

Estimating stand-scale biomass, nutrient contents, and associated uncertainties for tree species of Canadian forests

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Abstract: The growing demand for bioenergy feedstock from forest harvest residues is generating concerns about the potential loss of site productivity through nutrient removal. We used tree-level national biomass equations and a national database of forest plots to develop stand-level biomass equations for the different tree components of 30 major forest tree species found in Canada using basal area as the independent variable. We have also compiled more than 12 800 nutrient concentration values for different components of Canadian tree species from existing databases and the literature. Uncertainties were propagated across biomass equations and through conversion of nutrient concentrations to nutrient contents. Most of the uncertainty in nutrient contents estimates was found to be among the nutrient concentration measurements. The greatest levels of uncertainty were for estimates of phosphorus in woody components and of calcium in foliage. Grouping species into genera gave only a minor loss of precision. The coupling of biomass equations and nutrient concentration data can be used to provide first-order estimates of biomass and nutrients exported by tree component and species when harvesting any commercial stand in Canada. However, the associated uncertainties are important enough to warrant their inclusion in decision making.

Résumé : La demande croissante pour les résidus de coupe à des fins de bioénergie génère des préoccupations de perte de productivité suite à l'exportation d'éléments nutritifs. Nous avons développé des équations allométriques de biomasse à l'échelle du peuplement pour 30 espèces d'arbre dominantes de la forêt canadienne utilisant la surface terrière comme variable indépendante, à partir d'équations nationales de biomasse à l'échelle de l'arbre et de l'information provenant d'un inventaire national de parcelles forestières. Nous avons aussi compilé plus de 12 800 valeurs de concentrations de nutriments pour diverses composantes d'arbre et d'espèces qui provenaient de bases de données existantes et de la littérature. L'incertitude a été propagée dans les équations allométriques et au travers de la transformation des concentrations de nutriments en contenus. La plupart des incertitudes se retrouvent au niveau des mesures de concentrations de nutriments. Ce sont les estimés du phosphore dans les compartiments ligneux ainsi que ceux du calcium dans le feuillage qui sont les plus incertains. Le regroupement des espèces par genre n'a généré qu'une faible perte de précision. Le couplage des équations de biomasse et des mesures de concentrations en nutriments permet d'estimer les quantités de biomasse et de nutriments par composante d'arbre et par espèce exportées des peuplements commerciaux lors de leur récolte. Cependant, l'incertitude sur ces estimés est suffisamment importante pour nécessiter sa prise en compte pour les prises de décision.

Introduction

The increasing use of forest biomass as energy feedstock raises concerns over the sustainability of this practice because removing branches and foliage from sites can more than double nutrient removal compared with stem-only harvesting (Paré et al. 2002). Input–output nutrient budgets have been used to determine site suitability for intensive biomass harvesting and to evaluate the need for compensation with fertilization (Ranger and Turpault 1999; Raulund-Rasmussen et al. 2008; Klaminder et al. 2011). However, nutrient budgets have usually been calibrated for small, intensively studied sites (Watmough et al. 2005) and are associated with large uncertainties (Auchmoody and Greweling 1979; Ranger and Turpault 1999; Yanai et al. 2010). Several attempts have been made to expand nutrient budgets to regional scales (e.g., Grigal and Bates (1992), and Akselsson et al. (2004)), but errors are usually not reported and variability within species and tree components across sites is poorly understood. Uncertainties in regional-scale nutrient budgets are a strong limitation to their use in management guidelines (Klaminder et al. 2011).

Uncertainties vary among different nutrient budget components. For example, estimates of mineral-weathering rates and

related changes in soil-nutrient pools and fluxes vary greatly with the methodology used (Blum et al. 2002; Klaminder et al. 2011; Futter et al. 2012). By contrast, the accuracy of biomass and nutrient-pool estimates for aboveground tree components should be relatively good because of the simplicity of the methods used. Such differences must be explicitly acknowledged when developing tools for estimating site nutrient removals in harvested-tree component biomass and nutrient concentration data.

Biomass equations for individual trees have long been available for most regions and forest tree species in Canada (e.g., Ker 1980) and have recently been re-evaluated in a uniform manner across Canada (Lambert et al. 2005; Ung et al. 2008; also see the biomass calculator at <https://apps-scf-cfs.rncan.gc.ca/calc/en/calculateur-calculator>). However, in the stand-level world of forest management, information on basal area is more commonly used and reported than data on individual tree diameters, thereby making stand-level biomass difficult to assess. Once calculated, the biomass of the different tree components is then multiplied by nutrient concentrations to determine nutrient contents from which nutrient removals under different levels of harvesting intensity can be determined. Raulund-Rasmussen et al. (2008)

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suggest that when computing nutrient removal, species-level differences are inconsequential for stem-only harvesting but important to consider when branches and foliage are also removed from sites. However, managers have so far lacked the tools needed to move beyond this assertion when making decisions about harvesting intensities.

The aim of this study was, therefore, to develop an empirically based methodology to support sustainable harvesting decisions for forest biomass across Canada's forests. The specific objectives were (i) to develop a methodology to estimate stand-level biomass by species and tree component from basal area measurements, (ii) to estimate stand-level nutrient contents for five macroelements (nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg)) in each tree component, (iii) to evaluate the uncertainty associated with these estimates, and (iv) to evaluate information loss through species aggregation. Potential solutions for reducing levels of uncertainty are also discussed. The methodologies developed can be applied in other forested jurisdictions.

Material and methods

Estimating tree-component nutrient concentrations

We generated a database of nutrient concentrations for five macroelements (N, P, K, Ca, and Mg) for each of four aboveground tree components (stemwood, bark, branch, and foliage) for 30 of the most common commercial tree species found in Canada. We first created a database containing nutrient data for tree components taken from tables in [Kimmins et al. \(1985\)](#) and [Pardo et al. \(2004\)](#), and added nutrient concentration data compiled as part of two nutrient-cycling projects in Canada (Forest Nutrition Database compiled by the Forest Nutrition Group of the Sustainable Forest Management Network, J.W. Fyles and S. Welke (personal communication); Georgia Basin Critical Loads Project, B.D. Titus and D.G. Maynard (personal communication)). A literature search was also carried out to find additional data, especially for under-represented nutrients, tree species, or tree components. Priority was given to data from single sites, but regional averages were also entered. The database thus obtained contained nutrient values for over 600 categories (species \times tree components \times macroelements), with the actual number of concentration values per category depending on data availability. The database was then cleaned of obvious outliers, and values were expressed in standard units of mass of nutrients per unit of oven-dry mass of tree component.

Mean concentrations (C) and standard deviations (S) were computed by macroelement, tree species, and tree component; standard deviations were computed only for cells with five or more observations. Simple correlation analyses were used to explore the relationships among the concentrations of different nutrients within tree components. The possibility of aggregating tree species into higher taxonomic categories (genus and division) was examined by estimating changes in the proportion of variability explained at increasing levels of aggregation using the GLM procedure in SAS ([SAS Institute Inc. 2003](#)). At the division level we use the terms "conifers" and "hardwoods" as equivalent to Gymnospermae and Magnoliophyta (previously Angiospermae).

The means and standard errors for all species, all conifers, or all hardwoods were calculated using two different methods: (1) unweighted (botanical) mean: all species having the same weight and (2) weighted mean: species values being weighted by their relative frequency of plot-level occurrence in our aggregated field plot database (see the following for details) as given in Supplementary data Table S.1.¹ For the unweighted mean and variance:

$$(1) \quad \bar{Y} = \frac{\sum_{s=1}^{N_s} \bar{Y}_s}{N_s}$$

$$(2) \quad V(\bar{Y}) = V\left(\frac{\sum_{s=1}^{N_s} \bar{Y}_s}{N_s}\right) = \frac{\sum_{s=1}^{N_s} V(\bar{Y}_s)}{N_s^2}$$

For the weighted mean and variance:

$$(3) \quad \bar{Y}_w = \sum_{s=1}^{N_s} W_s \bar{Y}_s \quad \text{where} \quad \sum_{s=1}^{N_s} W_s = 1$$

$$(4) \quad V(\bar{Y}_w) = V\left(\sum_{s=1}^{N_s} W_s \bar{Y}_s\right) = \sum_{s=1}^{N_s} W_s^2 V(\bar{Y}_s)$$

where \bar{Y} is the mean concentration of a particular element within a given biomass component for a group of tree species, N_s represents the number of species in the group, \bar{Y}_s is the mean for species s within the group, $V(\bar{Y}_s)$ is the variance of Y_s , and W_s is the weight for species s calculated as the ratio of the number of National Forest Inventory plots in which species s is found to the number of plots in which at least one of the N_s species is found. The unweighted mean is to be used as a substitute for known tree species for which we do not have values of nutrient concentrations. The weighted mean is to be used when species are not identified, such as in some products from satellite imagery.

Modelling stand-level allometry

Plot-level data (plot size, species, and diameter at breast height (DBH) of each tree in the plot) for 68 317 forest plots were provided in 2004 by all 10 Canadian provinces and the Yukon Territory in support of the National Forest Inventory. The data set was first cleaned to remove obvious measurement or data-transcription errors. Since we used the equations of [Lambert et al. \(2005\)](#) and [Ung et al. \(2008\)](#) to estimate biomass values per tree component (stemwood, stem bark, branches, and foliage) per species, we removed from our data set all trees whose total biomass exceeded the range of species-level biomass used by these authors to fit their allometric equations. As will be expanded upon later, we added a random error term to each biomass estimate, a procedure that sometimes generated negative biomass values for the smaller trees; upon the initial screening, we, therefore, removed trees in which, for at least one component, the absolute value of the error term was equal to or greater than the error-free biomass estimate. Finally, we removed from the data set all trees belonging to a plot in which at least one tree had been deleted in the screening process previously described. In all, these measures resulted in the deletion of 6.3% of the initial plot population.

[Lambert et al. \(2005\)](#) and [Ung et al. \(2008\)](#) used a large Canada-wide data set of biomass measurements obtained by destructive sampling in the early 1980's (the ENFOR data set) to generate two sets of equations for estimating biomasses of individual tree components (stemwood, stem bark, branches, and foliage) by species. The first set of equations uses only the DBH as an independent variable, whereas the second set uses DBH and tree height as independent variables. Since height measurements were available only on a very small subset of trees within plots, we used the DBH-only equations to estimate biomass:

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2012-0454>.

$$(5) \quad m_{ij} = \alpha_{ij} D_i^{\beta_{ij}} + \varepsilon_{ij}$$

where m_{ij} is the biomass of component j (stemwood, bark, branch, and foliage) of tree i , D_i is the DBH of tree i , ε is the error term, and α and β are parameters whose estimates are provided in Lambert et al. (2005) and Ung et al. (2008). Heteroscedasticity had been addressed in these studies by incorporating a power function of D_i in the model to be adjusted:

$$(6) \quad \delta_{ij} = \varepsilon_{ij} / D_i^{c_{ij}^2}$$

where δ_{ij} , the normalized error term, is assumed to follow a multinormal distribution MVN ($0, \Sigma$), where Σ is the residual variance-covariance matrix among tree components from the original data set (see Lambert et al. (2005) for retrieval instructions from public archives), and where c_j is a weight term whose values by species and tree component are given in Lambert et al. (2005) and Ung et al. (2008).

Normally, users of eq. (5) would simply need the values of parameters α and β to estimate the biomasses of a component for a tree of a given species and DBH. However, our goal was to generate a set of tree-level biomass values by component that were realistically variable and, hence, needed the among-tree variability of the original ENFOR data set for this purpose. Single values of ε_{ij} were, therefore, estimated from eq. (6) independently for each tree and component using the published values of c_j as well as values of δ_{ij} randomly generated using the RANDNORMAL function of SAS (SAS Institute Inc. 2003) and the among-component variance-covariance matrices. The use of such matrices automatically overlaid the within-tree correlation structure among tree components on the random error terms. These error terms were then used in eq. (5) to produce realistic noisy tree-level estimates of biomass by component.

Biomass estimates were then summed to the plot level by tree component and species and expressed on a per-hectare basis. The resulting stand-level database was purged of outlier values, where outliers are defined as either (i) greater than the third quartile plus 3 times the interquartile range of the sample population values or (ii) smaller than the first quartile minus 3 times the interquartile range of the sample population values; these correspond to the upper and lower far fences of box plots, respectively. This last step removed 35 plots from the final data set, leaving data from 63 978 plots to be used for model fitting, with 30 species present in a number of plots sufficiently large to fit the models. A summary of the properties of this plot-level data set is presented in Supplementary data Table S.1.¹

We then adjusted the following stand-level biomass model to the stand-level biomass data generated by tree component and by species:

$$(7) \quad M_{sjk} = a_{sj} B_{sk}^b B_{tk}^c + \varepsilon_{sjk}$$

where M_{sjk} ($t \cdot ha^{-1}$) is the biomass of tree component j of species s in plot k , B_{sk} ($m^2 \cdot ha^{-1}$) is the basal area of species s in plot k , B_{tk} ($m^2 \cdot ha^{-1}$) is the total basal area of plot k , and a , b , and c are the parameters to be estimated. A power function of species basal area was fitted as part of the model to reduce heteroscedasticity, as in Lambert et al. (2005):

$$(8) \quad \delta_{sjk} = \varepsilon_{sjk} / B_{sk}^{w_{sj}/2}$$

where symbols and indices are as in eq. 5, and where the values of w_{sj} were obtained from

$$(9) \quad \ln \varepsilon_{sjk}^2 = \theta_{sj} + w_{sj} \ln B_{sk}$$

where θ_{sj} is a parameter whose value is of no further interest. The term δ_{sjk} was again assumed to follow a multinormal distribution, MVN ($0, \Sigma$), where Σ is the residual variance-covariance matrix among tree components.

Equations (7)–(9) were fitted in the following fashion: for a given species s , eq. (7) was first fitted as an allometric system of equations that included all four tree components simultaneously, as in eq. (6) of Lambert et al. (2005), using the MODEL procedure of the SAS software (SAS Institute Inc. 2003). We then extracted the values of ε_{sjk} , the modeling error, by plot and tree component for each species and used these values to fit eq. (9) using PROC GLM (SAS Institute Inc. 2003) to determine the values of w_{sj} . These values of w_{sj} were used as additional independent variables and eqs. (7) and (8) were refitted as an allometric system of equations that included all tree components simultaneously, as in eq. (6) of Lambert et al. (2005), using the MODEL procedure of SAS (SAS Institute Inc. 2003). The resulting stand-level allometric model (eq. (7)) has the same two fundamental properties as the tree-level model of Lambert et al. (2005) and Ung et al. (2008): (i) the sum of the four tree components gives an unbiased estimate of total aboveground biomass per species and (ii) the model is not log-transformed for adjustment and thus does not require a bias correction when applied (Lambert et al. 2005).

Modeling the standard deviation of biomass estimates

We also modeled the standard deviation of the stand-level biomass estimates to facilitate the generation of allometric model uncertainty by the user. As a first step, we applied a Monte Carlo approach to generate 1000 estimates of biomass M for every species s and tree component j in each plot k

$$(10) \quad M_{sjk} = \hat{M}_{sjk} + \varepsilon_{sjk}$$

where \hat{M}_{sjk} was estimated by eq. (7) and the error term ε_{sjk} was generated from eqs. (8) and (9) using the RANDNORMAL function of SAS (2003) for the generation of values of δ_{sjk} that accounted for the variance-covariance structure among the stand-level tree component biomasses. These 1000 estimates were then used to compute a standard deviation of the biomass estimate for each tree component, species, and plot. Through this process, we generated a synthetic data set of standard deviations (S) for calibrating the following a priori standard deviation model:

$$(11) \quad S_{M_{sjk}} = d_{sj} B_{sk}^e + \varepsilon_{sjk}$$

where d and e are parameters to be adjusted. We used the same method as in the stand-level allometric equation (eqs. (8) and (9)) to address the problem of heteroscedasticity.

Computing nutrient contents

We computed the nutrient contents (R) for every species, tree component, and macroelement combination as the product of biomass (M) and nutrient concentration (C)

$$(12) \quad R \pm S_R = (M \pm S_M) (C \pm S_C)$$

where S_R , S_M , and S_C are the standard deviations of nutrient content, biomass, and nutrient concentration, respectively, for a particular species, tree component, and macroelement. To simplify the procedure, we assumed that there was no interaction between the properties being multiplied. Therefore, S_R was computed as

$$(13) \quad S_R = MS_C + CS_M$$

Table 1. Nutrient concentrations (%) by tree component for seven species ranking amongst the top 10 species most commonly found in the National Forest Inventory database (greatest number of plots with presence of the species), as well as for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), a locally important species.

Tree component	Species' nutrient concentration (%)							
	<i>Abies balsamea</i>	<i>Betula papyrifera</i>	<i>Picea glauca</i>	<i>Picea mariana</i>	<i>Pinus banksiana</i>	<i>Pinus contorta</i>	<i>Populus tremuloides</i>	<i>Pseudotsuga menziesii</i>
N								
Stemwood	0.089	0.096	0.058	0.076	0.067	0.045	0.130	0.133
Foliage	1.351	2.063	1.175	0.951	1.176	1.070	2.179	2.197
Branch	0.370	0.394	0.363	0.284	0.296		0.498	0.370
Bark	0.449	0.364	0.303	0.240	0.246	0.273	0.450	0.396
P								
Stemwood	0.008	0.013	0.005	0.007	0.005	0.008	0.014	0.007
Foliage	0.155	0.211	0.169	0.130	0.119	0.127	0.213	0.171
Branch	0.085	0.053	0.050	0.040	0.029		0.074	0.063
Bark	0.052	0.034	0.042	0.047	0.026	0.049	0.054	0.023
K								
Stemwood	0.090	0.053	0.044	0.043	0.045	0.041	0.112	0.100
Foliage	0.558	0.889	0.579	0.552	0.409	0.551	0.962	0.974
Branch	0.241	0.159	0.260	0.134	0.155		0.277	0.252
Bark	0.250	0.120	0.164	0.154	0.115	0.171	0.263	0.119
Ca								
Stemwood	0.081	0.082	0.098	0.141	0.068	0.084	0.232	0.061
Foliage	0.547	0.672	0.508	0.133	0.258	0.227	1.152	0.785
Branch	0.373	0.437	0.656	0.075	0.216		0.979	0.902
Bark	0.726	0.685	1.152	0.139	0.461	1.436	1.204	2.358
Mg								
Stemwood	0.020	0.019	0.009	0.019	0.013	0.023	0.034	0.011
Foliage	0.105	0.202	0.101	0.107	0.093	0.108	0.224	0.180
Branch	0.048	0.054	0.054	0.049	0.040		0.114	0.066
Bark	0.062	0.041	0.060	0.056	0.042	0.130	0.105	0.039

Note: Values in boldface font indicate SD > 50%. Data for all 30 species as well as SDs are presented in Supplementary data Table S.1.¹

Results and discussion

Nutrient concentrations in biomass components

More than 12 800 nutrient concentration values were collected from 329 studies, but the resulting database is unbalanced, as data availability varies widely among species and tree components. The mean nutrient concentrations for each species × tree component × nutrient combination for eight of the most commonly found tree species within the NFI plot database are presented in Table 1, and the values for weighted and unweighted (botanical) groups are given in Table 2. The summary data set for all species is presented in Supplementary data Table S.2.¹ The species for which we found the largest number of nutrient measurements were black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.; 1755 measurements), balsam fir (*Abies balsamea* (L.) Mill.; 1216 measurements), jack pine (*Pinus banksiana* Lamb.; 1145 measurements), sugar maple (*Acer saccharum* Marshall; 1043 measurements), quaking aspen (*Populus tremuloides* Michx.; 988 measurements), white spruce (*Picea glauca* (Moench) Voss; 986 measurements), red pine (*Pinus resinosa* Aiton; 818 measurements), and white birch (*Betula papyrifera* Marshall; 692 measurements). At the other end of the spectrum, we found fewer than 100 measurements for each of the following species: red alder (*Alnus rubra* Bong.), gray birch (*Betula populifolia* Marshall), black ash (*Fraxinus nigra* Marshall), tamarack (*Larix laricina* (Du Roi) K. Koch), Engelmann spruce (*P. engelmannii*), Sitka spruce (*P. sitchensis*), balsam poplar (*Populus balsamifera* L.), and bigtooth aspen (*Populus grandidentata* Michx.).

There were 10 times the number of measurements for foliage (9766 values) as for bark, branches, and stemwood (901, 952, and 1046 values, respectively). Measurements were more evenly distributed amongst nutrients, with 2749, 2564, 2493, 2462, and 2397 measurements for N, P, K, Ca, and Mg, respectively (Supplementary data Table S.2).¹

The number of species showing a high level of uncertainty in nutrient concentration per tree component (defined as coefficient

of variation (CV) >30%) is presented in Table 3. Among the five nutrients, P and Ca showed the greatest variability; the coefficient of variation for P was greater mostly in stemwood, whereas variability in Ca was greater in foliage. Overall, the lowest level of uncertainty in nutrient concentrations was found in bark. The high levels of variability in nutrient concentrations in stemwood (64% of nutrient-species combinations having a CV greater than 30%; Table 3) may, in part, be explained by the inclusion in the data set of studies reporting on a wide range of tree sizes, from juvenile to mature trees. Sapwood is nutrient-rich (Augusto et al. 2000), and its proportional representation within the stem normally varies with stem diameter, but in a complex and nonlinear fashion (e.g., Rochon et al. 1998). With a larger data set, the use of different concentration values for different stem and branch size classes could help reduce variability. The overall variability of the results was also likely increased by the use of analytical laboratory protocols whose detection limit may fall close to the nutrient concentrations of nutrient-poor woody tissues.

We found strong correlations among the concentrations of the different nutrients in foliage, except for P and Ca (Table 4). In general, foliar nutrient concentrations were greater in hardwoods than in conifers (Table 2), as foliar concentrations of N, Ca, and Mg in hardwoods were nearly double those of conifers. This is in agreement with the observations of Sardans et al. (2011) for tree species in Spain. We found one notable exception to this pattern: *Thuja occidentalis* L. (Supplementary data Table S.2),¹ which showed foliar concentrations that were high compared with values found for conifers (Table 2). This species showed foliar K, Ca, and Mg values that were higher than the mean values found for hardwoods (Table 2), with mean Ca values of 1.132% being notably higher than mean hardwood values (0.945%) and much higher than the mean value found for conifers (0.473%). Ca concentration differences can be large between species and can reflect adaptation to calcareous or acidic soils (e.g., calcicole-calcifuge adaptation of

Table 2. Mean nutrient concentrations (%) by tree component for “all species”, “all conifers”, and “all hardwoods”.

Species	Component	Nitrogen			Phosphorus			Potassium			Calcium			Magnesium		
		N _s	Mean (%)	SE												
Unweighted mean values																
Conifers	Stemwood	12	0.075	0.003	12	0.007	0.001	11	0.060	0.003	11	0.086	0.006	11	0.015	0.001
	Foliage	18	1.289	0.012	18	0.156	0.002	18	0.653	0.017	18	0.473	0.018	18	0.120	0.003
	Branch	11	0.318	0.011	11	0.055	0.004	11	0.177	0.012	11	0.476	0.018	11	0.050	0.002
	Bark	12	0.314	0.009	12	0.046	0.002	12	0.173	0.013	12	0.939	0.058	12	0.058	0.004
Hardwoods	Stemwood	8	0.129	0.007	7	0.011	0.001	7	0.077	0.003	7	0.114	0.007	7	0.022	0.001
	Foliage	11	2.124	0.093	10	0.175	0.005	10	0.854	0.030	10	0.945	0.038	10	0.201	0.007
	Branch	7	0.379	0.013	8	0.069	0.013	8	0.348	0.061	8	0.645	0.042	8	0.074	0.014
	Bark	6	0.436	0.014	6	0.042	0.003	7	0.420	0.178	7	1.274	0.160	7	0.060	0.003
All	Stemwood	20	0.096	0.003	19	0.008	0.000	18	0.067	0.002	18	0.097	0.005	18	0.018	0.001
	Foliage	29	1.606	0.036	28	0.163	0.002	28	0.725	0.015	28	0.642	0.018	28	0.149	0.003
	Branch	18	0.342	0.009	19	0.061	0.006	19	0.249	0.027	19	0.547	0.021	19	0.060	0.006
	Bark	18	0.355	0.007	18	0.045	0.002	19	0.264	0.066	19	1.063	0.069	19	0.059	0.003
Weighted mean values																
Conifers	Stemwood	12	0.075	0.005	12	0.007	0.001	11	0.061	0.004	11	0.101	0.017	11	0.016	0.001
	Foliage	18	1.225	0.007	18	0.149	0.001	18	0.593	0.010	18	0.460	0.012	18	0.112	0.002
	Branch	11	0.329	0.015	11	0.058	0.005	11	0.197	0.013	11	0.449	0.018	11	0.050	0.002
	Bark	12	0.324	0.013	12	0.046	0.005	12	0.187	0.010	12	0.925	0.040	12	0.061	0.003
Hardwoods	Stemwood	8	0.107	0.004	7	0.011	0.001	7	0.072	0.003	7	0.12	0.009	7	0.022	0.001
	Foliage	11	2.088	0.025	10	0.195	0.005	10	0.884	0.017	10	0.865	0.020	10	0.208	0.005
	Branch	7	0.403	0.013	8	0.064	0.007	8	0.265	0.031	8	0.568	0.029	8	0.069	0.006
	Bark	6	0.423	0.017	6	0.041	0.002	7	0.247	0.045	7	1.088	0.061	7	0.058	0.003
All	Stemwood	20	0.086	0.004	19	0.008	0.001	18	0.065	0.003	18	0.107	0.011	18	0.018	0.001
	Foliage	29	1.513	0.010	28	0.164	0.002	28	0.689	0.009	28	0.594	0.010	28	0.144	0.002
	Branch	18	0.354	0.011	19	0.060	0.004	19	0.221	0.014	19	0.491	0.015	19	0.056	0.003
	Bark	18	0.357	0.010	18	0.045	0.004	19	0.207	0.017	19	0.981	0.033	19	0.060	0.002

Note: Unweighted mean values (same weight for all species) and weighted mean values (based on the frequency of occurrence in the National Forest Inventory (NFI) database; see Supplementary data Table S.1)¹ are presented. N_s is the number of species represented in the mean. See the text for information on the estimation of SE. “Botanical values” are to be used to estimate the nutrient concentrations of a known species that is not listed in the table. “Weighted values” are to be used to estimate nutrient concentrations for unidentifiable species, such as those derived from remote sensing products.

Table 3. Ratio of the number of tree species showing a high variability in tissue nutrient concentrations (defined as a coefficient of variation (CV) >30%) by tree biomass component and nutrient category (with average CV in parentheses) on the number of species with a number of data entries n ≥ 5.

Nutrient	Ratio				
	Tree biomass component				
	Stemwood	Foliage	Branch	Bark	Total
N	4:12 (36)	1:28 (18)	4:15 (26)	5:13 (27)	21% (25)
P	11:14 (62)	12:28 (31)	12:16 (47)	5:13 (31)	56% (41)
K	8:12 (37)	5:28 (29)	8:14 (43)	4:12 (35)	38% (34)
Ca	10:14 (45)	20:28 (40)	7:13 (29)	3:11 (27)	61% (37)
Mg	10:15 (37)	5:28 (25)	7:14 (29)	1:12 (24)	33% (28)
Total	64%	31%	38%	18%	

Note: Values given in percentages are totals per nutrient or per tree biomass component. This information is derived from the full database for 30 tree species. Values in boldface type indicate that a majority of species showed a high variability.

plant species reviewed in Lee (1998)). *Populus* trees had the highest Ca concentrations amongst deciduous species.

Similar to foliage, stemwood concentrations of nutrients were, in general, positively correlated with each other, but the correlations were weaker (Table 4). Ca and Mg, two of the least mobile nutrients that tend to accumulate in permanent plant structures (Rochon et al. 1998), were highly and positively correlated with each other. Correlation among nutrient concentrations was poor in branches and very poor in bark (Table 4). This result is impor-

Table 4. Correlation coefficients (r) among nutrient concentrations within tree components.

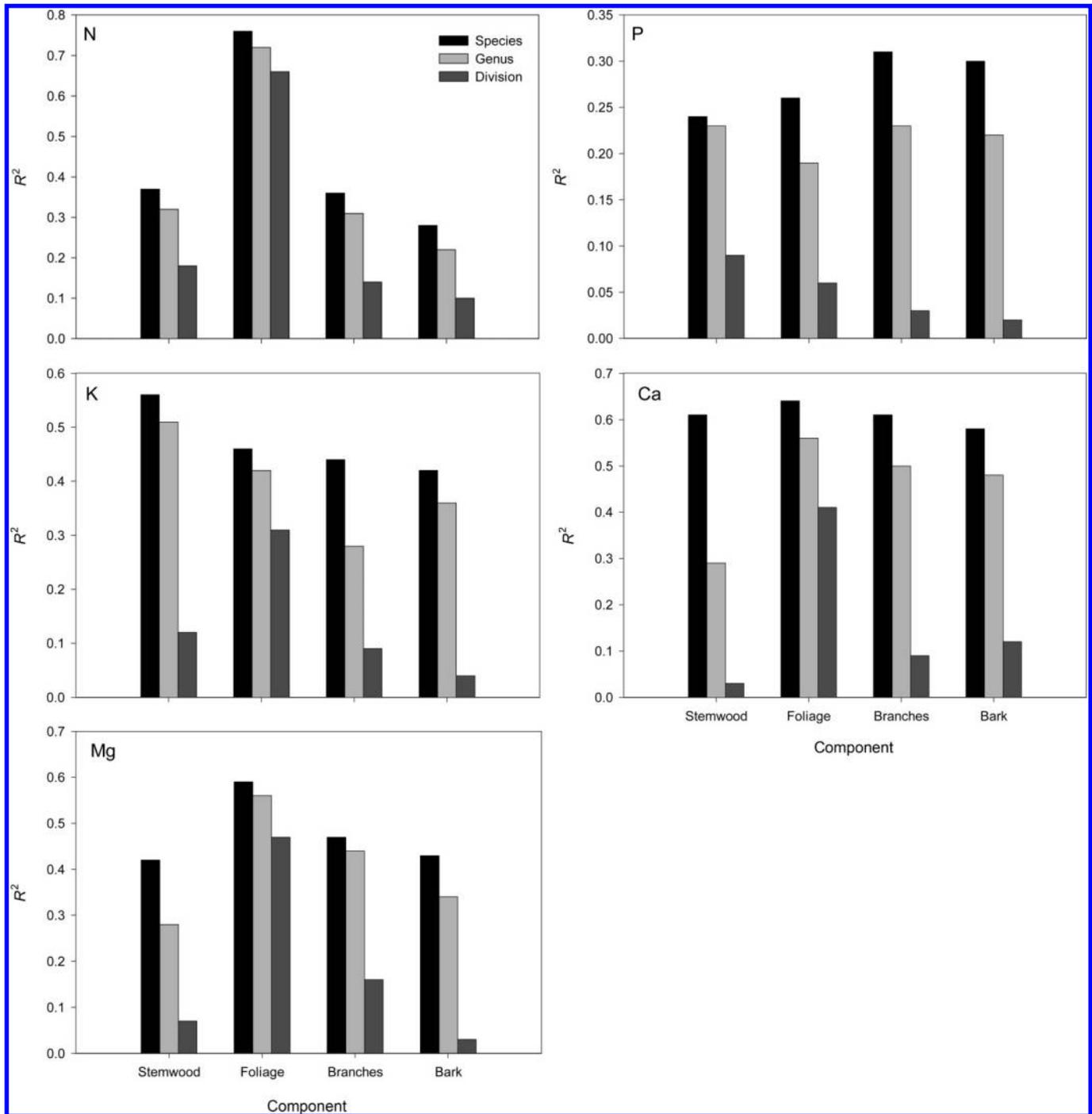
Tree component	Nutrient	r				
		N	P	K	Ca	Mg
Stemwood n (22–23)	N	1	0.410*	0.401*	0.375 ^{ns}	0.346 ^{ns}
	P		1	0.504*	0.557**	0.632***
	K			1	0.605**	0.780****
	Ca				1	0.902****
Foliage n (29–30)	N	1	0.587***	0.684****	0.498**	0.742****
	P		1	0.673****	0.339 ^{ns}	0.424*
	K			1	0.553**	0.632***
	Ca				1	0.674***
Branch n (21–22)	N	1	0.055 ^{ns}	0.245 ^{ns}	0.000 ^{ns}	0.607***
	P		1	0.746****	-0.071 ^{ns}	0.465*
	K			1	0.000 ^{ns}	0.712****
	Ca				1	0.292 ^{ns}
Bark n (20–21)	N	1	-0.063 ^{ns}	0.807****	0.300 ^{ns}	-0.077 ^{ns}
	P		1	0.000 ^{ns}	-0.437*	0.330 ^{ns}
	K			1	0.207 ^{ns}	0.055 ^{ns}
	Ca				1	0.239 ^{ns}
	Mg					1

Note: ns, not significant; *, p < 0.05; **, p < 0.01; ***, p < 0.001; ****, p < 0.0001.

tant because it suggests that a high export rate of one element (e.g., N), does not imply that there will be a high output of other elements (e.g., Ca).

Weighted means (Table 2) generally had slightly lower values than unweighted ones, showing that for both hardwoods and conifers, species with high nutrient concentrations are proportionally less abundant in the landscape. The standard errors

Fig. 1. Variation in R^2 , the portion of variability explained in nutrient concentrations with grouping from species to genus and to divisions (Gymnospermae and Magnoliophyta) per nutrient and biomass compartments.



associated with the weighted means were generally lower than those of the unweighted means (Table 2).

There was only a modest increase in unexplained variance in nutrient concentrations when species were aggregated by genus, with the exception of Ca in stemwood whose unexplained variance increased more (Fig. 1). Further aggregation of genera into conifers and hardwoods generated a large increase in unexplained variance in nutrient concentrations for all nutrients and tree components, with the exception of foliar N and Mg (Fig. 1).

In summary, uncertainty was highest for concentrations of P in woody components and Ca in foliage, and increased only slightly

when species were aggregated into genera. Relating nutrient concentrations within species or genera to variations in soil geochemistry, climate, and precipitation chemistry could decrease the uncertainty of the estimates (Yin 1993; Kang et al. 2011; Sardans et al. 2011).

Stand-level allometry

Equation parameters for estimates of biomass and of their associated standard deviations for eight of the most commonly found species within the NFI plot data set are presented in Tables 5a and 5b, respectively. Equation parameters and fit

Table 5. (a) Model parameter estimates and their standard error (SE) per tree species and biomass compartment for predicting biomass based on individual species basal area and total stand basal area (eq. (7)). (b) Model parameter estimates and their standard error (SE) per tree species and biomass compartment for eq. (11) predicting the standard deviation (SD) of biomass estimates (t·ha⁻¹) of biomass components based on individual species basal area and total stand basal area.

Parameter	Estimate	SE
(a) Model parameter estimates and SE per tree species and biomass component for eq. (7).		
<i>Abies balsamea</i>		
<i>a</i> _{stemwood}	1.6209	0.0080
<i>b</i> _{stemwood}	1.0571	0.0007
<i>c</i> _{stemwood}	0.0038	0.0017
<i>a</i> _{foliage}	0.6075	0.0035
<i>b</i> _{foliage}	0.9332	0.0008
<i>c</i> _{foliage}	-0.0142	0.0020
<i>a</i> _{Branch}	0.2860	0.0028
<i>b</i> _{Branch}	1.0598	0.0015
<i>c</i> _{Branch}	0.0219	0.0034
<i>a</i> _{bark}	0.3076	0.0014
<i>b</i> _{bark}	1.0512	0.0007
<i>c</i> _{bark}	0.0034	0.0016
<i>Betula papyrifera</i>		
<i>a</i> _{stemwood}	2.3069	0.0174
<i>b</i> _{stemwood}	1.0768	0.0011
<i>c</i> _{stemwood}	0.0371	0.0024
<i>a</i> _{foliage}	0.3599	0.0027
<i>b</i> _{foliage}	0.9357	0.0014
<i>c</i> _{foliage}	-0.0531	0.0025
<i>a</i> _{Branch}	0.5771	0.0057
<i>b</i> _{Branch}	1.0914	0.0013
<i>c</i> _{Branch}	0.0431	0.0031
<i>a</i> _{bark}	0.4133	0.0026
<i>b</i> _{bark}	1.0659	0.0008
<i>c</i> _{bark}	0.0312	0.0020
<i>Picea glauca</i>		
<i>a</i> _{stemwood}	2.1480	0.0163
<i>b</i> _{stemwood}	1.1042	0.0009
<i>c</i> _{stemwood}	-0.0044	0.0024
<i>a</i> _{foliage}	0.6012	0.0052
<i>b</i> _{foliage}	0.8858	0.0012
<i>c</i> _{foliage}	-0.0243	0.0028
<i>a</i> _{Branch}	0.4792	0.0043
<i>b</i> _{Branch}	0.9965	0.0013
<i>c</i> _{Branch}	-0.0065	0.0028
<i>a</i> _{bark}	0.3279	0.0020
<i>b</i> _{bark}	1.0518	0.0008
<i>c</i> _{bark}	-0.0013	0.0019
<i>Picea mariana</i>		
<i>a</i> _{stemwood}	1.6809	0.0076
<i>b</i> _{stemwood}	1.0156	0.0008
<i>c</i> _{stemwood}	0.0839	0.0016
<i>a</i> _{foliage}	0.8318	0.0034
<i>b</i> _{foliage}	0.9419	0.0010
<i>c</i> _{foliage}	-0.1022	0.0016
<i>a</i> _{Branch}	0.4148	0.0014
<i>b</i> _{Branch}	0.9964	0.0006
<i>c</i> _{Branch}	0.0204	0.0012
<i>a</i> _{bark}	0.3087	0.0008
<i>b</i> _{bark}	1.0110	0.0005
<i>c</i> _{bark}	0.0397	0.0009
<i>Pinus banksiana</i>		
<i>a</i> _{stemwood}	2.3317	0.0178
<i>b</i> _{stemwood}	0.9927	0.0013
<i>c</i> _{stemwood}	0.1023	0.0027
<i>a</i> _{foliage}	0.3055	0.0022
<i>b</i> _{foliage}	1.0069	0.0018

Table 5 (continued).

Parameter	Estimate	SE
<i>c</i> _{foliage}	-0.0884	0.0028
<i>a</i> _{Branch}	0.2317	0.0027
<i>b</i> _{Branch}	0.9736	0.0019
<i>c</i> _{Branch}	0.1240	0.0041
<i>a</i> _{bark}	0.2705	0.0010
<i>b</i> _{bark}	0.9978	0.0008
<i>c</i> _{bark}	0.0181	0.0014
<i>Pinus contorta</i>		
<i>a</i> _{stemwood}	2.0024	0.0155
<i>b</i> _{stemwood}	0.9608	0.0020
<i>c</i> _{stemwood}	0.1536	0.0029
<i>a</i> _{foliage}	0.3247	0.0022
<i>b</i> _{foliage}	1.0171	0.0033
<i>c</i> _{foliage}	-0.0988	0.0037
<i>a</i> _{Branch}	0.3368	0.0027
<i>b</i> _{Branch}	0.9920	0.0027
<i>c</i> _{Branch}	0.0328	0.0035
<i>a</i> _{bark}	0.2848	0.0010
<i>b</i> _{bark}	0.9880	0.0012
<i>c</i> _{bark}	0.0259	0.0015
<i>Populus tremuloides</i>		
<i>a</i> _{stemwood}	1.8931	0.0207
<i>b</i> _{stemwood}	1.0396	0.0015
<i>c</i> _{stemwood}	0.1264	0.0035
<i>a</i> _{foliage}	0.1828	0.0013
<i>b</i> _{foliage}	0.9616	0.0016
<i>c</i> _{foliage}	-0.1132	0.0027
<i>a</i> _{Branch}	0.2644	0.0036
<i>b</i> _{Branch}	1.0558	0.0015
<i>c</i> _{Branch}	0.1385	0.0043
<i>a</i> _{bark}	0.4470	0.0051
<i>b</i> _{bark}	1.0302	0.0016
<i>c</i> _{bark}	0.1102	0.0037
<i>Pseudotsuga menziesii</i>		
<i>a</i> _{stemwood}	1.9314	0.0316
<i>b</i> _{stemwood}	1.0586	0.0038
<i>c</i> _{stemwood}	0.0385	0.0059
<i>a</i> _{foliage}	0.6536	0.0064
<i>b</i> _{foliage}	0.9619	0.0026
<i>c</i> _{foliage}	-0.0268	0.0037
<i>a</i> _{Branch}	0.7817	0.0064
<i>b</i> _{Branch}	0.9976	0.0020
<i>c</i> _{Branch}	0.0127	0.0030
<i>a</i> _{bark}	0.4139	0.0066
<i>b</i> _{bark}	1.0393	0.0041
<i>c</i> _{bark}	0.0404	0.0058
(b) Model parameter estimates and SE per tree species and biomass component for eq. (11).		
<i>Abies balsamea</i>		
<i>d</i> _{stemwood}	0.4712	0.0001
<i>e</i> _{stemwood}	0.8495	0.0001
<i>d</i> _{foliage}	0.2095	0.0000
<i>e</i> _{foliage}	0.6936	0.0001
<i>d</i> _{Branch}	0.1363	0.0000
<i>e</i> _{Branch}	0.8149	0.0001
<i>d</i> _{bark}	0.0892	0.0000
<i>e</i> _{bark}	0.8151	0.0001
<i>Betula papyrifera</i>		
<i>d</i> _{stemwood}	0.8800	0.0001
<i>e</i> _{stemwood}	0.8490	0.0001
<i>d</i> _{foliage}	0.1225	0.0000
<i>e</i> _{foliage}	0.6764	0.0001
<i>d</i> _{Branch}	0.3351	0.0001
<i>e</i> _{Branch}	0.8151	0.0001
<i>d</i> _{bark}	0.1500	0.0000
<i>e</i> _{bark}	0.8147	0.0001

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Table 5 (concluded).

Parameter	Estimate	SE
<i>Picea glauca</i>		
d_{stemwood}	0.9702	0.0002
e_{stemwood}	0.7871	0.0001
d_{foliage}	0.2560	0.0000
e_{foliage}	0.6671	0.0001
d_{Branch}	0.1672	0.0000
e_{Branch}	0.7515	0.0001
d_{bark}	0.1009	0.0000
e_{bark}	0.7813	0.0001
<i>Picea mariana</i>		
d_{stemwood}	0.7653	0.0002
e_{stemwood}	0.7321	0.0001
d_{foliage}	0.2643	0.0001
e_{foliage}	0.7160	0.0001
d_{Branch}	0.1306	0.0000
e_{Branch}	0.5963	0.0001
d_{bark}	0.0781	0.0000
e_{bark}	0.6891	0.0001
<i>Pinus banksiana</i>		
d_{stemwood}	0.7876	0.0003
e_{stemwood}	0.7483	0.0002
d_{foliage}	0.0770	0.0000
e_{foliage}	0.6102	0.0002
d_{Branch}	0.1324	0.0001
e_{Branch}	0.6807	0.0002
d_{bark}	0.0488	0.0000
e_{bark}	0.5533	0.0002
<i>Pinus contorta</i>		
d_{stemwood}	1.2749	0.0007
e_{stemwood}	0.7246	0.0002
d_{foliage}	0.1087	0.0001
e_{foliage}	0.7053	0.0002
d_{Branch}	0.1782	0.0001
e_{Branch}	0.7067	0.0002
d_{bark}	0.0867	0.0000
e_{bark}	0.5574	0.0002
<i>Populus tremuloides</i>		
d_{stemwood}	0.9871	0.0003
e_{stemwood}	0.7540	0.0001
d_{foliage}	0.0592	0.0000
e_{foliage}	0.6297	0.0001
d_{Branch}	0.2225	0.0001
e_{Branch}	0.7523	0.0001
d_{bark}	0.2177	0.0001
e_{bark}	0.7377	0.0001
<i>Pseudotsuga menziesii</i>		
d_{stemwood}	1.4030	0.0012
e_{stemwood}	0.7141	0.0003
d_{foliage}	0.1956	0.0002
e_{foliage}	0.6702	0.0003
d_{Branch}	0.1768	0.0001
e_{Branch}	0.7274	0.0003
d_{bark}	0.2439	0.0002
e_{bark}	0.7163	0.0003

Note: Parameters are presented for the tree species listed in Table 1. Equation parameters and fit statistics for all 30 species and equations for functional groups (conifers and hardwoods) and for all species combined are presented in Supplementary data Tables S.3 and S.4.

statistics for all 30 species are presented in Supplementary data Tables S.3 and S.4.¹ The adjustment of stand-level allometric equations is generally excellent. The mean value of R^2 and of root mean squared error for the biomass model (eq. (7)) across all species are 0.95 and 5.24, respectively, for stemwood; 0.96 and 0.65, respectively, for bark; 0.93 and 1.33, respectively, for branches; and 0.93 and 0.66, respectively, for foliage. The mean value of R^2 for the standard deviation model (eq. (11)) is >0.99 . Foliage biomass had the worst fit among all tree components, as was found by Lambert

Table 6. Standard deviation (SD) of the error for plot-level biomass estimates by tree component for plots containing black spruce trees.

Tree component	SD of the error for biomass estimates		
	Tree level	Plot level	Ratio
Stem	1.56	8.99	5.77
Foliage	0.81	4.64	5.74
Branch	0.70	3.95	5.66
Bark	0.25	1.48	5.84

Note: The values are for estimates for which the error terms of the equation parameters have been propagated either at the tree or plot level.

et al. (2005) and by Ung et al. (2008) when adjusting the tree-level equations.

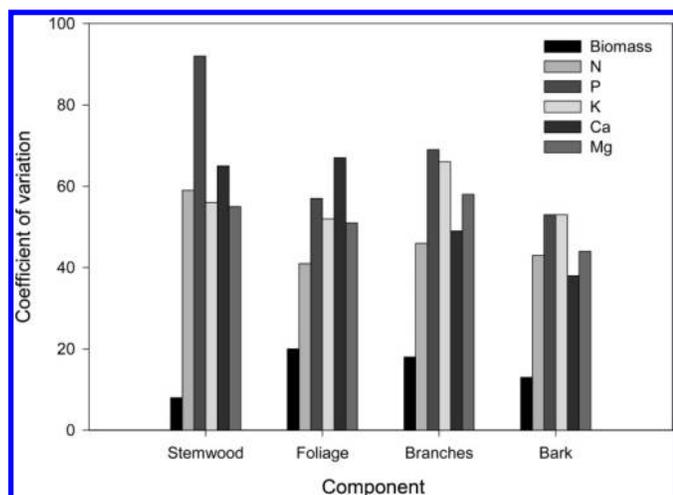
The choice of basal area as the main predictor is compatible with other stand-level allometric model derivations (e.g., Bi et al. 2010, Castedo-Dorado et al. 2012). The use of both total stand basal area and species basal area as independent variables in eq. (7) improves the fit by a small but important amount, and reduces the potential for bias in biomass estimates of individual species within mixed stands. In addition, because the model uses basal area as the only independent variable, biomass per species can thus be estimated from simple prism-based basal area measurements in variable-area plots, eschewing the need to measure tree diameters at breast height in fixed-area plots.

The propagation of error in such an exercise is always limited by the incomplete accounting of individual sources of error. Following the nomenclature of Yanai et al. (2012b), errors can come from four sources: measurement, sampling, modeling, and “among-model”. Measurement errors are those that are associated with actual field measurements of tree diameter and mass and, in this case, the decisions to include or exclude specific tree components such as stumps into the total biomass. This source of error was discussed in Lambert et al. (2005) but not quantified; since it is not explicitly parsed out in the current analysis, it contributes to the general error term.

The current work deals explicitly with the modelling error as we provide an estimate of the standard deviation of the model estimate (eq. (11)). By contrast, the among-model error is not explicitly considered in this exercise. Lambert et al. (2005) showed that other commonly used biomass equations for Canadian tree species were within the prediction intervals of the national equations. This observation does not preclude the possibility of divergence of the tree-level models from results of locally calibrated models. The tree-level equations of Lambert et al. (2005) and of Ung et al. (2008) were fitted to a data set acquired on about 9000 trees of more than 41 species sampled across Canada. Because of the large geographic sampling domain for individual tree species, there is a possibility for allometric relationships to generate a larger modelling error term for regional applications.

In addition, the original destructive sampling of trees was not carried out in a plot-based design and, hence, the resulting tree-level equations contain no information on between-plot variability. For their application, we therefore had to assume that the variability found in that data set rested fully among trees. In practical terms, this meant drawing a new set of random values of δ_{ij} in eq. (8) for each tree within the national data set. Distributing errors at the tree-level in this manner tends to reduce the overall variability among plot-level estimates of biomass, as positive and negative values cancel each other out, as discussed in Yanai et al. (2012b). Assuming that the error rested in the between-plot

Fig. 2. Mean values of the coefficient of variation (CV) obtained when predicting biomass and nutrient contents for hypothetical stands with a basal area of 25 m²·ha⁻¹ of a given species and 40 m²·ha⁻¹ total basal area for the eight species listed in Table 1.



variability would have meant drawing a single set of random values of δ_{ij} for all trees within a given plot, thus generating a noisier plot-level data set for model fitting. To illustrate this, we have estimated that a propagation of error terms at the plot level only instead of at the tree level would have increased the standard deviation of the error of the plot-level biomass estimates for black spruce by nearly a factor of six (Table 6). However, no attribution of the error to the plot level is valid, since, as previously mentioned, we have no information on between-plot variability.

Estimating nutrient contents

The combination of allometric models and nutrient concentrations enables us to estimate stand-level nutrient contents by species and component (eq. (12)), and the uncertainties associated with these estimates (eq. (13)). In general, the large uncertainty of nutrient content estimates is mostly due to the variability among measurements of nutrient concentrations. To illustrate this general observation, we estimated biomass, nutrient contents, and associated uncertainties for the species listed in Table 1 for a hypothetical stand. For the computations, we used 40 m²·ha⁻¹ as the total basal area (B_{tk} in eq. (7)) and 25 m²·ha⁻¹ as the basal area of the species of interest (B_{sk}). The resulting mean CV by nutrient-biomass and tree component is presented in Fig. 2. The CV for biomass estimates varies from 8% for stemwood to 20% for foliage; however, the values of CV for nutrient contents are generally >40% and some are very high (e.g., P in stemwood), reflecting the high variability in the nutrient concentration database. High estimates of variability are commonly reported in studies predicting forest ecosystem nutrient fluxes (Klaminder et al. 2011; Futter et al. 2012; Yanai et al. 2012a).

The high variability of nutrient content estimates makes their use in forest management decisions challenging because of the high possibility of making either type I or type II errors. Type I errors, rating sites as sensitive to nutrient removals when they are not, create lost opportunities for forestry. Type II errors, rating sites as nonsensitive to nutrient removals when they are, can result in long-term losses of productivity. The probability of occurrence of either error can be decreased over time through the implementation of an adaptive management approach in which postharvest monitoring programs are used to refine local forest management guidelines.

Conclusion

Large variability is an inescapable property of natural environments, although the levels shown in the present study could potentially be reduced through improvements in our understanding of soil, climate, age, or tree size effects on tree nutrition. In the short term, however, this very large variability must be considered for sound management decision making, and shows that we can make only very coarse determinations of nutrient fluxes in removals of biomass from individual sites in Canada. At the landscape level, however, we believe that the aggregated estimates over many sites will tend towards a population mean. It should also be borne in mind that biomass harvesting always leaves a large proportion of harvest residues on site because of technical constraints (e.g., 30%–50% in Ralevic et al. 2010). This must be taken into account when applying our equations to the evaluation of biomass removal projects. Finally, foliage is often used as an index of site fertility. Although standardization of sampling methodologies could reduce uncertainty in nutrient content estimates, some of the very high variability observed in nutrient concentrations probably reflects the response of individual trees and species to their local environment. Understanding this source of variability and its relation to site conditions should help us better manage Canada's forests from a nutritional perspective, especially regarding the cumulative effects of natural and anthropogenic disturbances.

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