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ORIGINAL PAPER

Generalized allometric volume and biomass equations for some tree species in Europe

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Abstract Since biomass is one of the key variables in ecosystem studies, widespread effort has aimed to facilitating its estimation. Numerous stand-specific volume and biomass equations are available, but these cannot be used for scaling up biomass to the regional level where several age-classes and structural types of stands coexist. Therefore simplified generalized volume and biomass equations are needed. In the present study, generalized biomass and volume regression equations were developed for the main tree species in Europe. These equations were based on data compiled from several published studies and are syntheses of the published equations. The results show that these generalized equations explain 64–99% of the variation in values predicted by the original published equations, with higher values for stem than for crown components.

Keywords Aboveground · Tree allometry · Dry weight · *Picea abies* · *Pinus sylvestris* · *Betula* spp. · *Fagus* spp. · *Quercus* spp.

Introduction

Rapid, easily implemented methods are needed for the assessment of standing biomass to estimate the degree of carbon sequestration by forest ecosystems. The method most often used for determining individual tree biomass and volume is the use of allometric relationships (Whittaker and Woodwell 1968). Normally, the volume or biomass of a tree is predicted as an equation of some easily measured variable, such as diameter-at-breast height (*dbh*) or height (*h*).

Whenever there is need for estimating the biomass of individual trees, the abundance of currently available predictive equations provides an alternative to the destructive sampling of trees for developing local equations. Comprehensive collections of stand-specific biomass equations are available in the literature (for North America Ter-Mikaelian and Korzukhin 1997, Jenkins et al. 2004; for Australia Eamus et al. 2000, Keith et al. 2000, Snowdon et al. 2000 and for Europe Zianis et al. 2005). Most published biomass equations were developed using trees sampled from specific study sites or from sites that represent small regions only. As a result, use of existing volume or biomass equations with forest inventory data at large spatial scales[1] is unreliable because the equations of previous studies may be site-specific, often disorganized and sometimes inconsistent (Pastor et al. 1983/1984; Jenkins et al. 2003; Wirth et al. 2004). Furthermore, unless an equation was developed exclusively for the species and study region of interest under conditions typical for the study site, it is impossible to know which equations to choose for a particular species and site. Reliable models of tree-level biomass to be used at large spatial scales are available mainly for Scandinavia and were compiled by Marklund (1987, 1988).

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[1] Forest inventories use as volume functions mostly equations other than allometric equations.

There may be additional value in deriving generalized equations for comparing different regions, since it is important to know that inconsistencies between regions are not due solely to the application of different regression equations, which yield contrasting values even for the same dataset but do not significantly vary among themselves (Pastor et al. 1983/1984). Despite these inconsistencies, or perhaps because of them, the need is clear for a consistent method and for generalized equations to estimate forest biomass at large scales (Jenkins et al. 2003).

To assess tree biomass on a large spatial scale one could (1) sample several trees of different sizes from a representative sample of species, regions and sites across the area of interest or (2) find an already existing equation for the geographically closest site (Ter-Mikaelian and Korzukhin 1997). Additionally, one could (3) use several available equations to estimate the range of biomass (Ter-Mikaelian and Korzukhin 1997) or (4) attempt as much as possible to collect sample data for reanalysis from all available sources of tree mensurational data (Wirth et al. 2004). Furthermore, one could (5) produce a generalized equation based on those reported in the literature (Schmitt and Grigal 1981; Pastor et al. 1983/1984; Zianis and Mencuccini 2003).

The first approach would ensure an unbiased sample of trees but would also be very expensive and time-consuming. The fourth approach is also difficult, since most scientists have not published the raw data from which their volume or biomass equations were developed. However, several authors reported that generalized regressions developed from field data can reasonably predict the biomass of trees from other sites (Schmitt and Grigal 1981; Wirth et al. 2004).

The aim here is to provide new generalized allometric volume and biomass equations using *dbh* for the most common tree species in Europe. The equations presented here should provide a consistent and unbiased basis for evaluating forest biomass across regional boundaries in analysis of the carbon budget of forests.

Methods

Material

Generalized allometric biomass (dry weight) and volume equations were developed for the most common tree species in Europe. Equations relating volume of the stem or biomass of the tree component (stem, branches, foliage and total aboveground) to *dbh* or *dbh* and *h* were compiled (Table 1) from the comprehen-

Table 1 Equations relating volume of stem or biomass of tree component (stem, branches, foliage and total aboveground) to diameter-at-breast height or diameter and height used in this study. The equations were compiled from the comprehensive study of Zianis et al. (2005) and ID numbers here correspond to the reference ID in Zianis et al. (2005)

	ID of equations
Temperate zone	
Picea abies	
Vol[a]	82–83, 94–95, 100–101, 127
AB[a]	140–142, 144–145, 148–151
ST[a,b]	258, 260, 272–273, 275–281, 290, 292
FL[a]	217, 219–220, 222, 229–238, 245
BR[a,c]	157–160, 162, 170–171, 175–177, 202, 205, 207–209, 305–307
Pinus sylvestris	
Vol	145–146, 155–157, 159–160, 169
AB	330–331, 352, 355–356
ST	492–494, 510, 514
FL	420–422, 445, 448–449, 454
BR	361–363, 390
Quercus spp.	
Vol	200–204, 206–211, 213–216
AB	569–578, 613
ST	–
FL	–
BR	–
Fagus spp.	
Vol	47–50, 52–53
AB	93–95, 97–9
ST	131–134
FL	114–115, 118–119
BR	105, 107–109
Boreal zone	
Picea abies	
Vol	88, 90, 92–93, 102–113, 116–119, 123
AB	146, 153–155
ST[b]	265–266, 270, 282–283, 286, 296–297, 300
FL	225, 227–228, 239–241, 243–245
BR[c]	178–180, 184–185, 210–211, 215
Pinus sylvestris	
Vol	148, 150–154, 161–164, 166, 170–173, 176–177
AB	344, 346–351
ST	473–482, 486, 507, 509, 516–520, 522–525, 528
FL	435, 437–444, 450, 452–453
BR	376–377, 383–389, 412–415, 418
Betula spp.	
Vol	26, 29–31, 33–34, 36, 38
AB	–
ST[b]	38, 43–47, 69, 72–73, 75
FL	35, 42, 67, 74
BR[c]	33, 41, 56–58, 61, 63, 65

[a] *Vol* is stem volume. *AB*, *ST*, *FL* and *BR* are biomass of tree compartments total aboveground, stem, foliage and branches, respectively

[b] In some cases separate equations are used for stem wood and for stem bark

[c] In some cases separate equations are used for living branches and for dead branches

sive study of Zianis et al. (2005). The equations were used to generate simplified specieswise and compartmentwise generalized regression equations.

When several equations based on independent tree samples from different sites were reported, all were included in this study. In the present study we analysed the following tree species in Europe: Norway spruce [*Picea abies* (L.) Karst.], Scots pine (*Pinus sylvestris* L.), birch (*Betula* spp. L.), oak (*Quercus* spp. L.) and beech (*Fagus* spp. L.).

Meta-analysis

The meta-analysis was used to formulate a generalized regression equation and to summarize studies on the same topic by different contributors to obtain a combined overall mean among studies (Iyengar 1991). The four stages of the meta-analysis included (1) identification of a study problem, (2) retrieval of relevant studies, (3) extraction of appropriate data and (4) formulation of a statistical model for combining data. Incorporating datasets produced by different authors into a single comprehensive analysis introduces some inhomogeneity that particularly affects assessment of the accuracy of the resulting predictions. Estimates for the uncertainty of predicted values rely heavily on the assumption of independence of residuals from the fitted model, an assumption hardly met if data from different authors are combined.

There are two ways to produce generalized regression equations for volume and biomass: formal and modified meta-analytic techniques (Jenkins et al. 2003). The formal meta-analytic technique combines regression coefficients (Peña 1997) and all equations used in such meta-analyses must have identical forms and identical variable transformations. Application of formal meta-analytic techniques for combining regression coefficients is not applicable to the present study, with its aim of developing generalized regression equations based on as many unpublished and published previous equations as possible. Therefore, a modified version was used of a type of meta-analysis that generates volume and biomass data using various published equations and that fits an equation to the generated data, thus summarizing previous equations (Schmitt and Grigal 1981; Pastor et al. 1983/1984).

Assessment of the variability of the original equations was performed in the following manner. Equally spaced points at a 1-cm interval for *dbh* were generated from each of the compiled equations to form specieswise and compartmentwise pseudoobservations (Fig. 1). In Fig. 1, the pseudoobservations represent the actual situation. Separate pseudoobservations for the Temperate and Boreal Zones were produced (for definitions of vegetation zones see Ahti et al. 1968). These points covered the range of diameter values specific to each equation and were used to generate generalized equations for each species and compartment, thus ensuring more weight to the equations with a wider diameter range. If the data range of the sample trees behind the original equation was not reported, the equation was assumed to cover the range from *dbh* of 10 cm up to the species-specific maximum limit. For *P. sylvestris*, *P. abies* and *Betula* spp., the maximum limit for *dbh* was set to 40 cm and for *Fagus* spp. and *Quercus* spp. to 50 cm. Since not all studies reported the number of sample trees used in developing the original regression, the equations compiled do not have different weights based on sample size.

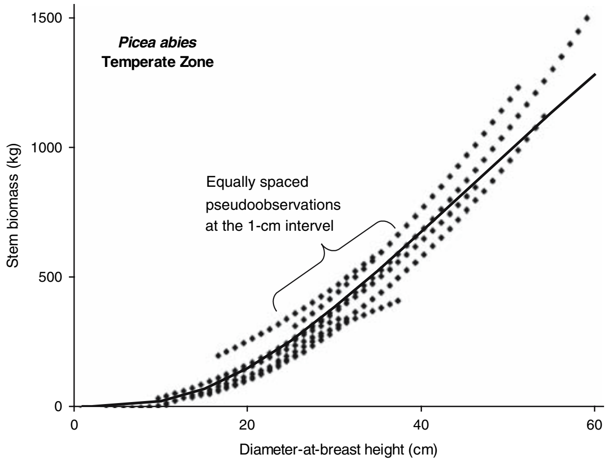

Fig. 1 Equally spaced points at a 1-cm interval for diameter-at-breast height were generated from each of the compiled equations to form specieswise and compartmentwise pseudoobservations that were used to estimate generalized equations

In some cases, the original equation has two explanatory variables: *dbh* and *h*. For these equations, the *dbh–h* relationships were utilized. For *Fagus* spp., *Quercus* spp., *P. abies* and *P. sylvestris* in the Temperate zone, the relationship between *dbh* and *h* was estimated based on data of forest management plans from the Czech Republic (Cienciala 2004, personal communication). For *P. abies*, *P. sylvestris* and *Betula* spp. in the Boreal Zone, tree measurements of permanent sample plots from the 8th National Forest Inventory of Finland were used. For both these datasets, the formula describing the *dbh–h* relationship developed by Näslund (1937) was fitted:

$$h = 1.3 + \frac{dbh^2}{(\beta_0 + \beta_1 \cdot dbh)^2} \tag{1}$$

(see Table 2).

Table 2 Relationship between tree height and diameter-at-breast height

	N	β_0	SE	β_1	SE	R^2	RMSE	RMSECV[a]	RMECV[a]
Temperate zone[b]									
Picea abies	–	1.609	–	0.153	–	–	–	–	–
Pinus sylvestris	–	1.543	–	0.168	–	–	–	–	–
Quercus spp.	–	1.315	–	0.180	–	–	–	–	–
Fagus spp.	–	1.573	–	0.154	–	–	–	–	–
Boreal zone[c]									
Picea abies	4365	2.088	0.0186	0.157	0.00097	86.16	2.128	2.214	0.186
Pinus sylvestris	5864	2.082	0.0204	0.170	0.00112	81.41	2.334	2.367	0.215
Betula spp.	3324	1.460	0.0192	0.184	0.00144	73.22	2.352	2.288	0.184

Diameter-at-breast height (*dbh*) in centimetres as an independent variable gives tree height (*h*) in metres by Eq. 1

[a] RMSECV and RMECV are the root-mean-square error and relative mean error of leave-one-out cross-validation, respectively (for calculation scheme see Appendix 1)

[b] Based on nationwide data of forest management plans in Czech Republic (Cienciala 2004, personal communication)

[c] Based on measurements of Finnish National Forest Inventory

Generalizing

Finally, the pseudoobservations generated with the published equations were used to predict the relationships between *dbh* and either stem volume or biomass of the aboveground tree compartment (total aboveground, stem, foliage, branches). In this respect, the regressions were syntheses of the published equations (Fig. 1). The commonly used mathematical model for biomass studies takes the form of the power equation

$$y_i = \beta_0 \cdot dbh^{\beta_1}, \tag{2}$$

where β_0 and β_1 are the scaling coefficients, y is either the volume of the stem or the biomass of tree component i (Zianis and Mencuccini 2004). Marklund (1987, 1988) developed an alternative

$$y_i = \exp\left(\beta_0 + \beta_1 \cdot \frac{dbh}{dbh + \beta_2}\right). \tag{3}$$

The units used for *dbh*, volume and biomass are cm, m^3 and kg, respectively. Both these equations were applied.

The *dbh* was used as the only predictive variable because it is the most common and the easiest variable to measure in the field (Pastor et al. 1983/1984). Although some previous biomass studies have also used h together with *dbh*, the advantage of such regressions over those using *dbh* alone is probably not practical with regard to the accuracy of h measurements and the increased fieldwork involved.

Model validation

Several procedures can be used to check the validity of a regression model: (1) comparison of the model predictions ($\hat{y}$) and coefficients with physical theory (see the global allocation rules below), (2) comparison of results with theoretical models and simulated data, (3) collection of new test data to check model predictions and (4) reservation of a portion of the available data to obtain an independent measure of the model prediction accuracy (Snee 1977).

When the validity of the generalized equations was checked, we first compared the model coefficients (β_1) of Table 4 with global allocation rules (West et al. 1999; Enquist and Niklas 2001). These authors concluded that the extending allometric theory predicts that y is proportional to the 8/3 (~2.667) power of the stem diameter *dbh* of any size class (i.e., $y \propto dbh^{8/3}$). They also suggested that this allometric theory is almost universally applied in biology and that it originated in the common geometric and hydrometric principles that govern the transport of essential materials to support cellular metabolism. The accuracies of the generalized equations were tested by comparing the model predictions with independent test data compiled from reported volume and biomass values (Burger 1937, 1953; Dietrich 1968; Vinš and Šika 1981; Vyskot 1990; Do-Hyung 2001).

Results and discussion

When the form of the equation reported by Marklund (1987, 1988) was used, the generalized equations for stem volume fitted well (R^2 = 96–100%)[2] with the

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[2] The R^2 and the root-mean-square error of the generalized volume and biomass equations were used to assess the variability of these equations relative to the original equations. These apply to the pseudoobservations generated and do not express the accuracy relative to the field data but indicate the amount of variation in predictions by the original equations accounted for by the generalized equations.

Table 3 Generalized volume and biomass equations (biomass kg dry matter)

	e^a	n^a	β_0	SE	β_1	SE	β_2	SE	$R^{2,b}$	RMSE^b
Temperate zone										
Picea abies										
Vol^c	13	330	–8.381	0.126	11.129	0.092	11.079	0.377	98.6	0.153
AB^c	9	144	–1.694	0.152	10.825	0.115	11.816	0.621	98.5	0.195
ST^c	11	240	–3.043	0.191	11.784	0.160	9.328	0.404	97.5	0.213
FL^c	14	308	–1.360	0.350	7.308	0.337	19.662	4.299	63.5	0.793
BR^c	10	265	–0.537	0.218	10.093	0.657	40.426	7.655	84.5	0.588
Pinus sylvestris										
Vol	9	266	–8.805	0.124	11.254	0.094	9.915	0.279	99.5	0.081
AB	4	56	–2.688	0.183	10.745	0.125	8.062	0.488	99.5	0.151
ST	5	104	–3.854	0.301	11.729	0.225	7.492	0.645	97.2	0.343
FL	7	103	–3.275	0.400	9.135	0.485	14.790	3.755	85.2	0.745
BR	4	82	–3.998	0.317	11.164	0.234	11.815	1.367	96.6	0.344
Quercus spp.										
Vol	14	596	–8.128	0.122	10.872	0.090	11.756	0.369	98.2	0.183
AB	11	335	–0.604	0.108	10.677	0.080	15.900	0.577	98.4	0.241
ST	–	–	–	–	–	–	–	–	–	–
FL	–	–	–	–	–	–	–	–	–	–
BR	–	–	–	–	–	–	–	–	–	–
Fagus spp.										
Vol	6	257	–7.087	0.460	10.691	0.289	16.184	1.994	95.9	0.236
AB	6	240	0.006	0.073	10.933	0.044	21.216	0.507	99.7	0.083
ST	4	167	–0.657	0.127	10.730	0.079	17.394	0.684	99.4	0.108
FL	4	146	–2.480	0.096	9.511	0.092	26.771	1.428	99.3	0.098
BR	4	167	–2.128	0.132	13.295	0.096	26.095	1.190	99.3	0.147
Boreal zone										
Picea abies										
Vol	21	810	–8.574	0.026	11.458	0.020	11.881	0.090	99.8	0.082
AB	4	70	–1.455	0.116	10.233	0.080	11.838	0.510	99.6	0.096
ST	6	154	–1.577	0.081	10.892	0.083	15.610	0.569	99.2	0.192
FL	9	247	–2.265	0.108	8.163	0.084	10.976	0.522	97.7	0.222
BR	7	191	–1.497	0.193	9.705	0.261	21.052	2.361	92.2	0.485
Pinus sylvestris										
Vol	17	538	–8.735	0.052	11.255	0.037	10.667	0.167	99.6	0.110
AB	7	128	–1.194	0.160	10.011	0.118	13.454	0.880	98.3	0.197
ST	13	275	–1.408	0.155	10.666	0.151	15.775	1.137	95.8	0.369
FL	12	284	–3.299	0.188	7.681	0.141	9.109	0.756	92.8	0.338
BR	9	177	–0.928	0.141	9.889	0.523	32.338	4.556	93.7	0.357
Betula spp.										
Vol	8	296	–9.481	0.166	11.359	0.124	8.293	0.352	98.2	0.216
AB	–	–	–	–	–	–	–	–	–	–
ST	7	114	–2.411	0.204	10.210	0.182	8.291	0.736	96.7	0.355
FL	4	52	–2.915	0.226	9.574	1.243	24.138	7.148	92.2	0.398
BR	5	87	–3.579	0.299	10.570	0.350	11.363	1.728	93.8	0.515

Dependent variables y, stem volume (m^3) or biomass of tree component i (kg) are given according to diameter–at-breast height (*dbh*) in Eq. 3

[a] Symbol e indicates the number of original equations behind the generalization and n gives the number of generated pseudoobservations

[b] The R^2 and the root-mean-square error (RMSE) of the generalized volume and biomass equations were calculated and used to assess the variability of these equations relative to the original equations. These apply to the pseudoobservations generated and do not express the accuracy relative to the field data but indicate the amount of variation in predictions by the original equations accounted for by the generalized equations

[c] *Vol* is stem volume. *AB*, *ST*, *FL* and *BR* are biomass of tree compartments total aboveground, stem, foliage and branches, respectively

Table 4 Generalized volume and biomass equations (biomass kg dry matter)

	e[a]	n[a]	β_0	SE	β_1	SE	R^2[b]	RMSE[b]
Temperate zone								
Picea abies								
Vol[c]	13	330	0.000247	0.000033	2.362	0.0375	96.5	0.085
AB[c]	9	144	0.255	0.0289	2.174	0.0317	98.3	33.269
ST[c]	11	240	0.314	0.0367	2.075	0.0307	96.8	63.250
FL[c]	14	308	0.0228	0.00842	2.032	0.0973	69.4	13.446
BR[c]	10	265	0.000989	0.000222	3.187	0.0832	91.5	19.409
Pinus sylvestris								
Vol	9	266	0.000168	0.000033	2.421	0.0541	93.1	0.116
AB	4	56	0.158	0.0108	2.237	0.0194	99.9	6.498
ST	5	104	0.0811	0.0369	2.380	0.1291	89.6	51.383
FL	7	103	0.00654	0.00713	2.362	0.3089	64.4	8.624
BR	4	82	0.00526	0.00253	2.724	0.1357	93.4	9.579
Quercus spp.								
Vol	14	596	0.000362	0.00006	2.226	0.0411	92.2	0.189
AB	11	335	0.230	0.00583	2.280	0.0060	99.9	42.450
ST	–	–	–	–	–	–	–	–
FL	–	–	–	–	–	–	–	–
BR	–	–	–	–	–	–	–	–
Fagus spp.								
Vol	6	257	0.000214	0.000043	2.429	0.0525	93.7	0.263
AB	6	240	0.240	0.0125	2.322	0.0127	99.5	88.474
ST	4	167	0.148	0.00938	2.360	0.0162	99.6	41.114
FL	4	146	0.00313	0.00027	2.438	0.0232	99.3	0.926
BR	4	167	0.00498	0.000586	3.045	0.0297	99.2	31.281
Boreal zone								
Picea abies								
Vol	21	810	0.000452	0.000023	2.149	0.0132	98.7	0.095
AB	4	70	0.116	0.0206	2.360	0.0505	98.8	22.674
ST	6	154	0.202	0.0160	2.121	0.0202	99.4	24.698
FL	9	247	0.386	0.0600	1.370	0.0416	89.2	9.694
BR	7	191	0.0443	0.00818	2.181	0.0474	95.3	18.254
Pinus sylvestris								
Vol	17	538	0.000707	0.000079	2.004	0.0315	94.3	0.096
AB	7	128	0.0835	0.0320	2.414	0.1087	90.9	57.345
ST	13	275	0.0654	0.0271	2.458	0.1154	81.0	91.514
FL	12	284	0.0663	0.0212	1.568	0.0917	69.5	4.441
BR	9	177	0.0111	0.00438	2.462	0.112	88.2	10.426
Betula spp.								
Vol	8	296	0.000249	0.00005	2.265	0.0563	92.9	0.094
AB	–	–	–	–	–	–	–	–
ST	7	114	0.206	0.0138	2.122	0.0201	99.6	6.058
FL	4	52	0.00139	0.000303	2.691	0.0685	98.9	0.300
BR	5	87	0.00607	0.0027	2.758	0.1317	93.1	7.134

Dependent variables y, stem volume (m^3) or biomass of tree component i (kg) are given according to diameter-at-breast height (*dbh*) in Eq. 2

[a] Symbol e indicates the number of original equations behind the generalization and n gives the number of generated pseudoobservations

[b] The R^2 and the root-mean-square error (RMSE) of the generalized volume and biomass equations were calculated and used to assess the variability of these equations relative to the original equations. These apply to the pseudoobservations generated and do not express the accuracy relative to the field data but indicate the amount of variation in predictions by the original equations accounted for by the generalized equations

[c] *Vol* is stem volume. *AB*, *ST*, *FL* and *BR* are biomass of tree compartments total aboveground, stem, foliage and branches, respectively

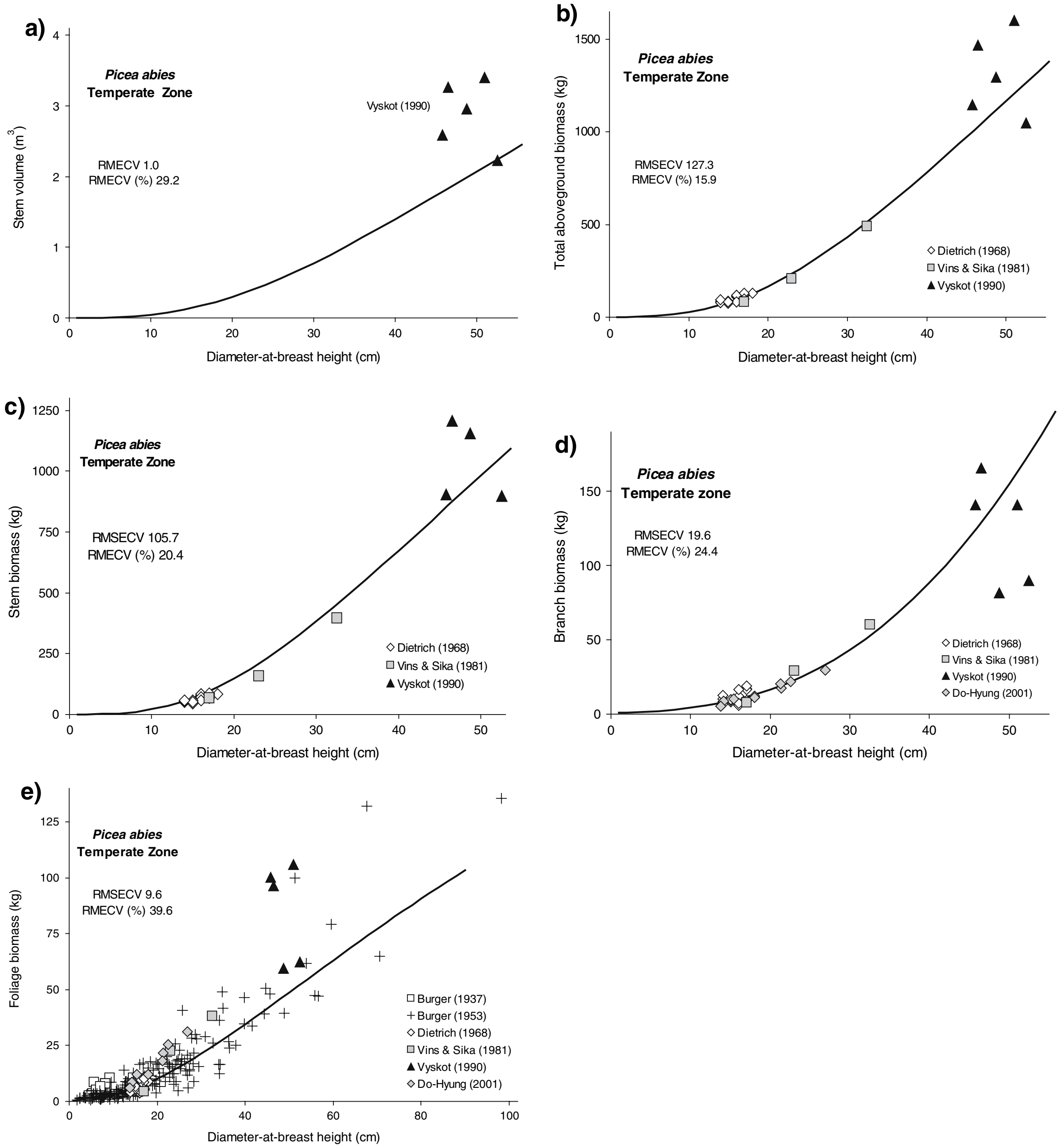

Fig. 2 Comparison of generalized biomass equations (Eq. 3, see Table 3) against reported volume and biomass values of Temperate zone *Picea abies* (Burger 1937, 1953; Dietrich 1968; Vinš and Šika 1981; Vyskot 1990; Do-Hyung 2001): **a** stem volume, **b** total aboveground biomass, **c** stem biomass, **d** branch biomass and **e** foliage biomass. For mPRESS, RMSECV and RMECV, see Eqs. 4, 5 and 6 in the Appendix 1

pseudoobservations generated with the original allometric equations (Table 3). The high values for R^2 are more or less self-evident, since the major parts of the variation had been removed before the pseudoobservations. Generalization accounted for 96–99% of the variation in values predicted by the original published equations for total aboveground biomass and stem biomass. Branch biomass was estimated accurately using generalized equations for *P. sylvestris* and *Fagus* spp. in the Temperate zone as well as for *P. abies*, *P. sylvestris* and *Betula* spp. under boreal conditions (R^2 = 92–99%). For *P. abies* under temperate conditions, generalization adequately fitted the pseudoobservations (R^2 = 85%). The gneralized equations for foliage biomass of *P. abies* and *P. sylvestris* in the Temperate Zone failed to predict the pseudoobservations accurately (R^2 = 71–85%). Nonetheless, the foliage biomass of *Fagus* spp. under temperate conditions and *P. abies*, *P. sylvestris* and *Betula* spp. under boreal conditions were estimated accurately ($R^2 = 92–99\%$).

The power equation, commonly used in biomass studies, predicted 92–99% of the total variation in pseudoobservations of stem volume (Table 4). Generalization explains 88–99% of the variation in values predicted by the original published equations for total aboveground biomass and branch biomass. Stem biomass was estimated accurately for *P. abies* and *Fagus* spp. in the Temperate zone and for *P. abies* and *Betula* spp. in the Boreal zone ($R^2 = 97–99\%$). For *P. sylvestris* under both temperal and boreal conditions, the generalizations fitted the pseudoobservations passably (81–90%). The generalized equations for the foliage biomass of *P. abies* and *P. sylvestris* under temperate conditions and *P. sylvestris* under boreal conditions failed to explain the variation in pseudodata (64–70%). Nonetheless, the generalized equations for foliage biomass of *Fagus* spp. in the Temperate Zone and *P. abies* and *Betula* spp. in the Boreal Zone fitted the pseudoobservations well (89–99%).

The results show that the coefficients of determination ranged from 64 to 99%, with higher values for stem volume, stem biomass, branch biomass and total aboveground biomass than for foliage biomass. The higher R^2 values for the generalizations indicate that the original equations used in the generalization are more similar or that only a few were used for the generalization. The equation form developed by Marklund (1987, 1988) (Eq. 3) appeared to fit better than power equation 2 (the most commonly used), especially in the lower diameters, where the power equation is rather stiff. Marklund's simplified equations scale the relationship according to the *dbh* of the stump diameter. Equations 2 and 3 predicted similar types of biomass or volume values for the higher *dbh* values.

Table 5 Dissimilarity of parameters β_1 (Table 3) between Temperate and Boreal zones. For calculation scheme, see Appendix 2

	t	*P*
Pinus sylvestris		
Vol[a]	7.23	<0.001
AB[a]	–10.73	<0.001
ST[a]	–18.67	<0.001
BR[a]	–5.84	<0.001
FL[a]	25.32	<0.001
Picea abies		
Vol	10.12	<0.001
AB	–10.11	<0.001
ST	–17.35	<0.001
BR	–17.47	<0.001
FL	31.50	<0.001

[a] *Vol* is stem volume. *AB*, *ST*, *FL* and *BR* are biomass of tree compartments total aboveground, stem, foliage and branches, respectively

The coefficients β_1 of Eq. 2 estimated in this study varied from 1.37 to 3.19, while the mean (~2.32) was quite similar to the empirical power values (1.16–3.32; $\bar{x}2.368$) reported by Zianis and Mencuccini (2004). The theoretical universal power value (~2.667) is slightly higher (West et al. 1999; Enquist and Niklas 2001), but Zianis and Mencuccini (2004) concluded that the mean of empirically determined coefficient β_1 gave more aacurate predictions than the theoretical universal power value.

When the generalizations were compared against the reported volume and biomass values, the generalized equations very closely predicted the total aboveground, branch and foliage biomasses for temperate *P. abies*, and there was virtually no difference between the generalized estimations and test data (Figs. 2b, d, e). In contrast, the generalized equations did not accurately predict the stem volume and stem biomass (Figs. 2a, c).

In general, inaccurate estimations may clearly be obtained from generalized equations when applied to any particular stand (Zianis and Mencuccini 2003). However, over- and underestimations from generalized predictions may cancel out when these are applied to large geographical areas. The results were assumed to be applicable to nationwide studies for European countries within the Temperate and Boreal zones (for definitions of vegetation zones see Ahti et al. 1968). The equations produced separately for the Temperate and Boreal zones differed in a statistically significant manner (Table 5).

The results of this study are applicable to *P. abies*, *P. sylvestris* and *Betula* spp. with *dbh* values of 10–40 cm. For *Fagus* spp. and *Quercus* spp. the suitable range is from 10 to 50 cm. Any meta-analysis must face the diversity of methods used in different studies. These differed with respect to the set of biomass components considered and the strategy involved in sample tree selection.

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Appendix 1

The modelled relationships between *dbh* and *h* were tested, reserving a portion of the available data to obtain an independent measure of the model prediction accuracy. When no test set is available for model validation, a cross-validation criterion can be used (Stone 1974; Snee 1977). Model validation was accomplished with the leave-one-out (LOO) cross-validation. The dataset is split into a training set, on which a model is estimated, and a test set on which the model is evaluated. In this case the response value $\hat{y}_{(\mathrm{i})}$ is predicted on a model that was estimated for the dataset minus the *i*th observation, while the test set contains only one observation (Stone 1974). The splitting procedure is repeated until all observations have once and only once been in the test set. Thus there are *n* models built, each using *n*–1 observations for model construction and the remaining observations for model validation. The LOO cross-validation criterion mPRESS (mean of the predictive error sum of squares) is most often used (Stone 1974; Snee 1977):

$$\mathrm{mPRESS} = \frac{1}{n}\sum_{i=1}^{n}\left(y_i - \hat{y}_{(i)}\right)^2, \tag{4}$$

in which n is the number of observations in the test set and y_i and $\hat{y}_{(\mathrm{i})}$ are, respectively, the experimental and predicted response values. Taking the square root of this, we can derive the root-mean-square error of cross-validation:

$$\mathrm{RMSECV} = \sqrt{\frac{1}{n}\sum_{i=1}^{n}\left(y_i - \hat{y}_{(i)}\right)^2}. \tag{5}$$

The relative mean error of cross-validation was also calculated:

$$\mathrm{RMECV} = \frac{1}{n}\sum_{i=1}^{n}\left|\frac{y_i - \hat{y}_{(i)}}{y_i}\right|. \tag{6}$$

Appendix 2

The dissimilarity $(H_0 : \beta_1^{\mathrm{BOR}} = \beta_1^{\mathrm{TEM}}; H_1 : \beta_1^{\mathrm{BOR}} \neq \beta_1^{\mathrm{TEM}})$ of parameters β_1^{BOR} and β_1^{TEM} (Table 3) was tested using the test statistic t (Ranta et al. 1999):

$$t = \frac{\beta_1^{\mathrm{BOR}} - \beta_1^{\mathrm{TEM}}}{s_{\beta_1^{\mathrm{BOR}} - \beta_1^{\mathrm{TEM}}}}, \tag{7}$$

where the standard error $s_{\beta_1^{\mathrm{BOR}} - \beta_1^{\mathrm{TEM}}}$ is given by

$$s_{\beta_1^{\mathrm{BOR}} - \beta_1^{\mathrm{TEM}}} = \sqrt{\frac{\left(s_{Y\cdot X}^2\right)_p}{\left(n^{\mathrm{BOR}} - 1\right)s_{X^{\mathrm{BOR}}}^2} + \frac{\left(s_{Y\cdot X}^2\right)_p}{\left(n^{\mathrm{TEM}} - 1\right)s_{X^{\mathrm{TEM}}}^2}}, \tag{8}$$

where the n_{BOR} and the n_{TEM} are the sample sizes. The error variance was assumed to be of equal size in both populations. The $\left(s_{Y\cdot X}^2\right)_p$ is the so-called pooled variance estimator and is given by

$$\left(s_{Y\cdot X}^2\right)_p = \frac{SS_{\mathrm{RESIDUAL}}^{\mathrm{BOR}} + SS_{\mathrm{RESIDUAL}}^{\mathrm{TEM}}}{\left(n^{\mathrm{BOR}} - 2\right) + \left(n^{\mathrm{TEM}} - 2\right)} \tag{9}$$

The $SS_{\mathrm{RESIDUAL}}^{j}$ follows:

$$SS_{\mathrm{RESIDUAL}}^{j} = \left[\sum\left(n^j - 1\right)s_X^2(j)\right] - \frac{\left[\sum\left(n^j - 1\right)s_{XY}(j)\right]^2}{\sum\left(n^j - 1\right)s_Y^2(j)}. \tag{10}$$

The $\left(n^j - 1\right)s_X^2(j)$, $\left(n^j - 1\right)s_Y^2(j)$ and $\left(n^j - 1\right)s_{XY}(j)$ were calculated from

$$\left(n^j - 1\right)s_X^2(j) = \sum_{i=1}^{n} x_i^2 - \frac{\left(\sum_{i=1}^{n} x_i\right)^2}{n}, \tag{11}$$

$$\left(n^j - 1\right)s_Y^2(j) = \sum_{i=1}^{n} y_i^2 - \frac{\left(\sum_{i=1}^{n} y_i\right)^2}{n} \tag{12}$$

and

$$\left(n^j - 1\right)s_{XY}(j) = \sum_{i=1}^{n} x_i y_i - \frac{\left(\sum_{i=1}^{n} x_i\right)\left(\sum_{i=1}^{n} y_i\right)}{n}, \tag{13}$$

respectively.

If the error variance is normally distributed and the errors of different values of the explanatory variable are independent, the test statistic follows the *t*-distribution with $n_{\mathrm{BOR}} + n_{\mathrm{TEM}} - 4$ degrees of freedom.

References

Ahti T, Hämet-Ahti L, Jalas J (1968) Vegetation zones and their sections in northwestern Europe. Ann Bot Fenn 5:169–211

Burger H (1937) Holz, Blattmenge und Zuwachs: Nadelmenge und Zuwachs bei Föhren und Fichten verschiedener Herkunft. Mitteilungen der Schweizerischen Anstalt für das Forstliche Versuchswesen 20:101–114

Burger H (1953) Holz, Blattmenge und Zuwachs: Fichten im gleichalterigen Hochwald. Mitteilungen der Schweizerischen Anstalt für das Forstliche Versuchswesen 29:38–130

Dietrich H (1968) Untersuchungen zur Nährstoffdynamik eines Fichtenbestandes. Archiv für Forstwesen 17:391–412

Do-Hyung L (2001) Relationship between above- and belowground biomass for Norway spruce (*Picea abies*): estimating root system biomass from breast height diameter. J Korean For Soc 90:338–345

Eamus D, McGuinness K, Burrows W (2000) Review of allometric relationship for estimating woody biomass for Queensland, the Northern Territory and Western Australia. Aust Greenhouse Office, Canberra. In: National Carbon Accounting System Technical Report 5A:1–56

Enquist BJ, Niklas KJ (2001) Invariant scaling relations across tree-dominated communities. Nature 410:655–660

Iyengar S (1991) Much ado about meta-analysis. Change 4:33–40

Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA (2003) National-scale biomass estimators for United States tree species. For Sci 49:12–35

Jenkins JC, Chojnacky DC, Heath LS, Birdsey R (2004) Comprehensive database of diameter-based biomass regressions for North American tree species. United States Department of Agriculture, Forest Service, General Technical Report NE-319:1–45

Keith H, Barrett D, Keenan R (2000) Review of allometric relationship for estimating woody biomass for New South Wales, the Australian Capital Territory, Victoria, Tasmania and South Australia. In: The Australian Greenhouse Office, Canberra, National Carbon Accounting System Technical Report 5B:1–113

Marklund LG (1987) Biomass functions for Norway spruce (*Picea abies* (L.) Karst.) in Sweden. Sveriges lantbruksuniversitet, Rapporter–Skog 43:1–127

Marklund LG (1988) Biomassafunktioner för tall, gran och björk i Sverige. Sveriges lantbruksuniversitet, Rapporter–Skog 45:1–73

Näslund M (1937) Skogsförsöksanstaltens gallringsförsök i tallskog. Meddelanden från Statens Skogsförsökanstalt 29:1–169

Pastor J, Aber JD, Melillo JM (1983/1984) Biomass prediction using generalized allometric regressions for some northeast tree species. For Ecol Manage 7:265–274

Peña D (1997) Combining information in statistical modeling. Am Stat 51:326–332

Ranta E, Rita H, Kouki J (1999) Biometria. Helsinki University Press, Helsinki

Schmitt MDC, Grigal DF (1981) Generalized biomass estimation equation for *Betula papyrifera* Marsh. Can J For Res 11:837–840

Snee RD (1977) Validation of regression models: methods and examples. Technometrics 19:415–428

Snowdon P, Eamus D, Gibbons P, Khanna P, Keith H, Raison J, Kirschbaum M (2000) Synthesis of allometrics, review of root biomass and design of future woody biomass sampling strategies. In: The Australian Greenhouse Office, Canberra, National Carbon Accounting System Technical Report 17:1–114

Stone M (1974) Cross-validatory choice and assessment of statistical predictions. J R Stat Soc 36:111–147

Ter-Mikaelian MT, Korzukhin MD (1997) Biomass equations for sixty-five North American tree species. For Ecol Manage 97:1–24

West GB, Brown JH, Enquist BJ (1999) A general model for the structure and allometry of plant vascular systems. Nature 400:664–667

Whittaker RH, Woodwell GM (1968) Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. J Ecol 56:1–25

Wirth C, Schumacher J, Schulze E-D (2004) Generic biomass functions for Norway spruce in central Europe—a meta-analysis approach toward prediction and uncertainty estimation. Tree Physiol 24:121–139

Vinš B, Šika A (1981) Biomasa smrkového porostu v chlumní oblasti. Práce VÚLHM 59:83–99

Vyskot M (1990) Aboveground biomass of adult Norway spruce. Acta Sc Nat Brno 24:1–36

Zianis D, Mencuccini M (2003) Aboveground biomass relationship for beech (*Fagus moesiaca* Cz.) trees in Vermio Mountain, Northern Greece, and generalised equations for *Fagus* spp. Ann For Sci 60:439–448

Zianis D, Mencuccini M (2004) On simplifying allometric analyses of forest biomass. For Ecol Manage 187:311–332

Zianis D, Muukkonen P, Mäkipää R, Mencuccini M (2005) Biomass and stem volume equations for tree species in Europe. Silva Fennica Monographs 4, 63 pp