

# Challenges in estimating forest biomass: use of allometric equations for three boreal tree species

Dingliang Xing, J.A. Colin Bergeron, Kevin A. Solarik, Bradley Tomm, S. Ellen Macdonald, John R. Spence, and Fangliang He

**Abstract:** Regionally fitted allometric equations for individual trees and root-to-shoot ratio values are normally used to estimate local aboveground and belowground forest biomass, respectively. However, uncertainties arising from such applications are poorly understood. We developed equations for both aboveground and belowground biomass using destructive sampling for three dominant upland boreal tree species in northwestern Alberta, Canada. Compared with our equations, the diameter-based national equations derived for use across Canada underestimated aboveground biomass for *Picea glauca* (Moench) Voss but gave reasonable estimates for *Populus balsamifera* L. and *Populus tremuloides* Michx. The national equations based on both tree diameter and height overestimated aboveground biomass for the *Populus* species but underestimated it for *Picea glauca* in our study area. The approach of root-to-shoot ratio proposed by the Intergovernmental Panel on Climate Change (IPCC) overestimated belowground biomass by 16%–41%, depending on forest cover type, in comparison with our values estimated directly on site, with the greatest bias in deciduous-dominated stands. When the general allometric equations for aboveground biomass and the root-to-shoot ratio for belowground biomass were combined to estimate stand biomass, overestimation could be as high as 18% in our study area. The results of our study support the development of improved regional allometric equations for more accurate local-scale estimations. Incorporating intraspecific variation of important traits such as tree taper may be especially helpful.

**Key words:** EMEND (Ecosystem Management Emulating Natural Disturbance), intraspecific trait variation, root-to-shoot ratio, tree taper, wood density.

**Résumé :** On utilise généralement des équations allométriques ajustées à l'échelle régionale pour les arbres individuels et des valeurs du rapport racines-tiges pour estimer respectivement la biomasse forestière locale, aérienne et souterraine. Cependant, les incertitudes découlant de telles applications sont mal comprises. Nous avons développé des équations de biomasse aérienne et souterraine en utilisant un échantillonnage destructif pour trois espèces d'arbres boréales dominantes dans les hautes terres du nord-ouest de l'Alberta, au Canada. Comparativement à nos équations, les équations nationales basées sur le diamètre développées pour être utilisées partout au Canada sous-estimaient la biomasse aérienne de *Picea glauca* (Moench) Voss, mais donnaient des estimations raisonnables pour *Populus balsamifera* L. et *Populus tremuloides* Michx. Les équations nationales basées sur le diamètre et la hauteur des arbres surestimaient la biomasse aérienne des espèces de *Populus* L., mais la sous-estimaient pour *Picea glauca* dans notre zone d'étude. L'approche du rapport racines-tiges, proposée par le Groupe d'experts intergouvernemental sur l'évolution du climat (GIEC), a surestimé la biomasse souterraine de 16 à 41% selon le type de couvert forestier par rapport à nos valeurs estimées directement sur le site, le biais le plus important étant observé dans les peuplements dominés par les feuillus. En combinant les équations allométriques générales pour la biomasse aérienne et le rapport racines-tiges pour la biomasse souterraine pour estimer la biomasse du peuplement, la surestimation pouvait atteindre 18% dans notre zone d'étude. Les résultats de notre étude justifient le développement d'équations allométriques régionales améliorées pour des estimations plus précises à l'échelle locale. L'incorporation des variations intraspécifiques des attributs importants, tels que le défilement de la tige des arbres, peut être particulièrement utile. [Traduit par la Rédaction]

**Mots-clés :** aménagement écosystémique, variations intraspécifiques des attributs, rapport racines-tiges, défilement de la tige, densité du bois.

## Introduction

Increasing pressure to reduce net carbon dioxide (CO<sub>2</sub>) emissions in light of climate change is spurring development of global strategies such as carbon markets that encourage carbon offsets through local efforts to enhance carbon sequestration. To calculate the impact of such efforts and properly manage sequestra-

tion, it is necessary to accurately quantify carbon stocks and fluxes. Forest ecosystems store a large amount of global terrestrial carbon (Pan et al. 2011), but methods to accurately quantify this carbon are still under development. In general, approaches to this quantification involve collecting data about forest composition via remote sensing and classifying forests by ecotype and density.

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**D. Xing, J.A.C. Bergeron, S.E. Macdonald,\* J.R. Spence, and F. He.** Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2H1, Canada.

**K.A. Solarik.** National Council for Air and Stream Improvement Inc., 2000 McGill College Avenue, 6th Floor, Montreal, QC H3A 3H3, Canada.

**B. Tomm.** Natural Resources Canada, Northern Forestry Centre, Edmonton, AB T6H 3S5, Canada.

**Corresponding author:** Dingliang Xing (email: [xingdingliang@gmail.com](mailto:xingdingliang@gmail.com)).

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Areas in these categories are then converted to carbon based on estimates derived using generalized allometric relationships between tree characteristics and biomass from representative plots (Goodale et al. 2002; Kurz et al. 2009; Pan et al. 2011). Such generalized equations (Jenkins et al. 2003; Lambert et al. 2005; Ung et al. 2008; Paul et al. 2016) are also widely used in growth and yield research to quantify biomass and (or) productivity for local forest plots. For instance, in Canada, the generalized, species-specific tree aboveground biomass equations developed by Lambert et al. (2005) and Ung et al. (2008) have been commonly used for investigating spatial and temporal patterns of forest productivity associated with biodiversity (Paquette and Messier 2011; Liang et al. 2016), climate change (Hogg et al. 2008; Chen et al. 2016), CO<sub>2</sub> fertilization (Girardin et al. 2011; Chen et al. 2016), and disturbances (Strukelj et al. 2015).

Generalized allometric equations are thus applied to forest data over widespread areas without much adjustment for possible local variation in the relationships. However, there is little understanding about the uncertainty in the local use of such generalized regional equations, as intraspecific geographical variation in these equations has been ignored. Several important predictors of tree biomass, including wood density (Wiemann and Williamson 2002; Fajardo and Piper 2011; Rossi et al. 2014) and tree architecture (Huang et al. 2000; Banin et al. 2012; Ung et al. 2013), vary across environmental gradients, but variation of these traits is ignored in generalized equations. This could result in poor estimation of biomass at locations where the traits depart significantly from the regional average. The extent to which this general approach adds uncertainty to estimation of carbon stock and forest productivity has not been studied in detail.

Another serious challenge in calculating forest biomass is the limited availability of allometric equations for belowground biomass. As a result, some studies simply ignore the belowground biomass, and many others estimate belowground biomass by multiplying aboveground biomass by a root-to-shoot ratio (RSR) (Intergovernmental Panel on Climate Change (IPCC) 2006); however, RSR can vary considerably with stand age and bioclimatic conditions (Mokany et al. 2006; Peichl and Arain 2007; Wang et al. 2008) and among tree species and sizes (Mokany et al. 2006; Sanquetta et al. 2011). Because implementing a general RSR value can exacerbate largely unexplored errors in biomass stock estimations, development and comparison of site- and species-specific allometric equations for belowground biomass would be useful.

Few studies have quantified errors resulting from local application of general biomass equations or use of a single RSR in boreal forests (but see Case and Hall (2008)), and thus, the magnitude of these potential errors is largely unknown. Here, we provide an example to consider this problem. Data collected through destructive whole-tree sampling in northwestern Alberta, Canada, were used to develop allometric equations for both above- and belowground biomass of three dominant boreal species (*Picea glauca* (Moench) Voss, *Populus tremuloides* Michx., and *Populus balsamifera* L.) from four different forest cover types. In this paper, we compare the estimates from the local equations we developed with those from the widely used Canadian national equations for aboveground biomass (Lambert et al. 2005; Ung et al. 2008) and with two RSR approaches commonly used for estimating belowground biomass (Li et al. 2003; IPCC 2006). Our goals were to (i) establish a credible basis for estimating both above- and belowground biomass for a forest for which we have detailed and destructively sampled biomass data and (ii) quantify the potential biases of using generalized models at both the tree and stand levels.

**Fig. 1.** Map of Canada showing the location of the present study (red star). The map was adapted from Ung et al. (2008), with the black dots showing sites used by Lambert et al. (2005) and Ung et al. (2008) to derive the Canadian national allometric equations. [Colour online.]



## Materials and methods

### Study area

The data for this study were collected in the boreal mixedwood forest of northwestern Alberta, Canada, at the Ecosystem Management Emulating Natural Disturbance (EMEND; Spence et al. 1999) research site (Fig. 1; 56°46'13"N, 118°22'28"W). The area is classified as the Lower Boreal Highlands Natural Subregion (Natural Regions Committee 2006) in which upland forest sites are dominated by *Picea glauca*, *Populus tremuloides*, and *Populus balsamifera* and lowland forest sites are dominated by *Picea mariana* (Mill.) Britton, Sterns & Poggenb. and *Larix laricina* (Du Roi) K. Koch (Bergeron et al. 2011).

Elevation at the EMEND site ranges from 677 to 880 m above sea level (a.s.l.). The climate at the EMEND site is characterized as follows (data from Eureka River, Alberta, ca. 42 km southwest of the EMEND site, 56°29'00"N, 118°44'00"W; Environment Canada 2013): a mean annual temperature of 0.0 °C, with a January mean of -16.9 °C and a July mean of 15.0 °C, and a mean annual precipitation of 440 mm, with 65% of this occurring during the growing season from May to September. Soils of the study area are primarily well-drained, fine-textured Orthic and Dark Gray Luvisols, with clay loam surface soil texture of glacial till and glaciolacustrine origin (Kishchuk et al. 2014).

### Field sampling

The EMEND project was laid out over 22 homogeneous composite forest polygons that were selected using the Alberta Vegetation Inventory and ground-truthing to represent sufficient areas of four forest cover types: (i) deciduous (broadleaf) dominated (>70% canopy cover), (ii) deciduous with coniferous understory, (iii) mixedwood, and (iv) coniferous dominated (>70% canopy cover) (see <https://emend.ualberta.ca/>). Stands representing each cover type were organized into three replicates, and each replicate was divided into ca. 10 ha compartments for subsequent application of disturbance treatments. If they could be located, two trees for each of *Picea glauca*, *Populus tremuloides*, and *Populus*

*balsamifera* were selected in each of the 22 original composite polygons for detailed stem and root analysis leading to biomass quantification. In total, we destructively measured 76 trees representing the range of variation in diameter at breast height (DBH; breast height = 1.30 m) for mature trees (Supplementary Table S1.1<sup>1</sup>) at the EMEND site as ascertained by detailed sampling in the previous 2 years. After recording DBH, these trees were felled, height was measured, and aboveground portions were immediately measured for biomass, as described in the following sections. Stumps and roots of these same trees were excavated and measured for belowground biomass quantification, as described in the following sections. We next describe how data were collected for each component of the tree.

### Stem

A cross section was obtained at ground level and at every metre to the top leader of the stem for *Populus* species and to a 5 cm diameter for *Picea glauca*. Stem volume was calculated for each 1 m section using the formula for the frustum of a cone, and values for each section were then summed to estimate stem volume (Husch et al. 2002). A cross section was also taken at breast height, and a wedge portion was dried at 70 °C to constant mass. Volume of this dried wedge was measured using the water displacement method, and specific gravity was obtained by dividing the dry mass of the wedge by its volume. Specific gravity was then multiplied by the volume of the stem to determine total biomass.

### Branches and foliage

All branches were counted, and their diameters near the trunk were recorded. The tree crown was divided into three sections of equal length (lower, middle, and upper), and two random branches per section were collected (except when a section had fewer than two branches). Each sampled main branch was divided into branches, twigs (current year's growth), and leaves, and all three components were dried at 70 °C to constant mass. Using all sampled branches for a given species, regressions were developed to estimate dry mass of leaves, twigs, and branches as a function of branch basal diameter (Supplementary Table S1.2<sup>1</sup>). Leaves and twigs were combined after separate estimation to represent the foliage component.

### Apex

For the upper portion of *Picea glauca* stems with diameter < 5 cm, a strategy similar to that for branches was used to quantify the mass of portions of leaves, twigs, and branches (stem). When the apex was ≤ 1 m in length, leaf, twig, and branch components of the whole apex were dried and weighed. Otherwise, the three components were each sampled from the basal and upper 50 cm sections of the apex separately, and dry masses of leaves, twigs, and branches for the whole apex were estimated using the samples.

### Roots and stumps

Roots and stumps within a 1 m radius from the pith and to a depth necessary to excavate the full stump and roots were carefully extracted using shovels, a chainsaw, and a hydraulic excavator. Limiting our sampling area to a 1 m radius allowed us to sample the majority of belowground biomass (Johansson and Hjelm 2012) while limiting field-sampling effort. Roots and stumps were washed using a water pump to remove soil. Volumes of stumps, large roots (>3 cm diameter), and small roots (≤3 cm diameter) were determined using water displacement. Cross sections taken at the top of the stump and from proximal, medial, and distal sections of one large root per tree were dried at 70 °C to constant mass. Samples of small roots were divided into four size categories: (i) <0.2 cm diameter, (ii) between 0.2 and 1 cm diameter, (iii) be-

**Table 1.** Regression parameters *a* and *b* for allometric equations ( $\log(B) = \log(a) + b\log(D)$ ) relating different components of tree biomass (*B*, in kilograms) to DBH (*D*, in centimetres) for three dominant species in the boreal forest of northwestern Alberta.

Component	<i>n</i>	$\log(a)$	<i>b</i>	SEE	<i>R</i> <sup>2</sup>
<b><i>Picea glauca</i></b>					
Stem	32	-3.668 (0.374)	<b>2.761 (0.115)</b>	0.212	0.95
Branch	34	-2.010 (0.683)	<b>1.671 (0.211)</b>	0.391	0.65
Foliage	34	-0.902 (0.521)	<b>1.213 (0.161)</b>	0.298	0.63
Belowground	32	-3.827 (0.397)	<b>2.419 (0.123)</b>	0.226	0.93
<b><i>Populus tremuloides</i></b>					
Stem	34	-1.402 (0.377)	<b>2.123 (0.114)</b>	0.112	0.91
Branch	34	-5.271 (1.085)	<b>2.581 (0.329)</b>	0.322	0.65
Foliage	34	-3.739 (0.714)	<b>1.431 (0.217)</b>	0.212	0.56
Belowground	32	-2.065 (0.670)	<b>1.833 (0.204)</b>	0.197	0.72
<b><i>Populus balsamifera</i></b>					
Stem	8	-0.965 (0.568)	<b>1.920 (0.165)</b>	0.076	0.95
Branch	8	-6.218 (2.289)	<b>2.761 (0.663)</b>	0.307	0.70
Foliage	8	-5.366 (1.919)	<b>1.953 (0.556)</b>	0.257	0.62
Belowground	7	-3.093 (2.178)	<b>2.038 (0.639)</b>	0.229	0.60

**Note:** Values in parentheses are standard errors. Significant coefficients ( $P < 0.05$ ) are indicated in boldface type. DBH is diameter at breast height (breast height = 1.30 m), *n* is sample size (the number of trees; the differences among different components of a species are due to missing values),  $\log$  is the natural logarithm, SEE is the residual standard error on logarithmic scale, and *R*<sup>2</sup> is the adjusted coefficient of determination of the linear regression.

tween 1 and 2 cm diameter, and (iv) between 2 and 3 cm diameter. The samples were then dried to constant mass. Dry mass and volume measured by water displacement were used to calculate specific gravity. Specific gravity of the stump, mean specific gravity of the three large-root samples, and mean specific gravity of all small-root size classes together were multiplied by the total volume of each of these components to determine belowground biomass for each tree.

### Development of tree-level allometric equations

To make our results comparable with previous studies (Lambert et al. 2005; Ung et al. 2008; Brassard et al. 2011), allometric equations based solely on DBH (eq. 1) or on both DBH and height (eq. 2) were developed for different biomass components (*i*), including stem, branches, foliage, and roots, for each species as follows:

$$(1) \quad B_i = aD^b$$

$$(2) \quad B_i = aD^bH^c$$

where *B<sub>i</sub>* is biomass; *D* is DBH; *H* is height; and *a*, *b*, and *c* are parameters estimated using linear regression on log-transformed data by assuming multiplicative lognormal error (Kerkhoff and Enquist 2009; Xiao et al. 2011). The system of equations for different biomass components may also be fitted simultaneously by including an additive model  $B_{\text{tot}} = \sum B_i$ , where  $B_{\text{tot}}$  is the total (or aboveground, if roots are not available) tree biomass, and *B<sub>i</sub>* is a biomass component modeled by either eq. 1 or eq. 2 (Parresol 1999). We explored this approach in Supplementary data S2 and found that this additive model does not perform better in biomass prediction as compared with the simple method of fitting each component separately (Supplementary Table S2.5).<sup>1</sup> Moreover, there are a few missing values in our data for different biomass components. The additive model cannot make any use of trees with even one missing component. In contrast, the separate fit-

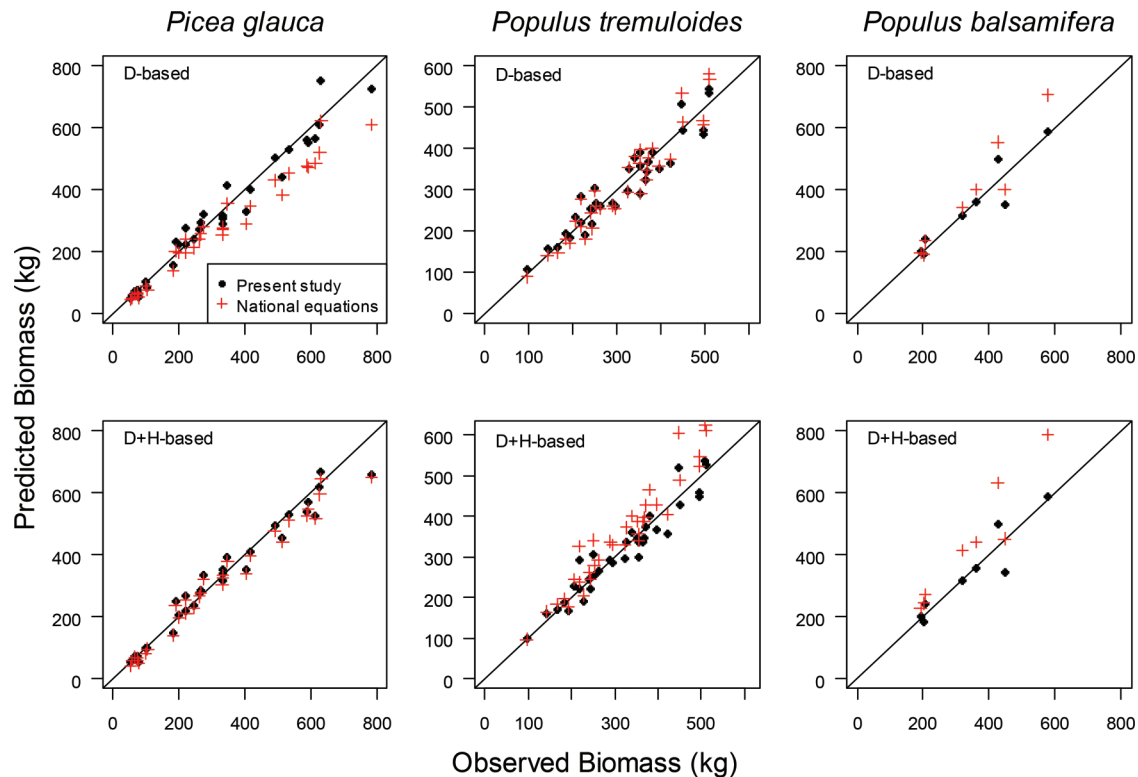
<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2019-0258>.

**Table 2.** Regression parameters  $a$ ,  $b$ , and  $c$  for allometric equations ( $\log(B) = \log(a) + b\log(D) + c\log(H)$ ) relating different components of tree biomass ( $B$ , in kilograms) to DBH ( $D$ , in centimetres) and tree height ( $H$ , in metres) for three dominant species in the boreal forest of northwestern Alberta.

Component	$n$	$\log(a)$	$b$	$c$	SEE	$R^2$
<b><i>Picea glauca</i></b>						
Stem	32	-3.904 (0.213)	<b>1.533 (0.166)</b>	<b>1.368 (0.170)</b>	0.118	0.98
Branch	34	-1.631 (0.414)	<b>3.835 (0.313)</b>	<b>-2.406 (0.318)</b>	0.232	0.87
Foliage	34	-0.624 (0.340)	<b>2.795 (0.256)</b>	<b>-1.759 (0.260)</b>	0.190	0.84
Belowground	32	-3.913 (0.393)	<b>2.003 (0.298)</b>	0.465 (0.305)	0.217	0.93
<b><i>Populus tremuloides</i></b>						
Stem	34	-2.827 (0.504)	<b>1.832 (0.126)</b>	<b>0.747 (0.204)</b>	0.093	0.94
Branch	34	-2.480 (1.610)	<b>3.152 (0.401)</b>	<b>-1.464 (0.653)</b>	0.298	0.69
Foliage	34	-1.426 (1.008)	<b>1.903 (0.251)</b>	<b>-1.213 (0.409)</b>	0.187	0.65
Belowground	32	-1.892 (1.070)	<b>1.870 (0.271)</b>	-0.092 (0.440)	0.197	0.71
<b><i>Populus balsamifera</i></b>						
Stem	8	-1.831 (2.007)	<b>1.798 (0.322)</b>	0.403 (0.889)	0.075	0.94
Branch	8	-1.248 (7.917)	<b>3.461 (1.271)</b>	-2.311 (3.507)	0.295	0.67
Foliage	8	-6.033 (6.912)	1.859 (1.110)	0.310 (3.062)	0.257	0.54
Belowground	7	-9.342 (5.989)	1.247 (0.944)	2.810 (2.518)	0.200	0.62

Note: Values in parentheses are standard errors. Significant coefficients ( $P < 0.05$ ) are indicated in boldface type. DBH is diameter at breast height,  $n$  is sample size (the number of trees),  $\log$  is the natural logarithm, SEE is the residual standard error on logarithmic scale, and  $R^2$  is the adjusted coefficient of determination of the linear regression.

**Fig. 2.** Relationship between observed and predicted tree-level aboveground biomass using the allometric equations developed in this study and the Canadian national equations (Lambert et al. (2005) for *Populus balsamifera* and Ung et al. (2008) for *Picea glauca* and *Populus balsamifera*). The solid diagonal lines are the 1:1 lines.  $D$ , diameter at breast height (DBH; breast height = 1.30 m);  $H$ , height. [Colour online.]



ting can make full use of the available data. Consequently, we chose to present results from the separate fitting in the main text and report the results from the additive model in Supplementary data S2.<sup>1</sup>

A problem with the linear regression on log-transformed data is that there will be a slight downward bias when back-transforming predicted biomass from logarithmic to arithmetic scales (Baskerville 1972). This bias has usually been remedied

by multiplying the back-transformed biomass by a correction factor (CF) defined as  $CF = \exp(SEE^2/2)$ , where SEE is the standard error of estimate of the regression on the logarithmic scale (Sprugel 1983). However, this correction itself is biased, especially when the sample size is small (Flewelling and Pienaar 1981), which is the case in our study. Thus, we followed Jenkins et al. (2003) and present uncorrected values but report the SEE values for completeness.

### Comparison with the widely used generalized approaches

Our locally developed equations were compared with the widely used Canadian national formulas for aboveground biomass (Lambert et al. 2005; Ung et al. 2008) and with the RSR approaches (Li et al. 2003; IPCC 2006) for belowground biomass. These comparisons were conducted at both tree and stand levels.

At the tree level, we used the previously described sampled trees. For each of these trees, the aboveground biomass components (i.e., stem, branches, and foliage) were predicted using both our equations parameterized from our local data, through a leave-one-out cross-validation procedure, and the national equations (Lambert et al. 2005; Ung et al. 2008). The belowground biomass of each tree was predicted using three methods: (i) a leave-one-out cross-validation procedure of the allometric equations developed in this study; (ii) the RSRs (for softwoods, root biomass =  $0.222 \times$  shoot biomass; for hardwoods, root biomass =  $1.576 \times$  shoot biomass<sup>0.615</sup>) developed by Li et al. (2003); and (iii) the RSR (root biomass =  $0.239 \times$  shoot biomass) proposed by IPCC (2006), which was adapted from Mokany et al. (2006) for our study species. For this comparison, we summed the biomasses of stem, branches, and foliage, after separate prediction, to represent aboveground biomass. Our predicted values based on both the  $D$  and  $D + H$  models, as well as those predicted by the national allometric equations (Lambert et al. 2005; Ung et al. 2008), were plotted against the measured biomass for every tree. We applied this same procedure for comparing belowground biomass estimations. All predicted values were also compared with the measured values to assess the prediction errors and biases (Supplementary Tables S1.3 and S1.4). To further understand the source of errors in estimates of aboveground biomass based on the national equations, the relationship between tree height and DBH was compared between our local data set and the national data set used by Ung et al. (2008) for *Picea glauca* and *Populus tremuloides*. To further understand the source of errors in estimates based on the RSR approaches, the relationships between the RSR and tree size (DBH and height) were fitted using regression models for *Picea glauca* and *Populus tremuloides* and compared with the relations proposed by Li et al. (2003) and IPCC (2006).

At the stand level, we used an independent inventory data set collected from the 100 EMEND experimental compartments as previously described. In each compartment, three to nine (most often six) permanent sampling transect plots (2 m  $\times$  40 m each) were randomly established, and DBH and height were measured for all living trees with DBH  $\geq$  5.0 cm in these plots in 1998 (Solarik et al. 2012). Here, we calculated the compartment-level biomass stocks (in kilograms per square metre) by summing all constituent trees in each compartment using both our own equations and the generalized above- and belowground approaches previously described and dividing these values by the summed area of the plots. A mean and standard deviation of the compartment-level values were then calculated and reported here for each of the four cover types. Percent difference of biomass between the stand-level estimations based on the generalized approaches and our own equations was then calculated to estimate errors that these generalized approaches generated.

All analyses in this study were performed in the statistical program R (R Core Team 2018).

## Results

### Allometric equations

Estimated parameters of the  $D$  and  $D + H$  allometric equations for different components of tree biomass are shown in Tables 1 and 2, respectively. Stem biomass, which on average accounted for 63.3% and 76.7% of total tree biomass for *Picea glauca* and *Populus* species, respectively, was the biomass component best fitted by the allometric models (Tables 1 and 2). DBH was a significant predictor of stem biomass for all three species, and the

**Table 3.** Comparison of stand-level aboveground biomass estimates ( $\pm 1$  standard deviation) for four forest cover types in the boreal forest in northwestern Alberta using allometric equations based on both DBH ( $D$ ) and DBH and tree height ( $D + H$ ) developed in the present study and the national equations (Lambert et al. (2005) for *Populus balsamifera* and Ung et al. (2008) for *Populus balsamifera* and *Picea glauca*).

Cover type	Present study (kg·m <sup>-2</sup> )	National (kg·m <sup>-2</sup> )	Absolute difference (kg·m <sup>-2</sup> )	Relative difference (%)
<b>D equation</b>				
DD	16.90 $\pm$ 2.83	16.94 $\pm$ 2.79	0.04 $\pm$ 0.69	0.35 $\pm$ 3.92
DU	22.00 $\pm$ 3.22	21.09 $\pm$ 3.25	-0.92 $\pm$ 0.84	-4.22 $\pm$ 4.23
MX	24.19 $\pm$ 4.93	22.19 $\pm$ 4.26	-2.00 $\pm$ 1.20	<b>-7.99<math>\pm</math>3.97</b>
CD	23.77 $\pm$ 5.43	21.31 $\pm$ 4.62	<b>-2.46<math>\pm</math>1.07</b>	<b>-9.90<math>\pm</math>4.01</b>
<b>D+H equation</b>				
DD	16.65 $\pm$ 2.78	18.58 $\pm$ 3.09	<b>1.93<math>\pm</math>0.74</b>	<b>11.68<math>\pm</math>4.18</b>
DU	21.76 $\pm$ 3.28	23.33 $\pm$ 3.69	1.56 $\pm$ 1.21	7.14 $\pm$ 5.81
MX	23.16 $\pm$ 4.37	23.80 $\pm$ 4.15	0.64 $\pm$ 0.76	3.09 $\pm$ 3.76
CD	23.06 $\pm$ 5.68	23.05 $\pm$ 5.33	-0.01 $\pm$ 0.67	0.56 $\pm$ 4.41

**Note:** Difference was calculated relative to estimates using equations developed in the present study. Differences significantly different from zero ( $P < 0.05$ ) are indicated in boldface type. DBH, diameter at breast height. Cover types: DD, deciduous-dominated stands; DU, deciduous stands with coniferous understorey; MX, mixedwood stands; and CD, coniferous-dominated stands. Sample sizes (number of compartments = 25) are the same for all cover types.

simple  $D$  model accounted for  $\geq 91\%$  variation in stem biomass. The effect of height was also significant for *Picea glauca* and *Populus tremuloides*, but including it in the model only slightly increased (by 3%) the coefficient of determination ( $R^2$ ) for these two species and did not improve the model for *Populus balsamifera*, possibly reflecting the relatively small sample size ( $n = 8$ ) for this species in our study (Table 2). For branch and foliage biomass, DBH was a significant predictor for all species, but the fit was understandably poorer than that of stem biomass ( $R^2 = 0.56$ – $0.70$  for branches and foliage versus  $R^2 = 0.91$ – $0.95$  for stems; Table 1). Incorporating height into these models increased the  $R^2$  by 4%–22% for *Picea glauca* and *Populus tremuloides* but did not improve the model for *Populus balsamifera* (Table 2).

For belowground biomass, which accounted for 17.9% and 15.0% of total tree biomass for *Picea glauca* and *Populus* species, respectively, both  $D$  and  $D + H$  models had very similar  $R^2$  values (Tables 1 and 2). DBH alone was a significant predictor of belowground biomass for all three species (Table 1).

### Comparing aboveground biomass estimates

For aboveground biomass of individual trees, both the national  $D$  and  $D + H$  equations were associated with larger prediction error, which is quantified by the root mean square error (RMSE), than the equations developed in the current study. This was expected and was the case for all three species (Supplementary Table S1.3). More importantly, the national equations underestimated aboveground biomass of individuals of *Picea glauca* by, on average, 14% for the  $D$  model and 5.3% for the  $D + H$  model (Fig. 2; Supplementary Table S1.3). The national  $D$  equations performed well for *Populus tremuloides* but overestimated tree-level aboveground biomass by 8% for *Populus balsamifera*. However, the national  $D + H$  equations overestimated biomass for both *Populus tremuloides* and *Populus balsamifera* by, on average, 11% and 26%, respectively (Fig. 2; Supplementary Table S1.3).

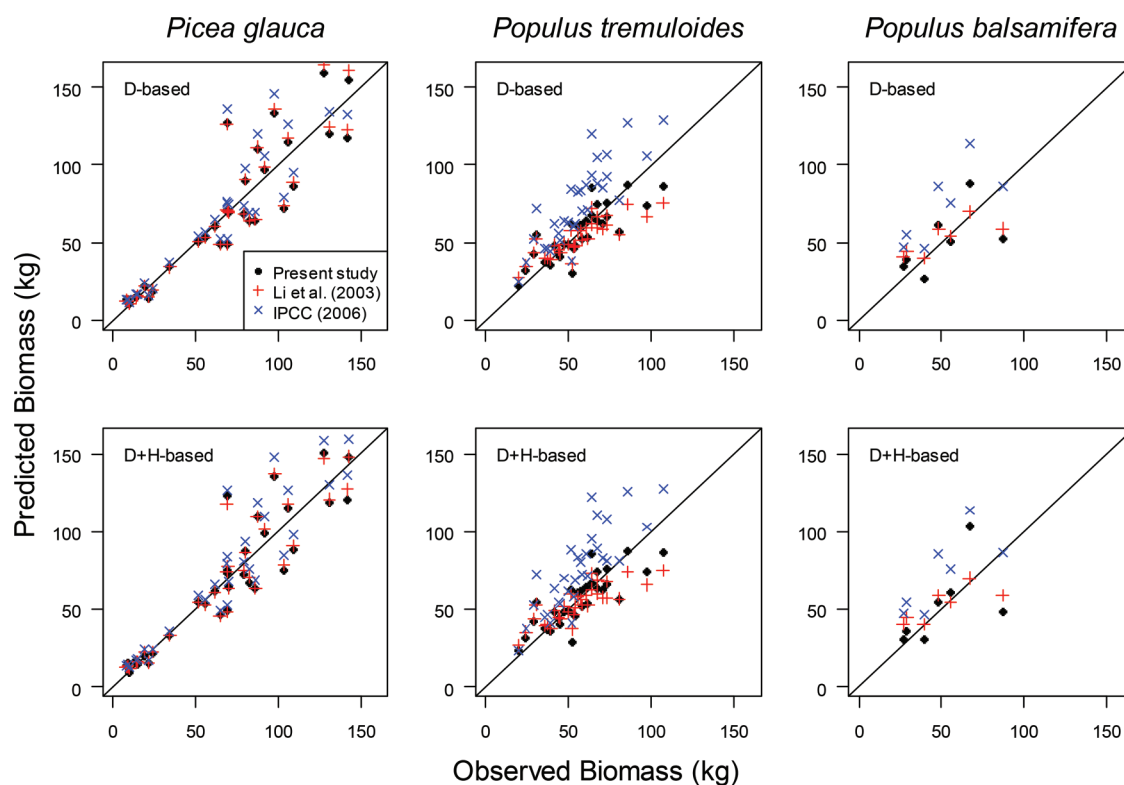
When scaled up to the stand level, the relative accuracy of the equations was naturally related to stand composition (Table 3). For instance, compared with the equations developed in this study, the national  $D + H$  equations resulted in larger estimated stand-level aboveground biomass in most stands (except the coniferous-dominated stands), with the largest overestimation (12%) observed for the deciduous-dominated stands.

**Table 4.** Comparison of stand-level belowground biomass estimates ( $\pm 1$  standard deviation) for the boreal forest in northwestern Alberta using allometric equations based on both DBH ( $D$ ) and DBH and tree height ( $D + H$ ) developed in the present study and the root-to-shoot ratio approaches proposed by Li et al. (2003) and IPCC (2006).

Cover type	Present study (kg·m <sup>-2</sup> )	Li et al. (2003) (kg·m <sup>-2</sup> )	IPCC (2006) (kg·m <sup>-2</sup> )	Difference (Li et al. 2003)		Difference (IPCC 2006)	
				Absolute (kg·m <sup>-2</sup> )	Percentage (%)	Absolute (kg·m <sup>-2</sup> )	Percentage (%)
<b>D equation</b>							
DD	2.96±0.56	3.14±0.59	4.04±0.68	0.19±0.20	6.57±7.51	<b>1.08±0.20</b>	<b>37.20±7.02</b>
DU	4.18±0.61	4.38±0.66	5.26±0.77	0.21±0.17	4.95±4.46	<b>1.08±0.24</b>	<b>25.96±5.11</b>
MX	4.76±1.02	4.85±1.07	5.78±1.18	0.10±0.18	1.97±3.98	<b>1.02±0.29</b>	<b>22.02±6.10</b>
CD	4.88±1.23	4.95±1.24	5.68±1.30	0.08±0.13	1.51±3.41	<b>0.81±0.16</b>	<b>17.64±6.57</b>
<b>D+H equation</b>							
DD	2.87±0.61	3.11±0.58	3.98±0.66	0.24±0.28	9.83±15.13	<b>1.11±0.29</b>	<b>40.73±16.41</b>
DU	4.20±0.65	4.34±0.66	5.20±0.78	0.14±0.29	3.53±6.57	<b>1.01±0.35</b>	<b>24.25±8.36</b>
MX	4.62±0.99	4.64±0.99	5.54±1.04	0.02±0.23	0.60±5.97	<b>0.91±0.24</b>	<b>20.59±7.69</b>
CD	4.79±1.28	4.80±1.30	5.51±1.36	0.02±0.10	0.21±3.26	<b>0.72±0.15</b>	<b>16.21±5.83</b>

**Note:** Difference was calculated relative to estimates using equations developed in the present study. Differences significantly different from zero ( $P < 0.05$ ) are indicated in boldface type. DBH, diameter at breast height. See Table 3 for abbreviations of cover type.

**Fig. 3.** Relationship between observed and predicted tree-level belowground biomass using the allometric equations developed in this study and the root-to-shoot ratio approaches proposed by Li et al. (2003) and IPCC (2006). The solid diagonal lines are the 1:1 lines.  $D$ , diameter at breast height (DBH);  $H$ , height. [Colour online.]



### Comparing belowground biomass estimates

The two RSRs applied in this study performed differently in estimating belowground biomass. The relationships proposed by Li et al. (2003) gave higher estimates for belowground biomass of individual trees (0.9%–14%), and this translated into an overall overestimation of 0.2%–9.8% for stand biomass, depending on forest cover type (Table 4; Supplementary Table S1.4<sup>1</sup>). Use of the IPCC (2006) ratio resulted in even higher estimates for both individual trees (12%–52%) and stands (16%–41%) compared with the estimates from our equations (Fig. 3; Table 4; Supplementary Table S1.4<sup>1</sup>). When the national allometric equations for aboveground biomass

and the RSRs for belowground biomass were combined to estimate stand biomass, overestimation could be as high as 18% in our study area (Table 5).

### Discussion

#### Aboveground biomass estimates

Allometric relationships for biomass are affected by many factors, both biotic and abiotic (see table 5 in Case and Hall (2008)). A close look into model performance for different biomass components shows that the biases observed in Fig. 2 for the national

**Table 5.** Comparison of stand-level total biomass estimates ( $\pm 1$  standard deviation) for the boreal forest in northwestern Alberta using allometric equations based on both DBH ( $D$ ) and DBH and tree height ( $D + H$ ) developed in the present study and previously available national aboveground biomass equations and the root-to-shoot ratio approaches for belowground biomass proposed by Li et al. (2003) and IPCC (2006).

Cover type	Present study (kg·m <sup>-2</sup> )	Li et al. (2003) (kg·m <sup>-2</sup> )	IPCC (2006) (kg·m <sup>-2</sup> )	Difference (Li et al. 2003)		Difference (IPCC 2006)	
				Absolute (kg·m <sup>-2</sup> )	Percentage (%)	Absolute (kg·m <sup>-2</sup> )	Percentage (%)
<b>D equation</b>							
DD	19.85±3.38	20.06±3.29	21.01±3.47	0.21±0.67	1.17±3.32	1.16±0.93	6.00±4.67
DU	26.18±3.81	25.28±3.78	26.17±4.04	-0.90±0.81	-3.46±3.38	-0.01±1.17	-0.12±4.99
MX	28.95±5.94	26.70±5.18	27.67±5.43	-2.25±1.24	<b>-7.51±3.46</b>	-1.28±1.47	-4.13±4.81
CD	28.65±6.64	25.71±5.70	26.46±5.74	<b>-2.93±1.18</b>	<b>-9.84±3.50</b>	-2.19±1.29	-7.04±4.80
<b>D+H equation</b>							
DD	19.52±3.33	21.87±3.63	23.02±3.83	<b>2.35±0.82</b>	<b>12.20±4.08</b>	<b>3.51±1.06</b>	<b>18.13±5.12</b>
DU	25.96±3.87	27.77±4.25	28.90±4.57	1.81±1.16	6.98±4.62	2.94±1.60	11.28±6.40
MX	27.79±5.34	28.42±5.00	29.49±5.14	0.63±0.82	2.64±3.47	1.70±1.07	6.58±4.69
CD	27.84±6.95	27.74±6.56	28.56±6.60	-0.10±0.71	0.16±3.80	0.72±0.87	3.34±5.31

**Note:** Difference was calculated relative to estimates using equations developed in the present study. Differences significantly different from zero ( $P < 0.05$ ) are indicated in boldface type. DBH, diameter at breast height. See Table 3 for abbreviations of cover type.

equations in predicting aboveground tree biomass is primarily caused by the stem models, although the crown models also showed considerable deviations. This is consistent with the fact that stem biomass accounts for the majority of aboveground biomass. Tree stem biomass is the product of stem volume and wood density, which are the primary drivers of variation in stem biomass and mediate the effects of other elements on stem biomass (Chave et al. 2014). Our measured wood density for the three dominant species, *Picea glauca*, *Populus tremuloides*, and *Populus balsamifera*, at the EMEND site were  $0.422 \pm 0.036$ ,  $0.458 \pm 0.036$ , and  $0.404 \pm 0.048$  g·cm<sup>-3</sup>, respectively. These values are close to those estimated for the same species from eastern Canada (Gonzalez 1990), where a large proportion of data used in developing the national equations was sampled. Hence, wood density may not be the most important factor for explaining variation in our results. Nevertheless, as shown by Gonzalez (1990), wood density of a particular species can vary considerably in space. Thus, although including intraspecific variation of wood density for use in allometric equations may be rewarding, this is not suggested by our results.

Although stem volume could be well predicted by tree DBH and height, tree taper should also be considered, as tree stems are not strictly conical. Thus, ignoring intraspecific variation in tree taper, which clearly exists for our three species (Ung et al. 2013), could be a source of discrepancy between generalized regional equations and locally derived equations. The different performances of the generalized  $D$  and  $D + H$  equations (e.g., the larger biomass estimates resulting from the Canadian national  $D + H$  models compared with those from the national  $D$  models (Fig. 2)) suggests that trees with a given DBH in our study area are taller than the mean tree height used in deriving the national equations. This inference is confirmed by a direct comparison of the relationships between  $H$  and  $D$  in our local data and the national data used in Ung et al.'s (2008) national studies (Fig. 4).

Clearly, the predictive accuracy of general regional or national biomass equations could be improved by incorporating measures of the important traits previously discussed. Additionally, many studies have shown that intraspecific variation in traits of a species can be partly captured by including factors such as ecoregion (Ung et al. 2013), climate (Rossi et al. 2014), and soil properties (Fajardo and Piper 2011) that reflect environmental conditions for tree growth. Although present opportunities to apply such relationships in large-scale allometric equations for estimating forest biomass are limited by lack of data, future work could usefully consider these factors.

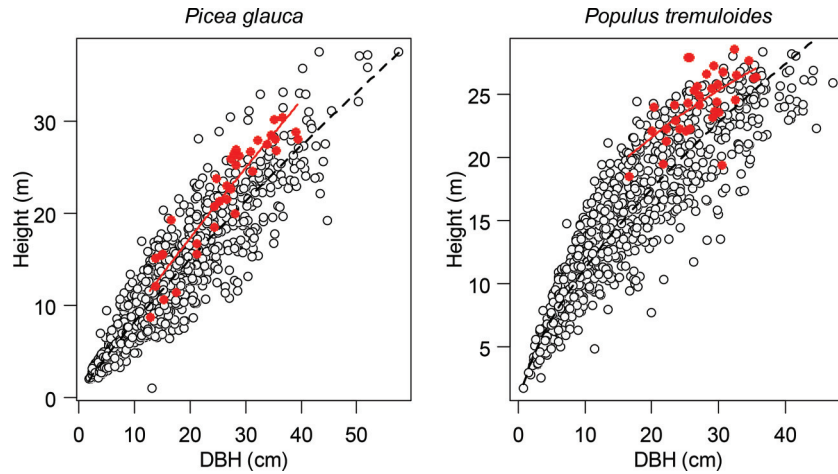
### Belowground biomass estimates

We acknowledge that our method of quantifying belowground biomass within only a 1 m radius may underestimate belowground biomass to some extent. However, Johansson and Hjelm (2012) found that *Populus* trees with DBH between 8 and 57 cm store 76% of belowground biomass in the stump alone. Adding both the large and small roots within a 1 m radius undoubtedly increases this percentage. Although roots of focal trees undoubtedly extend beyond the 1 m radius, expanding the radius leads to practical problems in distinguishing the rootstocks of individual trees. Thus, we feel that our estimates are credible and that the large overestimation based on the IPCC (2006) approach cannot be simply explained in terms of incompleteness in our sampling method.

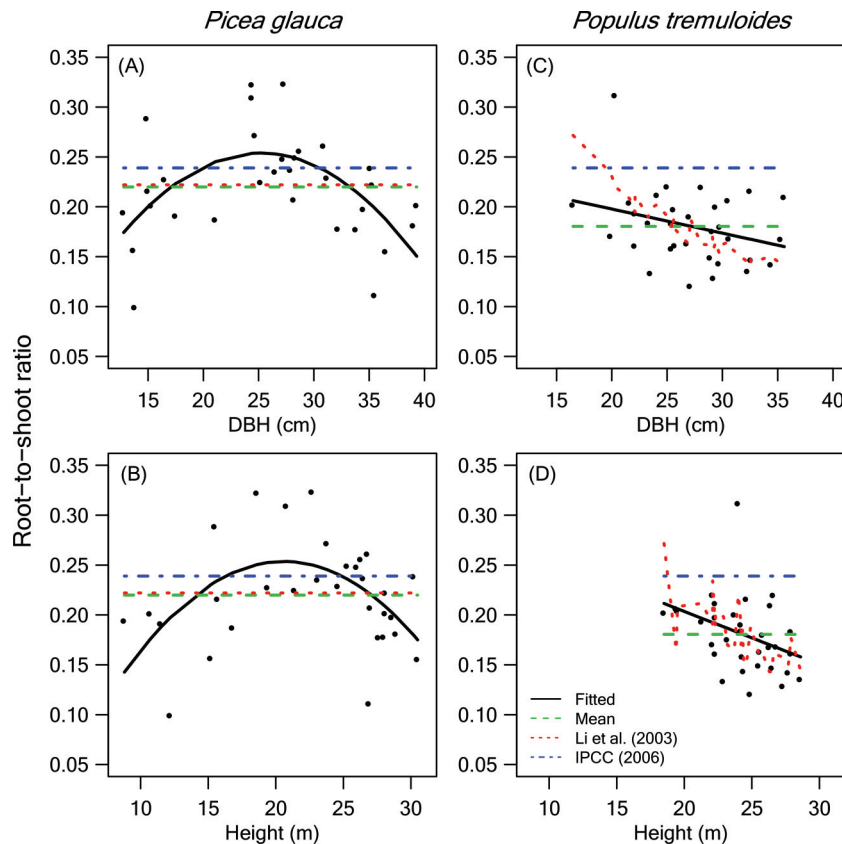
The discrepancy between our equations and the IPCC (2006) approach was especially prominent in estimation of belowground biomass in deciduous-dominated stands (41% overestimation; Table 4). This suggests that using the IPCC ratio for estimating belowground biomass of *Populus* species (Supplementary Table S1.4) is problematic, particularly for larger trees (Fig. 3). For our data, the RSR for *Populus tremuloides* was negatively related to tree size (Fig. 5; see also Sanquetta et al. (2011)). This explains why the use of the single IPCC RSR value (0.239) resulted in particularly large overestimation for the large trees at the EMEND site. This problem would significantly affect local results, as forests at the EMEND site are mature, with stand ages ranging between 100 and 225 years old (Bergeron et al. 2017), and about half of the *Populus tremuloides* trees in the deciduous-dominated stands had a DBH > 24 cm. Li et al. (2003) incorporated this size dependency for hardwood species, and we recommend that their generalized RSR for hardwoods (i.e., root biomass =  $1.576 \times$  shoot biomass<sup>0.615</sup>) be used to estimate belowground biomass when local allometric equations are not available. Although Li et al.'s (2003) single RSR for softwoods (i.e., root biomass =  $0.222 \times$  shoot biomass) performed well for our data, it should be used with caution, as we showed that the ratio for *Picea glauca* was also size dependent (Fig. 5). For instance, the single RSR would underestimate belowground biomass in stands dominated by medium-sized (20 cm < DBH < 30 cm) *Picea glauca* trees and overestimate belowground biomass in stands dominated by large-sized (DBH > 30 cm) *Picea glauca* trees (Fig. 5).

We did not compare our belowground biomass allometric equations with the few that have been previously published for the same species because Brassard et al. (2011) have already

**Fig. 4.** Relationship between tree height and diameter at breast height (DBH) for *Picea glauca* and *Populus tremuloides*. Open circles and dashed black lines represent data used in the Canadian national equations. Filled red circles and solid red lines represent data from the current study. Lines are the best fit power law regression with a multiplicative error. [Colour online.]



**Fig. 5.** Relationship of root-to-shoot ratio (below- to aboveground biomass) versus tree diameter at breast height (DBH;  $D$ ) and height ( $H$ ) for *Picea glauca* and *Populus tremuloides*. Black dots represent trees sampled in this study. The fitted regressions (solid black lines) are as follows: (A)  $y = -0.113 + 0.030D - 0.0006D^2$  ( $R^2_{adj} = 0.34$ ,  $P = 0.001$ ,  $n = 31$ ); (B)  $y = -0.116 + 0.037H - 0.0009H^2$  ( $R^2_{adj} = 0.25$ ,  $P = 0.007$ ,  $n = 31$ ); (C)  $y = 0.378 - 0.006D$  ( $R^2_{adj} = 0.21$ ,  $P = 0.012$ ,  $n = 32$ ); and (D)  $y = 0.513 - 0.012H$  ( $R^2_{adj} = 0.35$ ,  $P = 0.001$ ,  $n = 32$ ). [Colour online.]



shown that locally developed equations give inaccurate results when applied to different regions. This is expected, given the scarcely tested relationship between above- and belowground biomass and the sources of variation previously discussed for aboveground biomass. Besides, as correctly stated by Brassard et al. (2011), differences in sampling protocols and challenges in effectively extracting tree root systems likely contribute to the variation in estimation of belowground biomass among different studies.

**Limitations and recommendations**

Although our results favour locally developed allometric equations for reducing errors of local-scale biomass estimates, we must acknowledge that developing local equations is time consuming and difficult and, therefore, may be unlikely to occur in most cases. Moreover, when operating at multiple locations, the bias reduction achieved with use of multiple local equations will be balanced by a loss in the precision of

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predictions. For instance, the standard errors for parameters of our local models are one magnitude larger than those of the Canadian national models (order of 0.1 for our local models versus 0.01 for the national models; see Tables 1 and 2 and Ung et al. (2008)). Thus, in addition to supporting the development of local equations for use in intensive investigations at particular sites, our results highlight the need for improved regional allometric equations that could give more accurate local-scale estimations. This could be achieved both through increased understanding of how spatial variation affects biomass equations (e.g., Yuen et al. 2016) and by incorporating variation of traits that affect tree biomass allometry within species or by modeling the environmental factors that shape such variation. Resulting increases in predictive ability could, in turn, improve estimates used for development of regional carbon budgets.

## Conclusions

In this study, we developed allometric equations for both above- and belowground biomass components of three dominant, merchantable tree species in a boreal forest of northwestern Alberta. Comparison of results from these local equations with those from the Canadian national equations showed that the national general  $D + H$  biomass equations overestimated aboveground biomass for trees of two *Populus* species by more than 10% in our study area and slightly underestimated aboveground biomass for *Picea glauca*. These inaccuracies scaled up to provide up to 12% overestimation of stand-level aboveground biomass, depending on the forest cover type. We also compared our direct measurements of belowground biomass with estimates of two widely applied RSR approaches. The ratios proposed by Li et al. (2003) reasonably estimated the belowground biomass, although there were risks of error due to the unconsidered relationship between RSR and tree size for coniferous species. The RSR proposed by IPCC (2006), however, greatly overestimated belowground biomass at our study site. Thus, use of these ratios should be discouraged. Compared with the equations developed in this study, estimation of total stand-level biomass using the general national equations and the IPCC ratio resulted in up to 18% overestimation. The bias introduced by using regional models not only has important repercussions for local implementation of carbon management practices planned to offset carbon emissions through afforestation, but also has serious implications for biomass estimates when these practices are scaled up for large land bases. If the biomass of a stand is overestimated by as much as 18% in carbon budgets, a significant fraction of carbon emissions could be unaccounted for, leading to failure of carbon market systems designed to mitigate increases in global atmospheric  $\text{CO}_2$ . Nonetheless, developing local equations such as those reported in this study is time consuming and unrealistic in most cases. Thus, our study supports the development of improved regional allometric equations that could give more accurate local-scale estimations.

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