.2
	True fir/hemlock	395	−18.3	20.0
	Pine	331	−24.0	33.7
	Spruce	212	−24.4	28.7
Woodland[†]	Juniper/oak/mesquite	61	−32.2	38.5

* Number of data points generated from published equations (generally at 5 cm dbh intervals) for parameter estimation.

[†] Woodland group includes both hardwood and softwood species from dryland forests.

where

ratio = ratio of component to total aboveground biomass (dry weight) for trees 2.5 cm *dbh* and larger
dbh = diameter at breast height (cm)
Exp = exponential function
ln = log base e (2.718282)

Due to the scarcity of component biomass equations and the substantial variation in component estimates, no attempt was made to quantify variability among published estimates.

Results and Discussion

Aboveground Biomass Regressions

Aboveground biomass regression equations were developed for four hardwood and six softwood species groups (Table 4). In general, the hardwood species had greater biomass at a given dbh than did the softwood species (Figure 1). Two hardwood species groups—hard maple/oak/hickory/beech, and soft maple/birch—had the greatest biomass at a given dbh. The woodland species had the lowest biomass values for a given diameter, and three of the softwood species groups had the next-lowest biomass values: cedar/larch, pine, and spruce. The Douglas-fir species group had the largest of the softwood biomass values, while the aspen/alder/cottonwood/willow group had the smallest of the hardwood biomass values.

Hardwood species groups.—The aspen/alder/cottonwood/willow group, the lightest of the hardwood groups at a given dbh, is comprised of species belonging to the Salicaceae (*Populus* and *Salix* spp.) and Betulaceae (*Alnus* spp.) families. Though specific gravity was not used as the primary determinant of species grouping, these fast-growing species do have similar small bole wood specific gravity values (Table 1). Additional representatives of the Betulaceae family (*Betula* spp.) occur in the soft maple/birch species group. These species were grouped with the soft maple species separate from the members of the Betulaceae family in the aspen/alder/cottonwood/willow group. The pseudodata developed from published equations for *Betula* species indicated that they were heavier at a given dbh than the *Alnus* species, and that they were more similar to the soft maple species than to the other members of their taxonomic group.

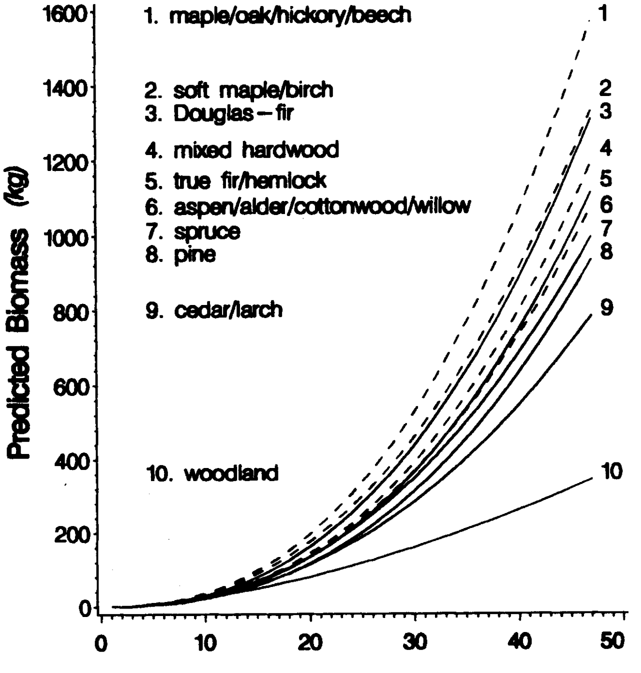

Figure 1. Graphs of ten equations for predicting total aboveground biomass by species group. Hardwoods are represented by dashed lines, softwoods by solid lines.

Sugar maple (*Acer saccharum*) was grouped with the hard maple/oak/hickory/beech group, apart from the other members of its family Aceraceae. This split reflects the different dbh/biomass relationships in the soft and hard maple species, as well as the higher bole wood specific gravity in sugar maple compared to other species in the Aceraceae family. Species in the family Fagaceae, including oak (*Quercus* spp.) and American beech (*Fagus grandifolia*), had pseudodata that matched sugar maple closely and were thus included in this group, as were members of the Juglandaceae family (*Carya* spp.).

Forty equations were included in the mixed hardwood group, compared with 36 in aspen/alder/cottonwood, 47 in soft maple/birch, and 49 in the hard maple/oak/hickory/beech group. However, more species and families are represented in the mixed hardwood group—21 and 14, compared with 8 species and 2 families in both the aspen/alder/cottonwood/willow and soft maple/birch groups, and 13 species in 3 families in the hard maple/oak/beech/hickory group. Because the pseudodata for different species and families, especially the species of intermediate bole wood specific gravity found in the mixed hardwood group, often overlapped with one another, we grouped the mixed hardwoods together unless it was clear that they belonged in one of the other three groups. This grouping was consistent with the pseudodata distribution, resulted in reasonable prediction intervals about each of the groups, and allowed for more systematic group assignment of species not represented in the published literature.

Softwood and woodland species groups.—Many of the softwood species in this analysis belong to the family Pinaceae. However, within the family, four genus groups—Douglas-fir, fir/hemlock, pine, and spruce—display distinct patterns of dbh/biomass relationships. The relative biomass of the groups [Douglas-fir is the heaviest at a given dbh, followed by fir/hemlock, then spruce and pine (Figure 1)] reflects roughly the mean bole wood specific gravities of the different groups, with the exception of pine, which has a higher mean specific gravity than the spruce and fir/hemlock groups. Several members of the Pinaceae family, particularly of the genus *Taxodiaceae*, are included with members of the genus *Cupressaceae* in the cedar/larch group. Despite the general agreement about the shape of the dbh/biomass relationship within all of the species groups, there was as much variation within a single species as between different species in a group (this is illustrated for the genus *Pinus* in Figure 2).

The woodland group includes both softwood and hardwood species with very low biomass values at a given dbh; these species come from the Leguminoseae, Rosaceae, Cupressaceae, Betulaceae, and Fagaceae families. The mean bole wood specific gravity for this group is higher than for any of the other groups (hardwood or softwood). Several factors may contribute to the low biomass of woodland species at a given dbh: (1) increased proportions of biomass in branches and foliage (Grier et al. 1992), putting greater emphasis on accurate measurement of these hard-to-measure components; (2) increased proportions of dead wood in live trees (Chojnacky 1994), potentially altering the allometric relationship for these species; and (3) potential errors in applying the drc to dbh conversion, which was based on a small sample of stems from western Colorado.

Prediction intervals.—For the hardwood species group equations, the regression residuals (expressed as a percentage of the predicted value) in the 10th percentile fell, on average, 25.7% below the predicted values (Table 5). The regression residuals in the 90th percentile fell, on average, 29.3% higher than the predicted values (Table 5). For the softwood species groups, on average the regression residuals falling in the 10th and 90th percentiles fell, respectively, 24.7% below and 29.1% above the predicted values (Table 5). The group with the smallest prediction interval (i.e., 80% of the standardized residuals fell the closest to the predicted values) was the true fir/hemlock group, and the groups with the largest intervals were the woodland and the cedar/larch groups. These prediction intervals are a tool for evaluating the variability among the pseudodata relative to the predicted values; while they are a guide for interpreting our results, they are not meant to be quantitative estimators of uncertainty.

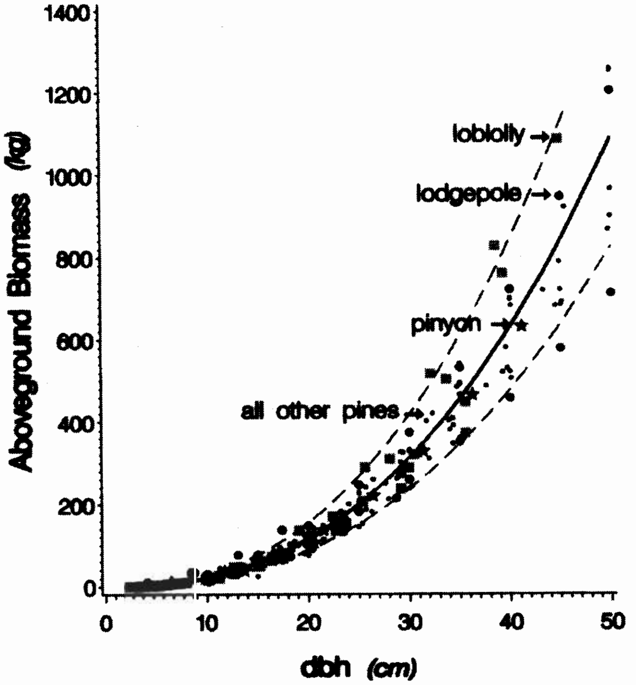

Figure 2. Example of pseudodata for *Pinus* species. Loblolly (gray square), lodgepole (large dot), and pinyon (star) species are highlighted. Smaller dots represent 11 other pine species. Dashed lines include 80% of the pseudo-data closest to regression equation (solid line).

Comparison with other datasets.—Our results suggest that softwood biomass is, on average, lower than hardwood biomass for a given tree diameter. This result is consistent with that of Schroeder et al. (1997) and Brown and Schroeder (1999), who developed generalized equations from a combination of measured data and predicted data points from other equations. They found that softwood biomass (including pine, spruce, and fir species) was slightly lower than hardwood biomass in the northeastern maple-beech-birch forest. This result is also consistent with that of Freedman (1984), who developed generalized softwood and hardwood biomass equations from 285 measured trees in Nova Scotia and found that hardwood biomass was slightly higher than softwood biomass over all dbh values.

For hardwood species, there is general (±30%) agreement between biomass predictions made for individual trees using our species-group equations and the general hardwood equation of Schroeder et al. (1997) (Figure 3). While the mean difference between approaches is not excessively large, our equations predict lower biomass for the aspen/alder/cottonwood/willow group, and higher biomass for the hard maple/oak/hickory/beech group than the Schroeder et al. (1997) equation at dbh values smaller than 110 cm. This difference is to be expected, as our equations are split by species group according to general trends in the dbh/biomass relationship, in contrast to the single hardwood equation published by Schroeder et al. (1997).

For softwood species, the mean difference between approaches was again less than 40%. However, our equation for pine biomass predicted lower biomass values for pine species in these four states than the Brown and Schroeder (1999)

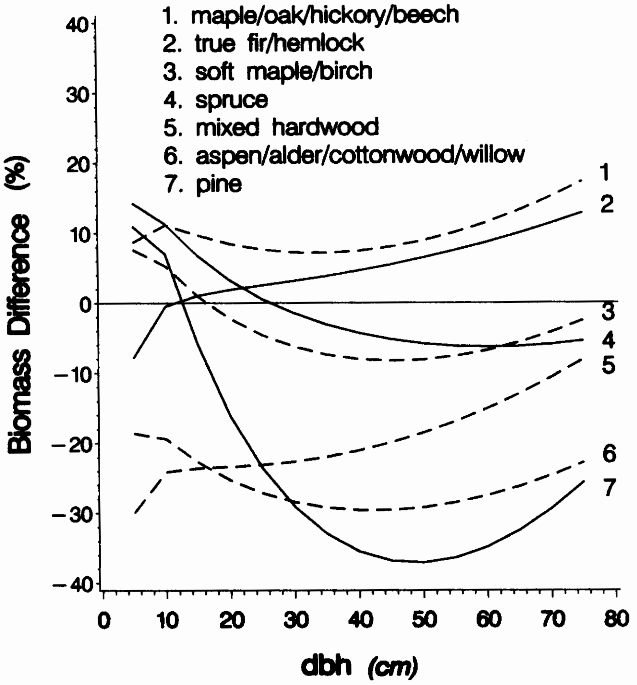

Figure 3. Our equations differ by up to 30% from regional equations developed by Brown and Schroeder (1999) and Schroeder et al. (1997). Difference is represented by our equation minus the Brown/Schroeder equation divided by the mean of the two sets of predictions.

equation. The rapidly increasing and decreasing shape of the difference between the two pine datasets suggests that the discrepancy is likely due more to equation-form differences than to actual differences in the overall biomass relationships represented by the two equations. We limited this comparison to the diameter range of the trees used to develop the Schroeder et al. (1997) and Brown and Schroeder (1999) equations; inclusion of additional large tree diameters show the Brown and Schroeder equations approach an asymptote while ours continue to increase (Figure 4).

Overall, the shape of the differences between the two approaches is due to different equation forms. The Schroeder et al. (1997) and Brown and Schroeder (1999) equations follow a log-transformed, nonlinear half-saturation shape with two inflection points, so that they increase quickly and begin to flatten out at dbh values above roughly 120 cm. The Schroeder et al. (1997) and Brown and Schroeder (1999) equations are based on trees with maximum diameter of 85.1 and 71.6 cm dbh for hardwoods and softwoods, respectively. Our analysis, which included predictions from equations developed using trees as large as 250 cm, suggests that the log-log equation form is more appropriate for very large trees.

While there is general agreement between our broad conclusions and those of other researchers, a similar comparison using these equations to predict biomass at the individual site level or at a local scale is problematic. Our equations were developed for application at regional to continental spatial scales and are designed to provide biomass estimates for regions containing a variety of site types. The most appropriate evaluation of our equations would be to compare against a large, representative, continental-scale set of biomass data taken from sites that span the observed range for each species. Such a large, unbiased, and representative data set does not exist, to our knowledge. If it could be developed, however, it would be immeasurably useful for endeavors like this one—indeed, this is absolutely the only way the accuracy of our equations (or of any set of generalized biomass equations) can be verified with certainty.

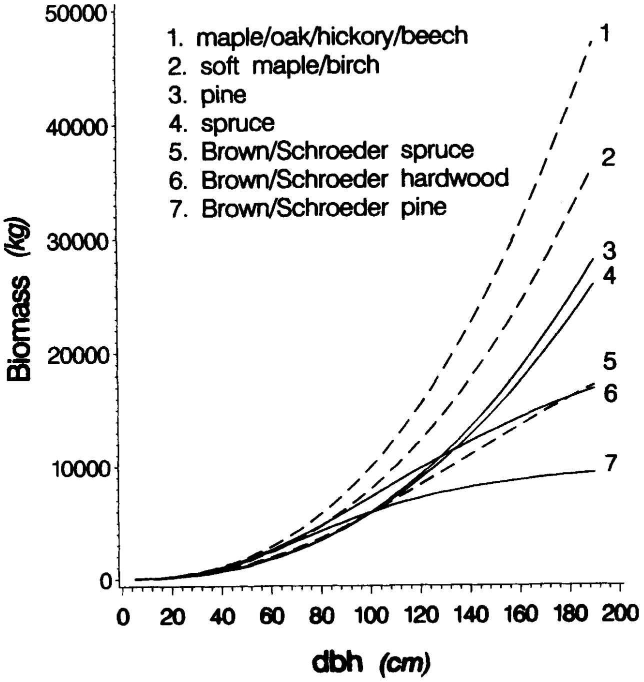

Figure 4. Our equations predict higher biomass for large trees than do those from Brown and Schroeder (1999) and Schroeder et al. (1997). Hardwoods are represented by dashed lines, softwoods by solid lines.

Component Biomass

We developed equations representing the average proportion of aboveground biomass in foliage, stem bark, stem wood, and coarse roots for hardwood and softwood species as a function of dbh (Tables 6 and 7, Figures 5 and 6). Branch (bark and wood) biomass was found by difference. Because our equations represent many species over a large variety of sites, we expect a larger range in component biomass than those equations from studies of smaller scope.

Comparisons with other datasets.—The range in softwood stem wood biomass reported here, roughly 30 to 60% of aboveground biomass, corresponds to the range (44 to 66% for softwoods larger than 8 cm dbh) reported by Freedman et al. (1982). For hardwood stem wood biomass, the same authors report a range from 45 to 71% of aboveground tree biomass for stems larger than 8 cm; this corresponds to the range we report for hardwoods larger than 10 cm, from 40 to 60% of aboveground biomass. Ker (1980a) reported that 67% of aboveground dry weight was contained in the merchantable stem for softwoods and 70% for hardwoods. Other authors have thus reported somewhat larger percentages of biomass in stem wood than we found in this study. However, this direct comparison may be misleading: the studies appropriate for this comparison include species such as birch, aspen, and sugar maple, which have the largest stem wood percentages in our dataset (Table 7). In addition, our approach emphasizes the change in these percentages with tree diameter, while the studies cited lump together a number of medium to large trees to develop one estimate across all diameters. Finally, most of these authors give little indication of potential variability in their ratio estimates.

Freedman et al. (1982) reported that the percentage of biomass in merchantable stem bark varied from 8 to 11% for softwoods, and from 8 to 19% for hardwoods. Ker (1980b) reported that stem bark comprised 8 and 12% of softwood and hardwood biomass, respectively. These data fall roughly within the bounds reported from this analysis of 8 to 14% for softwoods and 10 to 15% for hardwoods.

Freedman et al. (1982) report that foliage comprises from 7 to 19% of aboveground biomass for softwoods, and from 2 to 6% for hardwoods, while Ker (1980b) reported 8% for softwoods and 2% for hardwoods. Our results, that foliage makes up between 10 and 30% of aboveground biomass for softwoods and from 3 to 12% for hardwoods, were somewhat larger (at the upper end) than the mean published values. However, the upper portion of the percentage range in our data is based on very small trees, while the data from the studies cited include predominantly larger trees.

Freedman et al. (1982) report that softwood branch biomass comprises between 7 and 20% of aboveground biomass for softwoods, and between 15 and 96% for hardwoods (where branches comprise a larger proportion

Table 6. Parameters and equations* for estimating component ratios of total aboveground biomass for all hardwood and softwood species in the United States.

Species class	Biomass component	Parameters β_0	β_1	Data points†	R^2
Hardwood	Foliage	−4.0813	5.8816	632	0.256
	Coarse roots	−1.6911	0.8160	121	0.029
	Stem bark	−2.0129	−1.6805	63	0.017
	Stem wood	−0.3065	−5.4240	264	0.247
Softwood	Foliage	−2.9584	4.4766	777	0.133
	Coarse roots	−1.5619	0.6614	137	0.018
	Stem bark	−2.0980	−1.1432	799	0.006
	Stem wood	−0.3737	−1.8055	781	0.155

* Biomass ratio equation:

$$ratio = \mathrm{Exp}(\beta_0 + \frac{\beta_1}{dbh})$$

where

ratio = ratio of component to total aboveground biomass for trees 2.5 cm dbh and larger

dbh = diameter at breast height (cm)

Exp = exponential function

ln = log base e (2.718282)

† Number of data points generated from published equations (generally at 5 cm dbh intervals) for parameter estimation.

of aboveground biomass in smaller trees). Ker (1980b) writes that branch biomass comprises, on average, 17% of aboveground biomass for both hardwoods and softwoods. These figures are somewhat lower than the results from this study, which suggest branches comprise between 20 and 70% of aboveground biomass for hardwoods and between 20 and 30% for softwoods. However, Freedman et al. (1982) separated dead from live branches, while all branches were treated together in our study. In addition, both Freedman et al. (1982) and Ker (1980b) treated branches separately from the top of the stem (i.e., smaller than the minimum top diameter), while our method of finding branch biomass by subtraction lumps the unmerchantable stem portion together with the branches.

There is substantial within-species-group variability among the data used to develop our component ratio estimates (Table 7). We hypothesize that C allocation strategies may differ among individuals belonging to the same species (or species groups). The proportion of bio-mass in foliage, for example, might be different for an open-grown tree versus a

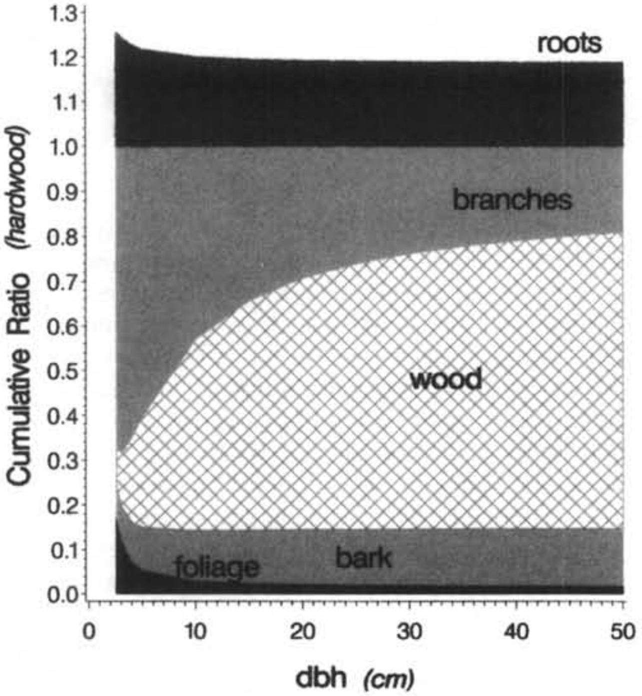

Figure 5. Proportion of aboveground biomass calculated from our generalized component ratio equations for hardwood foliage, stem bark, stem wood, branches, and roots.

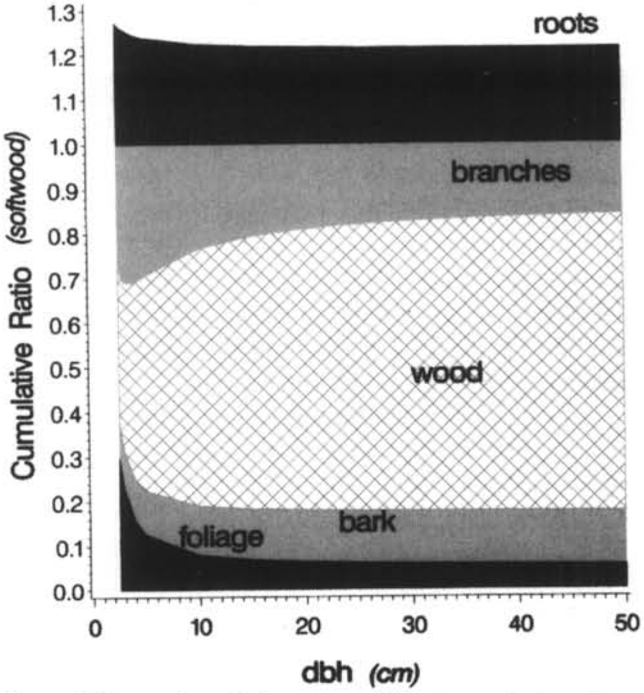

Figure 6. Proportion of aboveground biomass calculated from our generalized component ratio equations for softwood foliage, stem bark, stem wood, branches, and roots.

Table 7. Data ranges for biomass component ratios expressed as the ratio of total aboveground biomass) for all hardwood and softwood species in the United States.

	Biomass component	Species group	Ratio percentiles 5th	95th	*k**	dbh range min	max
						............(cm)............	
Hardwood	Foliage	Aspen/alder/cottonwood/willow	0.01	0.20	23	3	51
		Soft maple/birch	0.01	0.10	32	3	66
		Mixed hardwood	0.01	0.09	17	3	56
		Hard maple/oak/hickory/ beech	0.01	0.07	27	3	73
	Coarse roots	Aspen/alder/cottonwood/willow	0.16	0.33	6	3	51
		Soft maple/birch	0.10	0.29	7	3	66
		Mixed hardwood	0.21	0.37	5	3	23
		Hard maple/oak/hickory/ beech	0.13	0.30	4	3	66
	Stem bark	Aspen/alder/cottonwood/willow	0.09	0.21	7	11	50
		Soft maple/birch	0.08	0.14	4	12	42
		Mixed hardwood	0.10	0.20	1	6	36
		Hard maple/oak/hickory/ beech	0.07	0.10	1	14	34
	Stem wood	Aspen/alder/cottonwood/willow	0.49	0.74	6	12	50
		Soft maple/birch	0.44	0.80	5	12	42
		Mixed hardwood	0.44	0.75	8	6	53
		Hard maple/oak/hickory/ beech	0.39	0.64	9	11	56
Softwood	Foliage	Cedar/larch	0.02	0.18	14	3	61
		Douglas-fir	0.01	0.18	10	3	190
		True fir/hemlock	0.02	0.16	19	3	111
		Pine	0.02	0.20	29	3	99
		Spruce	0.06	0.20	17	3	78
		Woodland	0.02	0.46	7	3	78
	Coarse roots	Cedar/larch	0.15	0.34	3	3	51
		Douglas-fir	0.16	0.29	2	7	135
		True fir/hemlock	0.16	0.29	4	3	51
		Pine	0.08	0.23	3	3	66
		Spruce	0.20	0.33	4	3	66
	Stem bark	Cedar/larch	0.05	0.31	12	4	615
		Douglas-fir	0.09	0.20	8	3	215
		True fir/hemlock	0.07	0.29	19	7	235
		Pine	0.01	0.24	8	4	180
		Spruce	0.02	0.16	10	3	285
	Stem wood	Cedar/larch	0.54	0.84	12	4	615
		Douglas-fir	0.55	0.83	9	3	215
		True fir/hemlock	0.51	0.82	19	7	235
		Pine	0.43	0.76	8	4	180
		Spruce	0.37	0.87	10	3	285

* Number of dbh-based biomass component equations in literature used to develop ratio equations for each species group. All references included in Table 2 except for Baldwin (1989), McCain (1994), and Thies and Cunningham (1996).

tree growing in a dense stand, and the proportion of biomass in the stem might change with variables such as wind exposure or water availability. These differences appear as noise in component ratios, but they are most likely the predictable results of site-level variability in abiotic conditions.

Applying These Equations

Aboveground biomass.—Equation parameters for total aboveground biomass prediction for each of the species groups are presented in Table 4. For future use, species represented in the dataset used to develop these equations should be assigned to the groups shown in Tables 1 and 3. For species not included in this dataset, we suggest that the species key in Appendix A be used as a guideline for species group assignment.

Component biomass.—The proportion of total aboveground biomass in a given biomass component can be calculated from dbh as a ratio, using the parameters for hardwood and softwood species given in Table 6. To find total biomass in a particular component, multiply the total aboveground biomass (found as described above) by the proportion in that component. Total biomass in branches and treetops may be found by difference. Note that stem bark and stem wood are defined from a 12 in. (30.48 cm) stump height to a 4 in. (10.16 cm) dob top.

Large-scale biomass estimation.—The equations presented here are applicable to individual trees on a stem-by-stem basis. To estimate forest biomass at large scales using these equations, several approaches based on ground data are possible. For example, one might apply these equations directly to measured tree diameters from a large-scale forest mensuration dataset such as the FIA dataset. Alternatively, measured tree parameters from FIA plots could be used with biomass and volume prediction equations to develop ratios between merchantable volume and biomass; these ratios could then be used to estimate plot biomass given its volume, as the approach used in the FORCARB model.

There is potential error in using these equations. For clarity, we provide a summary of the potential errors inherent in using two different methods for large-scale biomass estimation (Table 8). For this purpose, we have compared errors potentially introduced in using individual species- and site-specific equations as they currently exist in the literature with the errors potentially introduced by using the generalized regression equations presented here. We emphasize, however, that: (1) errors are potentially introduced whenever an allometric method is used to estimate biomass, no matter what method and at what spatial scale; (2) it may not be feasible to ascertain whether any of these errors is actually introduced; and (3) our generalized equations represent the most comprehensive effort to date to develop consistent, accurate biomass equations for application all across the United States.

Conclusions

In this analysis, we performed a thorough review of available biomass literature and a rigorous analysis of a subset of pseudodata derived from that literature. We found that many of the published equations were unusable for large-scale application because of inconsistencies in methodology and definitions, incomplete reporting of methods, lack of access to original data, and sampling from narrow segments of the population of trees of the United States. Our equations may be applied for large-scale analyses of biomass or carbon stocks and trends, but should be used cautiously at very small scales where local equations may be more appropriate.

The clear variability in tree C allocation from site to site and from study to study suggests that more information is needed about the differences in biomass and allocation among different tree species and sites. This variability makes it difficult to estimate tree biomass accurately even when a site-specific regression equation is used. Development of continental-scale regressions of known accuracy requires a continental-scale measurement campaign, in which individuals of all species and sizes are measured, over the entire range of site conditions typical of each species. This would be a formidable task.

In future work, we strongly suggest that a consistent set of measurement and reporting protocols be adopted for biomass measurement studies (Clark 1979, Crow 1983) and that researchers publish the raw data from which their regressions were developed in addition to the equations themselves. This would facilitate future efforts to synthesize the biomass literature. We suggest that an effort be made to sample trees across the entire diameter range of a species, as well; any analysis of available biomass equations suffers from the clear lack of biomass equations for predicting biomass (especially for hardwoods) at large diameters.

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Table 8. Potential sources of error in allometric biomass estimation at large scales using species- and region-specific equations versus the generalized equations developed in this study.

Type of application	Potential source of error
Species- and site-specific equations applied to national scale	(a) Coefficients developed for one species (or species group) may not apply to another species (or species group). (b) Coefficients developed for one site may not apply to another site. (c) Sample trees and wood density samples may not be representative of the target population because of factors such as size range of sample trees and stand conditions. (d) Relationship of trees used to develop specific regression to the target population (i.e., all trees) is unknown. (e) Statistical error may be associated with estimated coefficients and form of selected equation. (f) Inconsistent standards, definitions, and methodology. (g) Use of indirect estimation methods may compound errors. (h) Measurement and data processing errors. (i) Regional boundaries may be sharply delineated due to differences in methodology.
Generalized equations (this study) applied to national scale	(a) Generalized equations may be biased in favor of species for which published equations exist. (b) Relationship of trees used to develop generalized regression to the target population (i.e. all trees) is unknown. (c) Potential bias in applying generalized equations to species where no published equations exist. (d) No obvious way to estimate uncertainty or variability. (e) Generalized equations may inherit shortcomings of published equations, including: (i) statistical error associated with estimated coefficients and form of selected equation, (ii) inconsistent standards, definitions, and methodology, (iii) use of indirect estimation methods that compound errors, and (iv) measurement and data processing errors.

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APPENDIX A. Species groups (SG*) identified for Forest Inventory and Analysis (FIA[†]) species list.

SG	Genus	Species	FIA	Common name
aa	*Alnus*	*rhombifolia*	352	White alder
aa		*rubra*	351	Red alder
aa		*rugosa*		Speckled alder
aa	*Populus*	*alba*	752	Silver poplar
aa		*angustifolia*	753	Narrowleaf cottonwood
aa		*balsamifera*	741	Balsam poplar
aa		*deltoides*	742	Eastern cottonwood
aa		*fremontii*	748	Fremont cottonwood
aa		*grandidentata*	743	Bigtooth aspen
aa		*heterophylla*	744	Swamp cottonwood
aa		*sargentii*	745	Plains cottonwood
aa		spp.	740	Cottonwood
aa		*tremuloides*	746	Quaking aspen
aa		*trichocarpa*	747	Black cottonwood
aa	*Salix*	*amygdaloides*	921	Peachleaf willow
aa		*eriocephala*	923	Diamond willow
aa		*nigra*	922	Black willow
aa		spp.	920	Willow
mo	*Acer*	*nigrum*	314	Black maple
mo		*saccharum*	318	Sugar maple
mo	*Carya*	*aquatica*	401	Water hickory
mo		*cordiformis*	402	Bitternut hickory
mo		*glabra*	403	Pignut hickory
mo		*illinoensis*	404	Pecan
mo		*laciniosa*	405	Shellbark hickory
mo		*ovata*	407	Shagbark hickory
mo		spp.	400	Hickory spp.
mo		*texana*	408	Black hickory
mo		*tomentosa*	409	Mockernut hickory
mo	*Fagus*	*grandifolia*	531	American beech
mo	*Quercus*	*agrifolia*	801	California live oak
mo		*alba*	802	White oak
mo		*bicolor*	804	Swamp white oak
mo		*chrysolepis*	805	Canyon live oak
mo		*coccinea*	806	Scarlet oak
mo		*douglasii*	807	Blue oak
mo		*durandii*	808	Durand oak
mo		*ellipsoidalis*	809	Northern pin oak
mo		*engelmannii*	811	Engelmann oak
mo		*falcata* var. *falcata*	812	Southern red oak
mo		*falcata* var. *pagodaefolia*	813	Cherrybark oak, swamp red oak
mo		*garryana*	815	Oregon white oak
mo		*ilicifolia*	816	Bear oak, scrub oak
mo		*imbricaria*	817	Shingle oak
mo		*incana*	840	Bluejack oak
mo		*kelloggii*	818	California black oak
mo		*laevis*	819	Turkey oak
mo		*laurifolia*	820	Laurel oak
mo		*lobata*	821	California white oak
mo		*lyrata*	822	Overcup oak
mo		*macrocarpa*	823	Bur oak
mo		*marilandica*	824	Blackjack oak
mo		*michauxii*	825	Swamp chestnut oak
mo		*muehlenbergii*	826	Chinkapin oak
mo		*nigra*	827	Water oak
mo	*Quercus*	*nuttalii*	828	Nuttall oak
mo		*palustris*	830	Pin oak
mo		*phellos*	831	Willow oak
mo		*prinus*	832	Chestnut oak
mo		*rubra*	833	Northern red oak
mo		*shumardii*	834	Shumard oak
mo		spp.	899	Scrub oak
mo		*stellata*	835	Post oak

APPENDIX A. (continued)

SG	Genus	Species	FIA	Common name
mo	*Quercus*	*stellata* var. *mississippiensis*	836	Delta post oak
mo		*velutina*	837	Black oak
mo		*virginiana*	838	Live oak
mo		*wislizeni*	839	Interior live oak
mh	*Aesculus*	*californica*	330	California buckeye
mh		*glabra*	331	Ohio buckeye
mh		*octandra*	332	Yellow buckeye
mh		spp.	330	Buckeye, horsechestnut
mh		spp.	333	Buckeye (except 331, 332)
mh	*Ailanthus*	*altissima*	341	Ailanthus
mh		*fordii*	980	Tung-oil tree
mh	*Amelanchier*	spp.	355	Serviceberry
mh	*Arbutus*	*menziesii*	361	Pacific madrone
mh	*Asimina*	*triloba*	367	Pawpaw
mh	*Bumelia*	*lanuginosa*	381	Chittamwood, gum bumelia
mh	*Carpinus*	*caroliniana*	391	American hornbeam, musclewood
mh	*Castanea*	*dentata*	421	American chestnut
mh		*ozarkensis*	423	Ozark chinkapin
mh		*pumila*	422	Allegheny chinkapin
mh	*Castanopsis*	*chrysophylla*	431	Golden chinkapin
mh		spp.	430	Chinkapin
mh	*Catalpa*	*bignonioides*	451	Southern catalpa
mh		*speciosa*	452	Northern catalpa
mh		spp.	450	Catalpa
mh	*Celtis*	*laevigata*	461	Sugarberry
mh		*occidentalis*	462	Hackberry
mh		spp.	460	Hackberry spp.
mh	*Ceriss*	*canadensis*	471	Eastern redbud
mh	*Cornus*	*florida*	491	Flowering dogwood
mh		*nuttallii*	492	Pacific dogwood
mh	*Cotinus*	*obovatus*	985	Smoketree
mh	*Crataegus*	spp.	500	Hawthorn
mh	*Diospyros*	*virginiana*	521	Common persimmon
mh	*Eucalyptus*	spp.	510	Eucalyptus
mh	*Fraxinus*	*americana*	541	White ash
mh		*latifolia*	542	Oregon ash
mh		*nigra*	543	Black ash
mh		*pennsylvanica*	544	Green ash
mh		*profunda*	545	Pumpkin ash
mh		*quadrangulata*	546	Blue ash
mh		spp.	540	Ash
mh	*Gleditsia*	*aquatica*	551	Waterlocust
mh		*triacanthos*	552	Honeylocust
mh	*Gordonia*	*lasianthus*	555	Loblolly-bay
mh	*Gymnocladus*	*dioicus*	571	Kentucky coffeetree
mh	*Halesia*	spp.	580	Silverbell
mh	*Hardwood*	spp.	1000	Hardwoods (general)
mh	*Ilex*	*opaca*	591	American holly
mh	*Juglans*	*cinerea*	601	Butternut
mh		*nigra*	602	Black walnut
mh		spp.	600	Walnut
mh	*Liquidambar*	*styraciflua*	611	Sweetgum
mh	*Liriodendron*	*tulipifera*	621	Yellow-poplar
mh	*Lithocarpus*	*densiflorus*	631	Tanoak
mh	*Maclura*	*pomifera*	641	Osage-orange
mh	*Magnolia*	*acuminata*	651	Cucumbertree
mh		*grandiflora*	652	Southern magnolia
mh		*macrophylla*	654	Bigleaf magnolia
mh		spp.	650	Magnolia spp.
mh		*virginiana*	653	Sweetbay
mh	*Malus*	spp.	660	Apple
mh	*Melia*	*azedarach*	983	Chinaberry
mh	*Morus*	*alba*	681	White mulberry
mh		*rubra*	682	Red mulberry

APPENDIX A. (continued)

SG	Genus	Species	FIA	Common name
mh	*Morus*	spp.	680	Mulberry spp.
mh	*Nyssa*	*aquatica*	691	Water tupelo
mh		*ogeche*	692	Ogeechee tupelo
mh		*sylvatica*	693	Blackgum
mh		*sylvatica* var. *biflora*	694	Swamp tupelo
mh	*Ostrya*	*virginiana*	701	Eastern hophornbeam, ironwood
mh	*Oxydendrum*	*arboreum*	711	Sourwood
mh	*Paulownia*	*tomentosa*	712	Paulownia, Empress tree
mh	*Persea*	*borbonia*	721	Redbay
mh	*Planera*	*aquatica*	984	Water-elm
mh	*Platanus*	*occidentalis*	731	Sycamore
mh		*racemosa*	730	California sycamore
mh	*Prunus*	*americana*	766	Wild plum
mh		*nigra*	765	Canada plum
mh		*pensylvanica*	761	Pin cherry
mh		*serotina*	762	Black cherry
mh		spp.	760	Cherry, plum spp.
mh		spp.	764	Plums, cherries, except 762
mh		*virginiana*	763	Chokecherry
mh	*Robinia*	*psuedoacacia*	901	Black locust
mh	*Sapium*	*sebiferum*	925	Chinese tallowtree
mh	*Sassafras*	*albidum*	931	Sassafras
mh	*Sorbus*	*americana*	935	American mountain-ash
mh		*aucuparia*	936	European mountain-ash
mh	*Tilia*	*americana*	951	American basswood
mh		*heterophylla*	952	White basswood
mh		spp.	950	Basswood
mh	*Ulmus*	*alata*	971	Winged elm
mh		*americana*	972	American elm
mh		*crassifolia*	973	Cedar elm
mh		*pumila*	974	Siberian elm
mh		*rubra*	975	Slippery elm
mh		*serotina*	976	September elm
mh		spp.	970	Elm
mh		*thomasii*	977	Rock elm
mh	*Umbellularia*	*californica*	981	California-laurel
mh	*Vaccinium*	*arboreum*	981	Sparkleberry
mb	*Acer*	*barbatum*	311	Florida maple
mb	*Acer*	*macrophyllum*	312	Bigleaf maple
mb		*negundo*	313	Boxelder
mb		*pensylvanicum*	315	Striped maple
mb		*rubrum*	316	Red maple
mb		*saccharinum*	317	Silver maple
mb		*spicatum*	319	Mountain maple
mb	*Betula*	*alleghaniensis*	371	Yellow birch
mb		*lenta*	372	Sweet birch
mb		*nigra*	373	River birch
mb		*occidentalis*	374	Water birch
mb		*papyrifera*	375	Paper birch
mb		*papyrifera* var. *commutata*	376	Western paper birch
mb		*populifolia*	379	Gray birch
mb		spp.	370	Birch spp.
cl	*Calocedrus*	*decurrens*	81	Incense-cedar
cl	*Chamaecyparis*	*lawsoniana*	41	Port-Orford-cedar
cl		*nootkatensis*	42	Alaska-cedar
cl		*thyoides*	43	Atlantic white-cedar
cl	*Juniperus*	*silicicola*	67	Southern redcedar
cl		*virginiana*	68	Eastern redcedar
cl	*Larix*	*laricina*	71	Tamarack (native)
cl		*lyallii*	72	Subalpine larch
cl		*occidentalis*	73	Western larch
cl		spp.	70	Larch (introduced)
cl	*Sequoia*	*sempervirens*	211	Redwood
cl	*Sequoiadendron*	*giganteum*	212	Giant sequoia

APPENDIX A. (continued)

SG	Genus	Species	FIA	Common name
cl	*Softwood*	spp.	0	Softwoods (general)
cl	*Taxodium*	*distichum*	221	Baldcypress
cl		*distichum* var. *nutans*	222	Pondcypress
cl	*Thuja*	*occidentalis*	241	White-cedar
cl		*plicata*	242	Western redcedar
df	*Pseudotsuga*	*macrocarpa*	201	Bigcone Douglas-fir
df		*menziesii*	202	Douglas-fir
pi	*Pinus*	*albicaulis*	101	Whitebark pine
pi		*aristata*	102	Bristlecone pine
pi		*arizonica*	135	Arizona pine
pi		*attenuata*	103	Knobcone pine
pi		*balfouriana*	104	Foxtail pine
pi		*banksiana*	105	Jack pine
pi		*clausa*	107	Sand pine
pi		*contorta*	108	Lodgepole pine
pi		*coulteri*	109	Coulter pine
pi		*discolor*	134	Border pinyon
pi		*echinata*	110	Shortleaf pine
pi		*edulis*	106	Pinyon pine
pi		*elliottii*	111	Slash pine
pi		*engelmannii*	112	Apache pine
pi		*flexilis*	113	Limber pine
pi		*glabra*	115	Spruce pine
pi		*jeffreyi*	116	Jeffrey pine
pi		*lambertiana*	117	Sugar pine
pi		*leiophylla*	118	Chihuahuan pine
pi		*monophylla*	133	Singleleaf pinyon
pi		*monticola*	119	Western white pine
pi		*muricata*	120	Bishop pine
pi	*Pinus*	*nigra*	133	Austrian pine
pi		*palustris*	121	Longleaf pine
pi		*ponderosa*	122	Ponderosa pine
pi		*pungens*	123	Table Mountain pine
pi		*radiata*	124	Monterey pine
pi		*resinosa*	125	Red pine
pi		*rigida*	126	Pitch pine
pi		*sabiniana*	127	California foothill pine
pi		*serotina*	128	Pond pine
pi		*strobiformis*	114	Southwestern white pine
pi		*strobus*	129	Eastern white pine
pi		*sylvestris*	130	Scotch pine
pi		*taeda*	131	Loblolly pine
pi		*virginiana*	132	Virginia pine
sp	*Picea*	*abies*	91	Norway spruce
sp		*breweriana*	92	Brewer spruce
sp		*engelmannii*	93	Engelmann spruce
sp		*glauca*	94	White spruce
sp		*mariana*	95	Black spruce
sp		*pungens*	96	Blue spruce
sp		*rubens*	97	Red spruce
sp		*sitchensis*	98	Sitka spruce
sp		spp.	90	Spruce
tf	*Abies*	*amabilis*	11	Pacific silver fir
tf		*balsamea*	12	Balsam fir
tf		*bracteata*	14	Bristlecone fir
tf		*concolor*	15	White fir
tf		*fraseri*	16	Fraser fir
tf		*grandis*	17	Grand fir
tf		*lasiocarpa*	19	Subalpine fir
tf		*lasiocarpa* var. *arizonica*	18	Corkbark fir
tf		*magnifica*	20	California red fir
tf		*magnifica* var. *shastensis*	21	Shasta red fir
tf		*procera*	22	Noble fir
tf		spp.	10	Abies

APPENDIX A. (continued)

SG	Genus	Species	FIA	Common name
tf	*Taxus*	*brevifolia*	231	Pacific yew
tf	*Torreya*	*californica*	251	California nutmeg
tf	*Tsuga*	*canadensis*	261	Eastern hemlock
tf		*caroliniana*	262	Carolina hemlock
tf		*heterophylla*	263	Western hemlock
tf		*mertensiana*	264	Mountain hemlock
tf		spp.	260	Hemlock
wo	*Acacia*	spp.	300	Acacia
wo	*Acer*	*glabrum*	321	Rocky Mountain maple
wo		*grandidentatum*	322	Bigtooth maple
wo	*Cercocarpus*	*intricatus*	479	Littleleaf mountain-mahogany
wo		*ledifolius*	475	Curlleaf mountain-mahogany
wo		*montanus*	476	True mountain-mahogany
wo		*montanus* var. *glaber*	478	Birchleaf mountain-mahogany
wo		*montanus* var. *pauciden*	477	Hairy mountain-mahogany
wo	*Cupressus*	*arizonica*	51	Arizona cypress
wo		spp.	50	Cypress
wo	*Juniperus*	*californica*	62	California juniper
wo		*communis*	60	Common juniper
wo		*deppeana*	63	Alligator juniper
wo		*erythrocarpa*	59	Redberry juniper
wo		*monosperma*	69	Oneseed juniper
wo		*occidentalis*	64	Western juniper
wo		*osteosperma*	65	Utah juniper
wo		*pinchotti*	58	Pinchot juniper
wo		*scopulorum*	66	Rocky Mountain juniper
wo	*Olneya*	*tesota*	990	Tesota (Arizona ironwood)
wo	*Prosopis*	spp.	986	Mesquite
wo	*Prunus*	*emarginata*	764	Bitter cherry
wo	*Quercus*	*arizonica, grisea*	803	Arizona white oak, Gray oak
wo		*emoryi*	810	Emory oak
wo		*gambelii*	814	Gambel oak
wo		*hypoleucoides*	843	Silverleaf oak
wo		*oblongifolia*	829	Mexican blue oak
wo		spp.	800	Deciduous oak spp.
wo		spp.	850	Evergreen oak spp.
wo	*Robinia*	*neomexicana*	902	New Mexico locust

* Species groups (SG) include aspen/alder/cottonwood/willow (aa), hard maple/oak/hickory/beech (mo), mixed hardwood (mh), soft maple/birch (mb), cedar/larch (cl), Douglas-fir (df), true fir/hemlock (tf), pine (pi), spruce (sp), and woodland conifer and softwood (wo).

† FIA species codes.