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Estimating foliage biomass in Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) plots

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Summary Dynamic decomposition models are needed to estimate changes in the carbon stock of boreal soil because these changes are difficult to measure directly. An important aboveground carbon flux to the soil is foliage litterfall. To estimate this flux, both the amount and the turnover rate of the foliage biomass component must be known. Several methods for estimating foliage biomass of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.), including biomass equations and biomass expansion factors (BEFs), were compared with predicted foliage biomass based on forest inventory plot-level measurements. Measured foliage biomass was upscaled from the branch-level to the plot-level by combining forest inventory variables (diameter, height, height at the crown base and crown base diameter) based on the assumptions of pipe model theory. Combining the foliage biomass: cross-sectional area ratio with the forest inventory variables provided accurate estimates of foliage biomass at the plot-level for plots in southern Finland. The results emphasize the need to test biomass equations with independent data, especially when the equations applied are based on neighboring regions.

Keywords: BEF, carbon, crown base, needle biomass, pipe model.

Introduction

Carbon dynamics of forest ecosystems depend on foliage biomass because of the short life span of the foliage. Although foliage biomass is not the most important biomass pool of the forest ecosystem in terms of quantity, it has a high turnover rate compared with other biomass pools, e.g., branches or stem, and so foliage litter is often the most important aboveground carbon input to soil. Foliage biomass is difficult to predict because of its great variation and dependence on various site and tree properties. As a consequence, direct measurements, which are laborious and involve destructive sampling, are often needed (e.g., Hoffman and Usoltsev 2002, Liski et al. 2002, Masera et al. 2003).

Several approaches have been used to predict biomass at the stand scale. For example, process-based models predict productivity mainly as a function of environmental variables, like radiation and soil properties. Most of these models estimate allocation of carbon to the foliage as a proportion of total photosynthetic production. These allocation parameters can be tested against alternative biomass estimates, such as biomass equations, which are based on empirical data. In contrast, statistical forest carbon models that utilize forest inventory data have used biomass equations, biomass expansion factors (BEFs) or percentages (Kellomäki et al. 1992) to quantify different biomass compartments.

In ecosystem studies on nutrient flows and photosynthesis, foliage biomass has traditionally been estimated based on analysis of a few stands (Mälkönen 1974, Helmisaari et al. 2002). However, several biomass studies comprise sample plots located across countries and include extensive sampling of branch and foliage biomass (Marklund 1988, Hakkila 1991). These country-level biomass equations have been used to estimate biomass at the stand-level; to obtain the foliage biomass of a stand, the tree-level biomass of foliage is summed. In the United States, stand biomass has also been estimated for groups of similar tree species by combining several biomass equations (Jenkins et al. 2003). These methods, which use stem volume as a predictor, are appropriate for large-scale assessments of biomass. Currently, national biomass stocks have been estimated by converting stem volumes to biomass (UN-ECE 2000), and similar biomass expansion factors (BEFs) have been used to estimate the stand-level biomass of foliage (Liski et al. 2002, Lehtonen et al. 2004).

An element common to all methods for estimating the regional biomass of foliage is that they have not been tested against other biomass measurements from the same region. To test methods for estimating regional biomass, an additional sampling of biomass across that specific area is required, but is often impossible to obtain.

Another challenge is quantifying the foliage biomass of large trees on mature plots; this is difficult because the canopy closes after self-thinning starts and because the applicability of biomass equations is often limited to smaller trees. With larger trees, biomass equations have higher variance, and as a result, the risk of bias increases with stand age, especially if the sample of large trees is small. Therefore, a method of bio-

Table 1. Description of the Vapu plots. Values are per hectare, including all species on a plot.

Species	Statistic	Stocking (n)	Basal area (breast height) (m^2)	Basal area (crown base) (m^2)	Quadratic mean diameter (cm)	Foliage mass[1] (Mg)	Stand age (years)	Stem volume (m^3)
Scots pine	Minimum	345	3	4[2]	5	1.78	8	10
	Mean	1803	16	10	12	4.29	54	105
	Maximum	4986	34	20	26	7.90	158	254
Norway spruce	Minimum	204	4	3	6	3.02	34	32
	Mean	1823	23	17	15	12.14	67	207
	Maximum	4455	38	26	31	19.45	159	444

[1] Dominant conifers only.

[2] In young stands, basal area at crown base can be more than at breast height.

mass estimation based on the functional properties of trees at the plot-level may be an attractive alternative.

According to the pipe model theory (Shinozaki et al. 1964), there is a strong relationship between foliage biomass and sapwood area. This relationship is fairly constant for trees of the same species, location (Hari et al. 1996, Vanninen et al. 1996) and crown condition (Eckmüllner and Sterba 2000). Therefore, the pipe model theory has been proposed as a good tool for predicting foliage biomass (Waring et al. 1982, Mäkelä et al. 1995). It has also been used successfully in process-based modeling (Mäkelä 1986, Berninger and Nikinmaa 1997, Mäkelä 2003).

The objective of this study was to test different methods of estimating foliage biomass against predicted estimates based on measurements at the plot level.

Materials and methods

Materials

The study is based on biomass measurements and detailed information about tree dimensions collected by the Finnish Forest Research Institute (Korhonen and Maltamo 1990) from 94 sample plots of the 8th National Forest Inventory during 1988–1990 (Vapu data, Table 1). Because destructive sampling was necessary, only sample plots located on land owned by state or forestry companies were included in the sampling. All sampled plots were located below 62°50′ N.

For each sample plot, three trees (with diameter at breast height (DBH) > 5 cm) closest to the center of the sample plot were felled in single-species stands, and an additional three trees were felled from the second-dominant stratum in mixed stands. The radius of the sample plot varied among plots from 5 to 13.78 m. A total of 196 Norway spruce (*Picea abies* (L.) Karst.) and 195 Scots pine (*Pinus sylvestris* L.) trees were included in the analysis.

Base diameter (in two directions at right angles to one another just above the butt swell), location (distance from ground) and status (live or dead) of every branch on each sample tree were measured. For each sample tree, stem diameter at the crown base was measured from two directions, and the height at the crown base was also determined. For Norway spruce trees, random selection of branches involved summing the diameters of living branches and dividing by 10 to give the quotient r. Then, a random integer between 1 and r was selected and used to locate the first sample branch. For Scots pines, the total number of branches was used for branch sampling instead of the diameter sum, because, unlike Norway spruce, Scots pines do not have many small branches between whorls. On average, 10 branches per tree were selected. Dry masses of the second, fifth and eighth sample branches were determined after drying for 48 h at 105 °C. After drying, foliage was separated from branches. Korhonen and Maltamo (1990) have described the sampling design and measurement methods in detail.

Estimates of foliage biomass

Foliage biomass was estimated for the Vapu plots by seven methods (Table 2). Four methods were based on stand-level measurements: biomass expansion factors (BEFs; Method 1), biomass to volume (Method 2) and Valentine's approach (Methods 3 and 4). Three methods (Methods 5, 6 and 7) were based on biomass equations that need tree-level data. To obtain estimates of foliage biomass by Method 1, stem volumes were multiplied by age-dependent BEFs as reported by Lehtonen et al. (2004). The volume-to-biomass estimates (Method 2) were

Table 2. Methods for estimating foliage biomass and the independent variables needed for these models. Abbreviations: W_f = foliage biomass; A_{cb} = basal area at the crown base; cr_m = modified mean crown ratio; cr = crown ratio; and DBH = diameter at breast height.

Method	Independent variables	Level of application
(1) BEF	Stem volume, stand age	Stand
(2) Volume-to-biomass	Stem volume	Stand
(3) Valentine (cr_m model)	Basal area (1.3 m), W_f:A_{cb} ratio	Stand
(4) Valentine	Basal area (1.3 m), W_f:A_{cb} ratio, cr_m	Stand
(5) Hakkila	DBH, cr	Tree
(6) Marklund	DBH, height	Tree
(7) Biomass equations of this study	DBH, height	Tree

similar to the BEF estimates except that stand age was not used as a predictor (Lehtonen et al. 2004). Estimates of foliage biomass were also derived based on the pipe model theory (Shinozaki et al. 1964) by applying the method described by Valentine et al. (1994) (Method 4). Foliage biomass (W_f) was assessed by multiplying basal area at breast height (G) by the modified mean crown ratio ($\mathrm{cr_m}$) at plot-level and by the mean $W_f{:}A_{cb}$ ratio for the whole Vapu region, where W_f is foliage biomass and A_{cb} is basal area at crown base:

$$W_f = G\mathrm{cr_m}\frac{W_f}{A_{cb}} \tag{1}$$

where $\mathrm{cr_m}$ is $\left[\dfrac{h-\mathrm{ch}}{h-1.3}\right]$, and h is tree height and ch is height at the crown base. The $\mathrm{cr_m}$ of each plot was used.

To simplify Valentine's method for situations where no information about the $\mathrm{cr_m}$ is available, $\mathrm{cr_m}$ was estimated from G by a simple linear model (Method 3):

$$\mathrm{cr_m}(G) = a + bG + e \tag{2}$$

where a and b are parameters (Table 3). Equation 2 reduces the input parameters from three to two, although it is known that basal area alone cannot explain crown ratio (Hynynen 1995).

Foliage biomass estimates that were obtained with modeled (Equation 2) $\mathrm{cr_m}$, G and regional mean W_f to A_{cb} ratio are described as Method 3 here (Table2).

For Method 5, the tree-level biomass equations of Hakkila (1991), which are based on DBH and crown ratio (cr), which equals $\left[\dfrac{h-\mathrm{ch}}{h}\right]$, were used to estimate foliage biomass (Table 2). Also, Marklund's (1988) equations (Method 6), based on DBH and h, were applied using the diameter and height of each tree in a plot.

Because the biomass equations by Marklund and Hakkila are based on separate data sets, additional nonlinear models for predicting foliage biomass were estimated by the Gauss-Newton method based on data obtained from trees felled at the Vapu plots (Method 7). Models had a similar form for both species, and DBH and h were used as predictors:

$$W_f(\mathrm{DBH}, h) = a\mathrm{DBH}^b h^c + e \tag{3}$$

where a, b and c are parameters (Table 4).

Table 3. Parameter estimates, standard deviation (SD), t statistics and sum of squares for the modified crown-ratio model: $\mathrm{cr}(G) = a + bG + e$ (Equation 2).

Parameter	Estimate	SD	t value	Sum of squares	
				Regression	Residual
Scots pine					
a	1.045	0.066	15.73	2.37	3.43
b	–0.022	0.003	–6.78		
Norway spruce					
a	1.400	0.070	20.02	1.97	4.70
b	–0.017	0.003	–5.49		

Table 4. Parameter estimates,[1] approximated standard deviation (SD) and sum of squares for foliage biomass models (Method 7) developed based on measurements of felled trees at the Vapu plots: $W_f(\mathrm{DBH,h}) = a\mathrm{DBH}^b h^c + e$ (Equation 3).

Parameter	Estimate	Approx. SD[2]	Sum of squares	
			Regression	Residual
Scots pine				
a	0.1179	0.0152		
b	2.1052	0.1234	9.69	1.22
c	–0.7931	0.1263		
Norway spruce				
a	0.1022	0.0113		
b	2.5947	0.1219	28.96	2.56
c	–0.8647	0.1328		

[1] Parameters were estimated by weighting with the inverse of modeled variance to account for heteroscedasticity of variance.

[2] Because of correlated observations (trees from the same plot), the standard errors were likely underestimated.

Foliage biomass of each plot estimated by each of the seven methods was plotted against foliage biomass predictions based on measurements on the sample (felled) trees. Methods for predicting foliage biomass of felled trees from weighed branches are explained in the next section.

Foliage biomass estimated based on branch-level measurements

Foliage biomass was up-scaled from the branch level to the plot level, with a sequence of models based on the assumptions of the pipe model theory (Shinozaki et al. 1964), and the relationship of foliage mass to sapwood area. The sapwood area of stems was approximated by basal area at crown base.

The models were based on hierarchical data, with several levels, such as branch, tree and plot, so it can be assumed that observations within the same class are correlated. This correlation was taken into account by linear mixed models to ensure unbiased estimates of standard errors of parameters. All mixed models were estimated by the restricted maximum-likelihood method (SAS 1999, SAS Institute, Cary, NC). These models include random parameters that have zero expectations, which can vary from zero (McCulloch and Searle 2000). Model selection was based on Akaike's Information Criterion (SAS 1999).

Proportion of foliage in the total biomass of the sample branches

Because only three branches out of ten sample branches were measured for the determination of foliage dry mass, to obtain an estimate of foliage biomass for the other branches, the proportion of foliage in the total branch biomass was modeled. The same explanatory variables were applied for Scots pine and Norway spruce trees. The arcsine transformation of square root of proportion of foliage biomass (s_{ki}) of Scots pine branch i on tree k was modeled as a function of branch diameter (d_{ki}), relative height of the branch (relative to tree height) in the crown (hr_{ki}) and diameter (DBH_k):

$$\begin{aligned}\text{Sin}^{-1}\sqrt{s_{ki}}(\text{hr},d,\text{DBH}) &= A_0 + A_1(\text{hr}_{ki})^{1.6} + A_2(d_{ki})\\ &+A_3(\text{DBH}_k)^{0.7} + a_{0k} + a_{1k}(\text{hr}_{ki})^{1.6} + e_{ki}\end{aligned} \tag{4}$$

and for Norway spruce:

$$\begin{aligned}\text{Sin}^{-1}\sqrt{s_{ki}}(\text{hr},d,\text{DBH}) &= A_0 + A_1(\text{hr}_{ki})^{0.5} + A_2(d_{ki})\\ &+A_3(\text{DBH}_k)^{0.6} + a_{0k} + a_{1k}(\text{hr}_{ki})^{0.5} + e_{ki}\end{aligned} \tag{5}$$

where A_0, A_1, A_2 and A_3 are fixed population parameters (Table 5), whereas a_{0k} and a_{1k} are random tree parameters with zero expectations. Powers for the explanatory variables were optimized according to residual figures by nonlinear models with the nlin procedure (SAS 1999) before the parameters for mixed models were estimated (Equations 4 and 5).

Model for foliage biomass

After the proportion of foliage was modeled and the total biomass of a branch was multiplied by the modeled proportion, there were 10 foliage biomass estimates per sample tree. Thereafter, the foliage biomass of branch i on tree k (w_{ki}) was modeled as a function of branch diameter (d_{ki}) and relative height of a branch in a crown (hr_{ki}):

$$\begin{aligned}\ln w_{ki}(d,\text{hr}) &= \ln A_0 + A_1\ln(d_{ki}) + A_2(\text{hr}_{ki})\\ &+A_3(\text{hr}_{ki}^2) + \ln a_{0k} + a_{1k}\ln(d_{ki}) + \ln e_{ki}\end{aligned} \tag{6}$$

where A_0, A_1, A_2 and A_3 are fixed population parameters (Table 6), and a_{0k} and a_{1k} are random tree parameters with zero expectations.

Table 5. Parameter values for the fixed part of the foliage proportion model. Note that independent variables have different powers in different species (see Equation 4 for Scots pine and Equation 5 for Norway spruce). Abbreviation: SD = standard deviation.

Parameter	Estimate	SD	*t* value	*P* value
Scots pine				
A_0	0.416	0.0144	28.92	< 0.0001
A_1	0.305	0.0175	17.36	< 0.0001
A_2	–0.0021	0.00041	–5.26	< 0.0001
A_3	–0.0147	0.00173	–8.52	< 0.0001
Norway spruce				
A_0	0.289	0.0163	17.75	< 0.0001
A_1	0.366	0.0168	21.87	< 0.0001
A_2	–0.0028	0.00045	–6.28	< 0.0001
A_3	–0.0131	0.00263	–4.98	< 0.0001

Table 6. Parameter values for the fixed part of the foliage–biomass model: $\ln w_{ki}(d, \text{hr}) = \ln A_0 + A_1\ln(d_{ki}) + A_2(\text{hr}_{ki}) + A_3(\text{hr}_{ki}^2) + \ln a_{0k} + a_{1k}\ln(d_{ki}) + \ln e_{ki}$ (Equation 6).

Parameter	Estimate	SD	*t* value	*P* value
Scots pine				
A_0	–3.586	0.0885	–40.54	< 0.0001
A_1	2.357	0.0320	73.66	< 0.0001
A_2	2.861	0.137	20.92	< 0.0001
A_3	–1.458	0.135	–10.80	< 0.0001
Norway spruce				
A_0	–3.022	0.112	–26.90	< 0.0001
A_1	2.210	0.0407	54.31	< 0.0001
A_2	5.573	0.168	33.19	< 0.0001
A_3	–4.207	0.170	–24.73	< 0.0001

Foliage biomass of trees

The model for the proportion of foliage biomass was used to estimate the foliage biomass of sampled branches, and random tree parameters were used for calibration of these biomass estimates. Thereafter, the foliage biomass of each branch was estimated based on the foliage biomass model, which was calibrated for each tree. To obtain total foliage biomass estimates for each sample tree, these estimates of foliage biomass for each branch in a given tree were summed. The basal area at the crown base for each sample tree was measured in the field, and the ratio between foliage biomass and cross-sectional area at the crown base (W_f:A_cb) calculated.

Basal area at the crown base

To up-scale foliage biomass of felled trees to the plot level, the basal area at the crown base of each plot is needed. Therefore, diameter at the crown base (dc) of trees k in plot l was modeled for Scots pine as a function of h, DBH, ch and slenderness (h/DBH):

$$\begin{aligned}\text{dc}_{lk}(h,\text{DBH},\text{ch},h/\text{DBH}) &= A_0 + A_1(h_{lk})\\ &+A_2(\text{DBH}_{lk}) + A_3(\text{ch}_{lk}) + A_4\left[\frac{h_{lk}}{\text{DBH}_{lk}}\right] + a_{0l} + e_{lk}\end{aligned} \tag{7}$$

and for Norway spruce as a function of DBH and ch:

$$\begin{aligned}\text{dc}_{lk}(\text{DBH},\text{ch}) &= A_0 + A_1(\text{DBH}_{lk}) + A_2(\text{ch}_{lk})\\ &+ a_{0l} + e_{lk}\end{aligned} \tag{8}$$

where A_0, A_1, A_2, A_3 and A_4 are fixed population parameters and a_{0l} is a random plot parameter with zero expectations (Table 7).

Foliage biomass at the plot level

Plot-level foliage biomass was assessed by generalizing the W_f:A_cb ratio from the sample trees to all trees on the same plot according to species. A variance component model was built

Table 7. Parameter values for the fixed part of the model for basal area at the crown base. Note that some of the independent variables are different for Scots pine (Equation 7) and for Norway spruce (Equation 8). Abbreviation: SD = standard deviation.

Parameter	Estimate	SD	t value	P value
Scots pine				
A_0	3.262	1.049	3.11	0.0032
A_1	0.506	0.093	5.43	< 0.0001
A_2	0.553	0.0531	10.42	< 0.0001
A_3	–0.846	0.0749	–11.30	< 0.0001
A_4	–2.099	1.143	–1.84	0.0686
Norway spruce				
A_0	1.890	0.411	4.60	< 0.0001
A_1	0.893	0.019	47.19	< 0.0001
A_2	–0.569	0.0743	–7.66	< 0.0001
A_3	–	–	–	–
A_4	–	–	–	–

Table 8. Parameter estimates for the fixed part of the model for the ratio of foliage biomass to basal area at the crown base, including also covariance parameter estimates (see Equation 9).

Parameter	Estimate	SD	t value	P value
Scots pine				
A_0	498.67	15.198	32.81	< 0.0001
Norway spruce				
A_0	796.23	22.867	34.46	< 0.0001

	Covariance parameter estimates		
	Parameter	Subject	Estimate
Scots pine	a_0	Plot	8,627
	Residual	–	10,984
Norway spruce	a_0	Plot	17,440
	Residual	–	35,206

for Scots pine and Norway spruce, where the W_f:A_{cb} ratio was explained with a class variable (sample plot), assuming that this ratio depends only on plot characteristics, which cannot be identified. The model for the W_f:A_{cb} ratio for plot l was:

$$\left[\frac{W_f}{A_{cb}}\right]_l = A_0 + a_{0l} + e_l \qquad (9)$$

where A_0 is a fixed population parameter and a_{0l} is a random parameter with zero expectation (Table 8). The foliage biomass of a plot was then estimated by multiplying the sum of modeled A_{cb} with the modeled W_f:A_{cb} ratio for each plot.

To test whether there was a significant difference between the estimate and the mean W_f:A_{cb} ratio, the estimated ratio was tested against the mean ratio based on the fixed part of the mixed model (Equation 9) with a t test, assuming that the ratio was normally distributed. The number of plots having a lower or higher ratio than the mean plus or twice the standard deviation was compared with the total number of plots.

Results

Estimates of foliage biomass for Scots pine plots obtained with BEF and both Valentine's methods were unbiased, having a slope close to one (Figure 1). According to the t test, these estimates did not differ from the reference estimate. Valentine's methods had only half of the variation of the BEF method, but Valentine's method with the modeled crown ratio had a systematic variance structure (Figure 1) that overestimated foliage biomass for stands with small A_{cb}, and underestimated

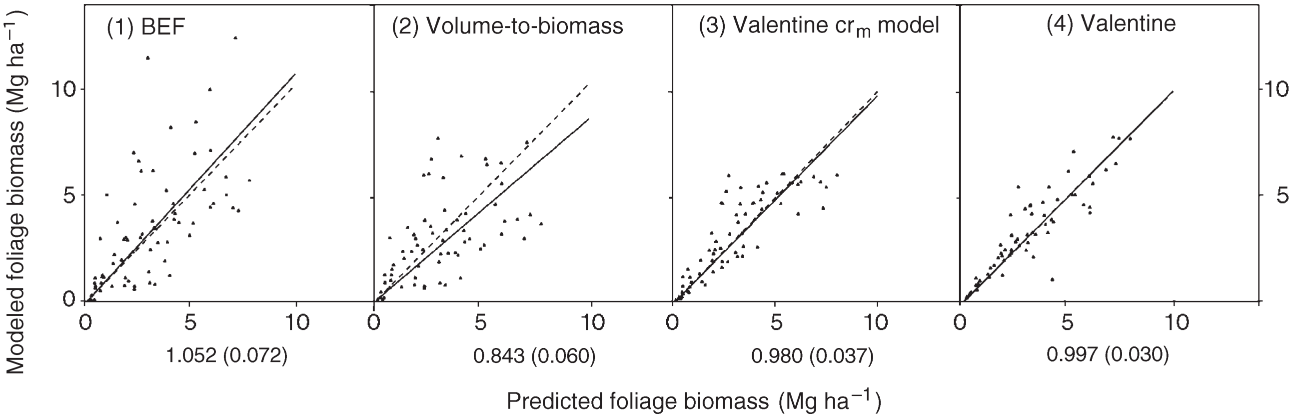

Figure 1. Comparison of methods for estimating foliage biomass (Mg ha^{-1}) for Scots pine plots with plot-level information. Predicted foliage biomass on the x-axis is based on the results of up-scaling measurements in this study. The biomass expansion factor, stem-volume-to-biomass and Valentine's methods are compared with the reference method. A linear regression trough (0,0) was fitted; slope and standard deviation of the slope are reported, and the dashed line denotes a 1:1 relationship.

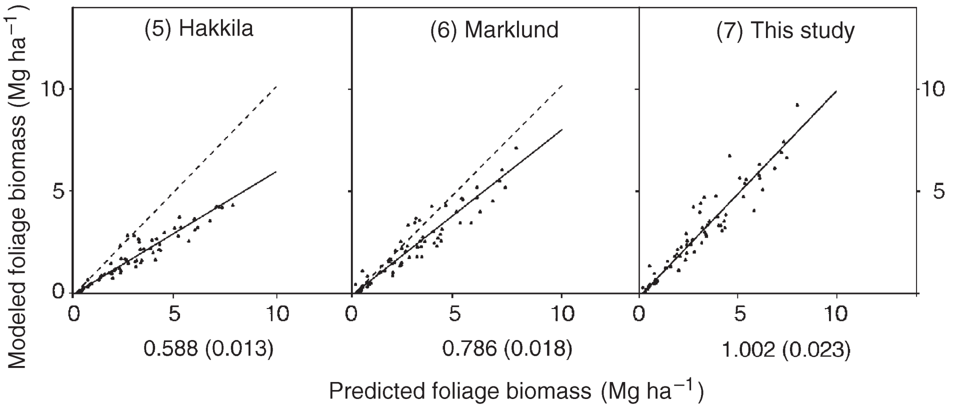

Figure 2. Comparison of methods for estimating foliage biomass for Scots pine plots with tree-level information. Predicted foliage biomass on the *x*-axis is based on the results of up-scaling measurements in this study. Hakkila (1991), Marklund (1988) and biomass equations developed in this study are compared with the reference method. A linear regression trough (0,0) was fitted; slope and standard deviation of the slope are reported, and the dashed line denotes a 1:1 relationship.

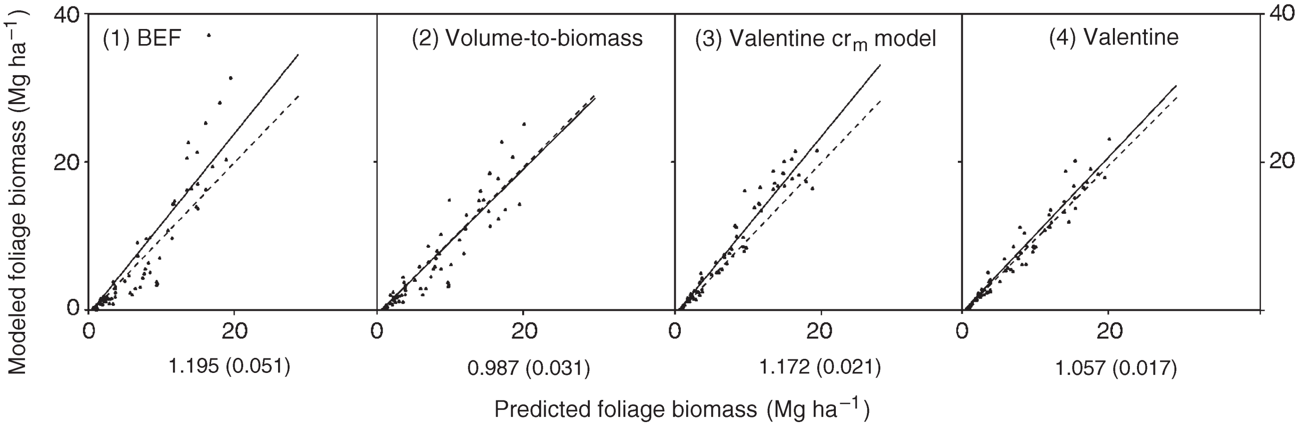

Figure 3. Comparison of methods for estimating foliage biomass for Norway spruce plots with plot-level information. Predicted foliage biomass on the *x*-axis is based on the results of up-scaling measurements in this study. Biomass expansion factor, stem-volume-to-biomass and Valentine's methods are compared to the reference method. A linear regression trough (0,0) was fitted; slope and standard deviation of the slope are reported, and the dashed line denotes a 1:1 relationship.

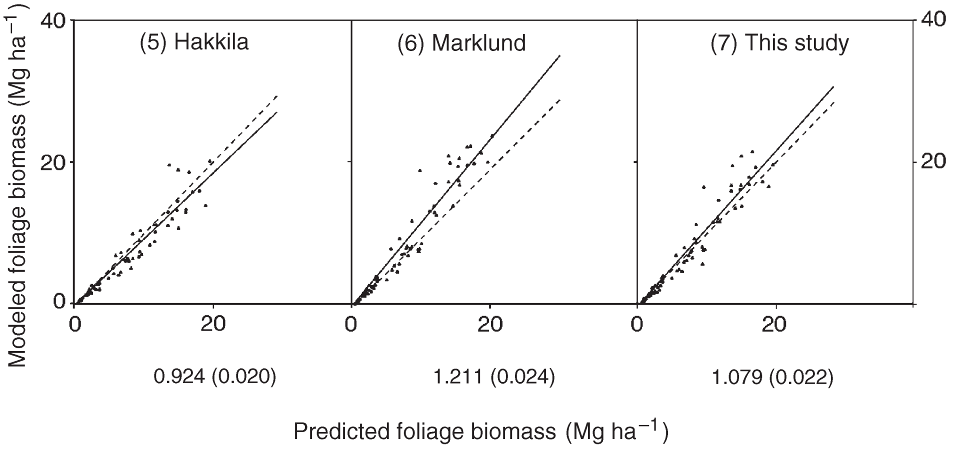

Figure 4. Comparison of methods for estimating foliage biomass for Norway spruce plots with tree-level information. Predicted foliage biomass on the *x*-axis is based on the results of up-scaling measurements in this study. Hakkila (1991), Marklund (1988) and biomass equations developed in this study are compared to the reference method. A linear regression trough (0,0) was fitted; slope and standard deviation of the slope are reported, and the dashed line denotes a 1:1 relationship.

that for stands with large A_{cb}. Biomass equations by Hakkila and Marklund systematically underestimated plot-level foliage biomass of Scots pine, whereas the equations developed in this study (Method 7) estimated foliage biomass of Scots pine plots well, having a slope of 1.002 and a slope variance of 0.023 (Figure 2).

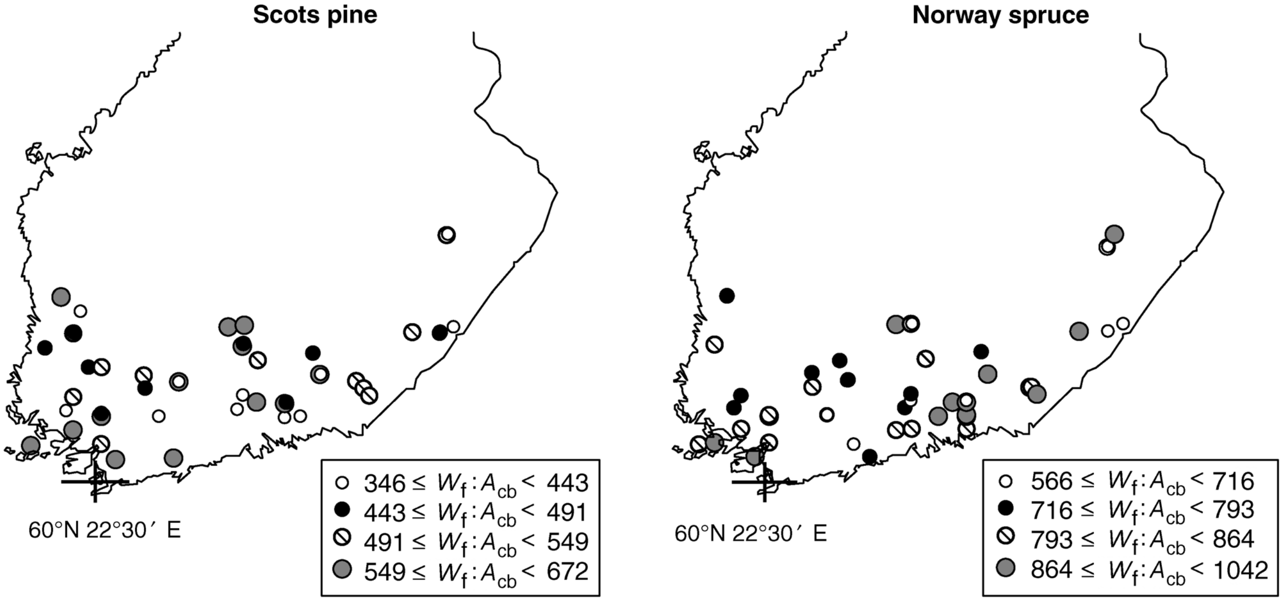

Figure 5. Foliage biomass (W_f): basal area at crown base (A_{cb}) ratio for Scots pine and Norway spruce by plot level. Values vary from 346 to 672 kg m^{-2} for Scots pine and from 566 to 1042 kg m^{-2} for Norway spruce. Size and symbol indicate the amount of foliage biomass per square meter of basal area at crown base.

For Norway spruce, the volume-to-biomass method and Valentine's method with mean crown ratio provided the least biased estimates of foliage biomass, having slopes of 0.987 and 1.057, respectively (Figure 3). In contrast, estimates of foliage biomass based on BEFs (Figure 3), Marklund's equations (Figure 4) and Valentine's method with modeled crown ratio had high bias, with the value of the slope being 1.195, 1.211 and 1.172, respectively (Figure 2). Biomass estimates by Hakkila (1991) slightly underestimated foliage biomass, whereas biomass equations developed in this study (Method 7) overestimated foliage biomass to some extent with a slope of 1.079 and a slope variance of 0.022 (Figure 4).

Comparison of W_f and A_{cb} revealed that the mean W_f:A_{cb} ratio for Scots pine was 499 kg m^{-2} compared with 796 kg m^{-2}, for Norway spruce, having standard deviations of 15 and 23 kg m^{-2}, respectively (Table 8), indicating low within-stand variance. The maximum W_f:A_{cb} ratios for Scots pine and Norway spruce were 672 and 1042 kg m^{-2}, respectively (Figure 5), whereas the corresponding minimum ratios were 346 and 566 kg m^{-2} (Figure 5). A large proportion of the variation in W_f:A_{cb} depended on plot characteristics: 33% of the variation in Norway spruce and 44% of that in Scots pine was explained by the class variable "plot." The W_f:A_{cb} ratio varied strongly between plots and also according to geographical location (Figure 5). According to the *t* test, 36% of Scots pine and 39% of Norway spruce plots had a statistically different W_f:A_{cb} ratio compared with the mean ratio based on the fixed part of a mixed model.

At the plot-level, the maximum foliage biomass for Scots pine was 7.9 Mg ha^{-1} for a basal area of 16.8 m^2 ha^{-1} at the crown base. For Norway spruce plots, the maximum foliage biomass was 19.5 Mg ha^{-1} for a basal area of 25.4 m^2 ha^{-1} at the crown base.

Discussion

Reliability of stand-level estimates of foliage biomass depends on the data and models used. Data can be obtained at the tree or plot level. When plot-level data are used, the variables available are averages for the tree population, such as mean stem volume, *G* and plot age, whereas tree-level data with DBH and *h* measurements provide a more solid basis for estimating foliage biomass, assuming that the biomass equations represent the region where they are applied. According to this study, the biomass equations of Marklund (1988) underestimated foliage biomass of Scots pine and overestimated it for Norway spruce. Marklund's equations are based on sampling across Sweden (Marklund 1988), whereas the biomass predictions based on measurements reported in this study were collected from southern Finland. On the other hand, Wirth et al. (2004) reported an overestimation of 25% for foliage biomass of Norway spruce by Marklund's (1988) equations compared with central European biomass studies. The BEFs reported by Lehtonen et al. (2004) were based on the equations of Marklund (1988). The difference between the BEF method and the Marklund method is that BEFs are based on Marklund's equations applied to Finnish tree-level data with DBH as an independent variable. Systematic differences between the BEF method and the Marklund method indicate that the diameter–height relationship or stand structure might differ between the Vapu plots, where the biomass measurements were made, and Marklund's sample plots in Sweden. Although the sampling by Marklund (1988) covers a wide range of sites with varying stand properties including basal area, altitude, site index and stand age, most of the sample plots are located above 100 m a.s.l. in inland Sweden. In contrast, most of the sample plots in the Vapu data set are located in southern Finland (Figure 5) and are less than 100 m a.s.l. The differences between Marklund's study and the biomass measurements of this study might also be partly due to different tree allometry in Sweden compared with southern Finland.

For Scots pine stands, the Finnish biomass equations developed by Hakkila (1991) underestimated foliage biomass (Figure 2), but were more accurate for Norway spruce stands, although lower than predictions based on measurements (Figure 4). The equations formulated by Hakkila (1991) were based on biomass sampling done in connection with loggings; therefore, the equations are applicable for estimating biomass of stands before thinning or clear-cutting, but might result in biased estimates for stands before canopy closure. Biomass equations parameterized with felled trees on the Vapu plots gave good predictions, especially for Scots pine plots, but predictions for Norway spruce plots were slightly overestimated.

Foliage biomass models developed by Hakkila (1991) for Norway spruce had a high coefficient of determination (0.88), whereas it was only 0.73 for Scots pine. Marklund (1988) also reported lower coefficients of determination for foliage biomass models of Scots pine compared with Norway spruce. The equations developed in this study had lower relative sum of squares for error with Norway spruce trees compared with Scots pines trees (Table 4). Together these studies indicate that there is more variation in foliage biomass in Scots pine trees than in Norway spruce trees.

Biomass estimates based on allometric equations assume that the plot-level biomass reflects the sum of each tree-level biomass. However, because the relative proportion of foliage biomass is reduced after canopy closure, while tree dimensions and stem volumes are still increasing (Satoo and Madgwick 1982, Vanninen et al. 1996, Mäkelä 1997), it is easy to overestimate foliage biomass at the plot-level, especially when the densities of the predicted plots have a different distribution compared with the density of those plots where the biomass sampling was originally made. Therefore, application of the approach that includes the pipe model (W_f:A_{cb}) ratio, which automatically takes into account the effect of canopy closure, would be a safer choice, especially when the foliage biomass of mature stands is being estimated. On the other hand, the results show that the W_f:A_{cb} ratio varies drastically even between neighboring plots, and in this study, the ratio differed significantly from the mean for a substantial number of plots. Therefore, when used in biomass assessments, W_f:A_{cb} ratios should be based on representative sampling and proper prediction techniques. Although the reasons for the variation in W_f:A_{cb} ratios were not studied here, high variation in site properties most likely introduces variation to the W_f:A_{cb} ratio.

For Scots pine, the mean W_f:A_{cb} ratio was 499 kg m^{-2}, which agrees well with earlier studies from Finland (Berninger and Nikinmaa 1997, Mäkelä and Vanninen 1998). The corresponding mean ratio for Norway spruce was 796 kg m^{-2}, compared with 1000 kg m^{-2} in Norway (Horntvedt 1993) and Austria (Eckmüllner and Sterba 2000) and 1020 kg m^{-2} in the Czech Republic (Dvorak et al. 1996). These differences in the W_f:A_{cb} ratio of Norway spruce between this and earlier studies might be associated with climatic conditions (Mencuccini and Bonosi 2001) or that sapwood area was approximated by overbark measurements of diameter at the crown base in this study, whereas others have used discs or cores to determine sapwood area. However, the W_f:A_{cb} ratio of Norway spruce varied from 566 to 1042 kg m^{-2} in this study, which covers the range of published ratios.

When information about the W_f:A_{cb} ratio and crown ratio is available, Valentine's method appears to be a good option, because it was found to be unbiased and had low variation. However, if only mean stem volume and plot ages are available for Scots pine plots, application of BEFs would provide unbiased estimates of foliage biomass for larger regions. For Norway spruce, the stem-volume-to-biomass model would provide good estimates for larger regions, at least in southern Finland. According to this study, when estimating the foliage biomass of single plots in southern Finland, either the Valentine's method or tailor-made biomass equations should be used. Models for crown ratio and W_f:A_{cb} ratio combined with measurements, such as DBH, tree height, upper diameter and height at the crown base from the national forest inventory, could be used to estimate foliage biomass for studies on the carbon cycle of forest ecosystems.

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