

Canadian national tree aboveground biomass equations

M.-C. Lambert, C.-H. Ung, and F. Raulier

Abstract: The estimation of aboveground biomass density (organic dry mass per unit area) is required for balancing Canadian national forest carbon budgets. Tree biomass equations are the basic tool for converting inventory plot data into biomass density. New sets of national tree biomass equations have therefore been produced from archival biomass data collected at the beginning of the 1980s through the ENergy from the FORest research program (ENFOR) of the Canadian Forest Service. Since the sampling plan was not standardized among provinces and territories, data had to be harmonized before any biomass equation could be considered at the national level. Two features characterize the new equations: estimated biomass of the compartments (foliage, branch, wood, and bark) are constrained to equal the total biomass, and dependence among error terms for the considered compartments of the same tree is taken into account in the estimates of both the model parameters and the variance prediction. The estimation method known to economists as “seemingly unrelated regression” allowed the inclusion of dependencies among the error terms of the considered biomass compartments. Sets of equations based on diameter at breast height (dbh) and on dbh and height have been produced for 33 species, groups of hardwood and softwood, and for all species combined. Biomass predicted by the new equations was compared with that estimated from provincial equations to evaluate the loss of accuracy when scaling up from the regional to the national scale. Bias and error of prediction from the set of national equations based on dbh and height were generally more similar to those from provincial equations than to those of predictions from the set of equations based on dbh alone.

Résumé : L'estimation de la densité de biomasse aérienne (matière organique sèche par unité de surface) est requise pour déterminer les bilans nationaux canadiens de carbone forestier. Les équations de biomasse d'arbre constituent l'outil de base pour convertir les données des placettes d'inventaire en densité de biomasse. C'est pour cette raison que les données de biomasse ont été récupérées d'archives nationales pour produire de nouvelles séries d'équations de biomasse d'arbre. Ces données ont été recueillies au début des années 80 par le Service canadien des forêts dans le cadre du programme de recherche appelé Énergie de la FORêt (ENFOR). Comme le plan d'échantillonnage n'était pas standardisé parmi les provinces et territoires, les données ont dû être uniformisées avant que les équations de biomasse puissent être considérées au niveau national. Deux propriétés caractérisent les nouvelles équations de biomasse : les estimés de composantes de biomasse (feuille, branche, bois et écorce) sont contraints à égaliser la biomasse totale et la dépendance parmi les termes d'erreurs pour les différentes composantes d'un même arbre est prise en considération dans les estimés des paramètres du modèle et dans la variance de la prédiction. La méthode d'estimation connue par les économistes comme une « méthode de régression sans corrélation apparente » permet l'inclusion des dépendances entre les termes d'erreurs des composantes de biomasse considérées. Les séries d'équations basées sur le diamètre à hauteur de poitrine (dhp), d'une part, et sur le dhp et la hauteur, d'autre part, ont été produites pour 33 essences, par groupe de feuillus et de conifères et pour toutes les essences réunies. Les biomasses prédictes par les nouvelles équations nationales sont comparées à celles estimées par des équations provinciales pour évaluer la perte de précision causée par l'agrégation de l'échelle régionale à l'échelle nationale. Le biais et l'erreur de prédiction obtenus avec la série d'équations nationales basées à la fois sur le dhp et la hauteur sont généralement beaucoup plus semblables à ceux obtenus des équations provinciales que le biais et l'erreur de prédiction des équations nationales basées uniquement sur le dhp.

Introduction

Between 1980 and 1995, the earth's biosphere actively removed approximately 30% of the new carbon added to the atmosphere by human activities (Houghton 2000; Apps 2003).

Atmospheric CO₂ is taken up by terrestrial ecosystems through photosynthesis, but most of this uptake is naturally and rapidly reemitted into the atmosphere (Schulze et al. 2000), and only a relatively small fraction of plant carbon enters long-

Received 14 December 2004. Accepted 4 May 2005. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 21 September 2005.

M.-C. Lambert, C.-H. Ung,¹ and F. Raulier.² Laurentian Forestry Centre, Natural Resources Canada, Canadian Forest Service, 1055 rue du P.E.P.S., P.O. Box 3800, Sainte-Foy, QC G1V 4C7, Canada.

¹Corresponding author (e-mail: Chhun-Huor.Ung@nrcan.gc.ca).

²Present address: Faculté de foresterie et de géomatique, Université Laval, Québec, QC G1K 7P4, Canada.

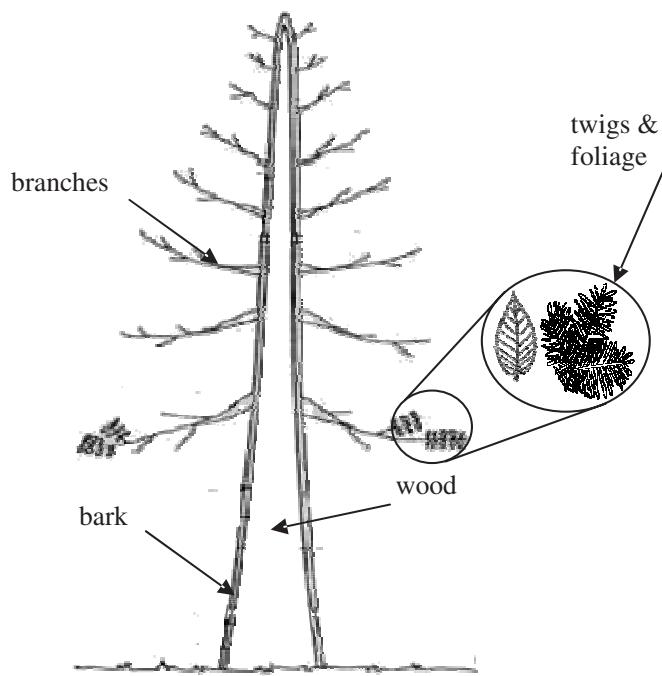
term storage, such as in wood and humus (Intergovernmental Panel on Climate Change 2001). Consequently, the earth's biosphere can oscillate between being a source or a sink of atmospheric CO₂, depending on ecosystem productivity and disturbance regime (Apps 2003). Because of their high carbon density, forests play an important role in the national net balance of global climate change induced by greenhouse gases, because changes in the carbon stock of trees determine the status of forests as an atmospheric source or sink (Kurz et al. 2002). National forest carbon budgets that have been constructed to address the source and sink topic can be based on biomass density estimation (organic dry mass per unit area) (Kurz and Apps 1999; Pacala et al. 2001). When forest inventory plot data are used for estimating biomass density, tree biomass equations that can be consistently applied on a national scale represent a basic tool for converting inventory plot data into biomass density.

Since the comprehensive review of biomass equations for 65 North American tree species by Ter-Mikaelian and Korzukhin (1997) there has been an increasing need for generalized and consistent biomass equations to model the carbon cycle at the national scale. Jenkins et al. (2003) responded to this need for the United States by adopting a so-called generalized regression method proposed by Pastor et al. (1984). Pastor et al.'s method (1984) is based on published equations and has two major weaknesses. Firstly, biomass pseudodata are generated from the published equations and are used as though they were real data for the estimation of the generalized parameters equations. The data set on which the generalized equations are based is then highly autocorrelated. This departure from the usual assumptions of least squares estimation does not bias the estimates of the regression coefficients of the generalized equations but they are neither best linear unbiased estimates (BLUE) nor efficient under these conditions (Kmenta 1986, p. 308). Moreover, the estimated variances are biased and the conventionally calculated confidence intervals and tests of significance are not valid (Kmenta 1986, p. 311). Finally, the reported R² values are meaningless. Secondly, the potential bias in sample selection at a nationwide scale cannot be addressed by the fact that a published equation based on a single site has the same weight in the final equation as another equation based on several sites. Moreover, the generation of pseudodata cannot take into account the relative precision of the regression coefficients, which must reflect the sample variability and the sample size effect. In addition, using a selection of publications can result in a publication bias.

In Canada, the existing biomass equations were established at the provincial and territorial scale during the 1980s through the ENergy from the FORest research project (ENFOR) of the Canadian Forest Service (Appendix A), which dealt with each province and territory separately. However, in terms of the need for a generalized and coherent set of biomass equations, these existing equations remain disparate, sometimes unpublished, and sometimes with undetermined error. National equations avoid the artificial presence of provincial and territorial frontiers, which are only administrative and not ecological limits.

Evert (1985) has already used the complete ENFOR data set to produce national biomass equations. For each of the 18 Canadian species considered, stem wood, stem bark, and crown were predicted by three independent equations using

Fig. 1. Biomass compartments. (Source: Alemdag 1984, p. 2; reproduced with permission of Natural Resources Canada, Canadian Forest Service, 2005.)



diameter at breast height (dbh) and height as explanatory variables. Evert's equations (1985) have, however, a major flaw in assuming independence among compartments (crown, wood, and bark) of the same tree, while, in fact, the three compartments considered are dependent. Moreover, Evert (1985) did not separate leaf biomass from branch biomass, even if leaf biomass is recognized to be an important input variable in carbon cycle modeling (Körner 1994). The purpose of this paper was to eliminate the weakness of Evert's equations (1985) by recovering the archival ENFOR biomass data, organizing it into a coherent biomass data set, and producing a national system of equations for the aboveground compartments of tree biomass with an estimated accuracy. This effort responds to the concern in accounting for the uncertainty in balancing the countrywide carbon budget.

Materials

The aboveground biomass compartments considered are illustrated in Fig. 1. The stem is delimited between ground level and tree top and is partitioned into stem wood and stem bark. All branches are cut at the stem base. Leaves and twigs represent the foliage compartment. According to Aldred and Alemdag (1988), stump biomass was determined based on the ratio of stump volume (stump height at 0.30 m) to the volume of the lower merchantable section. Dead branches, cones, and fruits are not included as part of aboveground biomass in this work (Aldred and Alemdag 1988). Details on field and laboratory procedures for each province can be found in ENFOR references (Appendix A).

Major efforts have been made to harmonize the data sets recovered from archival tapes of the ENFOR program (Fig. 2). However, all the data could not be recovered: British Columbia data are missing, and Maritimes data have been partially re-

Fig. 2. Distribution of plot biomass measured by ENFOR (when location is available).

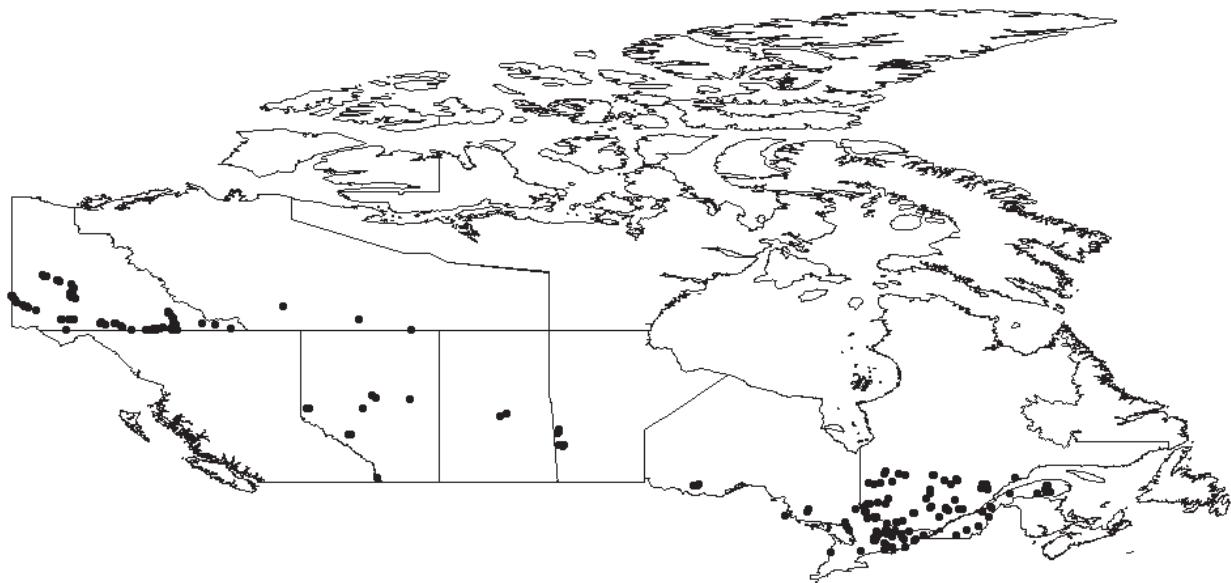
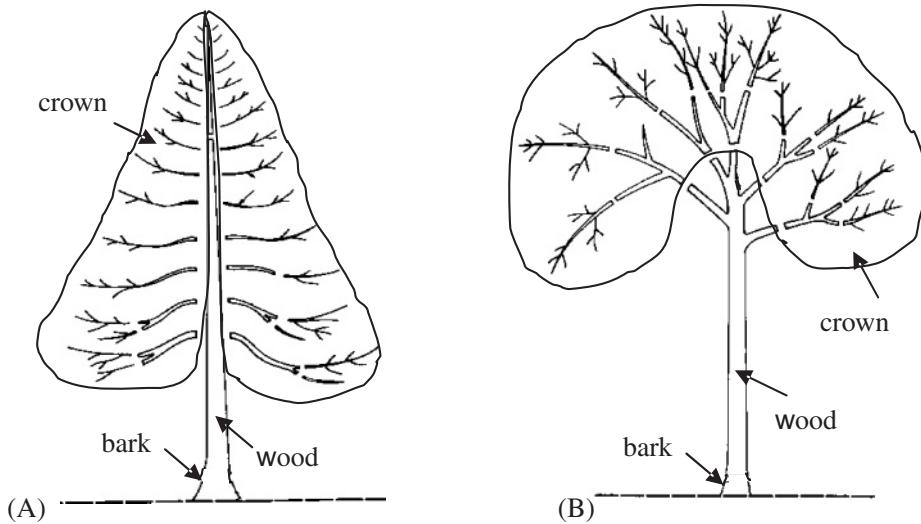


Fig. 3. Biomass compartments considered in Quebec: (A) softwood and (B) hardwood. (Source: Ouellet 1983, pp. 28 and 29; reproduced with permission of Natural Resources Canada, Canadian Forest Service, 2005.)



covered but it is not clear whether the information comes from New Brunswick or Nova Scotia. Moreover, as illustrated in Fig. 3, the sampling protocol was different for Quebec. For softwood species, branches and needles have not been separated (Fig. 3A). For hardwoods, the basal part of some branches was included in the stem, as branches were cut at the 9 cm diameter (Fig. 3B). Foliage has not been separated from branches (Fig. 3B). The following logit regression has been established for each species (Appendix B) from other provinces' data to separate foliage from branches:

$$[1] \quad \hat{p} = \frac{\exp(\hat{\alpha} + \hat{\beta}D)}{1 + \exp(\hat{\alpha} + \hat{\beta}D)}$$

where \hat{p} is the predicted proportion of branches, $\hat{\alpha}$ and $\hat{\beta}$ are model coefficients, and D is the diameter at breast height (dbh in centimetres).

Wood and bark were not separated for some trees from Newfoundland. Hence, proportions of stem wood were computed from the data of other provinces, as for the crown components in Quebec.

Trees were sampled within the plot, but plot information (identification of the plot, location, size, stand type, stand density, and stand height) was not always available. Some provinces' and territories' biomass definitions in the ENFOR information reports were not clear (Appendix A). Sometimes, specifications for stump, dead branches, or cones and fruits were not mentioned. It was thus assumed that the biomass of these compartments was measured according to Aldred and Alemdag's protocol (1988). In addition, the definition of twig might vary slightly. Detection of anomalous and influential data was done with graphical distributions of biomass values and by comparing green and dry masses. The distribution of the harmonized biomass data is presented in Table 1, while Table 2 presents descriptive statistics for dbh, height, and total biomass.

Table 1. Number of trees per province and territory and per species in the data set.

Species*	Provinces and territories†												Total
	AB	BC	MB	NB	NL	NS	NT	ON	PE	QC	SK	YT	
Alpine fir	60												60
Balsam fir	20	20		283	49			70		177	20		639
Balsam poplar	20	20					50	97			20		207
Basswood								80					80
Beech								81		96			177
Black ash								31		42			73
Black cherry								78					78
Black spruce	20	20		300	49	48		73		714	20	290	1534
Eastern hemlock								148		87			235
Eastern redcedar								33					33
Eastern white-cedar								91		93			184
Eastern white pine								144		55			199
Grey birch						43							43
Hickory								35		41			76
Hop-hornbeam								14					14
Jack pine	20	21			41	52		74		136	20		364
Largetooth aspen								100					100
Lodgepole pine	60											141	201
Red ash								27					27
Red maple						46		68		63			177
Red oak								117					117
Red pine						47		272		52			371
Red spruce										55			55
Silver maple								40					40
Sugar maple								113		122			235
Tamarack larch	20	20		232	46	56		84		97	20		575
Trembling aspen	20	19		67	46	54		226		133	20	188	773
White ash								73		36			109
White birch	20	20		270	44			134		98	20		606
White elm								81					81
White oak								61					61
White spruce	20	20		164	44	56		76		78	20	354	832
Yellow birch					53			98		129			280
Total	280	160		1369	455	316		2619		2304	160	973	8636

*Refer to Appendix B.

†AB, Alberta; BC, British Columbia; MB, Manitoba; NB, New Brunswick; NL, Newfoundland and Labrador; NT, Northwest Territories; NS, Nova Scotia; NU, Nunavut (Northwest Territories in the 1980s); ON, Ontario; PE, Prince Edward Island; QC, Quebec; SK, Saskatchewan; YT, Yukon.

Methods

As proposed by Parresol (1999, 2001), a set of nonlinear regression equations was specified in such a way that (i) each compartment regression contains its own independent variables, and the total tree regression is a function of all the specified independent variables; (ii) each regression can use its own weight function; and (iii) additivity is ensured by setting constraints on regression coefficients so that the predicted biomasses of the compartments add up to the prediction of the total biomass. The set of equations was calibrated with the procedure MODEL in SAS/ETS (SAS Institute Inc. 1999a), using joint generalized least squares, more commonly called seemingly unrelated regressions (Gallant 1987). This technique results in lower variance of the regression coefficients by taking into account the contemporaneous correlations among the regression residuals of the equations (Parresol 1999). In fact, it is more realistic to consider that compart-

Table 2. Descriptive statistics for dbh, height, and total biomass by tree species.*

Species	No. of trees	Total biomass	
		dbh (cm)	Height (m)
Alpine fir	60	19.6±1.3 (2.1;36.5)	14.8±0.8 (2.2;23.7) (1.7;461.8)
Balsam fir	639	16.4±0.4 (1.5;42.4)	12.2±0.2 (1.6;52.2) (0.5;649.0)
Balsam poplar	207	21.5±0.8 (2.0;53.2)	16.3±0.4 (3.3;27.0) (0.5;1516.3)
Basswood	80	26.5±1.6 (3.7;54.8)	17.5±0.7 (3.8;26.1) (2.1;1118.9)
Beech	177	23.5±0.9 (1.8;46.3)	17.5±0.4 (2.9;26.5) (0.7;1372.5)
Black ash	73	16.2±1.2 (2.0;43.1)	14.4±0.6 (2.6;22.9) (1.0;926.4)
Black cherry	78	22.0±1.3	16.6±0.6 (2.7;26.1) (2.1;29.1)

Table 2 (concluded).

Species	No. of trees	dbh (cm)	Height (m)	Total biomass (kg)
Black spruce	1534	(0.9;49.6) 13.9±0.2 (1.6;37.2)	(2.1;25.9) 11.6±0.1 (1.8;23.5)	(0.6;1183.5) 73.3±1.9 (0.6;556.1)
Eastern hemlock	235	24.1±0.9 (1.3;51.4)	14.4±0.4 (2.3;26.5)	286.9±20.5 (0.6;1406.6)
Eastern redcedar	33	12.3±1.4 (2.0;38.2)	7.2±0.4 (2.7;12.8)	52.7±12.3 (1.4;316.4)
Eastern white-cedar	184	20.8±0.9 (2.1;66.2)	11.8±0.3 (1.9;21.9)	117.2±9.3 (1.0;917.4)
Eastern white pine	199	28.7±1.1 (1.5;68.7)	18.7±0.5 (2.3;38.5)	425.8±33.0 (0.3;2183.1)
Grey birch	43	10.3±0.8 (2.2;22.7)	8.9±0.5 (2.3;14.9)	39.8±6.9 (0.6;181.0)
Hickory	76	20.8±1.2 (2.8;46.6)	19.3±0.8 (3.9;29.4)	363.3±42.4 (1.4;1335.1)
Hop-hornbeam	14	7.7±0.9 (5.2;18.5)	8.6±0.4 (6.3;11.9)	20.0±6.4 (6.3;86.8)
Jack pine	364	18.6±0.5 (1.7;41.0)	15.9±0.3 (2.9;27.0)	153.6±7.8 (0.7;784.7)
Largetooth aspen	100	15.8±0.7 (1.5;39.2)	16.9±0.6 (2.3;28.9)	114.8±12.2 (1.0;641.2)
Lodgepole pine	201	15.0±0.6 (2.5;39.0)	12.7±0.4 (2.5;25.9)	99.0±8.8 (0.8;694.4)
Red ash	27	21.1±1.8 (4.9;40.2)	18.0±1.1 (7.2;26.7)	207.9±33.6 (5.8;587.8)
Red maple	177	19.9±0.8 (2.4;56.0)	15.7±0.4 (3.8;25.4)	238.6±21.7 (1.1;1875.9)
Red oak	117	22.6±1.0 (1.1;55.3)	15.3±0.4 (2.5;23.0)	311.4±29.2 (0.4;1977.5)
Red pine	371	22.4±0.6 (1.3;55.1)	16.4±0.3 (1.8;34.4)	216.5±12.6 (0.3;1572.6)
Red spruce	55	22.9±1.2 (6.5;43.5)	15.9±0.4 (8.0;21.2)	207.7±22.4 (9.1;811.7)
Silver maple	40	22.8±2.0 (3.7;45.3)	19.4±0.9 (6.6;26.4)	351.7±58.1 (5.7;1163.7)
Sugar maple	235	24.6±0.9 (2.0;57.8)	17.3±0.3 (2.6;26.4)	466.9±30.7 (1.6;2421.1)
Tamarack larch	575	14.7±0.3 (1.8;44.5)	12.3±0.2 (2.2;30.5)	96.4±4.8 (0.4;938.9)
Trembling aspen	773	17.7±0.4 (0.7;47.2)	15.8±0.2 (1.8;28.3)	161.7±7.2 (0.1;1081.5)
White ash	109	22.3±1.1 (2.4;53.7)	17.6±0.4 (3.9;26.9)	296.2±28.5 (1.2;1850.1)
White birch	606	16.4±0.4 (1.5;43.6)	13.3±0.2 (2.6;23.9)	152.0±7.1 (0.4;1020.8)
White elm	81	20.3±1.1 (0.7;55.2)	13.5±0.5 (2.1;23.2)	203.5±28.8 (0.2;1832.2)
White oak	61	23.9±2.1 (2.2;74.3)	11.5±0.6 (2.8;21.5)	325.4±63.1 (1.3;2385.5)
White spruce	832	16.6±0.3 (1.8;51.9)	12.9±0.2 (1.1;37.5)	123.6±5.7 (0.4;1344.6)
Yellow birch	280	25.7±0.9 (0.8;70.3)	16.4±0.3 (2.7;25.6)	494.4±34.4 (0.1;2951.4)

*Each mean (\pm standard error) has been calculated from the number of trees. Values in parentheses indicate the range.

ments are dependent and that residuals are correlated, because the same tree gives values for more than one biomass compartment (Carvalho and Parresol 2003). The most important impact of using a simultaneous estimation is to have a statis-

Table 3. Model parameter estimates and their standard error (SE) for the dbh-based set of equations per species, genus, and all species combined.

Species	Parameter	Estimate	SE
Alpine fir	$b_{\text{wood}1}$	0.0528	0.0046
	$b_{\text{wood}2}$	2.4309	0.0268
	$b_{\text{bark}1}$	0.0108	0.0026
	$b_{\text{bark}2}$	2.3876	0.0739
	$b_{\text{branches}1}$	0.0121	0.0033
	$b_{\text{branches}2}$	2.3519	0.0845
	$b_{\text{foliage}1}$	0.0251	0.0086
	$b_{\text{foliage}2}$	2.0389	0.1070
	$b_{\text{wood}1}$	0.0534	0.0017
	$b_{\text{wood}2}$	2.4030	0.0103
Balsam fir	$b_{\text{bark}1}$	0.0115	0.0004
	$b_{\text{bark}2}$	2.3484	0.0127
	$b_{\text{branches}1}$	0.0070	0.0007
	$b_{\text{branches}2}$	2.5406	0.0347
	$b_{\text{foliage}1}$	0.0840	0.0046
	$b_{\text{foliage}2}$	1.6695	0.0199
	$b_{\text{wood}1}$	0.0510	0.0033
	$b_{\text{wood}2}$	2.4529	0.0205
	$b_{\text{bark}1}$	0.0297	0.0035
	$b_{\text{bark}2}$	2.1131	0.0375
Balsam poplar	$b_{\text{branches}1}$	0.0120	0.0014
	$b_{\text{branches}2}$	2.4165	0.0376
	$b_{\text{foliage}1}$	0.0276	0.0018
	$b_{\text{foliage}2}$	1.6215	0.0240
	$b_{\text{wood}1}$	0.0562	0.0045
	$b_{\text{wood}2}$	2.4102	0.0227
	$b_{\text{bark}1}$	0.0302	0.0068
	$b_{\text{bark}2}$	2.0976	0.0652
	$b_{\text{branches}1}$	0.0230	0.0069
	$b_{\text{branches}2}$	2.2382	0.0888
Basswood	$b_{\text{foliage}1}$	0.0288	0.0095
	$b_{\text{foliage}2}$	1.6378	0.0966
	$b_{\text{wood}1}$	0.1478	0.0202
	$b_{\text{wood}2}$	2.2986	0.0401
	$b_{\text{bark}1}$	0.0120	0.0010
	$b_{\text{bark}2}$	2.2388	0.0256
	$b_{\text{branches}1}$	0.0370	0.0042
	$b_{\text{branches}2}$	2.3680	0.0353
	$b_{\text{foliage}1}$	0.0376	0.0055
	$b_{\text{foliage}2}$	1.6164	0.0445
Beech	$b_{\text{wood}1}$	0.0941	0.0073
	$b_{\text{wood}2}$	2.3491	0.0245
	$b_{\text{bark}1}$	0.0323	0.0050
	$b_{\text{bark}2}$	2.0761	0.0474
	$b_{\text{branches}1}$	0.0448	0.0086
	$b_{\text{branches}2}$	1.9771	0.0781
	$b_{\text{foliage}1}$	0.0538	0.0088
	$b_{\text{wood}1}$		
	$b_{\text{wood}2}$		
	$b_{\text{bark}1}$		
Black ash	$b_{\text{bark}2}$		
	$b_{\text{branches}1}$		
	$b_{\text{branches}2}$		
	$b_{\text{foliage}1}$		
	$b_{\text{foliage}2}$		
	$b_{\text{wood}1}$		
	$b_{\text{wood}2}$		
	$b_{\text{bark}1}$		
	$b_{\text{bark}2}$		
	$b_{\text{branches}1}$		

Table 3 (continued).

Species	Parameter	Estimate	SE
Black cherry	b_{foliage2}	1.3584	0.0562
	b_{wood1}	0.3743	0.0573
	b_{wood2}	1.9406	0.0472
	b_{bark1}	0.0679	0.0204
	b_{bark2}	1.8377	0.0883
	$b_{\text{branches1}}$	0.0796	0.0108
	$b_{\text{branches2}}$	2.0103	0.0483
	b_{foliage1}	0.0840	0.0053
	b_{foliage2}	1.2319	0.0248
Black spruce	b_{wood1}	0.0477	0.0010
	b_{wood2}	2.5147	0.0075
	b_{bark1}	0.0153	0.0006
	b_{bark2}	2.2429	0.0139
	$b_{\text{branches1}}$	0.0278	0.0019
	$b_{\text{branches2}}$	2.0839	0.0253
	b_{foliage1}	0.1648	0.0088
	b_{foliage2}	1.4143	0.0208
	b_{wood1}	0.0619	0.0030
Eastern hemlock	b_{wood2}	2.3821	0.0150
	b_{bark1}	0.0139	0.0010
	b_{bark2}	2.3282	0.0210
	$b_{\text{branches1}}$	0.0217	0.0031
	$b_{\text{branches2}}$	2.2653	0.0420
	b_{foliage1}	0.0776	0.0069
	b_{foliage2}	1.6995	0.0292
	b_{wood1}	0.1277	0.0126
	b_{wood2}	1.9778	0.0320
Eastern redcedar	b_{bark1}	0.0377	0.0076
	b_{bark2}	1.6064	0.0707
	$b_{\text{branches1}}$	0.0254	0.0073
	$b_{\text{branches2}}$	2.2884	0.0948
	b_{foliage1}	0.0550	0.0172
	b_{foliage2}	1.8656	0.1079
	b_{wood1}	0.0654	0.0037
	b_{wood2}	2.2121	0.0170
	b_{bark1}	0.0114	0.0013
Eastern white-cedar	b_{bark2}	2.1432	0.0348
	$b_{\text{branches1}}$	0.0335	0.0034
	$b_{\text{branches2}}$	1.9367	0.0331
	b_{foliage1}	0.0499	0.0038
	b_{foliage2}	1.7278	0.0265
	b_{wood1}	0.0997	0.0129
	b_{wood2}	2.2709	0.0350
	b_{bark1}	0.0192	0.0016
	b_{bark2}	2.2038	0.0237
Eastern white pine	$b_{\text{branches1}}$	0.0056	0.0008
	$b_{\text{branches2}}$	2.6011	0.0381
	b_{foliage1}	0.0284	0.0024

Table 3 (continued).

Species	Parameter	Estimate	SE
Grey birch	b_{foliage2}	1.9375	0.0248
	b_{wood1}	0.0720	0.0043
	b_{wood2}	2.3885	0.0223
	b_{bark1}	0.0168	0.0011
	b_{bark2}	2.2569	0.0304
	$b_{\text{branches1}}$	0.0088	0.0027
	$b_{\text{branches2}}$	2.5689	0.1188
	b_{foliage1}	0.0099	0.0020
	b_{foliage2}	1.8985	0.0820
Hickory	b_{wood1}	0.2116	0.0547
	b_{wood2}	2.2013	0.0776
	b_{bark1}	0.0365	0.0046
	b_{bark2}	2.1133	0.0397
	$b_{\text{branches1}}$	0.0087	0.0025
	$b_{\text{branches2}}$	2.8927	0.0892
	b_{foliage1}	0.0173	0.0030
	b_{foliage2}	1.9830	0.0517
	b_{wood1}	0.1929	0.0431
Hop-hornbeam	b_{wood2}	1.9672	0.0833
	b_{bark1}	0.0671	0.0201
	b_{bark2}	1.5911	0.1317
	$b_{\text{branches1}}$	0.0278	0.0110
	$b_{\text{branches2}}$	2.1336	0.1417
	b_{foliage1}	0.0293	0.0081
	b_{foliage2}	1.9502	0.1018
	b_{wood1}	0.0804	0.0042
	b_{wood2}	2.4041	0.0168
Jack pine	b_{bark1}	0.0184	0.0009
	b_{bark2}	2.0703	0.0165
	$b_{\text{branches1}}$	0.0079	0.0011
	$b_{\text{branches2}}$	2.4155	0.0486
	b_{foliage1}	0.0389	0.0029
	b_{foliage2}	1.7290	0.0251
	b_{wood1}	0.0959	0.0144
	b_{wood2}	2.3430	0.0483
	b_{bark1}	0.0308	0.0035
Largetooth aspen	b_{bark2}	2.2240	0.0388
	$b_{\text{branches1}}$	0.0047	0.0006
	$b_{\text{branches2}}$	2.6530	0.0435
	b_{foliage1}	0.0080	0.0016
	b_{foliage2}	2.0149	0.0629
	b_{wood1}	0.0475	0.0029
	b_{wood2}	2.5437	0.0190
	b_{bark1}	0.0186	0.0018
	b_{bark2}	2.0807	0.0319
Lodgepole pine	$b_{\text{branches1}}$	0.0198	0.0027
	$b_{\text{branches2}}$	2.1287	0.0499
	b_{foliage1}	0.0432	0.0051

Table 3 (continued).

Species	Parameter	Estimate	SE
Red ash	$b_{foliage2}$	1.7166	0.0410
	b_{wood1}	0.1571	0.0287
	b_{wood2}	2.1817	0.0572
	b_{bark1}	0.0416	0.0075
	b_{bark2}	2.0509	0.0592
	$b_{branches1}$	0.0177	0.0058
	$b_{branches2}$	2.3370	0.1025
	$b_{foliage1}$	0.1041	0.0259
	$b_{foliage2}$	1.2185	0.0778
	b_{wood1}	0.1014	0.0052
Red maple	b_{wood2}	2.3448	0.0173
	b_{bark1}	0.0291	0.0027
	b_{bark2}	2.0893	0.0320
	$b_{branches1}$	0.0175	0.0034
	$b_{branches2}$	2.4846	0.0603
	$b_{foliage1}$	0.0515	0.0065
	$b_{foliage2}$	1.5198	0.0400
	b_{wood1}	0.1754	0.0149
Red oak	b_{wood2}	2.1616	0.0267
	b_{bark1}	0.0381	0.0051
	b_{bark2}	2.0991	0.0403
	$b_{branches1}$	0.0085	0.0028
	$b_{branches2}$	2.7790	0.0979
	$b_{foliage1}$	0.0373	0.0029
	$b_{foliage2}$	1.6740	0.0268
	b_{wood1}	0.0564	0.0034
Red pine	b_{wood2}	2.4465	0.0192
	b_{bark1}	0.0188	0.0006
	b_{bark2}	2.0527	0.0102
	$b_{branches1}$	0.0033	0.0005
	$b_{branches2}$	2.7515	0.0455
	$b_{foliage1}$	0.0212	0.0014
	$b_{foliage2}$	2.0690	0.0204
	b_{wood1}	0.0989	0.0068
Red spruce	b_{wood2}	2.2814	0.0212
	b_{bark1}	0.0220	0.0017
	b_{bark2}	2.0908	0.0257
	$b_{branches1}$	0.0005	0.0001
	$b_{branches2}$	3.2750	0.0591
	$b_{foliage1}$	0.0066	0.0012
	$b_{foliage2}$	2.4213	0.0545
	b_{wood1}	0.2324	0.0326
Silver maple	b_{wood2}	2.1000	0.0398
	b_{bark1}	0.0278	0.0023
	b_{bark2}	2.0433	0.0262
	$b_{branches1}$	0.0028	0.0010
	$b_{branches2}$	3.1020	0.1059
	$b_{foliage1}$	0.1430	0.0545

Table 3 (continued).

Species	Parameter	Estimate	SE
Sugar maple	$b_{foliage2}$	1.2580	0.1091
	b_{wood1}	0.1315	0.0084
	b_{wood2}	2.3129	0.0182
	b_{bark1}	0.0631	0.0103
	b_{bark2}	1.9241	0.0464
	$b_{branches1}$	0.0330	0.0038
	$b_{branches2}$	2.3741	0.0341
	$b_{foliage1}$	0.0393	0.0024
	$b_{foliage2}$	1.6930	0.0196
	b_{wood1}	0.0625	0.0028
Tamarack larch	b_{wood2}	2.4475	0.0153
	b_{bark1}	0.0174	0.0005
	b_{bark2}	2.1109	0.0101
	$b_{branches1}$	0.0196	0.0015
	$b_{branches2}$	2.2652	0.0269
	$b_{foliage1}$	0.0801	0.0063
	$b_{foliage2}$	1.4875	0.0291
	b_{wood1}	0.0605	0.0029
Trembling aspen	b_{wood2}	2.4750	0.0155
	b_{bark1}	0.0168	0.0007
	b_{bark2}	2.3949	0.0143
	$b_{branches1}$	0.0080	0.0008
	$b_{branches2}$	2.5214	0.0333
	$b_{foliage1}$	0.0261	0.0036
	$b_{foliage2}$	1.6304	0.0439
	b_{wood1}	0.1861	0.0142
White ash	b_{wood2}	2.1665	0.0251
	b_{bark1}	0.0406	0.0040
	b_{bark2}	1.9946	0.0308
	$b_{branches1}$	0.0461	0.0102
	$b_{branches2}$	2.2291	0.0695
	$b_{foliage1}$	0.1106	0.0276
	$b_{foliage2}$	1.2277	0.0753
	b_{wood1}	0.0593	0.0020
White birch	b_{wood2}	2.5026	0.0114
	b_{bark1}	0.0135	0.0008
	b_{bark2}	2.4053	0.0193
	$b_{branches1}$	0.0135	0.0009
	$b_{branches2}$	2.5532	0.0231
	$b_{foliage1}$	0.0546	0.0028
	$b_{foliage2}$	1.6351	0.0189
	b_{wood1}	0.0402	0.0040
White elm	b_{wood2}	2.5804	0.0286
	b_{bark1}	0.0073	0.0023
	b_{bark2}	2.4859	0.0974
	$b_{branches1}$	0.0401	0.0042
	$b_{branches2}$	2.1826	0.0356
	$b_{foliage1}$	0.0750	0.0031

Table 3 (concluded).

Species	Parameter	Estimate	SE
White oak	b_{foliage2}	1.3436	0.0164
	b_{wood1}	0.0762	0.0082
	b_{wood2}	2.3335	0.0373
	b_{bark1}	0.0338	0.0019
	b_{bark2}	1.9845	0.0181
	$b_{\text{branches1}}$	0.0113	0.0023
	$b_{\text{branches2}}$	2.6211	0.0583
	b_{foliage1}	0.0188	0.0041
	b_{foliage2}	1.7881	0.0671
	b_{wood1}	0.0359	0.0009
White spruce	b_{wood2}	2.5775	0.0088
	b_{bark1}	0.0116	0.0005
	b_{bark2}	2.3022	0.0140
	$b_{\text{branches1}}$	0.0283	0.0017
	$b_{\text{branches2}}$	2.0823	0.0222
	b_{foliage1}	0.1601	0.0085
	b_{foliage2}	1.4670	0.0184
	b_{wood1}	0.1932	0.0193
	b_{wood2}	2.1569	0.0269
	b_{bark1}	0.0192	0.0017
Yellow birch	b_{bark2}	2.2475	0.0243
	$b_{\text{branches1}}$	0.0305	0.0024
	$b_{\text{branches2}}$	2.4044	0.0230
	b_{foliage1}	0.1119	0.0121
	b_{foliage2}	1.3973	0.0313
	b_{wood1}	0.0871	0.0015
	b_{wood2}	2.3702	0.0052
	b_{bark1}	0.0241	0.0009
	b_{bark2}	2.1969	0.0116
	$b_{\text{branches1}}$	0.0167	0.0007
Hardwood	$b_{\text{branches2}}$	2.4807	0.0131
	b_{foliage1}	0.0390	0.0009
	b_{foliage2}	1.6229	0.0083
	b_{wood1}	0.0648	0.0012
	b_{wood2}	2.3927	0.0061
	b_{bark1}	0.0162	0.0002
	b_{bark2}	2.1959	0.0055
	$b_{\text{branches1}}$	0.0156	0.0005
	$b_{\text{branches2}}$	2.2916	0.0108
	b_{foliage1}	0.0861	0.0025
Softwood	b_{foliage2}	1.6261	0.0100
	b_{wood1}	0.0787	0.0012
	b_{wood2}	2.3702	0.0051
	b_{bark1}	0.0185	0.0002
	b_{bark2}	2.2159	0.0041
	$b_{\text{branches1}}$	0.0230	0.0006
	$b_{\text{branches2}}$	2.2678	0.0097
	b_{foliage1}	0.0767	0.0021
	b_{foliage2}	1.5720	0.0096
	b_{wood1}	0.0230	0.0008
All	b_{wood2}	2.3702	0.0051
	b_{bark1}	0.0185	0.0002
	b_{bark2}	2.2159	0.0041
	$b_{\text{branches1}}$	0.0230	0.0006
	$b_{\text{branches2}}$	2.2678	0.0097
	b_{foliage1}	0.0767	0.0021
	b_{foliage2}	1.5720	0.0096

Table 4. Model parameter estimates and their standard error (SE) for the dbh- and height-based set of equations per species, genus, and all species combined.*

Species	Parameter	Estimate	SE
Alpine fir	b_{wood1}	0.0268	0.0023
	b_{wood2}	1.7579	0.0577
	b_{wood3}	0.9871	0.0794
	b_{bark1}	0.0009	0.0004
	b_{bark2}	1.4460	0.2504
	b_{bark3}	1.8839	0.3653
	$b_{\text{branches1}}$	0.0470	0.0085
	$b_{\text{branches2}}$	2.9288	0.2044
	$b_{\text{branches3}}$	-1.1588	0.2155
	b_{foliage1}	0.0551	0.0151
Balsam fir	b_{foliage2}	1.7585	0.0885
	b_{foliage3}	—	—
	b_{wood1}	0.0294	0.0008
	b_{wood2}	1.8357	0.0163
	b_{wood3}	0.8640	0.0213
	b_{bark1}	0.0053	0.0004
	b_{bark2}	2.0876	0.0388
	b_{bark3}	0.5842	0.0506
	$b_{\text{branches1}}$	0.0117	0.0008
	$b_{\text{branches2}}$	3.5097	0.0667
Balsam poplar	$b_{\text{branches3}}$	-1.3006	0.0773
	b_{foliage1}	0.1245	0.0073
	b_{foliage2}	2.5230	0.0750
	b_{foliage3}	-1.1230	0.0878
	b_{wood1}	0.0117	0.0015
	b_{wood2}	1.7757	0.0541
	b_{wood3}	1.2555	0.0883
	b_{bark1}	0.0180	0.0036
	b_{bark2}	1.8131	0.0939
	b_{bark3}	0.5144	0.1438
Basswood	$b_{\text{branches1}}$	0.0112	0.0028
	$b_{\text{branches2}}$	3.0861	0.1464
	$b_{\text{branches3}}$	-0.7164	0.2179
	b_{foliage1}	0.0617	0.0103
	b_{foliage2}	1.8615	0.1264
	b_{foliage3}	-0.5375	0.1855
	b_{wood1}	0.0168	0.0014
	b_{wood2}	1.9844	0.0494
	b_{wood3}	0.8989	0.0767
	b_{bark1}	0.0057	0.0010

Table 4 (continued).

Species	Parameter	Estimate	SE
Beech	$b_{foliage3}$	—	—
	b_{wood1}	0.0432	0.0053
	b_{wood2}	2.0378	0.0443
	b_{wood3}	0.7000	0.0816
	b_{bark1}	0.0049	0.0015
	b_{bark2}	1.9057	0.0905
	b_{bark3}	0.6770	0.1709
	$b_{branches1}$	0.0355	0.0045
	$b_{branches2}$	2.3749	0.0381
	$b_{branches3}$	—	—
	$b_{foliage1}$	0.0452	0.0080
	$b_{foliage2}$	1.5567	0.0529
	$b_{foliage3}$	—	—
Black ash	b_{wood1}	0.0306	0.0081
	b_{wood2}	2.1836	0.0575
	b_{wood3}	0.5740	0.1344
	b_{bark1}	0.0897	0.0452
	b_{bark2}	2.2634	0.1301
	b_{bark3}	-0.5670	0.2761
	$b_{branches1}$	0.0994	0.0273
	$b_{branches2}$	2.1630	0.1432
	$b_{branches3}$	-0.4809	0.2285
	$b_{foliage1}$	0.0124	0.0047
	$b_{foliage2}$	1.0325	0.1425
	$b_{foliage3}$	0.8747	0.2638
Black cherry	b_{wood1}	0.0181	0.0050
	b_{wood2}	1.7013	0.0571
	b_{wood3}	1.3057	0.1157
	b_{bark1}	0.0101	0.0034
	b_{bark2}	1.5956	0.0767
	b_{bark3}	0.9190	0.1401
	$b_{branches1}$	0.0005	0.0004
	$b_{branches2}$	2.8004	0.1592
	$b_{branches3}$	0.8603	0.3067
	$b_{foliage1}$	0.1976	0.0291
	$b_{foliage2}$	1.4421	0.1099
	$b_{foliage3}$	-0.5264	0.1743
Black spruce	b_{wood1}	0.0309	0.0005
	b_{wood2}	1.7527	0.0120
	b_{wood3}	1.0014	0.0144
	b_{bark1}	0.0115	0.0004
	b_{bark2}	1.7405	0.0266
	b_{bark3}	0.6589	0.0303
	$b_{branches1}$	0.0380	0.0024
	$b_{branches2}$	3.2558	0.0543
	$b_{branches3}$	-1.4218	0.0606
	$b_{foliage1}$	0.2048	0.0087
	$b_{foliage2}$	2.5754	0.0496
	$b_{foliage3}$	-1.3704	0.0561

Table 4 (continued).

Species	Parameter	Estimate	SE
Eastern hemlock	b_{wood1}	0.0257	0.0019
	b_{wood2}	1.9277	0.0357
	b_{wood3}	0.8576	0.0549
	b_{bark1}	0.0118	0.0012
	b_{bark2}	1.9893	0.0614
	b_{bark3}	0.4700	0.0928
	$b_{branches1}$	0.0215	0.0044
	$b_{branches2}$	2.6553	0.1087
	$b_{branches3}$	-0.4682	0.1564
	$b_{foliage1}$	0.1471	0.0179
	$b_{foliage2}$	2.0108	0.0959
	$b_{foliage3}$	-0.6080	0.1416
Eastern redcedar	b_{wood1}	0.0520	0.0069
	b_{wood2}	1.7731	0.0347
	b_{wood3}	0.7054	0.0871
	b_{bark1}	0.0283	0.0040
	b_{bark2}	1.7079	0.0488
	b_{bark3}	—	—
	$b_{branches1}$	0.0219	0.0063
	$b_{branches2}$	2.3585	0.0899
	$b_{branches3}$	—	—
	$b_{foliage1}$	0.2575	0.1128
	$b_{foliage2}$	2.5136	0.1784
	$b_{foliage3}$	-1.5565	0.3393
Eastern white-cedar	b_{wood1}	0.0295	0.0018
	b_{wood2}	1.7026	0.0355
	b_{wood3}	0.9428	0.0600
	b_{bark1}	0.0076	0.0008
	b_{bark2}	1.7861	0.0628
	b_{bark3}	0.6132	0.1045
	$b_{branches1}$	0.0501	0.0066
	$b_{branches2}$	2.5165	0.1117
	$b_{branches3}$	-0.8774	0.1719
	$b_{foliage1}$	0.0813	0.0105
	$b_{foliage2}$	2.2180	0.1124
	$b_{foliage3}$	-0.7907	0.1708
Eastern white pine	b_{wood1}	0.0170	0.0008
	b_{wood2}	1.7779	0.0197
	b_{wood3}	1.1370	0.0305
	b_{bark1}	0.0069	0.0005
	b_{bark2}	1.6589	0.0369
	b_{bark3}	0.9582	0.0534
	$b_{branches1}$	0.0184	0.0020
	$b_{branches2}$	3.1968	0.0665
	$b_{branches3}$	-1.0876	0.0874
	$b_{foliage1}$	0.0584	0.0113
	$b_{foliage2}$	2.2389	0.0772
	$b_{foliage3}$	-0.5968	0.1038
Grey birch	b_{wood1}	0.0295	0.0022

Table 4 (continued).

Species	Parameter	Estimate	SE
Hickory	$b_{\text{wood}2}$	1.9064	0.0375
	$b_{\text{wood}3}$	0.9139	0.0604
	$b_{\text{bark}1}$	0.0148	0.0036
	$b_{\text{bark}2}$	1.8433	0.1463
	$b_{\text{bark}3}$	0.5021	0.2200
	$b_{\text{branches}1}$	0.0150	0.0058
	$b_{\text{branches}2}$	3.0347	0.2225
	$b_{\text{branches}3}$	-0.7629	0.3448
	$b_{\text{foliage}1}$	0.0455	0.0056
	$b_{\text{foliage}2}$	2.6447	0.1905
	$b_{\text{foliage}3}$	-1.4955	0.2381
	$b_{\text{wood}1}$	0.0139	0.0020
	$b_{\text{wood}2}$	1.5913	0.0472
	$b_{\text{wood}3}$	1.5080	0.0797
	$b_{\text{bark}1}$	0.0081	0.0021
	$b_{\text{bark}2}$	1.4943	0.0886
	$b_{\text{bark}3}$	1.1324	0.1413
	$b_{\text{branches}1}$	0.0050	0.0014
	$b_{\text{branches}2}$	3.0463	0.0900
	$b_{\text{branches}3}$	—	—
	$b_{\text{foliage}1}$	0.0121	0.0025
	$b_{\text{foliage}2}$	2.0865	0.0623
	$b_{\text{foliage}3}$	—	—
Hop-hornbeam	$b_{\text{wood}1}$	0.0083	0.0033
	$b_{\text{wood}2}$	1.6534	0.0532
	$b_{\text{wood}3}$	1.7479	0.1630
	$b_{\text{bark}1}$	0.0012	0.0009
	$b_{\text{bark}2}$	1.1486	0.1174
	$b_{\text{bark}3}$	2.2903	0.3428
	$b_{\text{branches}1}$	0.0009	0.0009
	$b_{\text{branches}2}$	1.9152	0.1380
	$b_{\text{branches}3}$	1.7769	0.4215
	$b_{\text{foliage}1}$	0.0247	0.0085
	$b_{\text{foliage}2}$	2.0056	0.1271
	$b_{\text{foliage}3}$	—	—
	$b_{\text{wood}1}$	0.0199	0.0010
Jack pine	$b_{\text{wood}2}$	1.6883	0.0185
	$b_{\text{wood}3}$	1.2456	0.0280
	$b_{\text{bark}1}$	0.0141	0.0010
	$b_{\text{bark}2}$	1.5994	0.0388
	$b_{\text{bark}3}$	0.5957	0.0553
	$b_{\text{branches}1}$	0.0185	0.0021
	$b_{\text{branches}2}$	3.0584	0.0551
	$b_{\text{branches}3}$	-0.9816	0.0654
	$b_{\text{foliage}1}$	0.0325	0.0035
	$b_{\text{foliage}2}$	1.7879	0.0359
	$b_{\text{foliage}3}$	—	—
	$b_{\text{wood}1}$	0.0128	0.0011
	$b_{\text{wood}2}$	2.0633	0.0314
Largetooth aspen	$b_{\text{wood}3}$	0.9516	0.0480
	$b_{\text{bark}1}$	0.0240	0.0022
	$b_{\text{bark}2}$	2.3055	0.0325
	$b_{\text{bark}3}$	—	—
	$b_{\text{branches}1}$	0.0131	0.0017
	$b_{\text{branches}2}$	3.1274	0.0766
	$b_{\text{branches}3}$	-0.8379	0.0902
	$b_{\text{foliage}1}$	0.0382	0.0028
	$b_{\text{foliage}2}$	2.1673	0.0547
	$b_{\text{foliage}3}$	-0.6842	0.0647

Table 4 (continued).

Species	Parameter	Estimate	SE
Lodgepole pine	$b_{\text{wood}1}$	0.0202	0.0008
	$b_{\text{wood}2}$	1.7179	0.0242
	$b_{\text{wood}3}$	1.2078	0.0341
	$b_{\text{bark}1}$	0.0099	0.0007
	$b_{\text{bark}2}$	1.6049	0.0535
	$b_{\text{bark}3}$	0.7456	0.0710
	$b_{\text{branches}1}$	0.0440	0.0066
	$b_{\text{branches}2}$	3.7190	0.1449
	$b_{\text{branches}3}$	-2.0399	0.1699
	$b_{\text{foliage}1}$	0.0785	0.0114
	$b_{\text{foliage}2}$	2.5377	0.1291
	$b_{\text{foliage}3}$	-1.1213	0.1558
	$b_{\text{wood}1}$	0.0224	0.0048
	$b_{\text{wood}2}$	1.7845	0.0816
	$b_{\text{wood}3}$	1.0660	0.1202
	$b_{\text{bark}1}$	0.0219	0.0051
	$b_{\text{bark}2}$	1.4190	0.0882
	$b_{\text{bark}3}$	0.8963	0.1307
Red ash	$b_{\text{branches}1}$	0.0176	0.0077
	$b_{\text{branches}2}$	2.3313	0.1358
	$b_{\text{branches}3}$	—	—
	$b_{\text{foliage}1}$	0.0761	0.0263
	$b_{\text{foliage}2}$	1.3077	0.1043
	$b_{\text{foliage}3}$	—	—
	$b_{\text{wood}1}$	0.0315	0.0042
	$b_{\text{wood}2}$	2.0342	0.0423
	$b_{\text{wood}3}$	0.7485	0.0770
	$b_{\text{bark}1}$	0.0283	0.0029
Red maple	$b_{\text{bark}2}$	2.0907	0.0332
	$b_{\text{bark}3}$	—	—
	$b_{\text{branches}1}$	0.0225	0.0034
	$b_{\text{branches}2}$	2.4106	0.0475
	$b_{\text{branches}3}$	—	—
	$b_{\text{foliage}1}$	0.0571	0.0064
	$b_{\text{foliage}2}$	1.4898	0.0358
	$b_{\text{foliage}3}$	—	—
	$b_{\text{wood}1}$	0.0285	0.0049
	$b_{\text{wood}2}$	1.8501	0.0368
Red oak	$b_{\text{wood}3}$	1.0204	0.0732

Table 4 (continued).

Species	Parameter	Estimate	SE
Red pine	$b_{\text{bark}1}$	0.0326	0.0066
	$b_{\text{bark}2}$	1.8100	0.0610
	$b_{\text{bark}3}$	0.4153	0.1090
	$b_{\text{branches}1}$	0.0013	0.0005
	$b_{\text{branches}2}$	3.0637	0.0863
	$b_{\text{branches}3}$	0.3153	0.1273
	$b_{\text{foliage}1}$	0.0582	0.0048
	$b_{\text{foliage}2}$	1.5438	0.0295
	$b_{\text{foliage}3}$	—	—
	$b_{\text{wood}1}$	0.0106	0.0005
	$b_{\text{wood}2}$	1.7725	0.0143
	$b_{\text{wood}3}$	1.3285	0.0229
	$b_{\text{bark}1}$	0.0277	0.0018
	$b_{\text{bark}2}$	1.5192	0.0425
	$b_{\text{bark}3}$	0.4645	0.0519
	$b_{\text{branches}1}$	0.0125	0.0010
	$b_{\text{branches}2}$	3.3865	0.0403
	$b_{\text{branches}3}$	-1.1939	0.0551
Red spruce	$b_{\text{foliage}1}$	0.0731	0.0068
	$b_{\text{foliage}2}$	2.3439	0.0494
	$b_{\text{foliage}3}$	-0.7378	0.0639
	$b_{\text{wood}1}$	0.0143	0.0016
	$b_{\text{wood}2}$	1.6441	0.0340
	$b_{\text{wood}3}$	1.4065	0.0690
	$b_{\text{bark}1}$	0.0274	0.0041
	$b_{\text{bark}2}$	2.0188	0.0481
	$b_{\text{bark}3}$	—	—
	$b_{\text{branches}1}$	0.0005	0.0001
	$b_{\text{branches}2}$	3.3136	0.0779
	$b_{\text{branches}3}$	—	—
	$b_{\text{foliage}1}$	0.0106	0.0022
	$b_{\text{foliage}2}$	2.2709	0.0649
	$b_{\text{foliage}3}$	—	—
Silver maple	$b_{\text{wood}1}$	0.0274	0.0055
	$b_{\text{wood}2}$	1.7126	0.0581
	$b_{\text{wood}3}$	1.1086	0.1198
	$b_{\text{bark}1}$	0.0123	0.0044
	$b_{\text{bark}2}$	1.8250	0.0955
	$b_{\text{bark}3}$	0.5010	0.1990
	$b_{\text{branches}1}$	0.0543	0.0391
	$b_{\text{branches}2}$	3.7343	0.2311
	$b_{\text{branches}3}$	-1.6497	0.4651
	$b_{\text{foliage}1}$	6.6808	3.3429
	$b_{\text{foliage}2}$	2.1092	0.2006
	$b_{\text{foliage}3}$	-2.1697	0.3733
Sugar maple	$b_{\text{wood}1}$	0.0301	0.0040
	$b_{\text{wood}2}$	2.0313	0.0307
	$b_{\text{wood}3}$	0.8171	0.0717

Table 4 (continued).

Species	Parameter	Estimate	SE
Tamarack larch	$b_{\text{bark}1}$	0.0103	0.0037
	$b_{\text{bark}2}$	1.7111	0.0749
	$b_{\text{bark}3}$	0.8509	0.1772
	$b_{\text{branches}1}$	0.0661	0.0161
	$b_{\text{branches}2}$	2.5940	0.0706
	$b_{\text{branches}3}$	-0.4933	0.1490
	$b_{\text{foliage}1}$	2.5019	0.2763
	$b_{\text{foliage}2}$	2.4527	0.0698
	$b_{\text{foliage}3}$	-2.3008	0.1089
	$b_{\text{wood}1}$	0.0276	0.0010
	$b_{\text{wood}2}$	1.6724	0.0208
	$b_{\text{wood}3}$	1.1443	0.0271
	$b_{\text{bark}1}$	0.0120	0.0004
	$b_{\text{bark}2}$	1.7059	0.0243
	$b_{\text{bark}3}$	0.5811	0.0318
	$b_{\text{branches}1}$	0.0336	0.0028
	$b_{\text{branches}2}$	3.1335	0.0694
	$b_{\text{branches}3}$	-1.1559	0.0864
Trembling aspen	$b_{\text{foliage}1}$	0.1324	0.0107
	$b_{\text{foliage}2}$	2.1140	0.0770
	$b_{\text{foliage}3}$	-0.8781	0.0983
	$b_{\text{wood}1}$	0.0142	0.0005
	$b_{\text{wood}2}$	1.9389	0.0176
	$b_{\text{wood}3}$	1.0572	0.0271
	$b_{\text{bark}1}$	0.0063	0.0005
	$b_{\text{bark}2}$	2.0819	0.0354
	$b_{\text{bark}3}$	0.6617	0.0527
	$b_{\text{branches}1}$	0.0137	0.0012
	$b_{\text{branches}2}$	2.9270	0.0445
	$b_{\text{branches}3}$	-0.6221	0.0633
	$b_{\text{foliage}1}$	0.0270	0.0018
	$b_{\text{foliage}2}$	1.6183	0.0231
	$b_{\text{foliage}3}$	—	—
White ash	$b_{\text{wood}1}$	0.0224	0.0046
	$b_{\text{wood}2}$	1.7438	0.0364
	$b_{\text{wood}3}$	1.1899	0.0917
	$b_{\text{bark}1}$	0.0126	0.0034
	$b_{\text{bark}2}$	1.6456	0.0607
	$b_{\text{bark}3}$	0.7893	0.1361
	$b_{\text{branches}1}$	0.0354	0.0084
	$b_{\text{branches}2}$	2.3046	0.0739
	$b_{\text{branches}3}$	—	—
	$b_{\text{foliage}1}$	0.0195	0.0093
	$b_{\text{foliage}2}$	1.0509	0.1073
	$b_{\text{foliage}3}$	0.7836	0.1980
White birch	$b_{\text{wood}1}$	0.0338	0.0011
	$b_{\text{wood}2}$	2.0702	0.0157
	$b_{\text{wood}3}$	0.6876	0.0233

Table 4 (continued).

Species	Parameter	Estimate	SE
White elm	$b_{\text{bark}1}$	0.0080	0.0006
	$b_{\text{bark}2}$	1.9754	0.0320
	$b_{\text{bark}3}$	0.6659	0.0466
	$b_{\text{branches}1}$	0.0257	0.0020
	$b_{\text{branches}2}$	3.1754	0.0492
	$b_{\text{branches}3}$	-0.9417	0.0684
	$b_{\text{foliage}1}$	0.1415	0.0086
	$b_{\text{foliage}2}$	2.3074	0.0513
	$b_{\text{foliage}3}$	-1.1189	0.0723
	$b_{\text{wood}1}$	0.0207	0.0039
	$b_{\text{wood}2}$	2.2276	0.0632
	$b_{\text{wood}3}$	0.6488	0.1171
	$b_{\text{bark}1}$	0.0078	0.0024
	$b_{\text{bark}2}$	2.4540	0.0954
	$b_{\text{bark}3}$	—	—
	$b_{\text{branches}1}$	0.0393	0.0059
	$b_{\text{branches}2}$	2.1880	0.0456
	$b_{\text{branches}3}$	—	—
White oak	$b_{\text{foliage}1}$	0.0516	0.0028
	$b_{\text{foliage}2}$	1.4511	0.0187
	$b_{\text{foliage}3}$	—	—
	$b_{\text{wood}1}$	0.0442	0.0049
	$b_{\text{wood}2}$	1.6818	0.0457
	$b_{\text{wood}3}$	1.0310	0.0844
	$b_{\text{bark}1}$	0.0308	0.0050
	$b_{\text{bark}2}$	1.7479	0.0672
	$b_{\text{bark}3}$	0.3504	0.1137
	$b_{\text{branches}1}$	0.0022	0.0006
	$b_{\text{branches}2}$	2.0165	0.0598
	$b_{\text{branches}3}$	1.3953	0.1278
	$b_{\text{foliage}1}$	0.0053	0.0017
	$b_{\text{foliage}2}$	1.2822	0.1077
	$b_{\text{foliage}3}$	1.1323	0.1905
White spruce	$b_{\text{wood}1}$	0.0265	0.0007
	$b_{\text{wood}2}$	1.7952	0.0180
	$b_{\text{wood}3}$	0.9733	0.0208
	$b_{\text{bark}1}$	0.0124	0.0006
	$b_{\text{bark}2}$	1.6962	0.0459
	$b_{\text{bark}3}$	0.6489	0.0517
	$b_{\text{branches}1}$	0.0325	0.0016
	$b_{\text{branches}2}$	2.8573	0.0522
	$b_{\text{branches}3}$	-0.9127	0.0578
	$b_{\text{foliage}1}$	0.2020	0.0094
	$b_{\text{foliage}2}$	2.3802	0.0524
	$b_{\text{foliage}3}$	-1.1103	0.0586
Yellow birch	$b_{\text{wood}1}$	0.0259	0.0038
	$b_{\text{wood}2}$	1.9044	0.0305
	$b_{\text{wood}3}$	0.9715	0.0709

Table 4 (concluded).

Species	Parameter	Estimate	SE
Hardwood	$b_{\text{bark}1}$	0.0069	0.0015
	$b_{\text{bark}2}$	2.0834	0.0534
	$b_{\text{bark}3}$	0.5371	0.1178
	$b_{\text{branches}1}$	0.0325	0.0025
	$b_{\text{branches}2}$	2.3851	0.0231
	$b_{\text{branches}3}$	—	—
	$b_{\text{foliage}1}$	0.1683	0.0222
	$b_{\text{foliage}2}$	1.2764	0.0380
	$b_{\text{foliage}3}$	—	—
	$b_{\text{wood}1}$	0.0359	0.0009
	$b_{\text{wood}2}$	2.0263	0.0100
	$b_{\text{wood}3}$	0.6987	0.0168
	$b_{\text{bark}1}$	0.0094	0.0005
	$b_{\text{bark}2}$	1.8677	0.0201
	$b_{\text{bark}3}$	0.6985	0.0327
	$b_{\text{branches}1}$	0.0433	0.0024
	$b_{\text{branches}2}$	2.6817	0.0309
	$b_{\text{branches}3}$	-0.5731	0.0461
Softwood	$b_{\text{foliage}1}$	0.0859	0.0038
	$b_{\text{foliage}2}$	1.8485	0.0266
	$b_{\text{foliage}3}$	-0.5383	0.0412
	$b_{\text{wood}1}$	0.0284	0.0003
	$b_{\text{wood}2}$	1.6894	0.0065
	$b_{\text{wood}3}$	1.0857	0.0086
	$b_{\text{bark}1}$	0.0100	0.0003
	$b_{\text{bark}2}$	1.8463	0.0174
	$b_{\text{bark}3}$	0.5616	0.0218
	$b_{\text{branches}1}$	0.0301	0.0008
	$b_{\text{branches}2}$	3.0038	0.0201
	$b_{\text{branches}3}$	-1.0520	0.0252
	$b_{\text{foliage}1}$	0.1554	0.0036
	$b_{\text{foliage}2}$	2.4021	0.0218
	$b_{\text{foliage}3}$	-1.1043	0.0271
All	$b_{\text{wood}1}$	0.0348	0.0005
	$b_{\text{wood}2}$	1.9235	0.0070
	$b_{\text{wood}3}$	0.7829	0.0092
	$b_{\text{bark}1}$	0.0139	0.0004
	$b_{\text{bark}2}$	1.5429	0.0176
	$b_{\text{bark}3}$	0.8189	0.0242
	$b_{\text{branches}1}$	0.0346	0.0008
	$b_{\text{branches}2}$	2.6706	0.0194
	$b_{\text{branches}3}$	-0.6033	0.0252
	$b_{\text{foliage}1}$	0.1822	0.0039
	$b_{\text{foliage}2}$	2.2864	0.0183
	$b_{\text{foliage}3}$	-1.1203	0.0239

*Missing values (—) correspond to parameter estimates not significantly different from zero ($\alpha = 0.05$).

Table 5. Nonlinear, seemingly unrelated regression-fitting statistics with weight functions.*

Species	Model	dbh-based set of equations					dbh- and height-based set of equations				
		$\hat{\sigma}_{\text{SUR}}^2$	$\hat{\sigma}_{ii}$	AdjRSq	RMSE	c	$\hat{\sigma}_{\text{SUR}}^2$	$\hat{\sigma}_{ii}$	AdjRSq	RMSE	c
Alpine fir	Wood	1.0125	0.0925	0.97	18.1	2.44	1.1353	0.0008	0.99	10.5	3.70
	Bark	0.0018	0.94		4.5	2.87		0.0001	0.94	4.6	3.93
	Stem	0.0595	0.97		20.7	2.67		0.0007	0.99	11.7	3.87
	Branches	0.0004	0.75		10.4	3.80		0.0009	0.72	11.0	3.56
	Foliage	0.0040	0.64		7.8	2.88		0.0065	0.65	7.7	2.78
	Crown	0.0047	0.72		18.0	3.32		0.0085	0.70	18.4	3.19
	Total	0.2380	0.96		30.8	2.44		0.0313	0.97	26.7	3.00
Balsam fir	Wood	1.0053	0.0012	0.96	16.9	4.04	1.0001	0.0005	0.99	9.6	3.96
	Bark	0.0001	0.90		5.0	4.08		0.0001	0.92	4.3	3.81
	Stem	0.0017	0.96		19.8	4.03		0.0010	0.99	11.6	3.83
	Branches	0.0003	0.74		9.6	3.90		0.0004	0.79	8.7	3.75
	Foliage	0.0305	0.58		6.9	2.41		0.1230	0.63	6.5	1.86
	Crown	0.0042	0.72		14.8	3.49		0.0319	0.77	13.4	2.67
	Total	0.0047	0.97		20.1	3.63		0.0073	0.98	17.6	3.38
Balsam poplar	Wood	1.0032	0.0008	0.90	50.5	4.49	1.0017	0.0364	0.94	39.8	3.06
	Bark	0.0003	0.88		9.2	3.86		0.0032	0.89	8.9	3.02
	Stem	0.0054	0.92		54.6	3.90		0.0149	0.95	43.4	3.39
	Branches	0.0002	0.71		24.4	4.27		0.0003	0.75	22.6	4.16
	Foliage	0.0005	0.68		2.3	2.97		0.0010	0.69	2.3	2.69
	Crown	0.0002	0.72		25.5	4.43		0.0002	0.76	23.9	4.47
	Total	0.0049	0.91		67.7	4.02		0.0241	0.94	56.9	3.41
Basswood	Wood	1.0101	0.0275	0.97	43.2	3.14	1.0049	0.0002	0.97	37.9	4.54
	Bark	0.0039	0.81		16.8	3.02		0.0010	0.86	14.5	3.33
	Stem	0.0539	0.96		53.9	3.04		0.0002	0.97	44.1	4.68
	Branches	0.0009	0.84		23.3	3.80		0.0004	0.85	22.6	4.09
	Foliage	0.0030	0.51		5.2	2.61		0.0030	0.51	5.2	2.62
	Crown	0.0025	0.85		25.0	3.60		0.0006	0.86	24.2	4.12
	Total	0.1755	0.96		62.5	2.91		0.0021	0.97	52.6	4.12
Beech	Wood	1.0102	0.3006	0.90	80.0	2.85	1.0874	0.0299	0.91	76.0	3.47
	Bark	0.0006	0.82		7.5	3.35		0.0002	0.84	7.0	3.65
	Stem	0.3312	0.90		84.7	2.86		0.0215	0.91	79.9	3.61
	Branches	0.0041	0.73		49.4	3.90		0.0116	0.73	49.4	3.57
	Foliage	0.2004	0.47		4.3	1.32		0.2318	0.48	4.3	1.27
	Crown	0.0217	0.72		52.8	3.43		0.1186	0.72	52.8	2.91
	Total	0.4720	0.90		115.9	2.92		0.1702	0.91	111.0	3.18
Black ash	Wood	1.0029	0.0033	0.97	27.1	3.96	1.0164	0.0529	0.97	23.0	2.89
	Bark	0.0192	0.93		5.3	2.31		0.0173	0.92	5.6	2.36
	Stem	0.0182	0.97		30.8	3.43		0.2132	0.97	27.4	2.52
	Branches	0.0011	0.72		10.9	3.93		0.0017	0.72	11.0	3.79
	Foliage	0.0542	0.57		1.7	1.35		0.0107	0.60	1.6	1.89
	Crown	0.0039	0.71		12.5	3.59		0.0059	0.70	12.6	3.44
	Total	0.0085	0.96		35.6	3.82		0.1349	0.97	32.9	2.76
Black cherry	Wood	1.0599	22.3981	0.73	85.4	1.61	1.1313	0.1302	0.91	50.5	2.84
	Bark	0.4492	0.71		10.9	1.58		0.0125	0.79	9.4	2.61
	Stem	30.8718	0.74		93.5	1.56		0.1773	0.90	56.5	2.80
	Branches	0.0015	0.58		54.6	4.28		0.0036	0.75	42.5	3.93
	Foliage	5.8842	0.56		2.4	—		0.0205	0.55	2.4	1.77
	Crown	0.0012	0.59		55.8	4.39		0.0032	0.74	44.1	3.97
	Total	60.7665	0.80		116.4	1.52		0.2573	0.92	73.8	2.93
Black spruce	Wood	1.0005	0.0118	0.93	14.3	3.30	1.0001	0.0006	0.98	6.8	3.94
	Bark	0.0006	0.90		2.2	3.05		0.0001	0.93	1.8	3.71
	Stem	0.0189	0.93		15.6	3.19		0.0009	0.98	7.4	3.85
	Branches	0.0017	0.61		7.2	3.43		0.0009	0.70	6.3	3.57
	Foliage	0.0105	0.53		4.9	2.78		0.0097	0.60	4.5	2.70
	Crown	0.0147	0.62		11.1	3.10		0.0079	0.71	9.7	3.21
	Total	0.0091	0.96		15.2	3.55		0.0093	0.97	12.5	3.38

Table 5 (continued).

Species	Model	dbh-based set of equations					dbh- and height-based set of equations				
		$\hat{\sigma}_{\text{SUR}}^2$	$\hat{\sigma}_{ii}$	AdjRSq	RMSE	c	$\hat{\sigma}_{\text{SUR}}^2$	$\hat{\sigma}_{ii}$	AdjRSq	RMSE	c
Eastern hemlock	Wood	1.0005	0.0005	0.93	56.3	4.58	1.0006	0.0080	0.96	42.3	3.41
	Bark	0.0001	0.90	11.9	4.10		0.0001	0.90	11.9	4.00	
	Stem	0.0013	0.94	59.5	4.31		0.0074	0.97	45.0	3.52	
	Branches	0.0036	0.73	30.2	3.40		0.0025	0.74	29.4	3.50	
	Foliage	0.0010	0.77	10.7	3.43		0.0008	0.74	11.4	3.53	
	Crown	0.0106	0.77	37.6	3.28		0.0094	0.77	37.4	3.30	
	Total	0.0156	0.94	78.0	3.60		0.1216	0.95	68.8	2.89	
Eastern redcedar	Wood	1.0903	0.2877	0.96	6.9	1.92	1.3423	0.0401	0.98	4.8	2.49
	Bark	0.0150	0.92	0.8	1.36		0.0099	0.91	0.8	1.54	
	Stem	0.4967	0.96	7.4	1.76		0.1072	0.98	5.3	2.15	
	Branches	0.0152	0.81	10.3	2.92		0.0135	0.81	10.5	2.94	
	Foliage	0.0120	0.81	5.3	2.70		0.1601	0.81	5.3	1.69	
	Crown	0.1964	0.86	13.0	2.25		0.8142	0.86	13.1	1.68	
	Total	2.1210	0.96	14.1	1.54		1.1460	0.95	15.0	1.72	
Eastern white-cedar	Wood	1.0009	0.0269	0.94	20.5	2.78	1.0052	0.0013	0.97	15.1	3.54
	Bark	0.0002	0.90	4.1	3.29		0.0007	0.91	4.0	2.81	
	Stem	0.0172	0.95	22.5	2.99		0.0013	0.97	16.7	3.62	
	Branches	0.0004	0.75	9.2	3.70		0.0023	0.75	9.2	3.07	
	Foliage	0.0021	0.70	6.6	2.94		0.0018	0.68	6.8	2.99	
	Crown	0.0030	0.75	15.1	3.35		0.0106	0.74	15.4	2.92	
	Total	0.0315	0.95	29.5	2.96		0.0140	0.96	26.6	3.15	
Eastern white pine	Wood	1.0016	0.4629	0.89	109.8	2.66	1.0032	0.0003	0.98	50.1	4.26
	Bark	0.0002	0.90	15.1	3.75		0.0001	0.93	12.5	3.97	
	Stem	0.3476	0.90	120.5	2.79		0.0003	0.98	54.5	4.34	
	Branches	0.0009	0.82	35.1	3.71		0.0000	0.89	27.3	4.66	
	Foliage	0.0009	0.82	10.1	3.25		0.0455	0.84	9.4	2.05	
	Crown	0.0006	0.85	40.5	4.04		0.0035	0.91	31.9	3.37	
	Total	0.3142	0.95	106.1	2.76		0.0119	0.98	65.6	3.40	
Grey birch	Wood	1.2562	0.0057	0.96	6.0	3.11	1.9853	0.0003	0.98	4.0	3.96
	Bark	0.0002	0.92	1.4	3.30		0.0001	0.94	1.2	3.65	
	Stem	0.0066	0.96	7.3	3.18		0.0035	0.98	4.8	3.11	
	Branches	0.0002	0.76	4.2	4.10		0.0005	0.69	4.7	3.69	
	Foliage	0.0001	0.81	0.5	2.90		0.0008	0.67	0.7	2.18	
	Crown	0.0005	0.76	4.7	3.88		0.0014	0.68	5.4	3.41	
	Total	0.0016	0.94	11.1	3.92		0.0050	0.96	9.0	3.33	
Hickory	Wood	1.0344	1.7733	0.86	79.4	2.40	1.0324	0.0031	0.97	36.8	3.94
	Bark	0.0065	0.91	7.9	2.89		0.0006	0.92	7.4	3.47	
	Stem	1.9675	0.88	83.7	2.42		0.0058	0.97	38.0	3.81	
	Branches	0.0012	0.72	70.6	4.46		0.0044	0.72	71.8	4.05	
	Foliage	14.3183	0.83	3.8	—		0.0025	0.83	3.8	2.64	
	Crown	0.0018	0.74	73.4	4.38		0.0024	0.73	74.6	4.27	
	Total	1.2935	0.87	131.6	2.76		0.0195	0.95	83.9	3.79	
Hop-hornbeam	Wood	0.7228	22.9024	0.91	4.8	—	0.7287	7.4768	0.97	2.7	—
	Bark	1.1138	0.74	1.1	—		0.3496	0.92	0.6	—	
	Stem	35.2605	0.89	5.9	—		0.0035	0.97	3.4	3.87	
	Branches	1.2060	0.92	1.1	—		0.5735	0.96	0.8	—	
	Foliage	0.2139	0.95	0.5	—		0.2043	0.95	0.5	—	
	Crown	1.2945	0.96	1.1	—		1.1057	0.97	1.1	—	
	Total	0.0679	0.92	6.9	2.73		15.6629	0.97	4.0	—	
Jack pine	Wood	1.0050	0.0282	0.91	35.5	3.28	1.0028	0.0010	0.98	17.3	3.96
	Bark	0.0001	0.88	3.0	3.40		0.0000	0.91	2.5	3.85	
	Stem	0.0329	0.92	37.2	3.26		0.0010	0.98	17.6	3.97	
	Branches	0.0001	0.71	10.3	4.29		0.0001	0.75	9.4	4.45	
	Foliage	0.0017	0.71	3.5	2.82		0.0015	0.70	3.5	2.86	
	Crown	0.0006	0.74	12.7	3.97		0.0010	0.77	12.0	3.68	
	Total	0.0227	0.94	37.5	3.38		0.0028	0.97	24.9	3.85	

Table 5 (continued).

Species	Model	dbh-based set of equations					dbh- and height-based set of equations				
		$\hat{\sigma}_{\text{SUR}}^2$	$\hat{\sigma}_{ii}$	AdjRSq	RMSE	c	$\hat{\sigma}_{\text{SUR}}^2$	$\hat{\sigma}_{ii}$	AdjRSq	RMSE	c
Largetooth aspen	Wood	1.0026	0.5138	0.93	23.3	2.16	1.0055	0.0001	0.98	12.5	4.80
	Bark	0.0034	0.92		5.4	2.95		0.0029	0.92	5.6	3.00
	Stem	0.4481	0.94		25.7	2.29		0.0011	0.98	14.7	3.94
	Branches	0.0000	0.85		5.9	5.08		0.0000	0.89	5.0	4.71
	Foliage	0.0021	0.81		1.2	2.11		0.0002	0.83	1.1	2.98
	Crown	0.0002	0.85		6.9	4.00		0.0000	0.89	5.8	4.94
	Total	0.3645	0.96		24.1	2.35		0.0006	0.98	16.3	4.28
Lodgepole pine	Wood	1.0004	0.0082	0.96	20.3	3.54	1.0003	0.0001	0.99	10.9	4.51
	Bark	0.0015	0.93		2.1	2.57		0.0003	0.93	2.2	3.02
	Stem	0.0250	0.96		21.0	3.18		0.0004	0.99	11.6	4.13
	Branches	0.0004	0.55		9.5	3.99		0.0006	0.68	8.0	3.60
	Foliage	0.0037	0.72		3.1	2.67		0.0050	0.71	3.2	2.48
	Crown	0.0037	0.65		11.4	3.39		0.0045	0.73	9.9	3.16
	Total	0.0357	0.97		21.6	3.00		0.0273	0.98	17.8	2.89
Red ash	Wood	1.4200	2.2096	0.86	46.8	2.01	1.4000	0.0097	0.95	28.7	3.41
	Bark	0.0149	0.85		7.9	2.47		0.0018	0.92	5.8	2.99
	Stem	2.6838	0.86		54.7	2.04		0.0155	0.95	34.1	3.35
	Branches	0.0225	0.83		11.4	2.68		0.0141	0.83	11.5	2.84
	Foliage	2.6898	0.67		1.6	—		2.8033	0.65	1.7	—
	Crown	0.0007	0.83		12.5	3.94		0.0084	0.83	12.6	3.09
	Total	6.2881	0.88		61.2	1.87		0.0130	0.95	39.5	3.51
Red maple	Wood	1.0006	0.0015	0.95	48.7	4.41	1.0021	0.0060	0.96	43.9	3.80
	Bark	0.0001	0.90		7.2	4.46		0.0001	0.90	7.1	4.26
	Stem	0.0025	0.95		53.3	4.31		0.0076	0.96	48.5	3.82
	Branches	0.0027	0.81		26.8	3.70		0.0046	0.81	26.5	3.53
	Foliage	0.0263	0.73		2.6	1.75		0.0263	0.73	2.6	1.75
	Crown	0.0054	0.81		28.7	3.56		0.0081	0.81	28.4	3.42
	Total	0.0050	0.96		58.8	4.25		0.0020	0.97	51.4	4.40
Red oak	Wood	1.0075	0.0722	0.85	67.3	3.23	1.0017	0.0255	0.94	41.8	3.26
	Bark	0.0172	0.82		12.6	2.78		0.0013	0.86	11.2	3.55
	Stem	0.1560	0.87		73.0	3.07		0.0524	0.95	43.4	3.09
	Branches	0.0029	0.85		46.6	3.94		0.0021	0.90	37.0	4.04
	Foliage	0.0012	0.73		3.8	2.81		0.0008	0.72	3.8	2.98
	Crown	0.0033	0.85		48.4	3.93		0.0026	0.90	38.9	3.98
	Total	0.0344	0.91		92.3	3.64		0.0618	0.97	59.1	3.25
Red pine	Wood	1.0005	0.0020	0.83	77.8	4.29	1.0004	0.0059	0.98	27.5	3.34
	Bark	0.0001	0.88		4.7	3.68		0.0001	0.88	4.6	3.49
	Stem	0.0022	0.84		80.5	4.31		0.0092	0.98	28.2	3.23
	Branches	0.0000	0.80		18.2	4.49		0.0002	0.87	14.7	3.95
	Foliage	0.0035	0.77		7.9	2.85		0.0522	0.82	7.0	1.95
	Crown	0.0003	0.81		24.2	4.13		0.0270	0.87	20.1	2.67
	Total	0.0052	0.92		68.7	3.95		0.0008	0.98	33.3	4.18
Red spruce	Wood	1.0956	0.0150	0.97	20.4	3.13	2.8567	0.0007	0.98	18.3	3.92
	Bark	0.0000	0.94		3.2	4.15		0.0000	0.94	3.2	3.92
	Stem	0.0630	0.97		22.8	2.74		0.0052	0.98	19.8	3.35
	Branches	0.0003	0.93		6.6	3.58		0.0004	0.93	6.6	3.48
	Foliage	0.0005	0.90		4.2	3.25		0.0002	0.89	4.3	3.53
	Crown	0.0004	0.92		10.7	3.82		0.0003	0.92	10.9	3.94
	Total	0.0059	0.97		29.1	3.64		0.0196	0.98	25.9	3.12
Silver maple	Wood	1.0217	6.4906	0.97	40.3	1.57	1.0361	0.0044	0.98	27.4	3.58
	Bark	0.0003	0.96		4.4	3.24		0.0008	0.96	4.0	2.85
	Stem	5.7763	0.97		44.2	1.65		0.0218	0.98	30.9	3.10
	Branches	0.0001	0.88		47.0	5.09		0.0007	0.89	44.7	4.25
	Foliage	10.0436	0.75		3.2	—		0.5099	0.82	2.7	0.82
	Crown	0.0064	0.88		49.3	3.72		0.0004	0.89	46.8	4.56
	Total	0.2735	0.97		63.9	2.78		0.0138	0.97	64.0	3.66

Table 5 (continued).

Species	Model	dbh-based set of equations					dbh- and height-based set of equations				
		$\hat{\sigma}_{\text{SUR}}^2$	$\hat{\sigma}_{ii}$	AdjRSq	RMSE	c	$\hat{\sigma}_{\text{SUR}}^2$	$\hat{\sigma}_{ii}$	AdjRSq	RMSE	c
Sugar maple	Wood	1.0002	0.0262	0.96	65.4	3.46	1.0008	0.0466	0.97	58.0	3.18
	Bark	0.0877	0.76		17.9	2.22		0.0146	0.76	18.0	2.73
	Stem	0.1279	0.95		76.6	3.05		0.1327	0.96	69.3	2.95
	Branches	0.0025	0.86		43.7	3.93		0.0042	0.85	45.3	3.77
	Foliage	0.0025	0.77		4.5	2.63		0.0076	0.65	5.5	2.49
	Crown	0.0027	0.86		46.5	3.98		0.0048	0.85	49.1	3.84
	Total	0.0828	0.97		87.6	3.28		0.1126	0.97	78.8	3.09
Tamarack larch	Wood	1.0003	0.0065	0.92	25.7	3.78	1.0001	0.0006	0.98	13.1	4.19
	Bark	0.0001	0.94		2.0	3.44		0.0001	0.96	1.6	3.38
	Stem	0.0070	0.92		26.9	3.80		0.0008	0.98	13.5	4.12
	Branches	0.0003	0.77		8.5	4.12		0.0002	0.82	7.5	4.04
	Foliage	0.0104	0.57		3.2	2.37		0.0114	0.52	3.4	2.30
	Crown	0.0039	0.79		9.9	3.39		0.0026	0.82	9.2	3.43
	Total	0.0052	0.95		25.7	3.88		0.0043	0.98	17.3	3.72
Trembling aspen	Wood	1.0000	0.0083	0.95	31.8	3.66	1.0000	0.0001	0.98	20.8	4.82
	Bark	0.0001	0.91		9.2	4.25		0.0000	0.93	8.4	4.59
	Stem	0.0092	0.95		37.6	3.74		0.0003	0.98	25.3	4.67
	Branches	0.0001	0.76		12.6	4.49		0.0003	0.76	12.4	4.05
	Foliage	0.0328	0.43		2.7	1.74		0.0234	0.43	2.7	1.85
	Crown	0.0021	0.75		14.2	3.60		0.0047	0.75	14.1	3.31
	Total	0.0199	0.95		42.6	3.54		0.0009	0.97	34.0	4.41
White ash	Wood	1.0053	0.0091	0.87	72.2	3.93	1.0034	0.4408	0.93	50.4	2.46
	Bark	0.0062	0.80		10.5	2.89		0.0011	0.84	9.4	3.40
	Stem	0.0119	0.87		80.3	3.91		0.3561	0.93	57.2	2.60
	Branches	0.0019	0.74		44.6	3.97		0.0017	0.75	43.6	3.99
	Foliage	0.4437	0.51		2.6	0.83		0.2082	0.49	2.7	1.08
	Crown	0.0099	0.74		45.4	3.49		0.0069	0.75	44.6	3.60
	Total	0.0363	0.91		91.0	3.62		0.0491	0.93	78.5	3.38
White birch	Wood	1.0001	0.0119	0.94	28.0	3.49	1.0001	0.0004	0.97	20.7	4.49
	Bark	0.0002	0.89		6.2	3.89		0.0001	0.91	5.6	4.09
	Stem	0.0113	0.94		32.2	3.62		0.0009	0.97	23.9	4.27
	Branches	0.0001	0.78		18.1	4.90		0.0001	0.80	17.2	4.70
	Foliage	0.0088	0.58		3.8	2.46		0.0135	0.60	3.7	2.27
	Crown	0.0009	0.78		20.3	4.20		0.0023	0.80	19.3	3.80
	Total	0.0067	0.96		35.5	3.81		0.0025	0.97	32.3	4.06
White elm	Wood	1.3426	0.0056	0.98	28.9	3.73	1.0869	0.0048	0.98	30.2	3.71
	Bark	0.0020	0.81		13.2	3.14		0.0016	0.79	13.7	3.21
	Stem	0.0265	0.97		36.3	3.27		0.0199	0.97	39.0	3.30
	Branches	0.0186	0.76		20.6	3.11		0.0435	0.76	20.6	2.84
	Foliage	0.0022	0.78		1.8	2.34		0.0017	0.79	1.7	2.40
	Crown	0.0054	0.79		20.8	3.56		0.0324	0.79	20.9	2.96
	Total	0.0377	0.97		43.7	3.28		0.0337	0.97	46.3	3.30
White oak	Wood	1.0043	0.0003	0.79	127.4	4.86	1.1128	0.0038	0.98	39.0	3.80
	Bark	0.0007	0.92		10.0	3.19		0.0035	0.93	9.2	2.66
	Stem	0.0003	0.82		133.4	4.92		0.0266	0.98	43.8	3.20
	Branches	0.0002	0.92		49.6	4.53		0.0038	0.98	23.1	3.41
	Foliage	0.0003	0.86		3.9	3.14		0.0015	0.89	3.4	2.44
	Crown	0.0007	0.92		51.7	4.26		0.0095	0.98	24.0	3.19
	Total	0.0011	0.87		177.8	4.70		0.0324	0.99	59.0	3.33
White spruce	Wood	1.0000	0.0001	0.93	33.1	5.02	1.0000	0.0004	0.98	18.0	4.11
	Bark	0.0000	0.91		4.5	4.25		0.0000	0.93	4.1	3.98
	Stem	0.0003	0.94		35.2	4.81		0.0004	0.98	18.7	4.19
	Branches	0.0005	0.67		11.3	3.88		0.0004	0.70	10.7	3.86
	Foliage	0.1008	0.63		6.8	2.00		0.1260	0.60	7.0	1.84
	Crown	0.0104	0.71		16.0	3.28		0.0239	0.72	15.5	2.85
	Total	0.0031	0.95		35.3	4.04		0.0062	0.98	24.9	3.60

Table 5 (concluded).

Species	Model	dbh-based set of equations					dbh- and height-based set of equations				
		$\hat{\sigma}_{\text{SUR}}^2$	$\hat{\sigma}_{ii}$	AdjRSq	RMSE	c	$\hat{\sigma}_{\text{SUR}}^2$	$\hat{\sigma}_{ii}$	AdjRSq	RMSE	c
Yellow birch	Wood	1.0003	3.5072	0.94	87.4	2.05	1.0006	0.4618	0.95	80.3	2.52
	Bark	0.0192	0.84		22.0	2.68	0.0094	0.84		22.0	2.88
	Stem	4.5487	0.94		95.5	2.03	0.7738	0.95		88.6	2.44
	Branches	0.0004	0.81		76.3	4.48	0.0005	0.81		76.5	4.45
	Foliage	0.3125	0.41		7.6	1.45	0.5722	0.45		7.4	1.25
	Crown	0.0150	0.81		80.0	3.47	0.0378	0.81		80.2	3.20
	Total	2.8971	0.94		145.5	2.34	0.9527	0.94		135.6	2.59
Hardwood	Wood	1.0000	0.0493	0.88	75.2	3.32	1.0013	0.0020	0.92	60.6	4.26
	Bark	0.0030	0.78		14.9	3.21	0.0001	0.81		13.5	4.24
	Stem	0.1099	0.89		81.5	3.12	0.0030	0.93		63.7	4.17
	Branches	0.0002	0.71		48.4	4.87	0.0002	0.70		50.0	4.91
	Foliage	0.0056	0.56		4.4	2.53	0.0089	0.56		4.4	2.37
	Crown	0.0006	0.72		50.7	4.52	0.0007	0.70		52.3	4.50
	Total	0.0373	0.90		104.8	3.63	0.0031	0.92		96.1	4.42
Softwood	Wood	1.0000	0.0107	0.88	46.2	3.59	1.0000	0.0003	0.97	24.8	4.46
	Bark	0.0000	0.84		7.4	4.42	0.0001	0.85		7.2	4.05
	Stem	0.0087	0.90		48.5	3.70	0.0006	0.97		26.5	4.24
	Branches	0.0005	0.74		15.1	3.90	0.0003	0.78		13.9	4.03
	Foliage	0.0066	0.70		6.8	2.92	0.0083	0.70		6.8	2.75
	Crown	0.0058	0.77		19.6	3.43	0.0046	0.80		18.3	3.41
	Total	0.0065	0.93		48.4	3.82	0.0033	0.96		36.3	3.91
All	Wood	1.0001	0.0152	0.87	63.1	3.64	1.0037	0.0003	0.91	51.6	4.76
	Bark	0.0001	0.79		11.6	4.32	0.0000	0.74		12.9	4.82
	Stem	0.0176	0.88		68.5	3.66	0.0005	0.92		57.0	4.74
	Branches	0.0001	0.56		41.8	4.82	0.0001	0.60		40.0	4.93
	Foliage	0.0057	0.50		7.5	2.94	0.0127	0.45		7.9	2.59
	Crown	0.0018	0.63		41.9	4.08	0.0021	0.67		39.7	3.96
	Total	0.0123	0.89		87.3	3.91	0.0017	0.89		85.5	4.55

* $\hat{\sigma}_{\text{SUR}}^2$ is the system variance; $\hat{\sigma}_{ii}$ is the variance of the error from each compartment i ; AdjRSq is the adjusted coefficient of determination; RMSE is the root mean square error on the original scale; and c is the exponent in the weight function (D^c). Missing values of c (—) correspond to parameter estimates not significantly different from zero ($\alpha = 0.05$).

tical model for efficient parameter estimation and reliable prediction intervals (Parresol 2001; Carvalho and Parresol 2003).

While many researchers have reported that dbh is an adequate biomass predictor at local or regional scales, others have suggested that both dbh and height must be used for larger scale applications (Jenkins et al. 2003). As dbh can easily be measured, while tree height is not always measured, two sets of equations were developed: dbh-based equations and dbh- and height-based equations. Allometric equations (sensu Smith 1980) were used to relate biomass compartments with dbh and height. The dbh-based equations are

$$\begin{aligned}
 y_{\text{wood}} &= \beta_{\text{wood}1} D^{\beta_{\text{wood}2}} + e_{\text{wood}} \\
 y_{\text{bark}} &= \beta_{\text{bark}1} D^{\beta_{\text{bark}2}} + e_{\text{bark}} \\
 y_{\text{stem}} &= \hat{y}_{\text{wood}} + \hat{y}_{\text{bark}} + e_{\text{stem}} \\
 [2] \quad y_{\text{foliage}} &= \beta_{\text{foliage}1} D^{\beta_{\text{foliage}2}} + e_{\text{foliage}} \\
 y_{\text{branches}} &= \beta_{\text{branches}1} D^{\beta_{\text{branches}2}} + e_{\text{branches}} \\
 y_{\text{crown}} &= \hat{y}_{\text{foliage}} + \hat{y}_{\text{branches}} + e_{\text{crown}} \\
 y_{\text{crown}} &= \hat{y}_{\text{wood}} + \hat{y}_{\text{bark}} + \hat{y}_{\text{foliage}} + \hat{y}_{\text{branches}} + e_{\text{total}}
 \end{aligned}$$

where y_i is the dry biomass compartment i of a living tree (kilograms); i is wood, bark, stem, foliage, branches, crown,

and total; \hat{y}_i is the prediction of y_i ; D is the dbh (centimetres); β_{jk} are model parameters with coefficient estimates b_{jk} ; j is wood, bark, foliage, and branches; $k = 1$ or 2; and e_i are the error terms.

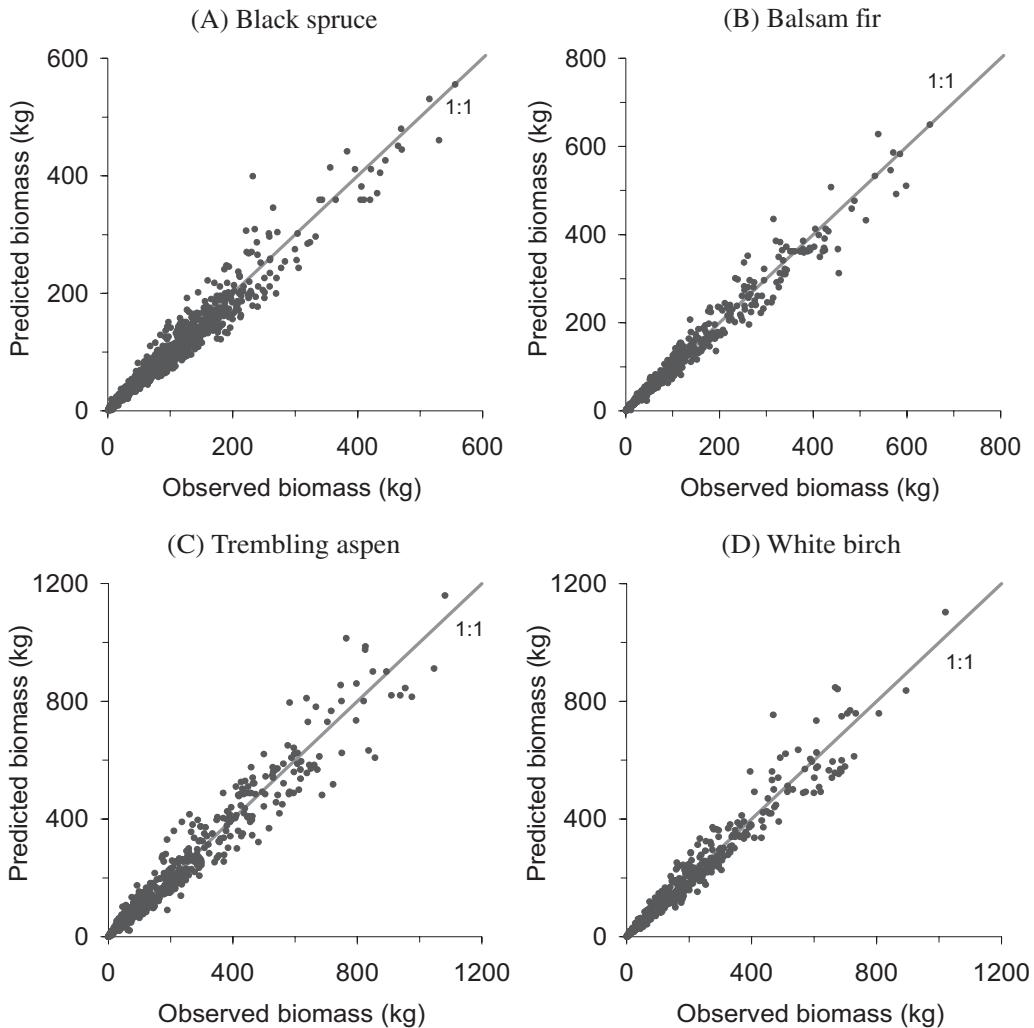
The dbh- and height-based equations are

$$\begin{aligned}
 y_{\text{wood}} &= \beta_{\text{wood}1} D^{\beta_{\text{wood}2}} H^{\beta_{\text{wood}3}} + e_{\text{wood}} \\
 y_{\text{bark}} &= \beta_{\text{bark}1} D^{\beta_{\text{bark}2}} H^{\beta_{\text{bark}3}} + e_{\text{bark}} \\
 y_{\text{stem}} &= \hat{y}_{\text{wood}} + \hat{y}_{\text{bark}} + e_{\text{stem}} \\
 [3] \quad y_{\text{foliage}} &= \beta_{\text{foliage}1} D^{\beta_{\text{foliage}2}} H^{\beta_{\text{foliage}3}} + e_{\text{foliage}} \\
 y_{\text{branches}} &= \beta_{\text{branches}1} D^{\beta_{\text{branches}2}} H^{\beta_{\text{branches}3}} + e_{\text{branches}} \\
 y_{\text{crown}} &= \hat{y}_{\text{foliage}} + \hat{y}_{\text{branches}} + e_{\text{crown}} \\
 y_{\text{total}} &= \hat{y}_{\text{wood}} + \hat{y}_{\text{bark}} + \hat{y}_{\text{foliage}} + \hat{y}_{\text{branches}} + e_{\text{total}}
 \end{aligned}$$

where H is the height in metres; stem, crown, and total aboveground biomasses are obtained by adding their respective compartments ($k = 1, 2$, or 3).

Heteroscedasticity often occurs in biomass data and is caused by an increase of residual variance when dbh or height increase. Usually, logarithmic transformation is used to address this problem. However, Parresol (2001) found that modeling the error structure on the original data scale gives

Fig. 4. Observed total biomass related to biomass predicted by the dbh-based set of equations: (A) black spruce, (B) balsam fir, (C) trembling aspen, and (D) white birch.



results as good as or even better than applying a transformation. Moreover, logarithmic transformation leads to predictions with a bias on the original scale. Various methods have been proposed for correcting this bias (Baskerville 1972; Ung and Végiard 1988). The Baskerville estimator may be biased for small sample sizes (Flewelling and Pienaar 1981), and it tends to overestimate the true bias (Hepp and Brister 1982). Hence, no data transformation has been used, and heteroscedasticity was addressed by considering that ordinary least squares residuals (e) are proportional to a power of D for each biomass compartment considered and total biomass:

$$[4] \quad \ln e_i^2 = b + c \ln D$$

The verification to check the normality of the standardized residuals for both equation systems was based on kurtosis and symmetry (SAS Institute Inc. 1999b). Variance homogeneity was verified with plots of standardized residuals (SAS Institute Inc. 1999b). Tests on dbh and height parameters were performed with a 5% significance level. The confidence limit formulas can be found in Parresol (2001, eq. 28) for mean value (eq. 5) and individual predictions (eq. 6) of each biomass equation:

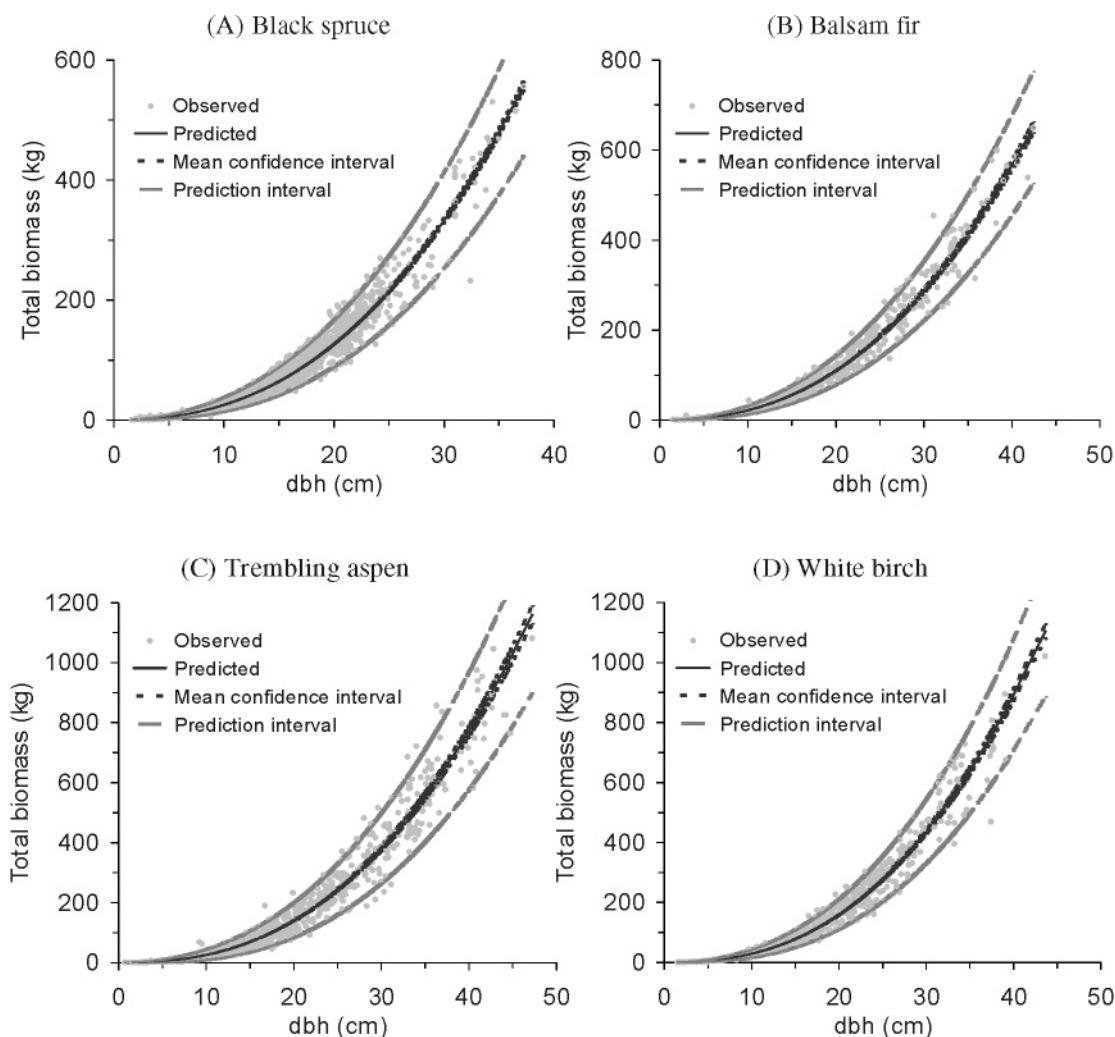
$$[5] \quad \hat{y}_i \pm t_{(\alpha/2)} \sqrt{S_{\hat{y}_i}^2}$$

$$[6] \quad \hat{y}_{i(\text{new})} \pm t_{(\alpha/2)} \sqrt{S_{\hat{y}_i}^2 + \hat{\sigma}_{\text{SUR}}^2 \hat{\sigma}_{ii} \psi_i(\hat{\theta}_i)}$$

where \hat{y}_i is the biomass prediction for component i (i is wood, bark, stem, foliage, branches, crown, and total); $S_{\hat{y}_i}^2$ is the estimated variance for the i th component of observation \hat{y}_i ; $\hat{\sigma}_{\text{SUR}}^2$ is the seemingly unrelated regression system variance; $\hat{\sigma}_{ii}$ is the variance of the error from each compartment i ; and $\psi_i(\hat{\theta}_i)$ is the estimated weight (D^c). Adopted fit statistics are the adjusted coefficient of determination (AdjRSq) and the root mean square error (RMSE).

To allow the assessment of biomass at local, regional, and continental scales, tree biomass data have been pooled at three progressive levels of aggregation: (i) species, (ii) groups of hardwood and softwood, and (iii) all species combined. Four species have been selected for a deeper comparison with already published equations: black spruce, trembling aspen, balsam fir, and white birch.

Fig. 5. Mean confidence interval and prediction interval for total biomass from the dbh-based set of equations: (A) black spruce, (B) balsam fir, (C) trembling aspen, and (D) white birch.



Results and discussion

Coefficient estimates and their standard error of dbh-based national system equations and of dbh- and height-based national system equations are presented in Tables 3 and 4, respectively.³ For both system equations, dbh coefficients (b_{j2}) are always positive either for stem compartments (j is wood and bark) or for crown compartments (j is branch and foliage). This clearly indicates an increase in all biomass compartments with increasing dbh. Two observations can be made on height coefficients (b_{j3}) in dbh- and height-based system equations. First, height predictor did not enter all equations. Second, b_{j3} is not always positive. When combined with dbh, the complementary information added by height can be interpreted as a proxy of the competitive environment of the tree, which involves the interactions between the level of species shade tolerance and the stand and site attributes. The positive sign of b_{j3} may indicate that, for two trees with the

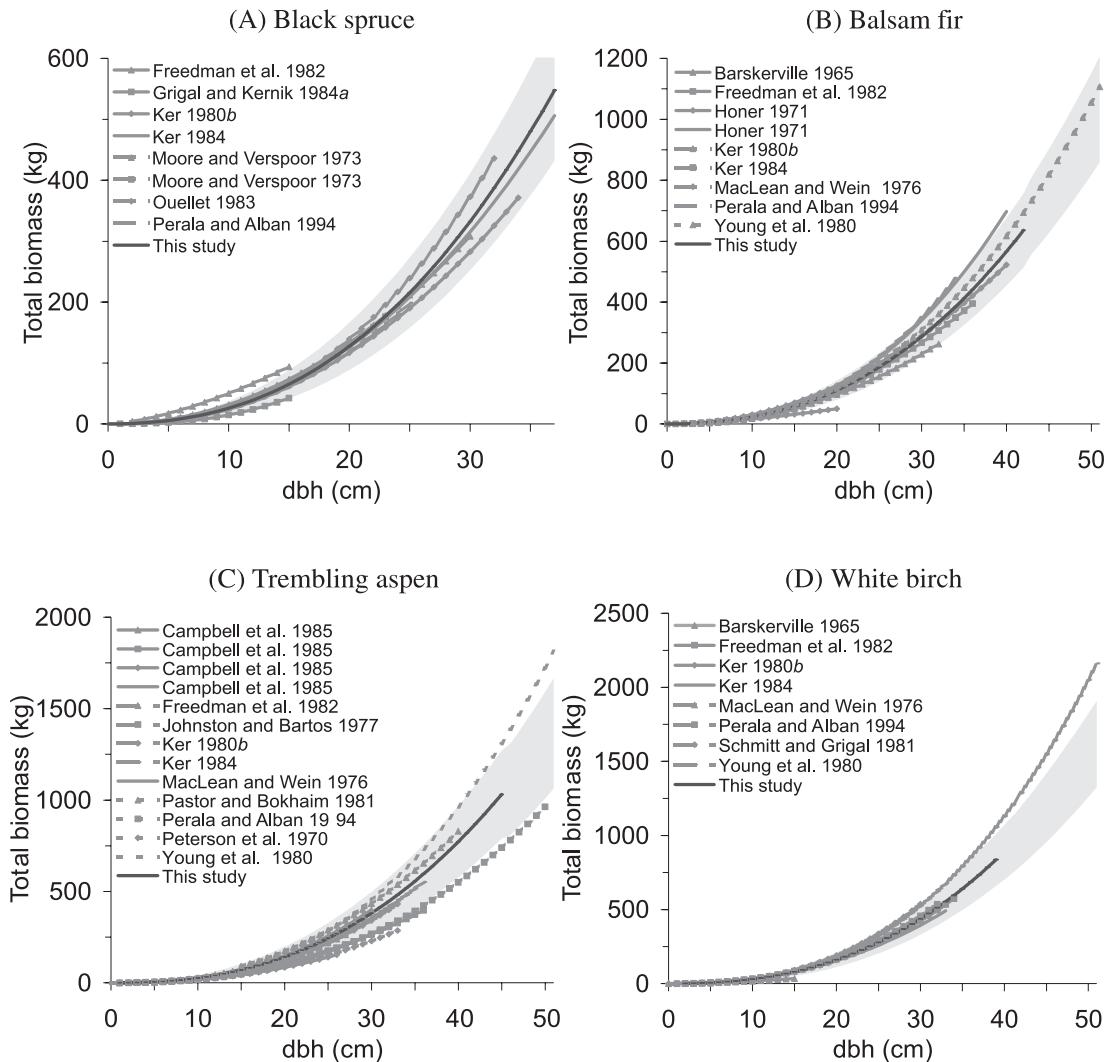
same dbh, the taller tree favoured height growth in relation to dbh growth and crown development. The negative sign of b_{j3} may indicate that trees competing for light exhibit a poorly developed crown (Vanninen and Mäkelä 2000).

When examining AdjRSq and RMSE in Table 5, two observations can be made. First, crown equations are associated with higher prediction error than are stem equations. Second, dbh is essential for predicting crown biomass compartments, while height is much less able to predict crown biomass compartments. Two consequences can be derived from both observations: (i) information added by height predictor improves the accuracy of the stem equations, but does not improve the accuracy of the crown equations; (ii) the role of height is significant, but secondary after dbh for predicting stem biomass compartments.

Graphically, by relating the observed total biomass to the predicted one, no apparent bias can be observed in the biomass predicted by dbh-based equations for all species. Figure 4

³The covariance matrices of parameter estimates are available from the corresponding author and on the Web site or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Ottawa, ON K1A 0S2, Canada. DUD 4004. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

Fig. 6. Comparison between the total biomass from national dbh-based equations and from Ter-Mikaelian and Korzukhin's (1997) equations.



illustrates this absence of bias for black spruce, trembling aspen, balsam fir, and white birch as examples. Mean confidence interval and prediction interval for total biomass from the dbh-based set of equations of four species are illustrated in Fig. 5. For equations based on dbh alone, Fig. 6 shows that the majority of total biomasses predicted by equations found in Ter-Mikaelian and Korzukhin (1997) are within the prediction intervals of national equations. The equations by Ter-Mikaelian and Korzukhin (1997) situated outside of the prediction interval of national equations are 2 of 8 for black spruce (2 of 6 if data from the United States are excluded), 4 of 9 for balsam fir (3 of 7 if data from the United States are excluded), 6 of 13 for trembling aspen (3 of 9 if data from the United States are excluded), and 2 of 8 for white birch (1 of 6 if data from the United States are excluded).

Biomass literature generally demonstrated that adding crown length as a predictor was generally much greater than height for improving the accuracy of the crown compartment equations (Pulkkinen 1991; Raulier et al. 1996; Monserud and Marshall 1999). However, crown length is not always available in the ENFOR data set, and particularly not measured

in inventory plots, rendering the eventual dbh- and crown-based equations inapplicable. We could not use a mixed-effect model (Pinheiro and Bates 2000) to combine the uncertainties of predictions for individual biomass compartments at the stand level and to consider the correlation structure of the errors because plot identification was frequently unavailable. Also, as plot identification was often lacking, stand variables such as site index (mean height of trees at a reference age), total basal area, or site attributes such as climatic variables (temperature, precipitation) were then unavailable for addressing the impact of stand and site attributes on crown compartment variability, especially.

Some provinces did not explicitly specify whether stumps were considered and whether dead branches and fruits and cones were excluded from the biomass definition. The proportion of stump biomass may represent as much as 72% of the total biomass, with an average of 5% ($\pm 4\%$). Stump biomass can be an important source of error if stumps were not harvested for some sampled trees. The number of trees sampled in each province is also quite dissimilar. In fact, sampled trees may not be representative of the species distribution in

Canada. Particularly, the 714 black spruce from Quebec (Table 1) represent nearly half of all black spruce sampled in Canada and thus have an excessive weight in the national equation estimates.

Branch and foliage biomasses in Quebec and stem wood and bark biomasses in Newfoundland were separated through a regression model based on data from other provinces. These two artifices were required to harmonize the data across Canada, but they introduced some correlation in the data and artificially reduced their variability. Also, for the hardwood species in Quebec, the branch portion between the branch base and the 9 cm diameter was included in the stem compartment. Unfortunately, no information was available to separate this branch portion from the stem. This causes a source of unknown bias in the national equations and could induce an overall overestimation of stem biomass and an underestimation of crown biomass. Furthermore, the estimation of the proportion of foliage and branches for the trees in Quebec should in turn introduce an overestimation of branch biomass compared with an underestimation of foliage biomass for a given crown biomass. This is due to the fact that the proportion equation (eq. 1) was estimated with trees from the other provinces that contain the branch portion between the branch base and the 9 cm diameter in their branch compartment.

In spite of the aforementioned limitations, both national system equations are well suited for policy-relevant purposes such as carbon accounting in the framework of the Kyoto Protocol. In fact, these generic biomass equations are directly applied to the dimensional tree scale of the national forest inventory data according to two possible scenarios: (*i*) dbh-based equations are recommended when tree height is not measured in the inventory plot, (*ii*) dbh- and height-based equations will be useful when both dbh and height data are available for all trees in the inventory plot. Moreover, the produced generic biomass equations can be used for verifying the allometry theory proposed by Enquist (2002) as an organizing principle for quantifying the relationship between tree size and biomass across spatial scales.

ENFOR did not consider all the Canadian tree species that are present in the national inventory data. To mitigate the consequences of the excluded species, additional equations by groups of hardwood and softwood species have been produced to allow the computation of biomasses of the missing species. The grouping of species is done on a genus basis, without any structural or physiological criteria. However, the grouped species equations may be useful to address the determination of functional groups within the framework of scaling up from a lower level to a higher level of vegetation responses to atmospheric changes (Körner 1993).

Conclusion

A major effort has been deployed to recover the archived ENFOR biomass data and to harmonize the data to develop national biomass equations. Sets of equations based on dbh and on dbh and height separate total tree biomass into foliage, branch, wood, and bark compartments. The seemingly unrelated regression method was used to estimate the parameter equations to consider both the correlation between compartments and the additivity property of the biomass compartments.

Even if they have been developed for national applications, they can also be used for provincial or territorial purposes when necessary. The limitations of the produced equations have been openly discussed. They are essentially caused by the absence of a standard sampling plan and of a standard tree harvesting protocol to collect the biomass. The national biomass equations were produced with particular emphasis on estimating their bias and error. Such estimations are essential to address the uncertainty of the biomass density estimated when balancing the national carbon budget.

Acknowledgements

The Panel on Energy Research and Development (PERD) of Natural Resources Canada funded this study. The authors thank Michèle Bernier-Cardou, Steen Magnussen, Werner A. Kurz, and Mark Gillis for their valuable advice. Gratitude is extended to Paul Boudewyn, Steve D'Eon, Marty Siltanen, and Mike Lavigne for their participation in recovering the ENFOR biomass data. The authors also thank Isabelle Lamarre and Pamela Cheers for their editorial comments and the anonymous reviewers for their helpful suggestions.

References

- Aldred, A.H., and Alemdag, I.S. 1988. Guidelines for forest biomass inventory. Can. For. Serv. Petawawa Natl. For. Inst. Inf. Rep. PI-X-77.
- Alemdag, I.S. 1983. Mass equations and merchantability factors for Ontario softwoods. Can. For. Serv. Petawawa Natl. For. Inst. Inf. Rep. PI-X-23.
- Apps, M.J. 2003. Forests, the global carbon cycle and climate change. In Congress Proceedings, B — Forests for the Planet. XII World Forestry Congress, Québec, Que., 21–28 September 2003. Edited by Organizing Committee. FAO, Rome. pp. 139–147.
- Baskerville, G.L. 1972. Use of logarithmic regression in the estimation of plant biomass. Can. J. For. Res. **2**: 49–53.
- Carvalho, J.P., and Parresol, B.R. 2003. Additivity in tree biomass components of Pyrenean oak (*Quercus pyrenaica* Willd.). For. Ecol. Manage. **179**: 269–276.
- Enquist, B.J. 2002. Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems. Tree Physiol. **22**: 1045–1064.
- Evert, F. 1985. Systems of equations for estimating oven dry mass of 18 Canadian tree species. Can. For. Serv. Petawawa Natl. For. Inst. Inf. Rep. PI-X-59.
- Flewelling, J.W., and Pienaar, L.V. 1981. Multiplicative regression with lognormal errors. For. Sci. **27**: 281–289.
- Gallant, A.R. 1987. Nonlinear statistical models. John Wiley & Sons, New York.
- Hepp, T.E., and Brister, G.H. 1982. Estimating crown biomass in loblolly pine plantations in the Carolina flatwoods. For. Sci. **28**: 115–127.
- Houghton, R.A. 2000. Interannual variability in the global carbon cycle. J. Geophys. Res. **105**: 20 121 – 20 130.
- Intergovernmental Panel on Climate Change. 2001. Climate change 2001: the scientific basis. Contribution of Working Group I to the third assessment report of the IPCC. Cambridge University Press, Cambridge.

- Jenkins, J.C., Chojnacky, D.C., Heath, L.S., and Birdsey, R.A. 2003. National-scale biomass estimators for United States tree species. *For. Sci.* **49**: 12–35.
- Kmenta, J. 1986. Elements of econometrics. 2nd ed. MacMillan Publishing Company, New York.
- Körner, C. 1993. Scaling from species to vegetation: the usefulness of functional groups. In *Biodiversity and ecosystem function*. *Ecol. Stud.* **99**: 117–140.
- Körner, C. 1994. Biomass fractionation in plants: a reconsideration of definitions based on plant functions. In *A whole plant perspective on carbon–nitrogen interactions*. Edited by J. Roy and E. Garnier. SPB Academic Publishers, The Hague. pp. 173–185.
- Kurz, W.A., and Apps, M.J. 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecol. Appl.* **9**: 526–547.
- Kurz, W.A., Apps, M., Banfield, E., and Stinson, G. 2002. Forest carbon accounting at the operational scale. *For. Chron.* **78**: 672–679.
- Monserud, R.A., and Marshall, J.D. 1999. Allometric crown relations in three northern Idaho conifer species. *Can. J. For. Res.* **29**: 521–535.
- Ouellet, D. 1983. Biomass prediction equations for twelve commercial species in Quebec. *Can. For. Serv. Laurentian For. Res. Cent. Inf. Rep.* LAU-X-62E.
- Parresol, B.R. 1999. Assessing tree and stand biomass: a review with examples and critical comparisons. *For. Sci.* **45**: 573–593.
- Parresol, B.R. 2001. Additivity of nonlinear biomass equations. *Can. J. For. Res.* **31**: 865–878.
- Pacala, S.W., Hurtt, G.C., Baker, D., Peylin, P., Houghton, R.A., Birdsey, R.A. et al. 2001. Consistent land- and atmosphere-based U.S. carbon sink estimates. *Science* (Washington, D.C.), **292**: 2316–2320.
- 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.
- Pinheiro, J.C., and Bates, D.M. 2000. Mixed-effects models in S and S-Plus. Springer-Verlag, New York.
- Pulkkinen, P. 1991. Crown structure and partitioning of above-ground biomass before the competition phase in a mixed stand of normal crowned Norway spruce (*Picea abies* (L.) Karst.) and pendulous Norway spruce (*Picea abies* f. *pendula* (Lawson) Sylven). *Tree Physiol.* **8**: 361–370.
- Raulier, F., Ung, C.H., and Ouellet, D. 1996. Influence of social status on crown geometry and volume increment in regular and irregular black spruce stands. *Can. J. For. Res.* **26**: 1742–1753.
- SAS Institute Inc. 1999a. SAS/ETS user's guide, version 8. SAS Institute Inc., Cary, N.C.
- SAS Institute Inc. 1999b. SAS procedures guide, version 8. SAS Institute Inc., Cary, NC.
- Schulze, E.-D., Wirth, C., and Heimann, M. 2000. Managing forests after Kyoto. *Science* (Washington D.C.), **289**: 2058–2059.
- Smith, R.J. 1980. Rethinking allometry. *J. Theor. Biol.* **87**: 97–111.
- Ter-Mikaelian, M.T., and Korzukhin, M.D. 1997. Biomass equations for sixty-five North American tree species. *For. Ecol. Manage.* **97**: 1–24.
- Ung, C.-H., and Végiard, S. 1988. Problèmes d'inférence statistique reliés à la transformation logarithmique en régression. *Can. J. For. Res.* **18**: 733–738.
- Vanninen, P., and Mäkelä, A. 2000. Needle and stem wood production in Scots pine (*Pinus sylvestris*) trees of different age, size and competitive status. *Tree Physiol.* **20**: 527–533.
- Aldred, A.H., and Alemdag, I.S. 1988. Guidelines for forest biomass inventory. *Can. For. Serv. Petawawa Natl. For. Inst. Inf. Rep.* PI-X-77.
- Alemdag, I.S. 1981. Aboveground-mass equations for six hardwood species from natural stands of the research forest at Petawawa. *Can. For. Serv. Petawawa Natl. For. Inst. Inf. Rep.* PI-X-6.
- Alemdag, I.S. 1982a. Aboveground dry matter of jack pine, black spruce, white spruce, and balsam fir trees at two localities in Ontario. *For. Chron.* **58**: 26–31.
- Alemdag, I.S. 1982b. Biomass of the merchantable and unmerchantable portions of the stem. *Can. For. Serv. Petawawa Natl. For. Inst. Inf. Rep.* PI-X-20.
- Alemdag, I.S. 1983. Mass equations and merchantability factors for Ontario softwoods. *Can. For. Serv. Petawawa Natl. For. Inst. Inf. Rep.* PI-X-23.
- Alemdag, I.S. 1984a. Total tree and merchantable stem biomass equations for Ontario hardwoods. *Can. For. Serv. Petawawa Natl. For. Inst. Inf. Rep.* PI-X-46.
- Alemdag, I.S. 1984b. Wood density variation of 28 tree species from Ontario. *Can. For. Serv. Petawawa Natl. For. Inst. Inf. Rep.* PI-X-45.
- 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.
- Alemdag, I.S., and Richardson, J. 1993. Annotated bibliography of ENFOR biomass reports 1979–1990. ENFOR Secretariat, For. Can. Inf. Rep. ST-X-6.
- Alemdag, I.S., and Stiell, W.M. 1982. Spacing and age effects on biomass production in red pine plantations. *For. Chron.* **58**: 220–224.
- Bella, I.E., and De Franceschi, J.P. 1980. Biomass productivity of young aspen stands in western Canada. *Can. For. Serv. North. For. Res. Cent. Inf. Rep.* NOR-X-219.
- Evert, F. 1985. Systems of equations for estimating ovendry mass of 18 Canadian tree species. *Can. For. Serv. Petawawa Natl. For. Inst. Inf. Rep.* PI-X-59.
- Ker, M.F. 1980a. Tree biomass equations for seven species in southwestern New Brunswick. *Can. For. Serv. Maritimes For. Res. Cent. Inf. Rep.* M-X-114.
- Ker, M.F. 1980b. Tree biomass equations for ten major species in Cumberland County, Nova Scotia. *Can. For. Serv. Maritimes For. Res. Cent. Inf. Rep.* M-X-108.
- Ker, M.F. 1984. Biomass equations for seven major Maritimes tree species. *Can. For. Serv. Maritimes For. Res. Cent. Inf. Rep.* M-X-148.
- Lavigne, M.B. 1982. Tree mass equations for common species of Newfoundland. *Can. For. Serv. Newfoundland For. Res. Cent. Inf. Rep.* N-X-213.
- Lavigne, M.B., and van Nostrand, R.S. 1981. Biomass equations for six tree species in central Newfoundland. *Can. For. Serv. Newfoundland For. Res. Cent. Inf. Rep.* N-X-199.
- Manning, G.H., Massie, M.R.C., and Rudd, J. 1984. Metric single tree weight tables for the Yukon Territory. *Can. For. Serv. Pac. For. Res. Cent. Inf. Rep.* BC-X-250.
- Ouellet, D. 1983a. Biomass equations for black spruce in Quebec. *Can. For. Serv. Laurentian For. Res. Cent. Inf. Rep.* LAU-X-60.
- Ouellet, D. 1983b. Biomass prediction equations for twelve commercial species in Quebec. *Can. For. Serv. Laurentian For. Res. Cent. Inf. Rep.* LAU-X-62.
- Ouellet, D. 1985. Biomass equations for six commercial tree species in Quebec. *For. Chron.* **61**: 218–222.

- Singh, T. 1982. Biomass equations for ten major tree species of the Prairie Provinces. Can. For. Serv. North. For. Res. Cent. Inf. Rep. NOR-X-242.
- Singh, T. 1984a. Biomass equations for six major tree species of the Northwest Territories. Can. For. Serv. North. For. Res. Cent. Inf. Rep. NOR-X-257.
- Singh, T. 1984b. Variation in the ovendry wood density of ten Prairie tree species. For. Chron. 17: 97–108.
- Singh, T. 1986. Generalizing biomass equations for the boreal forest region of west-central Canada. For. Ecol. Manage. 17: 97–107.
- Standish, J.T., Manning, G.H., and Demaerschalk, J.P. 1985. Development of biomass equations for British Columbia tree species. Can. For. Serv. Pac. For. Res. Cent. Inf. Rep. BC-X-264.
- Tunner, A., and Standish, J.T. 1986. Predicting logging residues in British Columbia. Can. For. Serv. Pac. For. Res. Cent. Inf. Rep. BC-X-284.

Appendix B

Table B1. List of species.

Alpine fir	Sapin subalpin	<i>Abies lasiocarpa</i> (Hook.) Nutt.
Balsam fir	Sapin baumier	<i>Abies balsamea</i> (L.) Mill.
Balsam poplar	Peuplier baumier	<i>Populus balsamifera</i> L.
Basswood	Tilleul d'Amérique	<i>Tilia americana</i> L.
Beech	Hêtre à grandes feuilles	<i>Fagus grandifolia</i> Ehrh.
Black ash	Frêne noir	<i>Fraxinus nigra</i> Marsh.
Black cherry	Cerisier tardif	<i>Prunus serotina</i> Ehrh.
Black spruce	Épinette noire	<i>Picea mariana</i> (Mill.) BSP
Eastern hemlock	Pruche du Canada	<i>Tsuga canadensis</i> (L.) Carr.
Eastern redcedar	Genévrier rouge	<i>Juniperus virginiana</i> L.
Eastern white-cedar	Thuya occidentalis	<i>Thuja occidentalis</i> L.
Eastern white pine	Pin blanc	<i>Pinus strobus</i> L.
Grey birch	Bouleau gris	<i>Betula populifolia</i> Marsh.
Hickory	Caryer	<i>Carya</i> Nutt.
Hop-hornbeam	Ostryer de Virginie	<i>Ostrya virginiana</i> (Mill.) K. Koch
Jack pine	Pin gris	<i>Pinus banksiana</i> Lamb.
Largetooth aspen	Peuplier à grandes dents	<i>Populus grandidentata</i> Michx.
Lodgepole pine	Pin lodgepole	<i>Pinus contorta</i> var. <i>latifolia</i> Engelm.
Red ash	Frêne rouge	<i>Fraxinus pennsylvanica</i> Marsh.
Red maple	Érable rouge	<i>Acer rubrum</i> L.
Red oak	Chêne rouge	<i>Quercus rubra</i> L.
Red pine	Pin rouge	<i>Pinus resinosa</i> Ait.
Red spruce	Épinette rouge	<i>Picea rubens</i> Sarg.
Silver maple	Érable argenté	<i>Acer saccharinum</i> L.
Sugar maple	Érable à sucre	<i>Acer saccharum</i> Marsh.
Tamarack larch	Mélèze laricin	<i>Larix laricina</i> (Du Roi) K. Koch
Trembling aspen	Peuplier faux-tremble	<i>Populus tremuloides</i> Michx.
White ash	Frêne blanc	<i>Fraxinus americana</i> L.
White birch	Bouleau à papier	<i>Betula papyrifera</i> Marsh.
White elm	Orme d'Amérique	<i>Ulmus americana</i> L.
White oak	Chêne blanc	<i>Quercus alba</i> L.
White spruce	Épinette blanche	<i>Picea glauca</i> (Moench) Voss
Yellow birch	Bouleau jaune	<i>Betula alleghaniensis</i> Britt. (<i>Betula lutea</i> Michx. F.)