Updated generalized biomass equations for North American tree species

David C. Chojnacky[1]*, Linda S. Heath[2] and Jennifer C. Jenkins[3]

[1]*Adjunct Faculty, Forest Biometrics, Forest Resources and Environmental Conservation Department, Virginia Tech,*
144 Rees Place, Falls Church, VA 22046, USA
[2]*US Department of Agriculture, Forest Service, Durham, NH 03824, USA*
[3]*US Environmental Protection Agency, Office of Air and Radiation, Climate Change Division, Washington, DC 20460, USA*

*Corresponding author. Tel./Fax.: +1 7033433288; E-mail: dchojnac@vt.edu

Historically, tree biomass at large scales has been estimated by applying dimensional analysis techniques and field measurements such as diameter at breast height (dbh) in allometric regression equations. Equations often have been developed using differing methods and applied only to certain species or isolated areas. We previously had compiled and combined (in meta-analysis) available diameter-based allometric regression equations for estimating total aboveground and component dry-weight biomass for US trees. This had resulted in a set of 10 consistent, national-scale aboveground biomass regression equations for US species, as well as equations for predicting biomass of tree components as proportions of total aboveground biomass. In this update of our published equation database and refinement of our model, we developed equations based on allometric scaling theory, using taxonomic groupings and wood specific gravity as surrogates for scaling parameters that we could not estimate. The new approach resulted in 35 theoretically based generalized equations (13 conifer, 18 hardwood, 4 woodland), compared with the previous empirically grouped 10. For trees from USDA Forest Inventory and Analysis Program (FIA) plots, with forest types grouped into conifers and hardwoods, previous and updated equations produced nearly identical estimates that predicted ~20 per cent higher biomass than FIA estimates. Differences were observed between previous and updated equation estimates when comparisons were made using individual FIA forest types.

Introduction

Tree biomass estimation has become critically important in recent years as the climate warms and estimates of fuel loads, biomass of forest products (including bioenergy products) and stored forest carbon (~50 per cent of forest biomass) are needed. However, biomass estimation procedures historically have been species- and site-specific, with a variety of different methods used. Our previous work (Jenkins *et al.*, 2003) was the result of an attempt to produce standardized, consistent and well-documented tree biomass estimation equations on a national scale, through compilation and synthesis of equations published in the literature, for use in the forest sector (Heath *et al.*, 2011) of the Inventory of US Greenhouse Gas Emissions and Sinks (e.g. EPA, 2012). We had used a meta-analysis to develop 10 generalized species-group-specific equations for estimating aboveground biomass from only diameter measurements using regression and log-transformation; two accompanying hardwood and conifer component ratio equations were also developed. Basing equations on diameter and not on height allowed for the most flexible usage. A companion publication (Jenkins *et al.*, 2004) supplied users with the full database of equations. This work could best have been improved by a thoughtfully designed collection of new data for study and/or use in replacing the generalized prediction equations. Such a dataset,

however, is an extensive undertaking and has not been generated in the 10 years since the previous study, so another more exhaustive meta-analysis was conducted with an updated set of literature equations.

In this study, we updated the Jenkins *et al.* (2004) database and refined our database and model. Instead of letting the statistical summary drive the final number of equations as it had in the previous study, we employed a more theoretically based approach, with generalized equation development based on factors whose importance was suggested by allometric scaling theory: taxonomic groupings (genus or family) and wood specific gravity. These factors were used as surrogates for scaling parameters that could not be estimated without collecting new data. We anticipated that the updated database and refined methodology would enable us to meet our objective of creating estimation equations for more species groupings and with enhanced predictive value.

Methods

Overview

Detailed descriptions of aspects of methods that were used and described in Jenkins *et al.* (2003), as well as citations for equation references in that work, will not be repeated here. Only changes made for the current work

will be described in detail. In brief, we compiled biomass estimation equations (based on measured data) from the literature, and using a meta-analysis, generated data for diameter-based published equations at intervals within the diameter ranges of the original equations – resulting in what we called 'pseudodata' following work of Pastor *et al.* (1984). This simply generated predicted values from equations (without any random component) to put all literature equations on a common basis, and is somewhat analogous to having original data from which to develop new generalized equations. We then fit the pseudodata to produce generalized national-scale equations by using regression and log transformation.

The study presented here included the following steps, detailed below:

(1) The biomass equation literature was updated with equations published on May 2011.
(2) Definitions were established and author measurement differences resolved prior to incorporation of published equations into the database.
(3) Preliminary analyses and modifications were conducted, enabling some equations excluded from Jenkins *et al.* (2003) to be incorporated.
(4) Pseudodata were generated for each equation within the diameter range of that equation.
(5) Total aboveground and belowground dry biomass and root component biomass models were constructed from pseudodata.

Updated literature search

Our initial database included 2626 equations but this study brought the total to 3464 aboveground biomass and component equations for North American tree species from 206 source studies. Our literature search encompassed bibliographies of relevant papers and the literature was identified using the search engines Academic Search Premier, AGRICOLA, CAB Direct, Environmental Science Complete, Geobase, Web of Science and Google Scholar. We included published equations up to May 2011 developed for the US or Canada that estimated total dry biomass for individual trees and/or components thereof, based on diameter alone or on diameter and height. We omitted equations for palms, citrus, dry tropical and non-native tree species.

Definitions

Biomass

Total aboveground biomass was defined as all material aboveground, which was fairly consistent among all studies except for some stump exclusion. Biomass components in the database were driven by author definitions; these included 58 unique categories that we collapsed into total above- and belowground biomass, and/or into the 6 categories of stem wood, stem bark, branches, foliage, coarse roots and fine roots. Component equations were used to calculate total aboveground biomass by summation when no total aboveground biomass equation was available. Breakpoints between coarse and fine roots varied among authors, but equations were so limited that we used all available studies and author breakpoints.

General tree groups

Tree groups that we refer to as hardwood, conifer and woodland correspond to trees that are angiosperms, gymnosperms and a mixed group of frequently multistemmed hardwood and conifer species generally measured near groundline, respectively. Species which comprise each of these groups are listed in the tables.
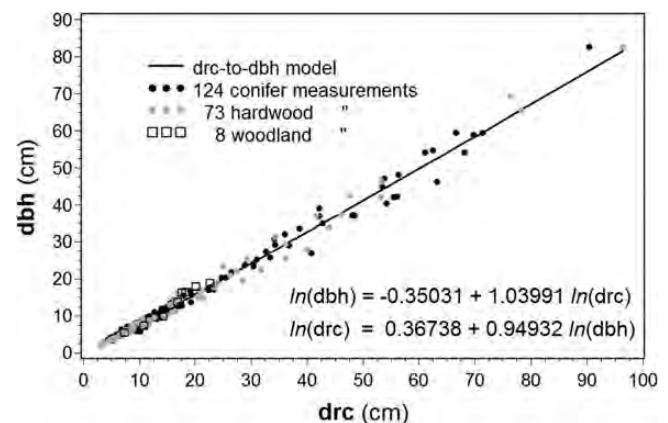

Figure 1 Diameter conversion based on 205 trees measured in VA, NM, OR and WA, including (a) conifer species: 34 pine, 26 spruce, 20 Douglas-fir, 17 hemlock, 15 cedar, and 12 fir; (b) hardwood species: 17 aspen, 11 alder, 10 oak, 7 tulip poplar, 6 maple, 3 sycamore, 3 hickory, 3 locust, 2 ash, 2 birch and 9 other hardwoods; (c) woodland species: 6 pinyon and 2 juniper. Regression R^2-statistic was 0.987 for logarithmic regression. (Contact corresponding author (D.C.C.) for further information).

Diameter measurements

Generally, diameter measurements at root collar (drc; generally near groundline but above root collar swell) are used only for woodland species, but some of the smaller trees of species for which a diameter at breast height (dbh; 1.37 m above groundline) measurement typically is used were also measured at drc. We measured 205 single-stem conifer and hardwood trees that had few to no branches between drc and dbh to obtain a diameter conversion for these small trees that was also useful for comparing biomass of all species at a common measurement point (Figure 1). Although this should be studied in more detail, our equation seemed to be reasonable for converting the few hardwood and small conifer drc measurements to dbh.

Specific gravity

Unless otherwise stated, 'specific gravity' refers to basic specific gravity of wood (on green volume to dry-weight basis) (Williamson and Wiemann, 2010). Specific gravity of wood was included in the database for each species for use in classifying species and grouping as described below. Specific gravity values are unitless and did not include any measure of variability. We used values from the US Department of Agriculture Forest Service, Forest Inventory and Analysis Program (FIA) (FIA, 2010), which for almost all US tree species were based on Miles and Smith (2009). We used our values from previous work for some woodland species (*Cercocarpus* = 0.81 (Chojnacky, 1984); Utah juniper (*Juniperus osteosperma*) = 0.54, oneseed juniper (*J. monosperma*) = 0.58, pinyon pine = 0.51 (*Pinus edulis*) (Chojnacky and Moisen, 1993)). Balsam fir (*Abies balsamea)* specific gravity (0.33) was used for Fraser fir (*A. fraseri*) instead of the genus average as suggested by Miles and Smith (2009), specific gravity for paloverde (*Cercidium microphyllum*) was set at 0.60 (National Academy of Sciences, 1980), and hybrid poplar (*Populus* spp.) was set at 0.34 (Hamilton and Wendel, 1967; Goyal *et al.*, 1999).

Stumps

Unless the author specified otherwise, we assumed stumps (5 – 30 cm, generally 15 cm above ground level) were included in aboveground biomass. Stump pseudodata were calculated for those equations where a stump

height was specified by the author and where stump biomass was explicitly excluded from aboveground biomass and/or included with coarse root biomass. We used the dbh-to-drc equation in Figure 1 (or drc directly if provided) and the author-reported stump height to approximate stump volume as a cylinder with drc as the diameter, then converted volume-to-biomass using specific gravity. Where the author excluded stump biomass from aboveground biomass, it was added to the total, and where stump biomass was included with coarse root biomass, it was subtracted from root. Stump correction affected only 25 per cent of final summarized biomass data and the median correction was <2.5 per cent increase in aboveground biomass. Large corrections >25 per cent occurred for <1 per cent of data and these were generally for trees <6-cm dbh.

Tree diameter ranges

Tree diameter ranges for which the original equations were developed were critical for our analyses so pseudodata were not generated outside ranges of original study trees. This information was generally available but in some cases was inferred from data graphs, text descriptions of sample sites or even auxiliary data as described below.

Preliminary analyses and equation modifications

The equations from the literature were generally recorded in our database in the exact mathematical form given by the author. However, when using this approach in our previous work (Jenkins *et al*., 2003) with 2626 literature equations for total or component biomass (not all usable), we were able to assemble only 318 aboveground biomass estimation equations for meta-analyses, which represented ~100 species or species groups. We wanted to fill gaps in the previous study's pseudodata, maximize the number of usable equations, and broaden the resultant applicability of the generalized estimation equations produced from the meta-analysis. Therefore, we combined studies or conducted preliminary analyses to modify some equations to fit our format for generating pseudodata. Of the 206 biomass studies (Table 1) compiled in this update that were not included in our previous study, equations from 55 were modified to fit criteria for estimating aboveground biomass. Details of these modifications are supplied in the Appendix. Pseudodata generated from these modified equations were later compared with those generated from unmodified equations to check for possible bias, as described below.

Pseudodata generation

We needed an estimate of aboveground biomass predicted from diameter that could be obtained from either a single equation or from the sum of component equations. After inclusion of modified equations, the final database for biomass meta-analyses included 2928 total or component equations for 129 species, from which we could assemble equations for 675 estimates of aboveground biomass and 82 estimates of belowground biomass. For each of the 2928 biomass equations, biomass values (pseudodata) were generated for diameters at equally spaced, ~5-cm intervals within the diameter (dbh or drc) range of the trees used to develop the original equation. However, several modifications were made to this data generation rule. Minimum diameter (dbh or drc) was set at 3 cm because only a few studies included trees with a minimum diameter of <3 cm, whereas in about half the studies this parameter was ≥3 cm. For small diameter ranges, the '5-cm interval rule' was modified to include a minimum number of pseudodata values. Four pseudodata values were generated for diameter ranges between 10 and 14 cm; 3 between 5 and 9 cm; and 2 between 3 and 5 cm. The number of pseudodata values for very large diameter ranges was restricted so as to not exceed the sample size of the original study; this increased diameter intervals in 8 studies generally to between 6 and 8 cm, with extremes of 11 and 15 cm. Of the total 21 521

pseudodata values generated in the study, the median number of pseudodata values generated per equation was 6.

After applying stump adjustments (as described above), pseudodata from each study's equations were used directly in regression meta-analyses, except for studies where biomass equations were reported for individual treatments within a designed experiment. For 8 such studies, pseudodata were averaged for each diameter across all treatments – essentially generating only one equation per species with these pseudodata. In addition to aboveground biomass equations, 34 per cent of the studies reported biomass component equations that also added to total aboveground biomass; for these studies we selected the estimate based on the aboveground biomass equation.

After summarizing all the pseudodata (combining components, averaging treatments, selecting best estimates and adjusting for stumps), we had 5031 pseudodata values for modeling aboveground biomass (as function of dbh) for 129 species or species groups – with 48 and 28 per cent of the pseudodata coming from equations developed for the eastern and western US, respectively, and 24 per cent from equations developed for Canada.

Although our database is structured to allow interested researchers to pursue modeling of biomass component equations, in this study we generated pseudodata only for root components, which were modeled as a ratio of aboveground biomass. A ratio model was used because it seemed to be the most consistent way to extrapolate our limited root data to many species. However, of the 82 root equations, 17 (from 10 studies) needed accompanying aboveground biomass pseudodata because only roots were measured (see Table 1). This was obtained by assembling aboveground biomass pseudodata from similar species in the other pseudodata, with stump corrections conducted as described above in definitions. A total of 700 pseudodata values for 39 species or species groups were generated for root component ratios.

Construction of above- and belowground biomass models

In our previous work (Jenkins *et al*., 2003), the pseudodata essentially drove classification of species into groups for regression modeling. But the ability to synthesize more than 300 equations into only 10 generalized equations suggested an underlying principle was at work, such as allometric scaling theory (Chojnacky, 2002). This generalized theory (see, e.g. West *et al*., 1997, 1999a, 1999b, 2009; Enquist *et al*., 1998, 1999, 2009) uses fractal dimensions of tree architecture and physics of fluid transport up a tree to produce a generalized aboveground biomass model; the biomass equation utilizes a diameter-to-mass scaling relationship, where primary predictor variables are diameter and *mean specific gravity of the entire tree*. Although we make no attempt to directly apply allometric scaling theory, we do include the importance of specific gravity in our formulation. Chave *et al*. (2005) also support the importance of specific gravity for aboveground biomass estimation.

Although specific gravity of wood is likely correlated with the *mean specific gravity of entire tree* (a parameter that is seldom measured), it did not make sense to directly use it in our modeling because differences in specific gravity as reported by various authors for stem sapwood, heartwood, bark, branches and/or tree sizes within an individual species often range from 0.05 to more than 0.10 units (Wahlgren and Fassnacht, 1959; Carpenter, 1983; Clark and Schroeder, 1986; Clark *et al*., 1986a). Instead the relative similarity of the specific gravity of tree species within genera and/or families led us to use taxonomy as an initial proxy for *mean specific gravity of entire tree* – but we also allowed for further splits into specific gravity classes when specific gravity was highly dissimilar within these taxonomic groupings. In this way we were able to utilize the principles of allometric scaling theory without having to precisely measure the *mean specific gravity of entire tree*. For example, Salicaceae (aspen/willow/poplar) species tend to be low in specific gravity whereas Fagaceae (oak/beech) tend to be high. For the purposes of our modeling, we used the words 'taxon' or 'taxa' to refer

Table 1 Key to author reference numbers in Tables 2–4 and 6, and to study modifications (see Appendix for details), for all biomass studies included in meta-analysis

Ref. no.	Author reference	Ref. no.	Author reference	Ref. no.	Author reference
1	Acker and Easter (1994)[1]	70	Grier *et al.* (1984)[1]	139	Petersen *et al.* (2008)
2	Adegbidi *et al.* (2002)	71	Grier *et al.* (1992)[1]	140	Peterson *et al.* (1970)[1]
3	Alban and Laidly (1982)[2]	72	Grigal and Kernik (1984)[1]	141	Phillips (1981)[1,3]
4	Arevalo *et al.* (2007)	73	Harding and Grigal (1985)[1]	142	Pike *et al.* (1977)
5	Aspinwall et al. (2011)	74	Harrington *et al.* (1984)[4]	143	Pitt and Bell (2004)
6	Baldwin (1989)[1,5]	75	Harris *et al.* (1973)[4]	144	Pollard (1972)[1]
7	Barclay *et al.* (1986)[1]	76	Harris *et al.* (1977)[6]	145	Ralston (1973)[1]
8	Barney *et al.* (1978)[1]	77	Harrison *et al.* (2009)	146	Ralston and Prince (1965)[2]
9	Baskerville (1965)[1]	78	Haynes and Gower (1995)[6]	147	Reid *et al.* (1974)
10	Bella and De Franceschi (1980)[2]	79	Hegyi (1972)[1]	148	Reiners (1972)[4]
11	Bickelhaupt *et al.* (1973)	80	Helgerson *et al.* (1988)[1]	149	Rencz and Auclair (1980)[1]
12	Binkley (1983)[1]	81	Hocker and Early (1983)[1,3]	150	Reynolds *et al.* (1978)[4]
13	Binkley *et al.* (1984)	82	Honer (1971)[1]	151	Ribe (1973)[1]
14	Bockheim and Lee (1984)[1]	83	Ishii and Kadotani (2006)[4,5]	152	Riemenschneider *et al.* (2001)[3]
15	Boerner and Kost (1986)[1]	84	Jacobs *et al.* (2009)	153	Rogerson (1964)[5]
16	Bormann (1990)[1]	85	Johnson (2009)	154	Rolfe *et al.* (1978)
17	Brenneman *et al.* (1978)[3]	86	Johnston and Bartos (1977)[7]	155	Ruark and Bockheim (1988)[1]
18	Bridge (1979)	87	Jokela and Martin (2000)[2]	156	Ruark *et al.* (1987)
19	Briggs *et al.* (1989)[1]	88	Jokela *et al.* (1981)[1]	157	Rubilar *et al.* (2005)[2]
20	Brown (1978)[4]	89	Jokela *et al.* (1986)[1]	158	Sabatia (2007)[7]
21	Busing *et al.* (1993)[1,3]	90	Kapeluck and Van Lear (1995)[6]	159	Sachs (1984)[4]
22	Callaway *et al.* (1994)	91	Karlik and McKay (2002)[7]	160	Samuelson *et al.* (2004)
23	Callaway *et al.* (2000)	92	Kaye *et al.* (2005)	161	Schmitt and Grigal (1981)[1]
24	Campbell *et al.* (1985)[1]	93	Ker (1980a)[1]	162	Schnell (1976)[7]
25	Carpenter (1983)	94	Ker (1980b)[1]	163	Schnell (1978)[4]
26	Carter and White (1971)[1]	95	Ker (1984)	164	Schroeder *et al.* (1997)[1]
27	Chapman and Gower (1991)[1]	96	Ker and van Raalte (1981)[4]	165	Seiler *et al.* (2009)[4]
28	Chen *et al.* (2004)[6]	97	Kimmins (1973)[5]	166	Shenoy *et al.* (2011)
29	Chojnacky (1984)[1,4]	98	Kinerson and Bartholomew (1977)[1]	167	Siccama *et al.* (1994)[1]
30	Chojnacky and Moisen (1993)[4]	99	King and Schnell (1972)	168	Singh (1984)[1]
31	Clark and Schroeder (1986)[3]	100	King *et al.* (2007)[7]	169	Smith and Wood (2006)
32	Clark and Taras (1976)[2]	101	Koerper and Richardson (1980)[1]	170	Snell and Little (1983)
33	Clark *et al.* (1985)[1]	102	Krumlik (1974)[1]	171	Snell and Max (1985)[5]
34	Clark *et al.* (1986a)	103	Lambert *et al.* (2005)	172	Sollins and Anderson (1971)[7]
35	Clark *et al.* (1986b)[1]	104	Landis and Mogren (1975)[1]	173	Sollins *et al.* (1973)
36	Clary and Tiedemann (1986)	105	Lavigne and Krasowski (2007)[6]	174	St. Clair (1993)[1]
37	Clary and Tiedemann (1987)[1]	106	Laxson *et al.* (1997)[4]	175	Standish *et al.* (1985)[2]
38	Cochran *et al.* (1984)[5]	107	Levia (2008)[5]	176	Storey *et al.* (1955)[5,7]
39	Coltrin (2010)	108	Lieffers and Campbell (1984)[1]	177	Strong and Roi (1983)[7]
40	Crow (1971)	109	Litton *et al.* (2003)[6]	178	Swank and Schreuder (1974)[1]
41	Crow (1976)[1]	110	Lojewski *et al.* (2009)	179	Telfer (1969)
42	Crow (1983)[1]	111	Loomis *et al.* (1966)[5]	180	Ter-Mikaelian and Lautenschlager (2001)[5]
43	Czapowskyj *et al.* (1985)	112	MacLean and Wein (1976)[1]	181	Thies and Cunningham (1996)[1,6]
44	Darling (1967)[1]	113	Mack *et al.* (2008)	182	Turner *et al.* (2004)
45	Davis and Trettin (2006)[3]	114	Marshall and Wang (1995)[1]	183	Tuskan and Rensema (1992)[4]
46	Dunlap and Shipman (1967)[5]	115	Martin *et al.* (1998)[1]	184	Vadeboncoeur *et al.* (2007)[6]
47	Duursma *et al.* (2007)[4]	116	Martin *et al.* (2005)	185	Van Lear *et al.* (1984)[1]
48	El Fadl *et al.* (1989)[4]	117	McCain (1994)[5]	186	Van Lear *et al.* (1986)[2]
49	Elliott *et al.* (2002)[3]	118	McGinnis *et al.* (2010)	187	Wade (1969)[5]
50	Espinosa-Bancalari and Perry (1987)	119	Means *et al.* (1994)[4]	188	Wang *et al.* (1995)[1]
51	Fassnacht (1996)[3]	120	Miller *et al.* (1981)[7]	189	Wang *et al.* (1996)
52	Fatemi *et al.* (2011)	121	Monk *et al.* (1970)	190	Wang *et al.* (2000)

Continued

Table 1 *Continued*

Ref. no.	Author reference	Ref. no.	Author reference	Ref. no.	Author reference
53	Felker *et al.* (1982)[1]	122	Monteith (1979)[1]	191	Wartluft (1977)[3]
54	Feller (1992)[1]	123	Moore and Verspoor (1973)[1]	192	Weaver and Forcella (1977)
55	Fortier *et al.* (2010)	124	Morrison (1990)[1]	193	Weetman and Harland (1964)[4]
56	Freedman (1984)[1]	125	Naidu *et al.* (1998)[4]	194	Westman (1987)[1]
57	Freedman *et al.* (1982)[1]	126	Navar (2009)	195	Westman and Whittaker (1975)
58	Gary (1976)[5]	127	Nelson and Switzer (1975)[1]	196	Whisenant and Burzlaff (1978)[4]
59	Gholz *et al.* (1979)[1]	128	Nicholas (1992)	197	Whittaker and Niering (1975)
60	Gholz *et al.* (1991)	129	Norris *et al.* (2001)	198	Whittaker and Woodwell (1968)[1]
61	Gilmore and Zenner (2005)[5]	130	Omdal *et al.* (2001)[6]	199	Whittaker *et al.* (1974)[4]
62	Goldsmith and Hocker (1978)[3]	131	Ouellet (1983)[1]	200	Wiant *et al.* (1977)[3]
63	Gower *et al.* (1987)[1]	132	Ouimet *et al.* (2008)[6]	201	Williams and McClenahen (1984)[1,3]
64	Gower *et al.* (1992)[1]	133	Parker and Schneider (1975)[1]	202	Xing *et al.* (2005)
65	Gower *et al.* (1993a)	134	Pastor and Bockheim (1981)[1]	203	Yarie *et al.* (2007)
66	Gower *et al.* (1993b)	135	Pastor *et al.* (1984)[1]	204	Young *et al.* (1980)[1]
67	Gower *et al.* (1997)	136	Pearson *et al.* (1984)[4]	205	Zabek and Prescott (2006)[2,3]
68	Green and Grigal (1978)[1]	137	Peichl and Arain (2007)	206	Zhou *et al.* (2011)[3]
69	Grier and Logan (1977)	138	Perala and Alban (1994)[4]		

[1] Complete reference in Jenkins *et al.* (2003).
[2] Equations refit to eliminate height variable.
[3] Foliage biomass taken from other similar studies.
[4] Multiple studies combined or other equation modifications.
[5] Study included component equations only, no total biomass.
[6] Total biomass for root study taken from other similar studies.
[7] Equations refit from author's data.

to a classification based on family or genus, although these were sometimes further split into groups based on specific gravity.

Classifying pseudodata into taxa

Classification into taxa and modeling of pseudodata were conducted concurrently because final grouping was based largely on regression results and diagnostics for finding the best data fit. However, our classification strategy is outlined here, with detailed modeling results discussed below. We began with a genus-based classification for conifer species, but for hardwoods, because there were so many genera, family was the starting point. Family was also used for initial classification of woodland species. Further separation was conducted based on specific gravity, sample size (i.e. quantity of pseudodata, numbers of underlying equations and diameter range of equations), and coarse geography (eastern *vs* western North America). Specific gravity was included in our database as previously described; for conifer species it ranged from 0.29 to 0.54 (most 0.35–0.45), for hardwoods from 0.31 to 0.66 (most 0.40–0.60), and for woodland species from 0.41–0.81. Final classification into taxa was an iterative process based on observing biomass-to-dbh patterns (from graphs), testing regression coefficients (using robust logarithmic regression described in more detail below), and observing regression residual patterns. In the end, 35 taxa – 13 conifers, 18 hardwood, and 4 woodland – were identified for one or more unique parameters in predicting biomass.

Conifer species were initially separated into 6 genera and the Cupressaceae family (Table 2). Further separation was made for the Cupressaceae family and for the genera *Abies*, *Picea*, *Pinus* and *Tsuga* based on geography and specific gravity. (Only two US coniferous genera – *Taxus* and *Torreya* – were missing from our taxa classification scheme; we suggest using Douglas-fir or hemlock genera equations for these.)

Aceraceae, Betulaceae, Fagaceae and Salicaceae comprised nearly three-fourths of the hardwood species (Table 3), so these families were initially separated out and considered for further separation based on specific gravity. Fabaceae and Juglandaceae had specific gravities >0.60 and were combined, as were Hippocastanaceae and Tiliaceae with specific gravities near 0.30. The remaining 9 families, which included mostly species with specific gravity 0.45–0.55, were initially grouped to construct a general hardwood taxon for those families having few published biomass equations; however, 3 warranted separation, leaving 6 families for the general taxon.

Pseudodata for woodland species separated naturally into family-based taxa including Cupressaceae (junipers), Pinaceae (pinyon), Fagaceae (evergreen oaks), Fabaceae (mesquite) and Rosaceae (mountain mahogany); but Fabaceae and Rosaceae were combined based on very high specific gravities and small numbers of pseudodata (studies) for each family (Table 4). (For woodland species not included in our pseudodata – hardwoods measured at drc (e.g. *Acer glabrum*, *Arbutus xalapensis*, *Robinia neomexicana*) – we suggest drc be converted to dbh (Figure 1) to estimate biomass from the appropriate hardwood taxa equations.)

Regression modeling of aboveground biomass

For regression modeling conducted simultaneously with the classification based on taxa as described above, we selected the two-parameter logarithmic regression model. It was selected because it rescales *unequal variation* in the biomass-to-diameter relationship into *equal variation* after logarithmic transformation [$\ln(\text{biomass}) = \beta_0 + \beta_1 \ln(\text{diameter})$, where diameter = dbh for conifer/hardwood species and drc for woodland species]. Also, this logarithmic model was the basis for most of the equations from which our pseudodata were generated. Regression modeling was conducted with Proc RobustReg (©SAS Institute Inc., 2011), which is a robust regression

Table 2 Thirteen taxa groupings for 265 biomass equations for 45 conifer species (or species groups), with diameter range given for all equations of each species or group

Taxa	Genus and species	Common name	FIA species code	Wood specific gravity	No. of equations	dbh range (cm)	Literature reference no. (see Table 1)
Abies < 0.35 spg*	*Abies balsamea*	Fir, balsam	12	0.33	12	3–51	9,57,82,94,95,96,103,112,138,202,204
	A. fraseri	Fir, Fraser	16	0.33	1	7–25	128
	A. lasiocarpa	Fir, subalpine	19	0.31	7	3–69	20,23,47,103,119,175,190
Abies ≥ 0.35 spg	*A. amabilis*	Fir, Pacific silver	11	0.40	4	4–109	59,102,119,175
	A. concolor	Fir, white	15	0.37	2	7–158	119,194
	A. grandis	Fir, grand	17	0.35	3	3–71	20,47,175
	A. magnifica	Fir, California red	20	0.36	2	19–143	119,194
	A. procera	Fir, noble	22	0.37	2	16–236	59,119
	Abies spp.	Fir, Pacific silver-noble-other	10	0.39	1	9–111	59
Cupressaceae < 0.30 spg	*Thuja occidentalis*	Cedar, northern white	241	0.29	6	3–66	93,103,138,148,204
Cupressaceae 0.30–0.39 spg	*Calocedrus decurrens*	incense-cedar	81	0.35	1	25–144	119
	Sequoiadendron giganteum	Sequoia, giant	212	0.34	1	97–614	119
	T. plicata	Cedar, western red	242	0.31	8	3–169	1,20,47,54,59,119,175
Cupressaceae ≥ 0.40 spg	*Chamaecyparis nootkatensis*	Cedar, Alaska	42	0.42	2	8–109	119,175
	Juniperus virginiana	Juniper, eastern redcedar	68	0.44	4	3–43	103,129,162,206
Larix	*Larix laricina*	Tamarack	71	0.49	6	3–51	25,94,103,168,204
	L. occidentalis	Tamarack, western larch	73	0.48	4	3–98	20,47,63,175
	L. spp.	Tamarack, larch (introduced)	70	0.49	1	6–35	66
Picea < 0.35 spg	*Picea engelmannii*	Spruce, Engelmann	93	0.33	5	3–90	20,47,104,119,175
	P. sitchensis	Spruce, Sitka	98	0.33	3	5–283	16,119,175
Picea ≥ 0.35 spg	*P. abies*	Spruce, Norway	91	0.36	2	6–44	66,89
	P. glauca	Spruce, white	94	0.37	12	3–58	9,57,73,94,95,96,103,138,143,168,175,203
	P. mariana	Spruce, black	95	0.38	21	3–40	8,43,57,67,72,94,103,113,116,123,131,138, 149,168,175,193,203
	P. rubens	Spruce, red	97	0.37	11	3–72	57,95,103,112,122,128,167,172,199,204

Pinus < 0.45 spg	*Pinus albicaulis*	Pine, whitebark	101	0.43	2	3–50	20,23
	P. arizonica	Pine, Arizona	135	0.43	1	10–45	126
	P. banksiana	Pine, jack	105	0.40	15	3–41	3,40,67,68,79,94,95,103,112,116,138,168
	P. contorta	Pine, lodgepole	108	0.38	11	3–60	20,47,63,103,119,136,147,175,182,195
	P. jeffreyi	Pine, Jeffrey	116	0.37	2	3–133	118,119
	P. lambertiana	Pine, sugar	117	0.34	3	3–180	69,118,119
	P. leiophylla	Pine, Chihuahua	118	0.43	1	10–35	126
	P. monticola	Pine, western white	119	0.36	2	4–115	47,175
	P. ponderosa	Pine, ponderosa	122	0.38	9	3–118	20,22,47,59,65,92,119,175
	P. resinosa	Pine, red	125	0.41	9	3–55	3,14,65,66,94,100,103,138,204
	Pinus spp.	Pine, ponderosa-lodgepole-sugar	100	0.37	1	16–80	59
	P. strobus	Pine, eastern white	129	0.34	14	3–69	66,81,93,98,103,112,122,135,137,138,172,178,204
Pinus ≥ 0.45 spg	*P. echinata*	Pine, shortleaf	110	0.47	3	4–50	32,158,172
	P. elliottii	Pine, slash	111	0.54	4	3–53	32,60,87
	P. palustris	Pine, longleaf	121	0.54	1	15–48	32
	P. rigida	Pine, pitch	126	0.47	1	3–31	198
	P. taeda	Pine, loblolly	131	0.47	19	3–56	2,5,32,87,125,127,145,157,160,172,185,186
Pseudotsuga	*Pseudotsuga menziesii*	Douglas-fir	202	0.45	23	3–215	7,20,47,50,54,59,63,64,69,70,77,80,114,119,139,142,174,175
Tsuga < 0.40 spg	*Tsuga canadensis*	Hemlock, eastern	261	0.38	9	3–85	17,21,81,93,103,122,172,204
Tsuga ≥ 0.40 spg	*T. heterophylla*	Hemlock, western	263	0.42	10	3–172	20,47,69,77,102,119,159,175
	T. mertensiana	Hemlock, mountain	264	0.42	4	9–126	59,102,119,175

*Where spg is specific gravity of wood of on green volume to dry-weight basis.

Table 3 Eighteen taxa groupings for 388 biomass equations for 70 hardwood species (or species groups), with diameter range given for all equations for each species or group

Taxa	Family	Genus and species	Common name	FIA species code	Wood specific gravity	No. of equations	dbh range (cm)	Literature reference no. (see Table 1)
Aceraceae < 0.50 spg*	Aceraceae	*Acer macrophyllum*	Maple, bigleaf	312	0.44	2	5–46	69,170
	Aceraceae	*A. pensylvanicum*	Maple, striped	315	0.44	3	3–13	81,85,204
	Aceraceae	*A. rubrum*	Maple, red	316	0.49	34	3–66	17,18,19,21,31,33,34,41,42,49,52,57,62,81,85, 94,95,98,103,112,115,122,135,138,141,148, 150,151,172,179,200,201,204
	Aceraceae	*A. saccharinum*	Maple, silver	317	0.44	1	4–45	103
	Aceraceae	*A. spicatum*	Maple, mountain	319	0.47	3	3–10	81,199,204
Aceraceae ≥ 0.50 spg	Aceraceae	*A. saccharum*	Maple, sugar	318	0.56	24	3–70	11,17,21,27,41,52,57,62,81,93,103,122,124,134, 135,138,151,167,172,199,201,204
Betulaceae < 0.40 spg	Betulaceae	*Alnus rubra*	Alder, red	351	0.37	9	3–64	12,80,119,133,151,170,175,204
	Betulaceae	*A.* spp.	Alder, sitka	350	0.37	1	3–7	13
Betulaceae 0.40–0.49 spg	Betulaceae	*Betula papyrifera*	Birch, paper	375	0.48	23	3–51	9,41,52,57,62,81,88,94,95,98,103,112,138,148, 151,161,175,189,190,203,204
	Betulaceae	*B. populifolia*	Birch, gray	379	0.45	6	3–23	81,94,103,151,204
Betulaceae 0.50–0.59 spg	Betulaceae	*B. alleghaniensis*	Birch, yellow	371	0.55	16	3–70	17,52,57,93,103,122,124,128,135,138,148, 151,167,199,204
Betulaceae ≥ 0.60 spg	Betulaceae	*B. lenta*	Birch, sweet	372	0.60	7	3–47	17,21,31,81,85,115,172
	Betulaceae	*Ostrya virginiana*	Hophornbeam	701	0.63	4	3–21	81,103,138,148
Cornaceae/Ericaceae/ Lauraceae/Platanaceae/ Rosaceae/Ulmaceae[1]	Cornaceae	*Cornus florida*	Dogwood	491	0.64	5	3–12	15,49,115,141,172
	Cornaceae	*Nyssa aquatica*	Tupelo, water	691	0.46	1	3–25	33
	Cornaceae	*N. sylvatica*	Tupelo, blackgum	693	0.46	5	3–50	31,33,141,150,201
	Ericaceae	*Arbutus menziesii*	Madrone, Pacific	361	0.58	2	3–64	74,170
	Ericaceae	*Oxydendrum arboreum*	Sourwood	711	0.50	3	4–35	85,115,141
	Ericaceae	*Umbellularia californica*	California bay laurel	981	0.51	1	8–61	39
	Lauraceae	*Sassafras albidum*	Sassafras	931	0.42	3	3–15	85,172,201
	Platanaceae	*Platanus occidentalis*	Sycamore	731	0.46	2	3–50	34,45
	Rosaceae	*Amelanchier* spp.	Serviceberry	356	0.66	2	3–25	148,172
	Rosaceae	*Prunus pensylvanica*	Cherry, pin	761	0.47	9	3–42	21,52,81,85,112,151,172,204
	Rosaceae	*P. serotina*	Cherry, black	762	0.47	5	3–50	17,85,103,200,201
	Rosaceae	*P. virginiana*	Cherry, Chokecherry	763	0.47	3	3–15	151,204
	Rosaceae	*Sorbus americana*	Sorbus, mtn. ash	935	0.60	1	7–26	172
	Ulmaceae	*Ulmus americana*	Elm	972	0.46	3	3–55	103,138,148
	Ulmaceae	*U.* spp.	Elm	970	0.54	1	3–27	34
Fabaceae/Juglandaceae, Carya	Juglandaceae	*Carya illinoinensis*	Pecan	404	0.60	1	22–33	169
	Juglandaceae	*C. ovata*	Hickory, shagbark	407	0.64	1	5–43	17
	Juglandaceae	*Carya* spp.	Hickory	400	0.62	11	3–70	31,33,34,35,103,115,141,146,163,172,200
Fabaceae/Juglandaceae, other	Fabaceae	*Robinia pseudoacacia*	Locust, black	901	0.66	2	4–42	31,49

Fagaceae, deciduous	Fagaceae	*Castanea dentata*	Chestnut, American	421	0.40	1	3–32	84
	Fagaceae	*Fagus grandifolia*	Beech	531	0.56	15	3–66	17,19,21,52,81,93,103,122,151,167,172, 179,199,204
	Fagaceae	*Quercus alba*	Oak, white	802	0.60	14	3–74	17,18,31,33,34,35,103,115,141,146,148, 172,198,200
	Fagaceae	*Q. coccinea*	Oak, scarlet	806	0.60	6	3–56	31,34,35,115,198,200
	Fagaceae	*Q. ellipsoidalis*	Oak, pin	809	0.59	1	3–50	148
	Fagaceae	*Q. falcata*	Oak, red southern	812	0.52	3	3–56	34,35,141
	Fagaceae	*Q. macrocarpa*	Oak, bur	823	0.58	1	6–25	138
	Fagaceae	*Q. nigra*	Oak, water	827	0.56	1	3–51	33
	Fagaceae	*Q. prinus*	Oak, chestnut	832	0.57	7	3–58	17,31,34,49,115,141,200
	Fagaceae	*Q. rubra*	Oak, red northern	833	0.56	18	3–73	17,21,27,31,49,62,66,81,98,103,115,122, 135,138,146,179,200,204
	Fagaceae	*Quercus* spp.	Oaks	800	0.59	3	3–73	121,154,172
	Fagaceae	*Q. stellata*	Oak, post	835	0.60	2	3–53	35,141
	Fagaceae	*Q. velutina*	Oak, black	837	0.56	5	3–89	18,31,99,200,201
Fagaceae, evergreen	Fagaceae	*Chrysolepis chrysophylla*	Chinkapin, golden	431	0.42	2	3–61	69,170
	Fagaceae	*Lithocarpus densiflorus*	Tanoak	631	0.58	2	3–66	74,170
	Fagaceae	*Q. douglasii*	Oak, blue	807	0.59	1	12–42	91
	Fagaceae	*Q. laurifolia*	Oak, laurel	820	0.56	1	3–44	33
	Fagaceae	*Q. minima*	Oak, dwarf live	841	0.59	1	3–3	165
Hamamelidaceae	Hamamelidaceae	*Liquidambar styraciflua*	Sweetgum	611	0.46	6	3–53	33,34,35,45,141,172
Hippocastanaceae/ Tiliaceae	Hippocastanaceae	*Aesculus flava*	Aesculus, yellow buckeye	332	0.33	2	8–56	21,172
	Tiliaceae	*Tilia americana*	Basswood	951	0.32	7	3–55	17,31,51,81,103,138,204
	Tiliaceae	*T. americana.* var. *heterophylla*	Basswood, white	952	0.32	2	8–33	21,172
Magnoliaceae	Magnoliaceae	*Liriodendron tulipifera*	Tulip poplar	621	0.40	13	3–65	17,21,31,33,34,35,49,85,115,141,172,200,201
	Magnoliaceae	*Magnolia fraseri*	Magnolia, Fraser	655	0.40	1	5–13	85
	Magnoliaceae	*M. virginiana*	Magnolia, sweetbay	653	0.42	1	3–19	150
Oleaceae < 0.55 spg	Oleaceae	*Fraxinus nigra*	Ash, black	543	0.45	4	3–43	103,133,148,204
	Oleaceae	*F. pennsylvanica*	Ash, green	544	0.53	3	3–42	33,103,206
	Oleaceae	*Fraxinus* spp.	Ash	540	0.51	2	4–32	138,172
Oleaceae ≥ 0.55 spg	Oleaceae	*F. americana*	Ash, white	541	0.55	7	3–55	17,31,93,103,122,201,204
Salicaceae < 0.35 spg	Salicaceae	*Populus balsamifera*	Populus, balsam poplar	741	0.31	6	3–53	10,103,116,138,168,203
	Salicaceae	*P.balsamifera.* ssp. *trichocarpa*	Populus, black Cottonwood	747	0.31	1	5–32	175
	Salicaceae	*Populus* spp.	Populus, cottonwood	740	0.34	3	3–40	152,183,205

Updated generalized biomass equations

Table 3 *Continued*

Taxa	Family	Genus and species	Common name	FIA species code	Wood specific gravity	No. of equations	dbh range (cm)	Literature reference no. (see Table 1)
Salicaceae ≥ 0.35 spg	Salicaceae	*P. deltoides*	Populus, cottonwood eastern	742	0.37	1	3–27	26
	Salicaceae	*P. grandidentata*	Populus, aspen bigtooth	743	0.36	6	3–55	57,101,103,122,138,201
	Salicaceae	*Populus* spp.	Populus, cottonwood	740	0.35	2	4–38	55,110
	Salicaceae	*P. tremuloides*	Populus, aspen quaking	746	0.35	36	3–70	10,24,57,62,67,81,86,94,95,103,108,112,113, 116,134,135,138,140,144,151,155,156,166, 168,175,179,188,203,204
	Salicaceae	*Salix alba*	Willow, white	927	0.36	1	3–4	4
	Salicaceae	*Salix* spp.	Willow	920	0.36	6	3–23	4,151,204

*Where spg is specific gravity of wood of on green volume to dry-weight basis.
[1]Might also use this equation for species not included in table, unless specific gravity more closely related to another taxon.

Table 4 Four taxa groupings for 23 biomass equations for 15 woodland species (or species groups), with diameter range given for all equations of each species or group

Taxa	Family	Genus and species	Common name	FIA species code	Wood specific gravity	No. of equations	dbh range (cm)	Literature reference no. (see Table 1)
Cupressaceae	Cupressaceae	*Cupressus* spp.	Cypress, pygmy	50	0.41	1	4–12	195
	Cupressaceae	*J. monosperma*	Juniper, oneseed	69	0.58	1	5–45	71
	Cupressaceae	*J. occidentalis*	Juniper, western	64	0.45	1	5–87	59
	Cupressaceae	*J. osteosperma*	Juniper, Utah	65	0.54	3	8–85	30,44,120
Fabaceae/Rosaceae	Fabaceae	*Cercidium microphyllum*	Paloverde, yellow	none	0.60	1	10–25	197
	Fabaceae	*Prosopis* spp.	Mesquite	755	0.78	4	3–60	48,53,106,196
	Rosaceae	*Cercocarpus ledifolius*	Mountain mahogany	475	0.81	1	5–56	29
	Rosaceae	*C. montanus.var.pauciden*	Mountain Mahogany	477	0.81	1	3–5	197
Fagaceae	Fagaceae	*Q. douglasii*	Oak, blue	807	0.59	1	15–50	91
	Fagaceae	*Q. gambelii*	Oak, Gambel	814	0.61	2	3–32	36,37
	Fagaceae	*Q. hypoleucoides*	Oak, silverleaf	843	0.59	1	4–37	197
	Fagaceae	*Quercus* (live) spp.	Oak, evergreen spp.	850	0.58	1	9–74	126
Pinaceae	Pinaceae	*P. cembroides*	Pine, pinyon	140	0.51	1	4–19	197
	Pinaceae	*P. edulis*	Pine, pinyon	106	0.51	2	5–45	44,71
	Pinaceae	*P. monophylla*	Pine, pinyon singleleaf	133	0.51	2	3–75	30,120

strategy that compromises between excluding outlying pseudodata entirely and treating them all equally as in Ordinary Least Squares regression. We used the M-estimation option (Maximum likelihood-like) which minimizes a weighted objective function – in this case, the bisquare weight, where all nonzero residuals were down-weighted (with weight between 1 and 0) in proportion to their distance from zero. This was particularly useful because our equation-generated observations (pseudodata) sometimes resulted in lines of points in divergent directions from the majority of other pseudodata: the weights captured the essence of these divergent equations (which we had no reason to exclude) and at the same time proportionately discounted outlying points.

Model fitting was conducted repeatedly, adjusting variable inclusions with each iteration to settle on taxa groupings (as described above), select specific gravity groups, and improve fit. Six factors were considered in final model selection: (1) statistical significance of model parameters, (2) favorable regression residual patterns, (3) avoidance of model extrapolation beyond data range, (4) Akaike Information Criterion (AIC) for robust regression, (5) sample size (numbers of equations as well as pseudodata number) and (6) geographic distribution of species (such as eastern or western North America). Nonsignificant parameters were not included in models but marginally significant parameters (*P*-values between 0.02 and 0.05) that would have further split taxa were sometimes ignored if pseudodata seemed to be too limited based on sample size considerations. All significance testing was based on a χ^2-statistic and significance level was set at 0.05 (for details on statistics see Proc RobustReg (© SAS Institute Inc., 2011)).

We also tested, within the robust regression (using binary (0,1-indicator) variables), pseudodata from the 55 modified equations (described in the 'Preliminary analyses and equation modifications' section) against pseudodata generated directly from published equations. These tests were conducted within the range of dbh overlap for the two equation types; generally there were no significant differences except for *Pseudotsuga* which was highly significant (Prob $\chi^2 < 0.001$). Even so, this did not seem sufficient cause to discard the pseudodata from 'modified equations' for *Pseudotsuga* because these data were only ~10 per cent lower (from graph not shown) than pseudodata from 'unmodified equations' and there was no way of knowing which equations –'modified' or 'unmodified' – were more accurate. Therefore, all pseudodata – whether from modified or unmodified equations – were used in final equation fitting.

Although our biomass modeling was based on logarithmic transformation of variables, we did not include a correction (Baskerville, 1972) for underestimation. First, extending use of Baskerville's correction to pseudodata (generated from equations) seemed to be unwise without some justification. Second, correction procedures may in fact introduce their own bias (for further information, see Jenkins *et al*. (2003) and Flewelling and Pienaar (1981)). The extensive research needed to determine if and how correction factors could be applied for this type of modeling was beyond the scope of our study.

Results

Aboveground biomass

Conifers

Regression analyses resulted in equations for 13 conifer taxa (Table 5). Modeling was done within the genus or family (e.g. the Cupressaceae).

The main advantage of splits within genera was better regression fit of pseudodata, often for small eastern-species trees. For *Abies*, *Picea* and *Tsuga*, specific gravity differences between eastern and western species nicely coincided with significant parameters, except for western *Abies lasiocarpa* which better fit with eastern *Abies* species. *Larix* included eastern and western species but

similar specific gravities and few pseudodata patterns precluded separation. The large *Pinus* genus was difficult to model because it encompassed North America, included considerable pseudodata variation, and differed little in specific gravity from east to west (e.g. ponderosa pine pseudodata spanned the entire range of variation for all pines). Southern pine species (*Pinus* subsection *Australes*) with specific gravity ≥0.45 were an exception, and were separated from the rest.

Modeling the Cupressaceae family was more challenging. Our first inclination was to subset the well-represented *Thuja* genera and further separate eastern and western species based on specific gravity, as all showed significant test results, but this left too few pseudodata to model the rest–particularly for small trees. However, a three-tier specific-gravity-based compromise was found where the lowest specific gravity (<0.30) *Thuja occidentalis* was separated from the midrange specific gravity (0.30–0.39) *Thuja placata* and other western Cupressaceae, and those from the highest specific gravity (≥0.40) Cupressaceae.

Comparison of prediction equations for the 13 conifer taxa illustrates the importance of specific gravity in the biomass-to-diameter relationship (Figure 2). High-specific-gravity southern pines (*Pinus* ≥ 0.45) and Douglas-fir (*Pseudotsuga*) show the most aboveground biomass for given diameter, low-specific-gravity Cupressaceae show the least, and although midrange trends are less clear, generally higher specific gravity is associated with more biomass for a given dbh.

Hardwoods

Eighteen taxa equations resulted from regression analyses of hardwood species (Table 5). Of the four families with the most pseudodata, Aceraceae split nicely at specific gravity thresholds corresponding to hard (*A. saccharum*) and soft maple (other *Acer* species) and higher specific gravity aspen (and a few other higher specific gravity species) split from lower specific gravity balsam poplar in the Salicaceae. Betulaceae and Fagaceae were more troublesome because they included so many species. Betulaceae was separated into *Alnus* spp. and three more classes based on specific gravity. Fagaceae pseudodata included many species of similar specific gravity that could only be statistically separated based on deciduous or evergreen species.

As previously mentioned, Fabaceae and Juglandaceae were combined, as were Hippocastanaceae and Tiliaceae, to represent the extreme high and low specific gravities for hardwood species. In order to better design for species in Fabaceae/Juglandaceae that were not included in our study (e.g. walnut (*Juglans*), butternut (*Juglans cinerea*), Kentucky coffeetree (*Gymnocladus dioicus*), yellowwood (*Cladrastis kentukea*)), this group was further separated into *Carya* and other. *Carya* showed particularly high biomass (for a given dbh), which we did not wish to presume applied to species not represented in our data. A check against Wang's (2006) walnut (*Juglans mandshurica*) equation from China showed a better match with the 'other' equation than the *Carya* equation, supporting our concern.

The rest of the hardwood families were initially grouped together, but Hamamelidaceae, Magnoliaceae and Oleaceae families were separated based on sufficient pseudodata that tested different from the rest and from each other; and Oleaceae was further separated based on specific gravity. Although some of these separations did not result in large prediction differences

Table 5 Aboveground biomass equation parameters for 13 conifer, 18 hardwood and 4 woodland taxa estimated from meta-analyses of 675[1] published equations, where (with biomass in kg and diameter in cm) the biomass equation is: ln(biomass) $= \beta_0 + \beta_1\ ln$(diameter)

Group	Taxa	Median specific gravity	β_0	β_1	No. of pseudodata	No. of equations[1]	Diameter	Diameter range (cm)	R^2-statistic
Conifer	Abies < 0.35 spg*	0.33	-2.3123	2.3482	131	20	dbh	3–69	0.75
Conifer	Abies ≥ 0.35 spg	0.37	-3.1774	2.6426	221	14	dbh	3–236	0.75
Conifer	Cupressaceae < 0.30 spg	0.29	-1.9615	2.1063	48	6	dbh	3–66	0.76
Conifer	Cupressaceae 0.30–0.39 spg	0.34	-2.7765	2.4195	164	10	dbh	3–614	0.76
Conifer	Cupressaceae ≥ 0.40 spg	0.43	-2.6327	2.4757	55	6	dbh	3–109	0.76
Conifer	Larix	0.49	-2.3012	2.3853	84	11	dbh	3–98	0.85
Conifer	Picea < 0.35 spg	0.33	-3.0300	2.5567	128	8	dbh	3–283	0.81
Conifer	Picea ≥ 0.35 spg	0.37	-2.1364	2.3233	289	46	dbh	3–72	0.81
Conifer	Pinus < 0.45 spg	0.39	-2.6177	2.4638	561	70	dbh	3–180	0.83
Conifer	Pinus ≥ 0.45 spg	0.47	-3.0506	2.6465	162	28	dbh	3–56	0.83
Conifer	Pseudotsuga	0.45	-2.4623	2.4852	253	23	dbh	3–215	0.86
Conifer	Tsuga < 0.40 spg	0.38	-2.3480	2.3876	65	9	dbh	3–85	0.85
Conifer	Tsuga ≥ 0.40 spg	0.42	-2.9208	2.5697	163	14	dbh	3–172	0.85
Hardwood	Aceraceae < 0.50 spg	0.44	-2.0470	2.3852	243	43	dbh	3–66	0.84
Hardwood	Aceraceae ≥ 0.50 spg	0.56	-1.8011	2.3852	200	24	dbh	3–70	0.84
Hardwood	Betulaceae < 0.40 spg	0.37	-2.5932	2.5349	46	10	dbh	3–64	0.81
Hardwood	Betulaceae 0.40–0.49 spg	0.47	-2.2271	2.4513	145	29	dbh	3–51	0.81
Hardwood	Betulaceae 0.50–0.59 spg	0.55	-1.8096	2.3480	134	16	dbh	3–70	0.81
Hardwood	Betulaceae ≥ 0.60 spg	0.62	-2.2652	2.5349	55	11	dbh	3–47	0.81
Hardwood	Cornaceae/Ericaceae/ Lauraceae/Platanaceae/ Rosaceae/Ulmaceae	0.47	-2.2118	2.4133	231	46	dbh	3–64	0.79
Hardwood	Fabaceae/Juglandaceae, Carya	0.62	-2.5095	2.6175	106	13	dbh	3–70	0.81
Hardwood	Fabaceae/Juglandaceae, other	0.66	-2.5095	2.5437	14	2	dbh	4–42	0.81
Hardwood	Fagaceae, deciduous	0.57	-2.0705	2.4410	606	77	dbh	3–89	0.84
Hardwood	Fagaceae, evergreen	0.58	-2.2198	2.4410	54	7	dbh	3–66	0.84
Hardwood	Hamamelidaceae	0.46	-2.6390	2.5466	44	6	dbh	3–53	0.79
Hardwood	Hippocastanaceae/ Tiliaceae	0.32	-2.4108	2.4177	77	11	dbh	3–56	0.83
Hardwood	Magnoliaceae	0.40	-2.5497	2.5011	114	15	dbh	3–65	0.83
Hardwood	Oleaceae < 0.55 spg	0.51	-2.0314	2.3524	54	9	dbh	3–43	0.84
Hardwood	Oleaceae ≥ 0.55 spg	0.55	-1.8384	2.3524	49	7	dbh	3–55	0.84
Hardwood	Salicaceae < 0.35 spg	0.31	-2.6863	2.4561	64	10	dbh	3–53	0.81
Hardwood	Salicaceae ≥ 0.35 spg	0.36	-2.4441	2.4561	299	52	dbh	3–70	0.81
Woodland	Cupressaceae[2]	0.50	-2.7096	2.1942	57	6	drc	4–87	0.91
Woodland	Fabaceae/Rosaceae	0.80	-2.9255	2.4109	41	7	drc	3–60	0.89
Woodland	Fagaceae	0.59	-3.0304	2.4982	36	5	drc	3–74	0.84
Woodland	Pinaceae	0.51	-3.2007	2.5339	45	5	drc	3–75	0.86

*Where spg is specific gravity of wood of on green volume to dry-weight basis.
[1]Table totals 676 equations because blue oak equation was used for both woodland and hardwood.
[2]As discussed in the text, woodland Cupressaceae (mostly juniper) equations seemed to predict low, possibly due to influence from early juniper diameter measurements. Another juniper equation fitted by adding pseudodata generated from unpublished studies (where drc was measured by current FIA definition) to those already utilized predicted 10–36% higher, depending on diameter [ln(biomass) $= -2.7190 + 2.2598\ ln$(drc)]. The corresponding author (D.C.C.) welcomes inquiries for further information.

among the resulting equations, they reduced lack-of-fit patterns apparent in residual graphs when modeled separately. This left the six remaining families – Cornaceae, Ericaceae, Lauraceae, Platanaceae, Rosaceae and Ulmaceae – as a mixed hardwood group covering specific gravity from ~0.45 to 0.65. US hardwood families (excluding nonnative species) not included in our study (Aquifoliaceae, Ebenaceae, Lauraceae, Moraceae, Styracaceae and Theaceae) can probably be included in the mixed hardwood group or
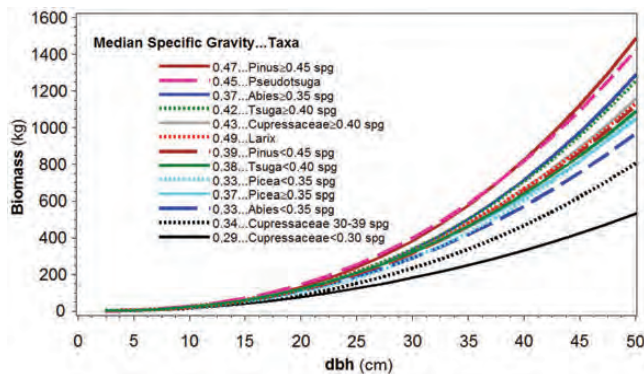
Figure 2 Conifer aboveground biomass predicted from 13 taxa-scale equations that include all conifer genera in the US except those in the Taxaceae family (which can be approximated by *Pseudotsuga*). Some taxa are split according to specific gravity of wood (spg). Median specific gravity is also calculated for respective taxa. Legend lists taxa in order of curves at 50-cm dbh. Model is $\ln(\text{biomass}) = \beta_0 + \beta_1 \ln(\text{dbh})$.
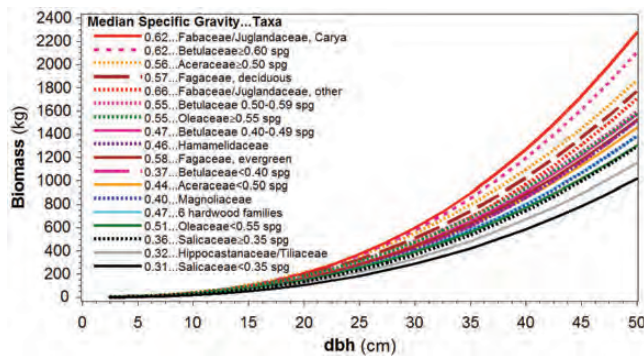

Figure 3 Hardwood aboveground biomass predicted from 18 taxa-scale equations that encompass almost all US hardwood families. Some taxa are split according to specific gravity of wood (spg). The '6 hardwood families' (mixed hardwoods) include Cornaceae, Ericaceae, Lauraceae, Platanaceae, Rosaceae, and Ulmacea with specific gravity from ∼0.45 to 0.65. (This equation could also be used for families not included in our study: Aquifoliaceae, Ebenaceae, Lauraceae, Moraceae, Styracaceae, and Theaceae.) Median specific gravity is also calculated for respective taxa. Legend lists taxa in order of curves at 50-cm dbh. Model is $\ln(\text{biomass}) = \beta_0 + \beta_1 \ln(\text{dbh})$.

with a more appropriate family if the specific gravity of the species in question is very high or very low.

For a given dbh, the resulting hardwood prediction equations generally estimated greater biomass for those taxa with higher specific gravity and lower biomass for those with lower specific gravity, but again this trend was less apparent for taxa that have midrange specific gravity values (Figure 3).

Woodland species

Biomass studies for woodland species were so limited that we grouped them as families and modeled them without further separation, except that we grouped Fabaceae and Rosaceae together
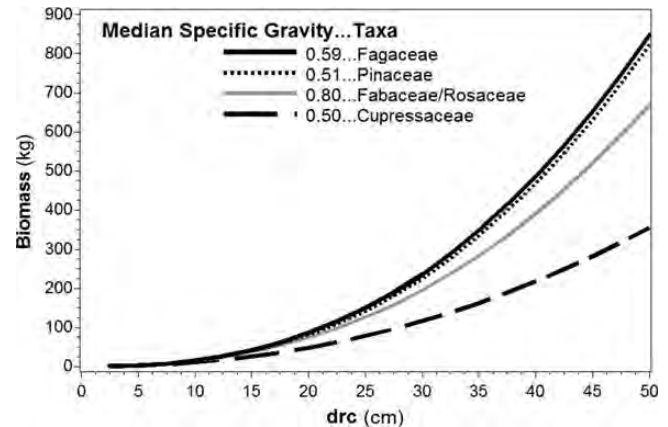
Figure 4 Woodland aboveground biomass predicted from four taxa-scale equations that include all woodland families in the US except Aceraceae, Boraginaceae, Ericaceae and Rhamnaceae (for which we suggest using the appropriate hardwood equation and diameter conversion). Median specific gravity (spg) is also calculated for respective taxa. Legend lists taxa in order of curves at 50-cm drc. Model is $\ln(\text{biomass}) = \beta_0 + \beta_1 \ln(\text{drc})$.

because of small sample sizes and similar specific gravity (Table 5). Although pseudodata for these two families did show wide variation, we chose to average the variation in a robust regression rather than use the otherwise minimal pseudodata to model the two extremes. The four woodland prediction equations (Figure 4) did not show a logical specific gravity trend and the equation for Cupressaceae (mostly juniper) seemed to predict low. Further examination of these old studies used to generate pseudodata raised concern that their juniper drc definitions may have led to larger drc measurements (and thus smaller biomass estimates) than those for other woodland species; FIA developed a drc definition beginning in the 1980s designed to address this issue. Overall the woodland biomass equations – particularly juniper – probably best show the need for new, carefully measured data.

Goodness of fit

Goodness-of-fit for the biomass equations showed R^2-statistics (see SAS, 2011 on Proc Robust for calculation details) between 0.75 and 0.91 (Table 5). Another graphical goodness-of-fit assessment was conducted by examining regression residuals for each taxon that were computed using robust regression weights and averaged within 10-cm diameter classes. Results showed residuals to be within ±10 per cent of predicted value for many conifers; exceptions within ±20 per cent included *Abies*, *Larix*, *Picea* and Cupressaceae taxa. For large-diameter predictions for *Pinus*, *Pseudotsuga* and *Tsuga* larger variations up to ±25–40 per cent were observed; most of these were positive residuals – indicating underprediction. Mean residuals for hardwood taxa showed variation within ±10–20 per cent of predicted values – and for some taxa all within ±10 per cent. Except for Pinaceae (within ±10 per cent), woodland residuals had much larger ranges, with ±30, ±40 and even ±70 per cent for Cupressaceae, Fagaceae and Fabaceae/Rosaceae, respectively. The Fabaceae/Rosaceae extreme was probably due to combining diverse families, as well as the very limited pseudodata.

Belowground biomass

Belowground biomass was modeled as the ratio of root component biomass to total aboveground biomass; fine and coarse roots were treated separately. The breakpoint between coarse and fine roots in published equations ranged from 2 to 10 mm diameter, with 5 or 10 mm most common. There were not enough species represented in our pseudodata to consider taxa separation for roots, and even hardwood and conifer separation was statistically nonsignificant. Therefore, one equation each for fine and coarse roots was fit from pseudodata by using robust regression (Table 6). Even though equations are presented, predictions are basically root-to-aboveground biomass ratios of 22 and 1 per cent for respective coarse and fine roots. Root equations can be used for woodland species by first converting drc to dbh (Figure 1).

Discussion

Our results provide a framework for selecting an aboveground biomass equation for every conifer, hardwood and woodland tree species in the US (except palm, citrus, dry tropical and other nonnative species) according to a taxa classification. The taxa framework was based in part on allometric scaling theory, where tree species with the densest wood (greatest specific gravity) were predicted to have more biomass for a given diameter, and species with the least dense wood predicted to have less biomass.

The biomass estimates for all US trees species compiled by the FIA program are the only ones available for comparison with predictions from these equations. FIA generates biomass estimates with a biomass expansion factor approach called the component ratio method (CRM) (Woodall *et al.*, 2011; Heath *et al.*, 2009); cubic volume estimates are converted to biomass through use of constant wood and bark specific gravity values and auxiliary information for branches, bark and stumps (Miles and Smith, 2009), and any other biomass added to the biomass of the merchantable stem is based on Jenkins *et al.* (2003) methods.

We used FIA (2010) plot data with our taxa-scale equations, as well as the Jenkins *et al.* (2003) equations, and compared results with FIA biomass estimates for the same trees. This was done by selecting from the FIA database only live noncull trees >2.5 cm (by using FIA coding statuscd = 1, treeclcd = 2 for diahtcd = 1 and treeclcd = (2 or 3) for diahtcd = 2; as described in Woudenberg *et al.* (2010)). About 2.3 million trees were selected from 119 000 plots. We summed biomass within the conditions established in FIA plots by using appropriate weights [see variables micrprop_unadj, subpprop_unadj, and macrprop_unadj in Woudenberg *et al.* (2010)]. Per-hectare plot estimates were then averaged by FIA forest type group (Woudenberg *et al.*, 2010, Appendix D). Several groups were combined due either to small sample size or similar per-hectare biomass values and nonstocked plots were excluded.

Comparison of all forest types (for trees measured at dbh) combined into conifer and hardwood groups (based on first species of type name) showed no difference between Jenkins *et al.* (2003) and our taxa-scale equations – both equations predicted 93 and 64 Mg ha^{-1} for conifers and hardwoods, respectively. This was not surprising because use of much of the same data and same modeling methodology should result in common results when summed over species. However, the species separation into

groups that was the main difference between the Jenkins *et al.* (2003) equations and those from this study produced marked differences among individual forest type groups for the two sets of equations, as discussed below. The FIA biomass estimates were ~20 per cent less than those from the Jenkins *et al.* (2003) and our new equations, at 78 and 53 Mg ha^{-1} for conifers and hardwoods, respectively (see Chojnacky (2012) for more details of comparison of new equations to FIA estimates).

Equations from this study and Jenkins *et al.* (2003) equations predicted 27 and 9 Mg ha^{-1}, respectively, for all woodland combined (trees measured at drc; FIA forest types pinyon/juniper and woodland hardwoods). This difference was attributed to addition of much more pseudodata for the new equations and a change in methodology – the Jenkins *et al.* (2003) equations were modeled at dbh based on a drc-to-dbh conversion that was probably not the best fit for the intended use. Because the FIA woodland estimates were based in part on the Jenkins *et al.* (2003) equations, they also estimated much lower biomass (15 Mg ha^{-1}) than the new equations (27 Mg ha^{-1}). In general, we suggest new woodland biomass data be collected to resolve estimation discrepancies but in the interim recommend our new equations based on the most thorough meta-analysis of published data to date.

For a more detailed examination of the conifer and hardwood equation comparisons to the FIA data, we looked at estimates at the forest type group scale. The pattern for conifer types showed equation differences from FIA ranging from −15 to ~80 per cent (Figure 5); the maximum difference for hardwood types was 38 per cent (Figure 6), the smaller differences likely resulting from the higher species diversity within hardwood forest types being averaged among equations. We expected FIA estimates to be lower because FIA excluded foliage, but the magnitude of the differences we found suggested more than just a foliage discrepancy between the equation sets. FIA's volume-to-biomass conversion may underestimate: Zhou *et al.* (2011) demonstrated for green ash (*Fraxinus pennsylvanica*), ponderosa pine (*P. ponderosa*) and eastern redcedar (*J. virginiana*) that volume-to-biomass conversion (using specific gravity similar to FIA's CRM method) consistently and significantly underestimates biomass from 6.3 to 16.6 per cent. Alternatively, use of pseudodata as in this study may not produce accurate biomass estimates. New biomass data are needed to uncover the reason(s) for these differences (Figures 5 and 6).

Conclusions and recommendations

Updating the Jenkins *et al.* (2004) database with more recent equations from the literature, conducting preliminary analyses and modifications for previously excluded literature equations (some of which addressed data gaps), and use of a theoretically based approach did, as anticipated, result in generalized biomass estimation equations for more species groupings. The previous (Jenkins *et al.*, 2003) approach produced 10 aboveground biomass equations. Our current work generated 35 biomass equations: 13 for conifers, 18 for hardwoods and 4 for woodland species.

There was little total difference between estimates from the equations in Jenkins *et al.* (2003) and those from the equations in this study for forest types combined into conifer and hardwood groups, which reflects different species groupings of much of the same data. However, there are some individual type differences, especially in the coniferous forest type groups of western pines

Table 6 Belowground biomass equation parameters for coarse and fine roots estimated from 82 published equations, where (with dbh in cm and the ratio defined as component biomass divided by total biomass), the biomass equation is: $ln(\text{ratio}) = \beta_0 + \beta_1 \, ln(\text{dbh})$

Component	β_0	β_1	R^2-statistic	Genus	No. of pseudodata	No. of equations	dbh range (cm)	Literature reference no. (see Table 1)
Coarse roots	−1.4485	−0.03476	0.0155[1]	Pinus	135	18	3–68	2,5,40,76,78,90,100,109,125,126, 130,132,136,138,145,160,195,204
				Acer	73	5	3–66	124,132,184,199,204
				Betula	73	6	3–66	9,124,184,190,199,204
				Pseudotsuga	68	3	3–163	59,69,181
				Picea	54	9	3–66	9,43,72,96,132,138,149,199,204
				Abies	43	7	3–51	9,82,96,105,190,202,204
				Fagus	37	3	3–66	184,199,204
				Quercus	35	3	4–89	99,126,154
				Hardwood	21	2	3–85	75,177
				Populus	21	2	3–51	138,204
				Thuja	19	2	3–51	54,204
				Larix	11	1	3–51	204
				Tsuga	11	1	3–51	204
				Prunus	9	1	3–23	204
				Conifer	5	1	3–22	177
				Salix	5	1	3–23	204
				Carya	4	1	22–33	169
				Alnus	3	1	3–8	204
				Cupressus	3	1	3–9	195
Fine roots	−1.8629	−0.77534	0.69	Pseudotsuga	37	1	3–161	28
				Pinus	10	1	3–41	28
				Hardwood	8	1	3–33	28
				Abies	6	1	3–28	105
				Picea	5	1	3–20	28
				Carya	4	1	22–33	169

[1]This low R^2-statistic indicates that the coarse root estimation is little more than a mean because the dbh term has very little effect. It is listed this way instead of as a mean to be consistent with other equations in the table and because this format is clearer for users such as computer programmers.
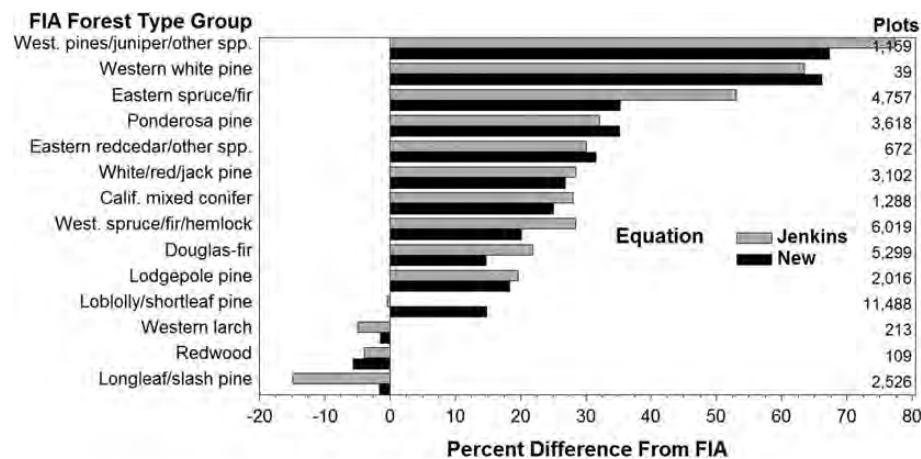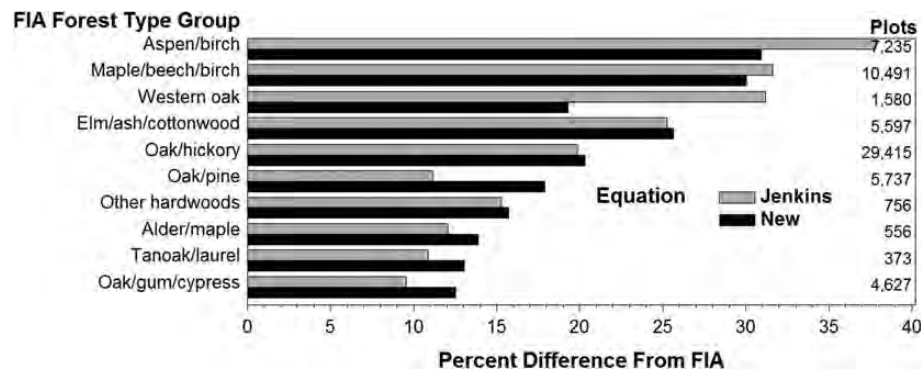
Figure 5 Percent difference from FIA (on plot basis) of conifer aboveground biomass estimates predicted from Jenkins *et al.* (2003) and this study's new taxa-scale equations. Percent difference from FIA = 100 × ([equation estimate − FIA estimate]/FIA estimate), where FIA plot estimates were first averaged within FIA forest type group.

Figure 6 Percent difference from FIA (on plot basis) of hardwood aboveground biomass estimates predicted from Jenkins *et al.* (2003) and this study's new taxa-scale equations. Percent difference from FIA = 100 × ([equation estimate − FIA estimate]/FIA estimate), where FIA plot estimates were first averaged within FIA forest type group.

(western pines/juniper/other spp.), spruce/fir (eastern spruce/fir and western spruce/fir/hemlock), Douglas-fir, loblolly/shortleaf pine and longleaf/slash pine (Figure 5); and in the hardwood types of aspen/birch, western oak and oak/pine (Figure 6). Although we consider the equations generated through the use of specific gravity and taxonomy in this study to be more soundly based than the empirical pseudodata groupings in Jenkins *et al.* (2003), a user's purpose may affect their preference as to which to use. If the user is primarily interested in total forest carbon, for hardwoods and conifers either set of equations could be used. We recommend the new equations for more detailed studies looking at species differences, and for woodland species.

We used allometric scaling theory as a theoretical basis for deriving consistent aboveground and belowground biomass estimation models through a meta-analysis approach. This theory suggests a tantalizingly simple model that would require only dbh and some proxy for *mean specific gravity of entire tree* as input variables, a concept supported by the clear importance of specific gravity in the biomass-to-diameter relationships modeled in this study. However, even if future studies prove this simple model inadequate, more careful study of whole-tree and within-tree variation in specific gravity – for a variety of species, diverse growth forms and specific gravities – could be useful. Recent work in tropical forest biomass estimation supports the usefulness of specific gravity (Chave *et al.*, 2005; Slik *et al.*, 2010; Vieilledent *et al.*, 2012).

Although this and our previous study make extensive use of existing data from independent studies, they are envisioned as an interim solution. The first study and this update, coming a decade later, together highlight the still-evident need in the US for generalized biomass estimation based on new data collection. We strongly recommend new data be collected across the US – particularly for woodland species – but using strategic, well-designed, theoretically based methods with agreed-upon protocols for data comparability. Such studies will better use scarce resources than more species-specific biomass studies based on data from small geographic areas, and could also provide data to definitively explain the differences between various approaches and determine which equations produce better estimates.

Acknowledgments

Conflict of interest statement

None declared.

Funding

References

(excluding literature cited in Jenkins *et al*. (2003) as indicated in Table 1).

Adegbidi, H.G., Jokela, E.J., Comerford, N.B. and Barros, N.F. 2002 Biomass development for intensively managed loblolly pine plantations growing on Spodosols in the southeastern USA. *For. Ecol. Manage.* **167**, 91–102.

Alban, D.H. and Laidly, P.R. 1982 Generalized biomass equations for jack and red pine in the Lake States. *Can. J. For. Res.* **12**, 913–921.

Alemdag, I.S. 1981 Aboveground-mass Equations for Six Hardwood Species from Natural Stands of the Research Forest at Petawawa. Information Report No. PI-X-6, Petawawa National Forestry Institute, 9 pp.

Alemdag, I.S. 1982 Aboveground dry matter of jack pine, black spruce, white spruce and balsam fir trees at two localities in Ontario. *For. Chron.* **58**, 26–30.

Alemdag, I.S. 1983 Mass Equations and Merchantability Factors for Ontario Softwoods. Information Report No. PI-X-23, Petawawa National Forestry Institute, 24 pp.

Alemdag, I.S. and Horton, K.W. 1981 Single-tree equations for estimating biomass of trembling aspen, large tooth aspen and white birch in Ontario. *For. Chron.* **57**, 169–173.

Arevalo, C.B.M., Volk, T.A., Bevilacqua, E. and Abrahamson, L. 2007 Development and validation of aboveground biomass estimations for four *Salix* clones in central New York. *Biomass Bioenergy.* **31**, 1–12.

Aspinwall, M.J., King, J.S., McKeand, S.E. and Bullock, B.P. 2011 Genetic effects on stand-level uniformity, and above- and belowground biomass production in juvenile loblolly pine. *For. Ecol. Manage.* **262**, 609–619.

Baldwin, V.C. 1987 A summary of equations for predicting biomass of planted southern pines. In *Estimating Tree Biomass Regressions and Their Error: Proceedings of the Workshop on Tree Biomass Regression Functions and Their Contribution to the Error of Forest Inventory Estimates, 1986 May 26–30, Syracuse, NY.* E.H. Wharton and T. Cunia (compilers). General Technical Report NE-117. US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, pp. 157–171.

Baskerville, G.L. 1966 Dry-matter production in immature balsam fir stands: roots lesser vegetation, and total stand. *For. Sci.* **12**, 49–53.

Baskerville, G.L. 1972 Use of the logarithmic regression in the estimation of plant biomass. *Can. J. For. Res.* **2**, 49–53.

Bella, I.E. and De Franceschi, J.P. 1980 Biomass Productivity of Young Aspen Stands in Western Canada. Information Report No. NOR-X-219. Northern Forest Research Centre, 30 pp.

Bickelhaupt, D.H., Leaf, A.L. and Richards, N.R. 1973 Effect of branching habit on above-ground dry weight estimates of *Acer saccharum* stands. In *IUFRO Biomass Studies, Nancy, France and Vancouver, BC*. H. Young (ed.). University of Maine, College of Life Sciences and Agriculture, pp. 221–230.

Binkley, D., Lousier, J.D. and Cromack, K. Jr. 1984 Ecosystem effects of Sitka alder in a Douglas-fir plantation. *For. Sci.* **30**, 26–35.

Bond-Lamberty, B., Wang, C. and Gower, S.T. 2002 Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. *Can. J. For. Res.* **32**, 1441–1450.

Bragg, D.C. 2001 A local basal area adjustment for crown width prediction. *North. J. Appl. Forest.* **18**, 22–28.

Brenneman, B.B., Frederick, D.J., Gardner, W.E., Schoenhofen, L.H. and Marsh, P.L. 1978 Biomass of species and stands of West Virginia hardwoods. In *Proceedings of Central Hardwood Forest Conference II*. P.E. Pope (ed.). Purdue University, pp. 159–178.

Bridge, J.A. 1979 *Fuelwood Production of Mixed Hardwoods on Mesic Sites in Rhode Island*. M.S. thesis, University of Rhode Island, 72 pp.

Brown, J.K. 1978 Weight and Density of Crowns of Rocky Mountain Conifers. Research Paper INT-197. US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, 56 pp.

Callaway, R.M., DeLucia, E.H. and Schlesinger, W.H. 1994 Biomass allocation of montane and desert ponderosa pine: an analog for response to climate change. *Ecology.* **75**, 1474–1481.

Callaway, R.M., Sala, A. and Keane, R.E. 2000 Succession may maintain high leaf area: sapwood ratios and productivity in old subalpine forests. *Ecosystems.* **3**, 254–268.

Carpenter, E.M. 1983 Above-Ground Weights for Tamarack in Northeastern Minnesota. Research Paper NC-245. US Department of Agriculture, Forest Service, North Central Forest Experiment Station, 9 pp.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q. and Eamus, D. *et al.* 2005 Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia.* **145**, 87–99.

Chen, W., Zhang, Q., Cihlar, J., Bauhaus, J. and Price, D.T. 2004 Estimating fine-root biomass and production of boreal and cool temperate forests using aboveground measurements: a new approach. *Plant Soil.* **265**, 31–46.

Chojnacky, D.C. 1984 Volume and Biomass for Curlleaf *Cercocarpus* in Nevada. Research Paper INT-332. US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, 8 pp.

Chojnacky, D.C. 1985 Pinyon-Juniper Volume Equations for the Central Rocky Mountain States. Research Paper INT-339. US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, 27 pp.

Chojnacky, D.C. 1987 Estimating singleleaf pinyon and Utah juniper volumes for several utilization standards. *West. J. Appl. For.* **2**, 51–55.

Chojnacky, D.C. 2002 Allometric scaling theory applied to FIA biomass estimation. In *Proceedings of Third Annual Forest Inventory and Analysis Symposium, 2001 October 17–19, Traverse City, MI*. R.E. McRoberts, G.A. Reams, P.C. Van Deusen and J.W. Moser (eds.). General Technical Report NC-230. US Department of Agriculture, Forest Service, North Central Forest Experiment Station, pp. 96–102.

Chojnacky, D.C. 2012 FIA's volume-to-biomass conversion method (CRM) generally underestimates biomass in comparison to published equations. In *Moving from Status to Trends: Forest Inventory and Analysis (FIA) Symposium 2012*. R.S. Morin and G. C. Liknes (eds.). GTR-NRS-P-105. US Department of Agriculture, Forest Service, Northern Research Station, pp. 396–402.

Chojnacky, D.C. and Moisen, G.G. 1993 Converting Volume to Biomass for Pinyon and Juniper. Research Note INT-411. US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, 5 pp.

Clark, A. III. 1987 Summary of biomass equations available for softwood and hardwood species in the southern United States. In *Estimating Tree Biomass Regressions and Their Error: Proceedings of the Workshop on Tree Biomass Regression Functions and Their Contribution to the Error of Forest Inventory Estimates, 1986 May 26–30, Syracuse, NY*. E.H. Wharton and T. Cunia (compilers). General Technical Report NE-117. US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, pp. 173–188.

Clark, A. III. and Schroeder, J.G. 1986 Weight, Volume, and Physical Properties of Major Hardwood Species in the Southern Appalachian Mountains. Research Paper SE-153. US Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, 78 pp.

Clark, A. III. and Taras, M.A. 1976 Comparison of aboveground biomasses of the four major southern pines. *For. Prod. J.* **26**, 25–29.

Clark, A. III., Phillips, D.R. and Frederick, D.J. 1986a Weight, Volume, and Physical Properties of Major Hardwood Species in the Piedmont. Research Paper SE-255. US Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, 84 pp.

Clary, W.P. and Tiedemann, A.R. 1986 Distribution of biomass within small tree and shrub form *Quercus gambelii* stands. *For. Sci.* **32**, 234–242.

Clebsch, E. 1971 Dry weight of trees and saplings from the Great Smoky Mountains National Park and eastern Tennessee. In *Dry Weight and Other Data for Trees and Woody Shrubs of Southeastern United States*. P. Sollins and R. Anderson (eds.). Ecol. Sci. Div. Publ. 407. Oak Ridge National Laboratory, pp. 15–21.

Cochran, P., Jennings, J. and Youngberg, C. 1984 Biomass Estimators for Thinned Second-Growth Ponderosa Pine Trees. Research Note PNW-RN-415. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, 6 pp.

Coltrin, W.R. 2010 *Biomass Quantification of Live Trees in a Mixed Evergreen Forest Using Diameter-Based Allometric Equations*. M.S. thesis, Humboldt State University, 52 pp.

Crow, T. 1971 Estimation of Biomass in an Even Aged Stand – Regression and 'Mean tree' Techniques. Forest Biomass Studies. Misc. Report 132. Maine Agricultural Experiment Station, pp. 35–48.

Czapowskyj, M.M., Robison, D.J., Briggs, R.D. and White, E.H. 1985 Component Biomass Equations for Black Spruce in Maine. Research Paper NE-564. US Department of Agriculture, Forest Service, Northeastern Research Station, 7 pp.

Davis, A.A. and Trettin, C.C. 2006 Sycamore and sweetgum plantation productivity on former agricultural land in South Carolina. *Biomass Bioenergy*. **30**, 769–777.

Dunlap, W.H. and Shipman, R.D. 1967 Density and Weight Production of Standing White Oak, Red Maple, and Red Pine. Report on Research Project No. 1524. Pennsylvania State University, School of Forest Resources, pp. 66–69.

Duursma, R.A., Marshall, J.D., Robinson, A.P. and Pangle, R.E. 2007 Description and test of a simple process-based model of forest growth for mixed-species stands. *Ecol. Model.* **203**, 297–311.

El Fadl, M.A., Gronski, S., Asah, H., Tipton, A., Fulbright, T.E. and Felker, P. 1989 Regression equations to predict fresh weight and three grades of lumber from large mesquite (*Prosopis glandulosa* var. *glandulosa*) in Texas. *For. Ecol. Manage.* **26**, 275–284.

Elliott, K.J., Boring, L.R. and Swank, W.T. 2002 Aboveground biomass and nutrient accumulation 20 years after clear-cutting a southern Appalachian watershed. *Can. J. For. Res.* **32**, 667–683.

Enquist, B.J., Brown, J.H. and West, G.B. 1998 Allometric scaling of plant energetics and population density. *Nature*. **395**, 163–166.

Enquist, B.J., West, G.B., Charnov, E.L. and Brown, J.H. 1999 Allometric scaling of production and life history variation in vascular plants. *Nature*. **401**, 907–911.

Enquist, B.J., West, G.B. and Brown, J.H. 2009 Extensions and evaluations of a general quantitative theory of forest structure and dynamics. *Proc. Natl. Acad. Sci. USA*. **106**, 7046–7051.

[EPA] Environmental Protection Agency. 2012 *Inventory of U.S. Greenhouse Gas Emissions and Sinks: 1990–2010*. L. Hockstad and B. Cook (compilers). EPA 430-R-12-001. US Environmental Protection Agency, 481 pp.

Espinosa-Bancalari, M.A. and Perry, D.A. 1987 Distribution and increment of biomass in adjacent young Douglas-fir stands with different early growth rates. *Can. J. For. Res.* **17**, 722–730.

Evert, F. 1983 A National System of Equations for Estimating Ovendry Mass of Trembling Aspen *Populus tremuloides* Michx. Information Report No. PI-X-24. Petawawa National Forestry Institute, 23 pp.

Fassnacht, K. 1996 *Characterization of the Structure and Function of Upland Forest Ecosystems in North Central Wisconsin*. Ph.D. dissertation, University of Wisconsin, 370 pp.

Fatemi, F.R., Yanai, R.D., Hamburg, S.P., Vadeboncoeur, M.A., Arthur, M.A. and Briggs, R.D. *et al*. 2011 Allometric equations for young northern hardwoods: the importance of age-specific equations for estimating aboveground biomass. *Can. J. For. Res.* **41**, 881–891.

Felker, P., Meyer, J.M. and Gronski, S.J. 1990 Application of self-thinning in mesquite (*Prosopis glandulosa* var. *glandulosa*) to range management and lumber production. *For. Ecol. Manage.* **31**, 225–232.

Flewelling, J.W. and Pienaar, L.V. 1981 Multiplicative regression with lognormal errors. *For. Sci.* **27**, 281–289.

[FIA] Forest Inventory and Analysis. 2010 *FIA Data Mart: Download Files, FIADB4.0*. US Department of Agriculture, Forest Service, FIA Program. Accessed online at http://199.128.173.17/fiadb4-downloads/datamart. html/; last accessed November 2010. [No longer available; current version FIADB5.1 is available online at http://apps.fs.fed.us/fiadb-downloads/ datamart.html/; last accessed April 6, 2012].

Fortier, J., Gagnon, D., Truax, B. and Lambert, F. 2010 Biomass and volume yield after 6 years in multiclonal hybrid poplar riparian buffer strips. *Biomass Bioenergy*. **34**, 1028–1040.

Fujimori, T., Kawanabe, S., Saito, H., Grier, C.C. and Shidei, T. 1976 Biomass and primary production in forests of three major vegetation zones in northwestern United States. *J. Jpn. For. Soc.* **58**, 360–373.

Gary, H.L. 1976 Crown Structure and Distribution of Biomass in a Lodgepole Pine Stand. Research Paper RM-165. US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 20 pp.

Gholz, H.L., Vogel, S.A., Cropper, W.P., McKelvey, K. and Ewel, K.C. 1991 Dynamics of canopy structure and light interception in *Pinus elliotii* stands, north Florida. *Ecol. Monogr.* **6**, 33–51.

Gilmore, D.W. and Zenner, E.K. 2005 Foliage–sapwood area relationships for balsam fir in north-central Minnesota. *North. J. Appl. Forest.* **22**, 203–210.

Goldsmith, L.J. and Hocker, H.W. 1978 Preliminary Small-Tree Aboveground Biomass Tables for Five Northern Hardwoods. Res. Report No. 68. University of New Hampshire, Agricultural Experiment Station.

Gower, S.T., Haynes, B.E., Fassnacht, K.S., Running, S.W. and Hunt, E.R. 1993a Influence of fertilization on the allometric relations for two pines in contrasting environments. *Can. J. For. Res.* **23**, 1704–1711.

Gower, S.T., Reich, P.B. and Son, Y. 1993b Canopy dynamics and aboveground production of five tree species with different leaf longevities. *Tree Physiol.* **12**, 327–345.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J. and Stow, T.K. 1997 Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. *J. Geophys. Res.* **102**, 29029–29041.

Goyal, G.C., Fisher, J.J., Krohn, M.J., Packood, R.E. and Olson, J.R. 1999 Variability in pulping and fiber characteristics of hybrid poplar trees due to

their genetic makeup, environmental factors, and tree age. *TAPPI J.* **82**, 141–147.

Grier, C.C. and Logan, R.S. 1977 Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecol. Monogr.* **47**, 373–400.

Hamilton, J.R. and Wendel, G.W. 1967 Specific Gravity and Fiber Length of Some Hybrid Poplars Growing in West Virginia. Bulletin 556T. West Virginia University, Agricultural Experiment Station, 6 pp.

Harrington, T.B., Tappeiner, J.C. and Walstad, J.D. 1984 Predicting leaf area and biomass of 1- to 6-year-old tanoak (*Lithocarpus densiflorus*) and Pacific madrone (*Arbutus menziesii*) sprout clumps in southwestern Oregon. *Can. J. For. Res.* **14**, 209–213.

Harris, W.F., Goldstein, R.A. and Henderson, G.S. 1973 Analysis of forest biomass pools, annual primary production and turnover of biomass for a mixed deciduous forest watershed. In *IUFRO Biomass Studies, Nancy, France and Vancouver, BC*. H. Young (ed.). University of Maine, College of Life Sciences and Agriculture, pp. 41–64.

Harris, W.F., Kinerson, R.S. and Edwards, N.T. 1977 Comparison of belowground biomass of natural deciduous forest and loblolly pine plantations. *Pedobiologia.* **17**, 369–381.

Harrison, R.B., Terry, T.A., Licata, C.W., Flaming, B.L., Meade, R. and Guerrini, I.A. *et al.* 2009 Biomass and stand characteristics of a highly productive mixed Douglas-fir and western hemlock plantation in coastal Washington. *West. J. Appl. Forest.* **24**, 180–186.

Haynes, B.E. and Gower, S.T. 1995 Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. *Tree Physiol.* **15**, 317–325.

Heath, L.S., Hansen, M.H., Smith, J.E., Miles, P.D. and Smith, B.W. 2009 Investigation into calculating tree biomass and carbon in the FIADB using a biomass expansion factor approach. In *Forest Inventory and Analysis (FIA) Symposium 2008*. W. McWilliams, G. Moisen and R. Czaplewski (compilers). Proceedings RMRS-P-56CD. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, 26 pp. [1 CD].

Heath, L.S., Smith, J.E., Skog, K.E., Nowak, D.J. and Woodall, C.W. 2011 Managed forest carbon estimates for the US greenhouse gas inventory, 1990–2008. *J. For.* **109**, 167–173.

Hu, H. and Wang, G.G. 2008 Changes in forest biomass carbon storage in the South Carolina Piedmont between 1936 and 2005. *For. Ecol. Manage.* **255**, 1400–1408.

Ishii, H. and Kadotani, T. 2006 Biomass and dynamics of attached dead branches in the canopy of 450-year-old Douglas-fir trees. *Can. J. For. Res.* **36**, 378–389.

Jacobs, D.F., Selig, M.F. and Severeid, L.R. 2009 Aboveground carbon biomass of plantation-grown American chestnut (*Castanea dentata*) in absence of blight. *For. Ecol. Manage.* **258**, 288–294.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S. and Birdsey, R.A. 2003 National-scale biomass estimation for United States tree species. *For. Sci.* **49**, 12–35.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S. and Birdsey, R.A. 2004 A Comprehensive Database of Diameter-Based Biomass Regressions for North American Tree Species. General Technical Report NE-319. US Department of Agriculture, Forest Service, Northeastern Research Station, 45 pp. [1 CD-ROM].

Johnson, B.A. 2009 *Acidic Deposition Effects on Above- and Belowground Wood Biomass and Nutrient Status in a Young Hardwood Forest*. M.S. thesis, West Virginia University, p. 126.

Johnston, R.S. and Bartos, D.L. 1977 Summary of Nutrient and Biomass Data from Two Aspen Sites in Western United States. Research Paper INT-227. US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, 15 pp.

Johnstone, W.D. and Peterson, E.B. 1980 Above-ground Component Weights in Alberta *Populus* Stands. Information Report No. NOR-X-226. Northern Forest Research Centre, 18 pp.

Jokela, E.J. and Martin, T.A. 2000 Effects of ontogeny and soil nutrient supply on production, allocation, and leaf area efficiency in loblolly and slash pine stands. *Can. J. For. Res.* **30**, 1511–1524.

Kapeluck, P.R. and Van Lear, D.H. 1995 A technique for estimating below-stump biomass of mature loblolly pine plantations. *Can. J. For. Res.* **25**, 355–360.

Karlik, J.F. and Chojnacky, D.C. unpublished. Biomass and carbon data from blue oaks in a California oak savanna. Draft document available from D.C. Chojnacky, Virginia Tech, 144 Rees Place, Falls Church, VA 22046, USA, dchojnac@vt.edu. Accepted 2013 to Biomass and Bioenergy.

Karlik, J.F. and McKay, A.H. 2002 Leaf area index, leaf mass density, and allometric relationships derived from harvest of blue oaks in a California oak savanna. In *Oaks in California's Changing Landscape: Proceedings of the Fifth Symposium on Oak Woodlands*. R.B. Standiford, D. McCreary and K.L. Purcell (technical coordinators). General Technical Report PSW-GTR-184. US Department of Agriculture, Forest Service, Pacific Southwest Research Station, pp. 719–729.

Kaye, J.P., Hart, S.C., Fule, P.Z., Covington, W.W., Moore, M.M. and Kaye, M.W. 2005 Initial carbon, nitrogen, and phosphorus fluxes following ponderosa pine restoration treatments. *Ecol. Appl.* **15**, 1581–1593.

Ker, M.F. 1984 Biomass Equations for Seven Major Maritimes Tree Species. Information Report No. M-X-148. Maritime Forest Research Center, 54 pp.

Ker, M.F. and van Raalte, G.B. 1981 Tree biomass equations for *Abies balsamea* and *Picea glauca* in northwestern New Brunswick. *Can. J. For. Res.* **11**, 13–17.

Kimmins, J.P. 1973 Nutrient Removal Associated with Whole-Tree Logging on Two Different Sites in the Prince George Forest District. Unpublished Report submitted to British Columbia Forest Service Productivity Committee, 100 pp. [Equations also listed in Stanek and State (1978)].

King, W.W. and Schnell, R.L. 1972 Biomass Estimates of Black Oak Tree Components. Technical Note B1. Tennessee Valley Authority; Division of Forestry, Fisheries, and Wildlife Development; 24 pp.

King, J.S., Giardina, C.P., Pregitzer, K.S. and Friend, A.L. 2007 Biomass partitioning in red pine (*Pinus resinosa*) along a chronosequence in the Upper Peninsula of Michigan. *Can. J. For. Res.* **37**, 93–102.

Lambert, M.C., Ung, C.H. and Raulier, F. 2005 Canadian national tree aboveground biomass equations. *Can. J. For. Res.* **35**, 1996–2018.

Lavigne, M.B. 1982 Tree Mass Equations for Common Species of Newfoundland. Information Report No. N-X-213. Newfoundland Forest Research Centre, 40 pp.

Lavigne, M.B. and Krasowski, M.J. 2007 Estimating coarse root biomass of balsam fir. *Can. J. For. Res.* **37**, 991–998.

Lavigne, M.B. and Van Nostrand, R.S. 1981 Biomass Equations for Six Tree Species in Central Newfoundland. Information Report No. N-X-199, Newfoundland Forest Research Centre, 51 pp.

Laxson, J.D., Schacht, W.H. and Owens, M.K. 1997 Above-ground biomass yields at different densities of honey mesquite. *J. Range Manage.* **50**, 550–554.

Levia, D.F. 2008 A generalized allometric equation to predict foliar dry weight on the basis of trunk diameter for eastern white pine (*Pinus strobus* L.). *For. Ecol. Manage.* **255**, 1789–1792.

Lieurance, D.M. 2007 Biomass allocation of the invasive tree *Acacia auriculiformis* and refoliation following hurricane-force winds. *J. Torrey Bot. Soc.* **134**, 389–397.

Litton, C.M., Ryan, M.G., Tinker, D.B. and Knight, D.H. 2003 Belowground and aboveground biomass in young postfire lodgepole pine forests of contrasting tree density. *Can. J. For. Res.* **33**, 351–363.

Lojewski, N.R., Fischer, D.G., Bailey, J.K., Schweitzer, J.A., Whitham, T.G. and Hart, S.C. 2009 Genetic basis of aboveground productivity in two native *Populus* species and their hybrids. *Tree Physiol.* **29**, 1133–1142.

Long, J.N. and Turner, J. 1975 Aboveground biomass of understory and overstorey in an age sequence of four Douglas-fir stands. *J. Appl. Ecol.* **12**, 179–188.

Loomis, R.M., Phares, R.E. and Crosby, J.S. 1966 Estimating foliage and branchwood quantities in shortleaf pine. *For. Sci.* **12**, 30–39.

Mack, M.C., Treseder, K.K., Manies, K.L., Harden, J.W., Schuur, E.A.G. and Vogel, J.G. *et al.* 2008 Recovery of aboveground plant biomass and productivity after fire in mesic and dry black spruce forests of interior Alaska. *Ecosystems.* **11**, 209–225.

Martin, J.L., Gower, S.T., Plaut, J. and Holmes, B. 2005 Carbon pools in a boreal mixedwood logging chronosequence. *Global Change Biol.* **11**, 1883–1894.

McCain, C. 1994 Unpublished old-growth Douglas-fir foliage biomass equation. Oregon State University, Forest Science Department, Corvallis, OR. Foliage data described in Massman, W.J. 1982 Foliage distribution in old-growth coniferous tree canopies. *Can. J. For. Res.* **12**, 10–17.

McGinnis, T.W., Shook, C.D. and Keeley, J.E. 2010 Estimating aboveground biomass for broadleaf woody plants and young conifers in Sierra Nevada, California, forests. *West. J. Appl. Forest.* **25**, 203–209.

Means, J.E., Hansen, H.A., Koerper, G.J., Alaback, P.B. and Klopsch, M.W. 1994 Software for Computing Plant Biomass – BIOPAK Users Guide. General Technical Report PNW-GTR-340. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, 184 pp.

Miles, P.D. and Smith, W.B. 2009 Specific Gravity and Other Properties of Wood and Bark for 156 Tree Species Found in North America. Research Note NRS-38. US Department of Agriculture, Forest Service, Northern Research Station, 35 pp.

Miller, E.L., Meeuwig, R.O. and Budy, J.D. 1981 Biomass of Singleleaf Pinyon and Utah Juniper. Research Paper INT-273. US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, 18 pp.

Monk, C.D., Child, G.I. and Nicholson, S.A. 1970 Biomass, litter and leaf surface area estimates of an oak-hickory forest. *Oikos.* **21**, 138–141.

Naidu, S.L., DeLucia, E.H. and Thomas, R.B. 1998 Contrasting patterns of biomass allocation in dominant and suppressed loblolly pine. *Can. J. For. Res.* **28**, 1116–1124.

National Academy of Sciences. 1980 Firewood Crops: Shrub and Tree Species for Energy Production. Report of an ad hoc panel of the advisory committee on technology innovation. 237 pp.

Navar, J. 2009 Allometric equations for tree species and carbon stocks for forests of northwestern Mexico. *For. Ecol. Manage.* **257**, 427–434.

Nicholas, N.S. 1992 *Stand Structure, Growth, and Mortality in Southern Appalachian Spruce-Fir*. Ph.D. dissertation, Virginia Polytechnic and State University, 77 pp.

Norris, M.D., Blair, J.M., Johnson, L.C. and Mckane, R.B. 2001 Assessing changes in biomass, productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass prairie. *Can. J. For. Res.* **31**, 1940–1946.

Omdal, D.W., Jacobi, W.R. and Shaw, C.G. III. 2001 Estimating large-root biomass from breast–height diameters for ponderosa pine in northern New Mexico. *West. J. Appl. Forest.* **16**, 18–21.

Oswald, B.P., Botting, R.R., Coble, D.W. and Farrish, K.W. 2010 Aboveground biomass estimation for three common woody species in the post oak savannah of Texas. *South. J. Appl. Forest.* **34**, 91–94.

Ouellet, D. 1985 Biomass equations for six commercial tree species in Quebec. *For. Chron.* **61**, 215–222.

Ouimet, R., Camire, C., Brazeau, M. and Moore, J.D. 2008 Estimation of coarse root biomass and nutrient content for sugar maple, jack pine, and black spruce using stem diameter at breast height. *Can. J. For. Res.* **38**, 92–100.

Pastor, J., Aber, J.D. and Melillo, J.M. 1984 Biomass prediction using generalized allometric regressions for some northeast tree species. *For. Ecol. Manage.* **7**, 265–274.

Pearson, J.A., Fahey, T.J. and Knight, D.H. 1984 Biomass and leaf area in contrasting lodgepole pine forests. *Can. J. For. Res.* **14**, 259–265.

Peichl, M. and Arain, M.A. 2007 Allometry and partitioning of above- and belowground tree biomass in an age-sequence of white pine forests. *For. Ecol. Manage.* **253**, 68–80.

Perala, D.A. and Alban, D.H. 1994 Allometric Biomass Estimators for Aspen-Dominated Ecosystems in the Upper Great Lakes. Research Paper NC-314. US Department of Agriculture, Forest Service, North Central Forest Experiment Station, 38 pp.

Petersen, K.S., Ares, A., Terry, T.A. and Harrison, R.B. 2008 Vegetation competition effects on aboveground biomass and macronutrients, leaf area, and crown structure in 5-year old Douglas-fir. *New Forest.* **35**, 299–311.

Pike, L.H., Rydell, R.A. and Denison, W.C. 1977 A 400-year-old Douglas-fir tree and its epiphytes: biomass, surface area, and their distributions. *Can. J. For. Res.* **7**, 680–699.

Pitt, D.G. and Bell, F.W. 2004 Effects of stand tending on the estimation of aboveground biomass of planted juvenile white spruce. *Can. J. For. Res.* **34**, 649–658.

Ralston, C.W. and Prince, A.B. 1965 Accumulation of dry matter and nutrients by pine and hardwood forests in the lower Piedmont of North Carolina. In *Forest–Soil Relationships in North America*. Oregon State University Press, pp. 77–94.

Ramseur, G.S. and Kelly, J.M. 1981 Forest characterization and biomass estimates for two sites on the Cumberland Plateau. *J. Tenn. Acad. Sci.* **56**, 99–104.

Rauscher, M.H. 1984 Growth and Yield of White Spruce Plantations in the Lake States (a Literature Review). Research Paper NC-253. US Department of Agriculture, Forest Service, North Central Forest Experiment Station, 46 pp.

Reid, C.P.P., Odegard, P.J., Hokenstrom, J.C., McConel, W.J. and Frayer, W.E. 1974 Effects of Clearcutting on Nutrient Cycling in Lodgepole Pine Forests. Research Paper. Colorado State University, College of Forestry and Natural Resources, 321 pp.

Reiners, W.A. 1972 Structure and energetics of three Minnesota forests. *Ecol. Monogr.* **42**, 71–94.

Reynolds, P.E., Carlson, K.G., Fromm, T.W., Gigliello, K.A. and Kaminski, R.J. 1978 Phytosociology, biomass, productivity and nutrient budget for the tree stratum of a southern New Jersey hardwood swamp. In *Proceedings, Central hardwood forest conference II*. P. Pope (ed.). Purdue University, pp. 123–139.

Riemenschneider, D.E., Berguson, W.E., Dickmann, D.I., Hall, R.B., Isebrands, J.G. and Mohn, C.A. *et al.* 2001 Poplar breeding and testing strategies in the north-central U.S.: Demonstration of potential yield and consideration of future research needs. *For. Chron.* **77**, 245–253.

Rogerson, T.L. 1964 Estimating Foliage on Loblolly Pine. Research Note SO-16. US Department of Agriculture, Forest Service, Southern Forest Experiment Station, 3 pp.

Rolfe, G.L., Akhtar, A.M. and Arnold, L.E. 1978 Nutrient distribution and flux in a mature oak-hickory forest. *For. Sci.* **41**, 122–130.

Rowell, C.E. and Carpenter, S.B. 1983 Black locust biomass prediction on eastern Kentucky strip mines. *South. J. Appl. Forest.* **7**, 27–30.

Ruark, G.A. and Bockheim, J.C. 1987 Below-ground biomass of 10-, 20- and 32-year-old *Populus tremuloides* in Wisconsin. *Pedobiologia.* **30**, 207–217.

Ruark, G.A., Martin, G.L. and Bockheim, J.G. 1987 Comparison of constant and variable allometric ratios for estimating *Populus tremuloides* biomass. *For. Sci.* **33**, 294–300.

Rubilar, R.A., Allen, H.L. and Kelting, D.L. 2005 Comparison of biomass and nutrient content equations for successive rotations of loblolly pine plantations on an Upper Coastal Plain site. *Biomass Bioenergy*. **28**, 548–564.

Sabatia, O.S. 2007 *Effect of Thinning on Partitioning of Aboveground Biomass in Naturally Regenerated Shortleaf Pine (*Pinus echinata *mill.)*. M.S. thesis, Oklahoma State Uniersity, 84 pp.

Sachs, D. 1984 *Management Effects on Nitrogen Nutrition and Long-Term Productivity of Western Hemlock Stands*. M.S. Thesis, Oregon State University, 72 pp.

Samuelson, L.J., Johnsen, K. and Stokes, T. 2004 Production, allocation, and stemwood growth efficiency of *Pinus taeda* L. stands in response to 6 years of intensive management. *For. Ecol. Manage*. **192**, 59–70.

Santantonio, D., Hermann, R.K. and Overton, W.S. 1977 Root biomass studies in forest ecosystems. *Pedobiologia*. **17**, 1–31.

SAS Institute Inc. 2011 SAS/STAT® 9.3 User's Guide. Copyright © SAS Institute Inc. Cary, NC. SAS and all other SAS Institute Inc. product or service names are registered trademarks or trademarks of SAS Institute Inc.

Schaegel, B.E. 1975 Estimating Aspen Volume and Weight for Individual Trees, Diameter Classes or Entire Stands. General Technical Report NC-20. US Department of Agriculture, Forest Service, North Central Forest Experiment Station, 16 pp.

Schnell, R.L. 1976 Biomass Estimates of Eastern Redcedar Tree Components. Technical Note B15. Tennessee Valley Authority; Division of Forestry, Fisheries, and Wildlife Development, 15 pp.

Schnell, R.L. 1978 Biomass Estimates of Hickory Tree Components. Technical Note B30. Tennessee Valley Authority; Division of Forestry, Fisheries, and Wildlife Development, 39 pp.

Seiler, T.J., Rasse, D.P., Li, J.H., Dijkstra, P., Anderson, H.P. and Johnson, D.P. *et al*. 2009 Disturbance, rainfall and contrasting species responses mediated aboveground biomass response to 11 years of CO_2 enrichment in a Florida scrub-oak ecosystem. *Glob. Change Biol*. **15**, 356–367.

Shenoy, A., Johnstone, J.F., Kasischkea, E.S. and Kiellanda, K. 2011 Persistent effects of fire severity on early successional forests in interior Alaska. *For. Ecol. Manage*. **261**, 381–390.

Singh, T. 1982 Biomass Equations for Ten Major Tree Species in the Prairie Provinces. Information Report No. NOR-X-242. Northern Forest Research Centre, 35 pp.

Slik, J.W.F., Aiba, S-I., Brearley, F.Q., Cannon, C.H., Forshed, O. and Kitayama, K. *et al*. 2010 Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. *Global Ecol. Biogeogr*. **19**, 50–60.

Smith, M.W. and Wood, B.W. 2006 Pecan tree biomass estimates. *HortScience*. **41**, 1286–1291.

Snell, J.A.K. and Little, S.N. 1983 Predicting Crown Weight and Bole Volume of Five Western Hardwoods. General Technical Report PNW-GTR-151. US Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, 37 pp.

Snell, J.A.K. and Max, T.A. 1985 Estimating the Weight of Crown Segments for Old-Growth Douglas-fir and Western Hemlock. Research Paper PNW-329. US Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, 22 pp.

Sollins, P. and Anderson, R.M. 1971 Dry-Weight and Other Data for Trees and Woody Shrubs of the Southeastern United States. Ecological Sciences Publication No. ORNL-IBP-71-6. Oak Ridge National Laboratory, 75 pp.

Sollins, P., Reichle, D.E. and Olson, J.S. 1973 Organic Matter Budget and Model for a Southern Appalachian *Liriodendron* Forest. Oak Ridge National Laboratory Report No. EDFB-IBP-73-2. Oak Ridge National Laboratory, 150 pp.

Standish, J.T., Manning, G.H. and Demaerschalk, J.P. 1985 Development of Biomass Equations for British Columbia Tree Species. Information Report No. BC-X-264. Pacific Forest Research Centre, 48 pp.

Stanek, W. and State, D. 1978 Equations Predicting Primary Productivity (Biomass) of Trees, Shrubs and Lesser Vegetation Based on Current Literature. Information Report No. BC-X-183. Pacific Forest Research Centre, 58 pp.

Storey, T.G., Fons, W.L. and Sauer, F.M. 1955 Crown Characteristics of Several Coniferous Tree Species. Report No. AFSWP-416. US Department of Agriculture, Forest Service, Division of Fire Research, 95 pp.

Strong, W.L. and La Roi, G.H. 1983 Root-system morphology of common boreal forest trees in Alberta, Canada. *Can. J. For. Res*. **13**, 1164–1173.

Telfer, E.S. 1969 Weight–diameter relationships for 22 woody plant species. *Can. J. Bot*. **47**, 1851–1855.

Ter-Mikaelian, M.T. and Korzukhin, M.D. 1997 Biomass equations for sixty-five North American tree species. *For. Ecol. Manage*. **97**, 1–24.

Ter-Mikaelian, M.T. and Lautenschlager, R.A. 2001 Predictive equations for leaf area and biomass for sugar bushes in eastern Ontario. *For. Chron*. **77**, 643–649.

Tritton, L.M. and Hornbeck, J.W. 1982 Biomass Equations for Major Tree Species of the Northeast. General Technical Report NE-69. US Department of Agriculture, Forest Service, Northeastern Forest Experimental Station, 46 pp.

Tufekcioglu, A., Raich, J.W., Isenhart, T.M. and Schultz, R.C. 2003 Biomass, carbon and nitrogen dynamics of multi-species riparian buffers within an agricultural watershed in Iowa, USA. *Agroforest. Syst*. **57**, 187–198.

Turner, M.G., Tinker, D.B., Romme, W.H., Kashian, D.M. and Litton, C.M. 2004 Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). *Ecosystems*. **7**, 751–775.

Tuskan, G.A. and Rensema, T.R. 1992 Clonal differences in biomass characteristics, coppice ability, and biomass prediction equations among four *Populus* clones grown in eastern North Dakota. *Can. J. For. Res*. **22**, 348–354.

Vadeboncoeur, M.A., Hamburg, S.P. and Yanai, R.D. 2007 Validation and refinement of allometric equations for roots of northern hardwoods. *Can. J. For. Res*. **37**, 1777–1783.

Van Hooser, D.D. and Chojnacky, D.C. 1983 Whole Tree Volume Estimates for the Rocky Mountain States. Resource Bulletin INT-RB-29. US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, 69 pp.

Van Lear, D.H., Taras, M.A., Waide, J.B. and Augspurger, M.K. 1986 Comparison of biomass equations for planted vs. natural loblolly pine stands of sawtimber size. *For. Ecol. Manage*. **14**, 205–210.

Vielledent, G., Vaudry, R., Andriamanohisoa, S.F., Rakotonarivo, O.S., Randrianasolo, H.Z. and Razafindrabe, H.N. *et al*. 2012 A universal approach to estimate biomass and carbon stock in tropical forests using generic allometric models. *Ecol. Appl*. **22**, 572–583.

Wade, D.D. 1969 Estimating Slash Quantity from Standing Loblolly Pine. Research Note SE-125. US Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, 4 pp.

Wahlgren, H.E. and Fassnacht, D.L. 1959 Estimating Tree Specific Gravity from a Single Increment Core. Report 2146. US Department of Agriculture, Forest Service, Forest Products Laboratory, 26 pp.

Wang, C. 2006 Biomass allometric equations for 10 co-occurring tree species in Chinese temperate forests. *For. Ecol. Manage*. **222**, 9–16.

Wang, J.R., Zhong, A.L., Simard, S.W. and Kimmins, J.P. 1996 Aboveground biomass and nutrient accumulation in an age sequence of paper birch (*Betula papyrifera*) in the Interior Cedar Hemlock Zone, British Columbia. *For. Ecol. Manage*. **83**, 27–38.

Wang, J.R., Letchforda, T., Comeaub, P. and Kimmins, J.P. 2000 Above- and below-ground biomass and nutrient distribution of a paper birch and subalpine fir mixed-species stand in the Sub-Boreal Spruce Zone of British Columbia. *For. Ecol*. *Manage*. **130**, 17–26.

Waring, R.H., Emmingham, W.H., Gholz, H.L. and Grier, C.C. 1978 Variation in maximum leaf area of coniferous forests in Oregon and its ecological significance. *For. Sci.* **24**, 131–140.

Wartluft, J.L. 1977 Weights of Small Appalachian Hardwood Trees and Components. Research Paper NE-366. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, 4 pp.

Weaver, T. and Forcella, F. 1977 Biomass of fifty conifer forests and nutrient exports associated with their harvest. *Great Basin Nat.* **37**, 395–401.

Weetman, G.F. and Harland, R. 1964 Foliage and wood production in unthinned black spruce in northern Quebec. *For. Sci.* **10**, 80–88.

West, G.B., Brown, J.H. and Enquist, B.J. 1997 A general model for the origin of allometric scaling laws in biology. *Science.* **276**, 122–126.

West, G.B., Brown, J.H. and Enquist, B.J. 1999a The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science.* **284**, 1677–1679.

West, G.B., Brown, J.H. and Enquist, B.J. 1999b A general model for the structure and allometry of plant vascular systems. *Nature.* **400**, 664–667.

West, G.B., Enquist, B.J. and Brown, J.H. 2009 A general quantitative theory of forest structure and dynamics. *Proc. Natl. Acad. Sci. USA.* **106**, 7040–7045.

Westman, W.E. and Whittaker, R.H. 1975 The pygmy forest region of northern California: studies on biomass and primary productivity. *J. Ecol.* **63**, 493–520.

Whisenant, S.G. and Burzlaff, D.F. 1978 Predicting green weight of mesquite (*Prosopis glandulosa* Torr.). *J. Range Manage.* **31**, 396–397.

Whittaker, R.H. and Niering, W.A. 1975 Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient. *Ecology.* **56**, 771–790.

Whittaker, R.H., Bormann, F.H., Likens, G.E. and Siccama, T.G. 1974 The Hubbard Brook ecosystem study: forest biomass and production. *Ecol. Monogr.* **44**, 233–254.

Wiant, H.V. Jr., Sheetz, C.E., Colaninno, A., DeMoss, J.C. and Castaneda, F. 1977 Tables and Procedures for Estimating Weights of some Appalachian Hardwoods. Bulletin 659T. West Virginia University, Agricultural and Forestry Experiment Station, 36 pp.

Williamson, G.B. and Wiemann, M.C. 2010 Measuring wood specific gravity. . .correctly. *Am. J. Bot.* **97**, 519–524.

Woodall, C.W., Heath, L.S., Domke, G.M. and Nichols, M.C. 2011 Methods and Equations for Estimating Aboveground Volume, Biomass, and Carbon for Trees in the U.S. Forest Inventory, 2010. General Technical Report NRS-88. US Department of Agriculture, Forest Service, Northern Research Station, 30 pp.

Woudenberg, S.W., Conkling, B.L., O'Connell, B.M., LaPoint, E.B., Turner, J.A. and Waddell, K.L. 2010 The Forest Inventory and Analysis Database: Database Description and User's Manual Version 4.0 for Phase 2. General Technical Report RMRS-GTR-245. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, 336 pp.

Xing, Z., Bourque, C.P., Swift, D.E., Clowater, C.W., Krasowski, M. and Meng, F.R. 2005 Carbon and biomass partitioning in balsam fir (*Abies balsamea*). *Tree Physic.* **25**, 1207–1217.

Yarie, J., Kane, E. and Mack, M. 2007 Aboveground Biomass Equations for Trees of Interior Alaska. Bulletin 115. University of Alaska, Agricultural and Forestry Experiment Station, 16 pp.

Zabek, L.M. and Prescott, C.E. 2006 Biomass equations and carbon content of aboveground leafless biomass of hybrid poplar in Coastal British Columbia. *For. Ecol*. *Manage*. **223**, 291–302.

Zhou, X., Brandle, J.R., Awada, T.N., Schoeneberger, M.M., Martin, D.L., Xin, Y. and Tang, Z. 2011 The use of forest-derived specific gravity for the conversion of volume to biomass for open-grown trees on agricultural land. *Biomass Bioenergy.* **35**, 1721–1731.

Appendix

Preliminary analyses and equation modifications

As discussed above, equations from 55 biomass studies were modified to fit our criteria for estimating aboveground biomass. Nine of these 55 were complete regression refits of raw biomass data published (Storey *et al.*, 1955; Sollins and Anderson, 1971; Schnell, 1976; Johnston and Bartos, 1977; Miller *et al.*, 1981; Strong and Roi, 1983; Sabatia, 2007) or graciously obtained from the authors (Karlik and Chojnacky unpublished (biomass data collected by Karlik and McKay, 2002), King *et al.*, 2007). Twelve were relatively minor algebraic manipulations of available study information to obtain desired equation forms (Weetman and Harland, 1964; Harris *et al.*, 1973; Whittaker *et al.*, 1974; Reynolds *et al.*, 1978; Schnell, 1978; Whisenant and Burzlaff, 1978; Harrington *et al.*, 1984; Sachs, 1984; Tuskan and Rensema, 1992; Laxson *et al.*, 1997; Naidu *et al.*, 1998; Seiler *et al.*, 2009). The remaining 34 studies involved modifications where 9 were regression refits of equations to eliminate height as a predictor variable, 7 combined biomass components among similar studies, 15 needed an auxiliary foliage equation to estimate total aboveground biomass (1 also needed height elimination), and 4 required other analyses.

When regression was involved in these modifications, three principles were followed:

- Models were devised to best fit data only within the diameter range of the particular study, either by polynomial regression (with weight as a function of diameter where needed) or logarithmic regression that sometimes included an additional diameter-term for more flexibility in regression [ln(biomass) = $a + b$ ln(diameter) + c diameter].
- If predicted data from equations (pseudodata) were needed for regression refit, these were generated uniformly within the diameter ranges of the equations given in studies (extrapolation outside this range was avoided except for a few cases).
- If auxiliary FIA data (FIA, 2010) were needed (for elimination of height or for other calculations, as described below), they were selected so as to correspond to the original study's geographic area, species, stand origin (plantation or natural stand), and explicit diameter range.

Eliminating height variable

Equations from 9 studies were refit as a function of diameter either by using author-published height-to-diameter equations (Ralston and Prince, 1965; Bella and De Franceschi, 1980) or by using select FIA (2010) data to predict biomass (using published equation) from height and diameter, then refitting as a function of diameter. In other words, the regression refit averaged the effect of the height variable by fitting a new equation based on diameter only.

The 7 studies needing additional data to estimate biomass from height and diameter were matched with FIA data for a large

population of trees of similar geography (generally a state), similar stand origin, and within the diameter range of species of respective studies (Clark and Taras, 1976; Alban and Laidly, 1982; Van Lear et al., 1986; Jokela and Martin, 2000; Rubilar et al., 2005). Geographic exceptions included use of Alaska and Washington FIA data for a British Columbia study (Standish et al., 1985), and use of all plantation poplar data in the FIA database for a Washington study (Zabek and Prescott, 2006) because less than 2,000 plantation poplar trees were measured in the entire US and less than 50 in Washington.

Combining studies

There were few biomass equations for western North American species – particularly large-diameter trees – but there were some studies that reported either crown (foliage and branch) or bole (wood and bark) biomass equations, suggesting opportunities for combining equations among studies:

- A large study excluding crown biomass (Means et al., 1994) included 40 stem wood and bark biomass equations for 18 California, Oregon, and Washington conifer species for trees up to 100- to over 200-cm dbh. We first reduced Means' equations to 18 by refitting when there was more than 1 equation per species and then matched these refitted equations with auxiliary crown equations refit from other studies. Auxiliary crown equations were constructed by generating genus-scale pseudodata from 76 foliage and/or branch equation estimates from 34 studies for the western US and Canada.
- We combined a study of stem material by Duursma et al. (2007) with Brown's (1978) study of crown biomass for the same 10 conifer species in the Inland Northwest; auxiliary bark ratios were obtained from Van Hooser and Chojnacky (1983).
- A Nevada mountain mahogany (Cercocarpus ledifolius) study (Chojnacky, 1984) lacked foliage, so a 6 per cent foliage-to-(wood + bark + branch) ratio devised from Whittaker and Niering (1975) C. breviflorus data were used, and missing branch material less than 3.8 cm was extrapolated from ratios of known branch material mass (for diameters between 3.8 and 7.6 cm). Also for Nevada, a pinyon and juniper study (Chojnacky and Moisen, 1993) required volume equations (Chojnacky, 1985; Chojnacky, 1987) for a conversion method that also used FIA data.
- A large-tree mesquite (Prosopis spp.) equation was gained by combining green-weight biomass equations from El Fadl et al. (1989) with wood moisture content data from Felker et al. (1990).
- Finally, a Douglas-fir (Pseudotsuga menziesii) crown biomass equation for trees 85 to 155 cm dbh was obtained by combining Ishii and Kadotani's (2006) branch biomass equation with McCain's (1994) foliage equation.

Foliage equation additions

There were 15 studies including 35 species in 19 genera where, because it was winter, stem wood, bark, and branches were measured but foliage (a minor part of tree biomass) was not. Forty-four percent of these species were oaks (Quercus) and maples (Acer). The rest were eastern hardwoods, except for poplar (in British Columbia), eastern redcedar (J. virginiana), and eastern hemlock

(Tsuga canadensis). We grouped 190 foliage equations from our database by genus, and used them to estimate foliage at a genus scale for the 15 studies. However, the maple equation was also used for 6 other genera (dogwood (Cornus), sassafras (Sassafras), sourwood (Oxydendrum), sycamore (Platanus), tupelo (Nyssa), and locust (Robinia)) because pseudodata for these were based on 3 or fewer equations each and their pseudodata variation was within that of maple.

Miscellaneous modifications

Four other studies required modification:

- Biomass equations reported by Perala and Alban (1994) were recalculated by averaging pseudodata from equations developed for different soil types, and in a few cases also by using author-published height-to-dbh equations, to eliminate soil types and height in refits.
- Reiners (1972) published biomass equations for Minnesota species but did not report a maximum dbh needed to generate pseudodata; basal area and trees per area for each species were reported instead of dbh range. Therefore, FIA (2010) data were used for counties included in the study area to model 'a maximum dbh for each species' from basal area and trees per acre (0.4047 ha); this maximum dbh was between 20 and 37 cm dbh for most species, but two extremes of 67 and 80 cm were set to 50 cm to guard against possible extrapolation error.
- Pearson et al. (1984) reported lodgepole pine (P. contorta) equations segmented into irregular diameter categories that were refit into single-diameter equations.
- Ker and van Raalte (1981) equations were refit using crown width and length equations obtained from Bragg (2001).

Excluded studies

Twelve studies were excluded because they summarized or duplicated biomass equations reported in other studies that we used (Baskerville, 1966; Clebsch, 1971; Fujimori et al., 1976; Santantonio et al., 1977; Stanek and State, 1978; Waring et al., 1978; Tritton and Hornbeck, 1982; Rauscher, 1984; Baldwin, 1987; Clark, 1987; Felker et al., 1990; Ter-Mikaelian and Korzukhin, 1997). Five studies were not used because the reported equations were not clear (Long and Turner, 1975; Ramseur and Kelly, 1981; Ruark and Bockheim, 1987; Tufekcioglu et al., 2003; Lieurance, 2007). Four studies that would have required modification to eliminate height were excluded either because study trees were very small or because species were already well represented by other studies (Schaegel, 1975; Rowell and Carpenter, 1983; Bond-Lamberty et al., 2002; Oswald et al., 2010). Ten Canadian studies that fit biomass equations as a function of dbh and height were not used because these data were included with the recent reanalysis by Lambert et al. (2005) of older Canadian biomass data (Johnstone and Peterson, 1980; Alemdag and Horton, 1981; Lavigne and Van Nostrand, 1981; Alemdag, 1981, 1982, 1983; Lavigne 1982; Singh 1982; Evert, 1983; Ouellet, 1985). Lastly, equations developed by Hu and Wang (2008) were not used because they were developed from FIA biomass estimates, which are based on volume-to-biomass conversion and other auxiliary information instead of direct measurement of biomass.