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Biomass in a Norway spruce–Scots pine forest: a comparison of estimation methods

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In order to compare different methods for estimating forest biomass, the dry mass of needles, branches, stem and roots at tree to stand levels was investigated in a mixed Norway spruce (*Picea abies*)–Scots pine (*Pinus sylvestris*) stand in southern Finland by means of direct weighing to allometric functions. The results revealed a substantial difference among estimations made with various methods. For instance, at the stand level, with the above-ground tree biomass (170.8 Mg ha^{-1}) estimated using partial harvesting methodas a baseline, tree biomass had a higher estimate (+10%) based on the dry mass of selected understorey, medium and dominant trees as the sample trees, but a lower estimate (–18%) by means of the allometric functions established based on the data gathered from nearby trees. At the individual tree level, the allometric functions overestimated dry weight of needles and branches by 20%–207% and 38%–263% for dominant pine and understorey spruce, respectively, but underestimated the stem weight. These results imply the utmost importance of considering the estimate error when calculating the tree biomass in a forest stand with an indirect approach.

Introduction

Worldwide forests constitute an important pool in the global carbon balance (Dixon *et al*. 1994, Houghton 2005). Consequently, in the context of the Kyoto Protocol with forest management as a strategy to mitigate atmospheric CO_2 increase, it is important to quantify carbon storage in forest ecosystems with less uncertainty, and thus an absolute necessity to gather accurate and precise data on forest biomass at both stand and regional levels (Laitat *et al*. 2000, Brown 2002).

In the Eurasian boreal climate zone covering 794 million ha across the continent and comprising 20% of the total global forested area (FAO 2001), Scots pine (*Pinus sylvestris*) and, in particular, Norway spruce (*Picea abies*) commonly form climax forests (Sarvas 1964). Much knowledge exists concerning high precision calculation of merchantable timber quantity on the basis of nationally accepted stem volume functions for such forests (e.g. Eriksson 1976, Laasasenaho 1982, Brandel 1990). However, merchantable timber in stands does not equal stand biomass, and although biomass functions for Scots pine, Norway spruce and also birch have been presented in many studies over the last decades (Braekke 1986, Marklund

1987, 1988, Finér 1989, Korsmo 1995, Usol'tsev and Vanclay 1995, Ter-Mikaelin and Korzhukin 1997), few comparisons regarding the accuracy of different methods of estimating stem dry mass or non-merchantable tree compartments like branches and foliage, not to mention stumps and roots, have been made. For instance, Marklund's (1988) functions were developed based on a comprehensive data set consisting of about 493 Scots pine and 551 Norway spruce trees, and these sample trees were collected in Swedish forests spanning a broad range of boreal climate conditions (Petersson & Ståhl 2006). These allometric functions (Marklund 1988) have since been used to estimate spruce and pine tree biomass in Finland (e.g. Liski & Westman 1995, Lehtonen *et al*. 2004) with an assumption that both countries have a similar boreal climate, but accuracy of the estimations has not been examined. On the other hand, general allometric functions for plants as well as all organisms have long been sought; hence, more case investigations of different organisms (including trees) could be very useful for validating allometric parameters (Niklas 1994, West *et al*. 1999, Pilli *et al*. 2006).

In order to obtain more appropriate national level forest biomass estimates, Biomass Expansion Factors (BEFs) have been introduced in recent decades (e.g. Fang *et al*. 1998, Fang and Wang 2001, Lehtonen *et al*. 2004). The BEFs are, in best case, biomass–volume relationships truly measured for appropriate tree species in tree stands of varying age and on sites of different fertility. By applying such sound BEFs to statistically reliable national forest inventory data for stands of equal properties, stem volume can then be converted to mass units as well as the dry mass of non-commercial components accounted for.

However, accuracy of BEFs to apply is, indeed, dependent on the precision of data used for the calculation of the biomass-volume relationships. Stand volume (explanatory variable) can most often be assessed with appropriate accuracy on the basis of generally accepted measures, but biomass or any separate compartment to be explained, may be either truly measured, estimated upon various samplings or even estimated based on some allometric relationships [*see* a review by Parresol (1999)]. For instance, in Fang *et al*. (1998) and Fang and Wang (2001), BEFs are obtained by combining data presented in literature (more than 700 sites), while Lehtonen *et al*. (2004) estimated biomass by using sets of the allometric functions (Marklund 1988) and then calculated biomass-volume relationships for a large variety of tree stand conditions. To conclude, although Fang and Wang (2001) presented the BEFs method as superior in comparison with e.g. mean biomass density methods, which certainly is true, it still remains necessary to analyse the effects of the various primary approaches on the estimation of forest biomass on a landscape or regional level by means of BEFs conversions.

The most reliable method for above-ground biomass determination is, indeed, harvesting and weighing of all trees or some sample trees within a site. Complete harvest is, however, both a laborious and an expensive measure. Thus, biomass data presented in literature is most often some estimates based on sampling and the application of regression models using e.g. breast height diameter (DBH) solely or together with height (*H*) or other easily measurable tree parameters to predict the dry mass of a tree or any given tree compartment (e.g. Satoo 1982, Parresol 1999). Stand biomass is then simply calculated by multiplying biomass of a class average tree by the number of trees in the class and summing over the stand (e.g. Zhai 1982, Rana *et al*. 1988). Methods may also be based on the assumption that the biomass of sample trees is related to the biomass of the stand as the ratio of respective basal areas. This, however, adds bias because trees standing in different positions have differing stem forms, and consequently the relationship between stem and branch biomass varies.

In order to obtain an accurate estimate of stand biomass, as discussed above, one of the key measures is how to determine the dry mass of various components (e.g. roots, stem, branches, needles, etc.) of a sample tree. For determining the dry mass of branches and needles of a sample tree, the most accurate method is to separate the needles from branches and directly determine dry mass of both components by collecting all branches. With this method, however, the main problem is extensive work. An alterna-

tive method would be to select sample branches, and then measure the dry mass of the samples. Based on the total number of branches and the dry mass of components of sample branches, corresponding dry mass of components for the whole tree can be obtained by up-scaling (e.g. Zhai 1982, Bhartari 1986, Liu 1987, Rawat and Singh 1988). A more precise approach for estimating branch biomass would be to apply the pipe-model theory (Shinozaki *et al*. 1964), and determine the relationship between branch neck cross-sectional area and branch biomass for sample branches. In any case, an important issue would be to compare the estimated results of such different methods in measuring stand biomass.

In comparison with above-ground biomass, the estimation of biomass in the below-ground compartment is an order of magnitude more complicated and laborious. Usually, in order to measure below-ground biomass of trees in a stand, the stumps and all roots of sample trees have to be excavated and weighed by size class. Then, based on the data from these sample trees, the root mass of all the trees in the stand is estimated (e.g. Zhai 1982, Bhartari 1986, Liu 1987). Alternatively, with data of these sample trees, the regression equations between the root mass of the respective trees and their DBH can be obtained, and are then used to estimate the dry mass of different root size fractions in the stands (Satoo 1982, Bao *et al*. 1984). The dry weight of fine roots (less than 2 mm or 5 mm depending on definition by researchers) in a stand can be estimated systematically by core sampling and determining all roots in a given soil layer (e.g. Zhai 1982, Liu *et al*. 1985, Pietikäinen *et al*. 2000).

The objective of this study is to conduct a case study on the tree biomass in an old boreal Norway spruce and Scots pine stand. In this context, particular focus will be set on comparing different approaches for estimating the dry mass of branches and needles (e.g. sample branch method, regression technique, whole branch harvesting method) for a tree and the biomass of trees (e.g. sample tree method, allometric functions of Marklund (1988), partial harvesting method) in a stand as well as discussing tree stand biomass as a basis for BEFs assessment.

Experimental forest and methods

Study forest

The study site was a naturally established mixed Norway spruce and Scots pine stand located in southern Finland (61°50´N, 24°22´E). The site lay on a south-facing slope with an average inclination of 3.4% and a mean elevation a.s.l. of 152 m. The forest site type changed along the slope, from dry VT on the top of the slope, over a mesic MT to moist OMT at the bottom [site type nomenclature according to Cajander (1949)]. Correspondingly, the groundwater table level during growing seasons ranged between 4 and 10 m. In the middle part of the slope, a plot (30 × 30 m) was set up, and DBH and height of all trees were measured. Based on the survey of trees in the plot, stand density was 792 stems ha^{-1} (589 spruce and 203 pine trees, respectively), and the overall stem volume was 240 m^3 ha^{-1}, of which 63% was Norway spruce and 37% Scots pine. Tree age varied from 100 to 140 years.

Mean annual temperature is 2.9 °C and annual precipitation 709 mm in the region. The soil was composed of glacio-fluvial sorted sand with a mean particle size of 0.43 mm. The soil order was a Spodosol, and the soil group a Typic Haplocryod (Soil Survey Staff 1992). The average thickness of the organic, eluvial, and illuvial horizons were 45, 52 and 176 mm, respectively.

Selection of sample trees

All trees in the plot were tallied by DBH class (1 cm). Because of highly varying size, spruce trees were stratified into three size groups: small trees (DBH < 15 cm), medium size trees (DBH = 15–21 cm), and large trees (DBH > 21 cm). Within each group, one spruce representing the average diameter was then selected to be a sample tree. Since all pine trees present were dominating crown layer trees and consequently rather uniformly sized, we selected only one average tree randomly. Basic properties of sample trees are listed in Table 1.

In the field, sample trees were felled on a large tarpaulin to enable quantitative harvesting of selected tree compartments. After felling, the

stem of each tree was partitioned into 2-m sections starting at the highest point of the root neck of the tree.

Stem mass of sample trees

For each sample tree, the stem dry mass was estimated in three different ways: (i) by direct weighing (StemW), (ii) by applying the allometric functions of Marklund (1988) (StemM), and (iii) by applying stem-form functions for volume (StemF).

For StemW determination, after removal of living and dead branches and partitioning into sections, each stem section was weighed fresh in the field. To determine the proportion of stem wood and bark components as well as their fresh-/dry-mass ratio, a 2-cm-thick disc was cut at the lower end of each section. The disc was separated into bark and wood for calculating the percentage of bark in the total mass, and both components were dried at 80 °C for 24 hours to obtain their dry weight. Based on the percentage of bark in the total mass, the fresh weight of bark and wood could be obtained for each stem section. The fresh-to-dry mass ratios of bark and wood were applied to calculate the total dry mass of respective fractions of each stem section. For a sample tree, total mass of stem wood and bark were finally obtained by summing over the stem. For StemM determination, DBH of each sample tree was measured and used as an independent variable in calculating stem dry mass by applying the allometric functions of Marklund (1988).

For StemF determination, DBH and height of each sample tree were used as independent variables in calculating stem volume by applying stem form functions of Laasasenaho (1972). Dry mass of the stem was then calculated by applying wood density figures from Hakkila (1971).

Branch and needle mass of sample trees

For each sample tree, dry mass of branches and needles were estimated in four different ways: (i) by direct weighing (BranchW, NeedleW), (ii) by systematic sampling (BranchS, NeedleS), (iii) on the basis of average branch (BranchA, NeedleA), and (iv) by applying the allometric functions of Marklund (1988) (BranchM, NeedleM)

After felling of sample trees, living branches of each tree were numbered in running order from the bottom of the crown to the top and according to stem section. The diameter at the neck of each branch was then measured. Finally, the cross-sectional area was calculated for all branches from neck diameter. For each method, a detailed description was made as follows.

Systematic sampling was conducted for BranchS and NeedleS determinations. For Norway spruce trees, every fifth branch was taken as a sample branch from the small and medium trees; from the large tree every eighth branch was taken. For the Scots pine tree, every fifth branch was taken as a sample branch. Altogether, 53 branches for Norway spruce and 16 branches for Scots pine were sampled. Linear regressions with neck cross-sectional area as an independent variable and branch mass (and the needle mass) as a dependent variable were fitted to measure

Table 1. Age and dimensions of sample trees. Age was estimated by counting the rings at the root neck of each sample tree.

Sample trees	Age (yr)	DBH* (cm)	Height (m)	Height position of first dead branch (m)	Height position of first living branch (m)	Crown width (m)	Number of living branches	Total basal neck area of living branches (cm^2)
Small spruce	106	12.3	13.5	3.12	7.6	3.4	67	43.4
Medium spruce	133	18.6	19.9	2.1	3.9	3.9	119	181.8
Large spruce	131	24.5	23.4	6.0	13.8	4.1	194	326.4
Average pine	137	28.8	24.1	6.0	16.0	5.7	84	310.9

*The DBH of each sample tree was close to the arithmetic mean of DBH of relevant tree class group.

sample branch material. Regressions were fitted individually for each sample tree (BranchS-1 and NeedleS-1) and in addition, jointly for all Norway spruce trees (BranchS-2 and NeedleS-2). The equations were then used to estimate the mass of individual branches and needles on the branches based on measured neck cross-sectional area. Total dry mass of branches and needles were finally obtained by summing over the sample tree.

For BranchA and NeedleA determinations, all branches of each 2-m stem section were classified according to branch neck diameter into three size classes, and from each size class one average branch was taken and amalgamated to form a compounded sample representative of the respective stem section. As a result, 4, 8 and 6 compound samples were obtained for small, medium and dominant spruces, respectively, and 4 compounded samples for the pine tree. For the systematic and average branch samples, needles were separated immediately upon sampling and, needles and branch matter were weighed fresh and re-weighed after drying at 80 °C for 24 hours. BranchA (or NeedleA) was simply calculated by first multiplying average sample branch (or needle) dry mass by number of branches on respective stem section, and then summing masses over the whole sample tree.

To determine BranchW and NeedleW, all remaining living branches were collected by stem section, weighed fresh in the field, and transported to the laboratory in paper bags. After air-drying, the needles could be separated from the branches, and thereafter the samples were dried at 80 °C for 24 hours and then weighed. For one sample tree, the dry mass of branches and needles was the sum of these branch materials and those which were used in other sampling methods.

For BranchM and NeedleM determinations, DBH of each sample tree was used as an independent variable in calculating needle and branch dry mass by applying the allometric functions of Marklund (1988).

Additionally, for each sample tree, the dead branches were collected by stem section, weighed fresh in the field, and the dry weight was obtained from the sample after drying at 80 °C for 24 hours.

Root and stump mass of sample trees

For each sample tree, root and stump dry mass was estimated in two different ways: (i) by direct weighing (RootW, StumpW), and (ii) by applying the allometric functions of Marklund (1988) (MCRootM, StumpM).

To determine below-ground biomass of sample trees, three concentric circular areas having radii of 1, 2 and 3 meters, and the space outside 3 m were delimited with the core of the stump of each sample tree serving as the centre. Within each concentric area, all roots were collected down to 100-cm depth. The roots were cleared from mineral soil and sorted according to diameter: < 2 mm, 2–20 mm, and > 20 mm. Root fractions are accordingly denoted fine (FRootW), medium (MRootW) and coarse (CRootW). To obtain dry mass, the sample from each class was oven-dried at 80 °C for 24 hours.

For MCRootM (including 2–20 and > 20 mm roots) and StumpM determinations, DBH of each sample tree was used as an independent variable in calculating root and stump dry mass by applying the allometric functions of Marklund (1988).

Estimating the biomass of the trees in the stand

The biomass of the tree stand was estimated in four different ways: (i) by weighing aboveground components of a sub-sample of harvested trees (StandW), (ii) on the basis of sample trees (StandS), (iii) by applying the allometric functions of Marklund (1988) (StandM), and (iv) by applying stem form functions for stem volume (StandF). In addition, stand root biomass in the 60-cm top soil layer was determined by systematic sampling and up-scaling (StandRootS).

For StandW determination, one third of stems in the plot were selected to derive their mass, i.e. 17 spruce and 7 pine trees. Each tree was weighed in its entirety, and the stem was weighed separately after de-branching and lopping off the top of the tree. Weighing was done with a harvester equipped with a load weighing head (1.0 kg accuracy). After harvesting, a disc

from the root end of each stem was cut in order to deduce the fresh-/dry-weight ratio. The representative branches from the lower, middle and upper crown of each cut tree were collected and freshly weighed. In the laboratory, the branches were oven-dried to ascertain the fresh/dry ratio. The mass of the stem and crown of each tree was then calculated. According to their DBH, these trees were divided into different diameter classes and correspondingly the dry mass of their biomass compartments was viewed as the mean of tree biomass in the respective diameter class. Tree stand biomass was then obtained by up-scaling dry mass of harvested trees by multiplying the mean of tree biomass by stem number of respective diameter-class trees.

For StandS determination, StemW, BranchW, NeedleW, StumpW and RootW of each sample tree were multiplied with the number of stems in the class, which the sample tree represented. This enabled calculation of the biomass of the respective fraction by tree species and sample tree size class (Norway spruce). The stand biomass was then obtained by summing over the stand.

For StandM determination, stand DBH distribution was used to calculate dry mass of branches, needles, dead branches, roots and stump for each 1-cm DBH class by applying the allometric functions of Marklund (1988). Total dry mass by fraction was then obtained by multiplying by stem number in each class, and the total for the stand by summing over DBH class.

For StandF determination, the volume of each tree stem was first calculated by stem form functions (Laasasenaho 1972). The stem mass was then calculated by employing wood density values according to Hakkila (1971). Total stem mass in the stand was deduced by summing up the mass of all trees.

For StandRootS determination, 72 core samples from the O horizon and top soil layer to 60 cm depth, distributed evenly over the site in a 4 × 10 m grid, were taken. In the laboratory, the roots were separated from the sands through washing and partitioned into the following tree root categories: < 2 mm, 2–20 mm, and other live roots. The dry mass was obtained by drying the sample from each class in the oven at 80 °C for 24 hours.

Comparison among the estimates

When comparing different estimates, the values obtained through direct weighing were used as a baseline, and percent deviations from observed values were calculated as follows:

$$\text{Percent deviation} = (M_E - M_W)/M_W \times 100$$

where M_E is any estimated dry mass, and M_W corresponding dry mass fraction determined through direct weighing.

All calculations were done using SYSTAT statistical packages (Systat Software Inc.).

Results

Sample tree biomass

Dimensions of sample trees

All sample trees were fairly evenly aged. The medium and large spruce trees and the pine tree were some 130 years old, and even the small spruce was no more than 25 years younger. The DBH of the large spruce tree was double that of the small spruce tree, which displayed typical features of understorey trees: first living branches situated high up in the crown while having a wide crown in relation to height (Table 1). Total neck basal area of living branches was 326 and 311 cm^2 for the large spruce and the pine, respectively, being 8 times greater than that of the small spruce. The pine, being a primary tree species on sites like the one investigated, was the oldest and also the largest among the sample trees (Table 1).

Dry mass of sample trees

Overall total dry mass of the sampled spruce trees ranged from 56 to 367 kg, and the dry mass of the pine tree was almost 1.5 times that of the largest spruce. Among biomass components, above-ground compartments constituted 75% to 87% of the total tree biomass. The greatest above-ground fraction was found for the medium spruce tree, which had the longest living crown (Table 1). The small spruce tree had

the greatest relative fraction of below-ground biomass. The high below-ground biomass of the understorey tree was allocated to the coarse (> 20 mm) root compartment and the fractions of medium and fine roots were in line with the other spruce trees (Table 2).

Estimation of the sample tree biomass

Regressions of needle and branch biomass on branch neck cross-sectional area

In regression models, regression slopes in all cases deviated significantly from zero, and the models explained 75% to 85% of variance in needle dry mass of sample branches of spruce trees (Table 3). For the pine tree, the degree of explanation was somewhat smaller (72%). Correspondingly, for branch biomass, the degrees of explanation of models were even higher (from 84% to 96%) (Table 3).

Likewise, when all sample branches from the three spruce trees were lumped together, coefficients were significant as for individual trees, and degrees of explanation for needles and branch material were 86% and 93%, respectively (Table 3).

Table 2. Dry mass (kg) of stem wood and bark (StemW), stump (StumpW), living branches (BranchW), dead branches, needles (NeedleW), coarse roots (CRootW), medium roots (MRootW) and fine roots (FRootW) for the sample trees. The mass was obtained by direct weighing.

Sample trees	StemW		StumpW	BranchW	Dead branches	NeedleW	CRootW	MRootW	FRootW
	Stem wood	Bark							
Small spruce	29.1	3.4	3.9	2.8	4.2	2.4	8.7	1.4	0.36
Medium spruce	114.8	13.9	14.9	18.3	7.7	10.5	5.3	4.4	0.44
Large spruce	202.5	23.6	30.5	26.0	20.8	19.2	37.2	7.6	0.46
Average pine	333.7	25.1	46.1	27.2	22.5	9.7	62.2	7.2	0.31

Table 3. Parameters for regression equations of branch (BranchS) and needle (NeedleS) dry mass (g) (*y*) against neck cross-sectional area of sample branches (cm^2) (*x*). The equations were obtained based on the data of single sample trees as well as the data of three spruce trees as a whole. The linear model used here is $y = a + bx$.

	a				*b*				*n*	r^2
	Coeff.	SE	*t*	*p*	Coeff.	SE	*t*	*p*		
Average pine										
BranchS	–46.97	31.31	1.50	= 0.16	108.32	6.49	16.68	< 0.001	16	0.95
NeedleS	5.45	23.24	0.23	= 0.82	29.29	4.82	6.08	< 0.001	16	0.72
Large spruce										
BranchS-1	–35.26	9.28	3.80	< 0.001	97.71	3.92	24.91	< 0.001	28	0.96
NeedleS-1	– 9.20	14.41	0.64	= 0.53	73.06	6.09	11.99	< 0.001	28	0.85
Medium spruce										
BranchS-1	–35.82	21.47	1.67	= 0.12	120.21	13.20	9.11	< 0.001	13	0.88
NeedleS-1	13.52	16.29	0.83	= 0.42	57.23	10.01	5.71	< 0.001	13	0.75
Small spruce										
BranchS-1	4.18	5.74	0.73	0.48	73.35	7.33	10.01	< 0.001	12	0.91
NeedleS-1	3.90	7.03	0.55	0.59	64.31	8.98	7.16	< 0.001	12	0.84
All spruces*										
BranchS-2	–16.52	7.17	2.30	= 0.025	94.31	3.70	25.46	< 0.001	53	0.93
NeedleS-2	–2.04	7.50	0.27	= 0.79	69.62	3.88	17.96	< 0.001	53	0.86

* With data of the sample branches obtained from all three spruce trees, regressions were fitted.

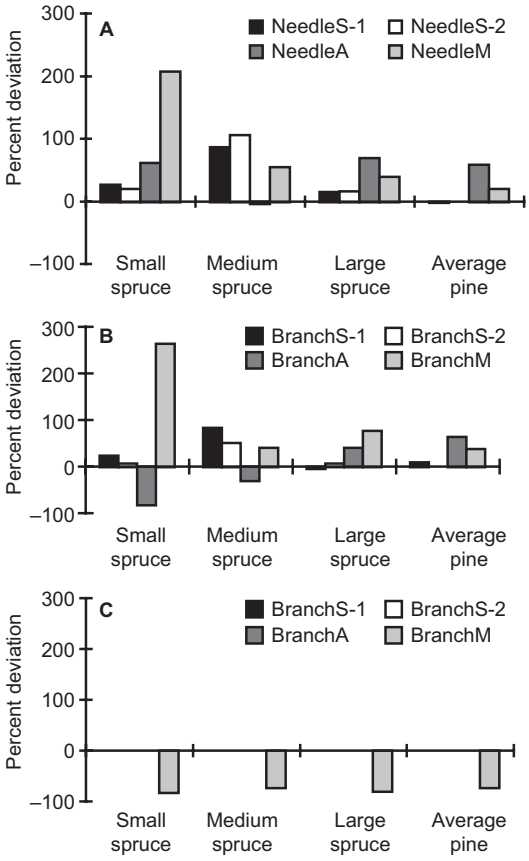

Fig. 1. Percent deviation for estimated dry mass of (**A**) needles (NeedleS-1, NeedleS-2, NeedleA and NeedleM), (**B**) living branches (BranchS-1, BranchS-2, BranchA and BranchM), and (**C**) dead branches (BranchM) on the baseline obtained by direct weighing (NeedleW, BranchW) (*see* Table 2) in the sample trees. The percent deviations were calculated with the formula: $(M_E - M_W)/M_W \times 100$, where M_E is any estimated dry mass and M_W corresponding dry mass fraction determined through direct weighing.

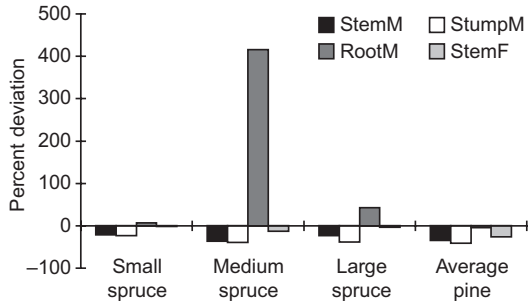

Fig. 2. Percent deviation for dry mass of stem (StemM, StemF), stump (StumpM), and coarse roots (RootM) estimated by the allometric functions of Marklund (1988) and stem form functions by Laasasenaho (1972) on the baseline obtained by direct weighing (StemW, StumpW and RootW) (*see* Table 2) in the sample trees. The percent deviations were calculated with the formula: $(M_E - M_W)/M_W \times 100$, where M_E is any estimated dry mass and M_W corresponding dry mass fraction determined through direct weighing. For RootM, the root means the coarse roots with diameter ≥ 2 mm.

Estimates of needle and branch biomass for the sample trees

Estimated sample tree needle biomass varied depending on the method, from slightly low to high estimates and in the worst case being more than twice the measured needle biomass (Fig. 1A). The spread of estimates for branch material biomass varied even more: from very low, less than a fifth of that measured, to very high, more than two and a half times the measured mass (Fig. 1B). When comparing among methods, the best estimates were indeed obtained by regressions on branch neck cross-sectional area. However, variation between trees was substantial. Both single spruce tree models and the models for all spruces together overestimated the biomass of the medium spruce, which had the longest and best developed crown among sample trees (*see* Table 1). At the same time, estimates for the small spruce and in particularly for the large spruce tree produced needle and branch biomass values reasonably close to measured values. For the estimated results of 3 sample trees, no consistent trend was discerned between the two methods (NeedleS-1 *vs*. NeedleS-2 as well as BranchS-1 *vs*. BranchS-2) (Figs. 1 and 2). For the pine tree, models on branch neck cross-sectional area produced estimates well within ±10% of measured values.

The estimates based on average branch (NeedleA and BranchA) were inaccurate and varied among sample trees in a non-systematic manner between low and high estimates (Fig. 1). In three of four cases the needle biomass was overestimated, and for branch material both over and under estimations were encountered. However, based on the average branch method (NeedleA and BranchA), medium spruce needle and branch material biomass were underestimated.

Estimates based on the allometric functions (Marklund 1988) (NeedleM and BranchM) systematically overestimated living biomass fractions for all sample trees. Nonetheless, except for the small spruce tree whose branch and needle mass was strongly overestimated, estimates were no worse than those obtained by the average branch method (Fig. 1). Mass of dead branches was estimated to be less than one-fifth of the measured mass.

Table 4. Above-ground biomass (Mg ha^{-1}) of Scots pine and Norway spruce trees based on partial harvesting method (StandW) in the stand.

Tree species	Crown*	Stem	Total in stand
Scots pine	8.2	85.0	93.2
Norway spruce	19.6	58.0	77.6
Total in stand	27.8	143.0	170.8

* The crown indicates the branches and needles combined.

Estimates of dry mass of stem, stump and roots for the sample trees

When applying average wood density to stem volume, biomass estimates closely resembled measured values for spruce trees (Fig. 2). Only for the medium spruce was the estimate low, by somewhat more than one-tenth. In the case of the pine tree, stem mass was underestimated by one-fourth (Fig. 2). The use of the allometric functions (Marklund 1988), however, seemed to systematically underestimate both stem and stump compartments. In the case of the coarse root compartment based on RootM, the outcome was highly variable among sample trees; coarse roots for the small spruce tree and the pine tree were estimated correctly, while the estimate was extremely high for the medium spruce tree.

Estimation of standing biomass in the stand

Measured tree biomass

Above-ground biomass (stumps excluded) determined by tree species upon partial harvest method (StandW) totalled 170.8 Mg ha^{-1} (Table 4). Total above-ground biomass was distributed evenly among the two tree species (54 to 44%). The crown compartment of spruce, however, was more than double that of pine, while the stem compartment of pine was 1.5 times that of spruce.

Root biomass (less than 20 mm) in the compounded humus layer and 0–60 cm top mineral soil layer totalled 28.8 Mg ha^{-1} (Table 5). Most of the roots were woody roots (86%), of which the majority were allocated to the humus layer and top 20 cm mineral soil layer: 70%–75% of woody roots and as much as 96% of the non-woody roots of ground vegetation.

Estimated tree biomass

Based on the sample tree method (StandS), estimated stand biomass totalled 239.9 Mg ha^{-1} including medium and fine roots, while the allometric functions of Marklund (1988) (StandM) produced an estimate of 183 Mg ha^{-1} excluding fine roots (Table 6). In comparison to measured above-ground biomass by means of StandW

Table 5. Root biomass (Mg ha^{-1}) in the stand by soil layer on the basis of core samples (StandRootS). Root fractions less than 2 and 2–20 mm are accordingly denoted fine and medium roots.

Soil layers	Roots			Total in stand
	Woody medium	Woody fine	Non-woody fine	
Humus layer	4.8	3.3	2.8	10.9
Mineral soil 0–20 cm	3.5	6.1	1.1	10.6
Mineral soil 20–40 cm	1.3	1.9	0.1	3.3
Mineral soil 40–60 cm	1.5	2.3	0.1	3.9
Total in stand	11.1	13.7	4.0	28.8

(Table 4), StandS overestimated biomass by some 10%, whilst StandM returned an estimate which was some 20% lower. The allometric functions (Marklund 1988) overestimated crown compartment biomass by 15% and 66% for spruce and pine, respectively, and underestimated stem compartment by 20% and 30%, correspondingly.

Biomass of the stump and below-ground compartment represented a substantial fraction (21%) of total stand biomass (Table 6). Exclusion of fine roots would create only a minor error in the estimate as they amounted to only 0.5% of the total. However, the medium root biomass estimated based on StandS (Table 6) was low in comparison to those calculated from StandRootS in the stand (Table 5). The estimated medium roots based on StandS comprised only one-third of the mass of sampled roots (StandRootS), and the estimated return of fine root biomass was even much lower, one-tenth of the mass according to StandRootS. Further, 14% of total biomass of roots less than 2 mm was found among non-woody roots (Table 5).

Discussion

Measurement of biomass is, by definition, the process of direct measurement of the mass of any entire tree compartment of interest, and the estimation of biomass involves the extraction of some sub-samples followed by data arrangement for the calculation of the mass of the respective compartments (Satoo 1982, Parresol 1999). The process of collecting complete samples of trees for weight measurement is overly time consuming and, consequently, direct measurements of the mass of tree compartments are infrequent; the majority of reported data are estimates based on sub-samples selected by some procedure from the respective tree compartments. Such sub-samples are most often selected arbitrarily, but in best case systematically, and the estimates and variances from such samples are known to be biased. The most appropriate approach would be randomised sampling of trees or, to conduct importance sampling, which would produce truly unbiased estimates (Cunia 1979, Valentine *et al*. 1994).

In our study, we determined fresh weight of sample trees by compartments by direct measuring and subsequently respective dry weight on the basis of ratio-type estimators after subsampling. For simplicity we used systematic sampling, i.e. we chose trees to be sampled after stratification based on tree stand DBH distribution, and sample branches either by taking every *n*th branch on the stem or, average branches after sorting according to the size of branches before which the stem had been partitioned into sub-sections of equal length. We judge that such

Table 6. Tree biomass (Mg ha^{-1}) in the stand determined by means of both the sample tree method (StandS) and the allometric functions of Marklund (1988) (StandM). Root fractions less than 2, 2–20 and over 20 mm are accordingly denoted fine, medium and coarse roots.

	Above-ground biomass				Below-ground biomass				Grand total
	Crown*	Stem	Stump	Total	Coarse roots**	Medium roots	Fine roots	Total	
Sample tree method									
Scots pine	14.9	90.3	11.6	116.8	15.6	1.8	0.1	17.4	134.3
Norway spruce	19.0	65.6	8.5	93.1	9.0	2.2	1.2	12.4	105.5
Total	33.9	155.9	20.2	210.0	24.6	4.0	1.3	29.9	239.9
Allometric functions									
Scots pine	13.6	59.7	6.9	80.2	15.0	–	–	15.0	95.2
Norway spruce	22.5	45.8	5.1	73.4	14.4	–	–	14.4	87.8
Total	36.1	105.6	11.9	153.6	29.4	–	–	29.4	183.0

* The crown indicates the branches and needles combined.

** For the allometric functions of Marklund (1987, 1988), the coarse roots should include the coarse roots and medium roots obtained by the sample tree method (StandS).

straightforward systematic sampling was sufficient for our purpose if it is merely to compare between different sampling and estimation approaches. However, some inferiority of these sampling approaches, in particular, average branch method, would be discussed below.

When estimating biomass of the non-merchantable crown compartment by applying the average-branch method and regressions on branch neck cross-section to all branches over the entire tree stem, we found substantial variation in return accuracy among the two estimation approaches. Closest, even good fit was obtained by applying regressions based on the extraction of every *n*th branch on the tree, while calculating biomass by multiplying average branch dry weight with number of branches for each sampled section returns inconsistent estimates: low for the smaller trees and high for the larger ones. It is obvious that systematic sampling of branches for determining ratio estimators is a more cost-effective method; the overall number of extracted sample branches is approximately equal in the systematic and average branch methods: 69 and 63, respectively.

The average sample branch method and similar sampling idea have been popularly used in some literature published (e.g. Zhai 1982, Bhartari 1986, Liu 1987, Rawat and Singh 1988). However, the method is impaired by serious obstacles, and caution should be taken if applying it. The inferiority of the average branch method is a result of structural sampling among branch variation. Although three branches were selected after stratification according to branch neck diameter and lumped for dry mass determination by stem section, such averaging could not remedy inaccuracy arising from random variation. Branches with equal neck diameter may be highly differing with respect to other size parameters. According to the pipe model theory (Shinozaki *et al* 1964), branch material and needle mass is not dependent on total neck cross-sectional area of the branch, but is explained rather by the fraction of sapwood. Thus, in any case, the application of a single tree-wise regression on branch neck cross-sectional area returns systematically biased values: the sapwood/heartwood ratio is certainly not constant over the entire stem length. Combining data from several sample trees into one tree-wise regression, as we tried with the spruce trees, certainly does not remedy this error because combining does not influence the cross-sectional area-sapwood ratio. Further, Fang and Wang (2001) noted that such measurement, as in this case the collecting of the average branch, may overestimate biomass as direct sampling tends to be carried out on specimens being slightly better than average. In our case, however, no such overestimation was the case as biomass estimates varied non-systematically around true values.

The allometric functions consistently overestimated crown compartment biomass; indeed, the estimation for the small understorey spruce completely failed. Stem and stump compartments, however, were consistently underestimated by one-fourth to almost one-half, while returns for coarse roots varied from correct to totally incorrect. The inability of Marklund's (1988) functions to return acceptable biomass estimates for our sample trees may be a result of differing population properties. For instance, a comparably more continental and northerly climate in Finland may result in phenotypes of trees differing from those in Sweden. However, Lehtonen *et al*. (2004) suggested that such a difference would be less than 5% for both pine and spruce. Differing silvicultural practices in the past have undoubtedly influenced tree structure at the stand level. In our forest, based on observations, no cuttings have been performed during the recent 40-year period, and the land area, in which our forest is situated, was in its early stages of stand development, i.e. 70 to 140 years ago, a relatively sparsely inhabited frontier area receiving little forestry management. However, during the course of stand development, old growth Scots pine timber has most probably been harvested occasionally through selective cuttings on the site leaving understorey spruce to develop (Levula *et al*. 2003). In contrast, Marklund's (1988) functions are based on random sampling in managed populations of Swedish Forest Service forests from all over Sweden.

According to Mälkönen (1974) and Hakkila (1971), tree dry mass can be estimated from stem volume. Stem volume is also most often used as the basis when calculating BEF values (Fang and Wang 2001, Fang *et al*. 1998, Lehtonen

et al. 2004). When we applied density values for Norway spruce and Scots pine suggested by Hakkila (1971) to stem volume calculated by Laasasenaho's (1982) stem functions, we obtained almost correct dry mass estimates for the stem compartment of the spruce trees. However, the estimate for the pine tree exceeded the true value by one-fourth. It is obvious that stem volume would be a reliable independent variable for dry mass estimation assuming that appropriate density values are available. In light of this case, Hakkila (1971) suggested reasonable values for Norway spruce (392 kg m^{-3}), and for old growth Scots pine stem wood (394 kg m^{-3}). On the basis of dry weight/volume ratios determined for sample trees in this study, we found that average density values were 405 kg m^{-3} for three Norway spruce trees (ranging form 376–439 kg m^{-3}) and 446 kg m^{-3} for a Scots pine sample tree.

Given tree species and environmental conditions in any specific area, the accumulation of biomass in a forest is a saturating function of tree stand age (Sprugel 1984, Paré & Bergeron 1995). On a broad geographical (e.g. continental or biome) scale, the maximum tree biomass which can be accumulated is mainly associated with prevailing climate (*see* Cannell 1982, Satoo 1982). On a local scale, standing biomass in a forest varies with site factors, stand properties like age, number of stems per hectare, species composition etc., which largely may be a result of past anthropogenic activities. According to the forest biomass data set by Cannell (1982) and the data set of boreal tree biomass by Gower *et al*. (2001), the maximum biomass in the forest near our study stand at 120–150 years of age would be about 230 Mg ha^{-1} dry matter. In comparison with such an average trend, the estimate on tree stand biomass in our forest, attained by means of partial harvesting method and assuming that stump and coarse roots equal 26% of above-ground biomass (average fraction on basis of sample tree method and allometric models), totals 215.2 Mg ha^{-1}. The biomass of the tree stand would be 238.6 Mg ha^{-1} using the sample tree method, but 186.1 Mg ha^{-1} by applying Marklund's (1988) allometric functions. The discussion above indicates that the tree biomass in our mixed spruce–pine forest approaches the maximum for boreal forests, but that attention should be paid to methodological differences behind various estimates when the literature is cited.

When comparing compounded stem and crown fractions among methods, the sample tree method, in this case, returns an overestimate of approximately 10% while the allometric functions still underestimate pools by about one-fifth. In short, different fractions are estimated randomly with varying accuracy and the return may be either low or high. This non-conformity mostly arises from redundant crown compartment biomass of the pine sample tree. As the biomass of pine trees in the forest is calculated based on only one sample tree by weighing, tree breast height cross-sectional area non-normality in this single sample tree may seriously bias the overall estimate. Other compartments (spruce stem and crown, pine stem) are approximately within ±10% of measured values. Further, stump and root compartments seem particularly difficult to estimate. The allometric functions return a much lower stump compartment than the sample tree method, and, roots determined by up-scaling after systematic sampling in the forest are much higher than roots determined by the sample tree method. When combining biomass estimates into various applications or, comparing between estimates, complications arise from the fact that biomass is frequently estimated by different methods and else foreseeable trends are consequently obscured by methodological nonconformities. Differing methods are also frequently modified to apply to specific research conditions. For instance, biomass regression equations have been established using the data of sample trees collected from different stands at a regional scale, instead of within a plot (Marklund 1987, 1988), and then such equations have been applied to individual forest stands (plots) within other regions (Liski *et al*. 1995, Westman and Laiho 2003). In determining branch and needle biomass the neck diameter of the branch solely or together with branch length has been used as an independent variable in the regression method (Ilvesniemi and Liu 2001). In applications of the ratio method, respective basal area has been used and, in other applications the average size branch has been considered representative for all branches of a tree or a section of a

tree (Zhai 1982, Bhartari 1986, Liu 1987, Rawat and Singh 1988).

Nonconformity in methods producing biomass estimates is also impinging on the calculation of biomass expansion factors. Thus, from Fang and Wang's (1998) it is not clear on what grounds or how they approved different biomass estimates for their calculations. It is certain that among 758 observations, a variety of estimation approaches have been used. Lehtonen *et al*. (2004) again consistently applied allometry to a large set of National Forest Inventory (NFI) data and consequently reported consistent BEF values. However, although NFI data and stem volume functions (Laasasenaho 1982) produce accurate estimates with known error, errors arising from the application of Marklund's (1988) allometric functions are not known. When we apply BEF values for Norway spruce and Sots pine aged 120–139 years according to Lehtonen *et al*. (2003), the calculation returns 179 Mg ha^{-1} for our forest. This approximately equals the biomass we obtained by applying Marklund's (1988) functions to our data, and is some 22% below the true value.

In conclusion, to be able to construct applicable BEFs, more consistently measured forest biomass data, which is also as equally representative as NFI data, is needed. For instance, Gower *et al*. (2001), when summarising net primary production and carbon allocation patterns for boreal forests, found a total of only 24 stands for which a complete budget had been described and another 45 stands for which data on the aboveground compartment had been collected. They concluded that with such a number of stands, each stand, if evenly distributed worldwide in boreal forests, would represent approximately 0.64×10^6 km^2. Although data on biomass pools from substantially more sites are available, e.g. some 750 already in Fang and Wang's (1998) study, this certainly demonstrates the need to produce sufficient data and develop databases having geographic coverage.

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