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Generic biomass functions for Common beech (*Fagus sylvatica L.*) in Central Europe – predictions and components of uncertainty

Abstract This study provides a comprehensive set of functions for predicting biomass for Common beech (Fagus sylvatica L.) in Central Europe for all major tree compartments. The equations are based on data of stem, branch, timber, brushwood (wood with diameter below 5 or 7 cm), foliage, root and total above-ground biomass of 443 trees from 13 studies. We used non-linear mixed-effects models to assess the contribution of fixed effects (tree dimensions, site descriptors), random effects (grouping according to studies) and residual variance to the total variance and to obtain realistic estimates of uncertainty of biomass on aggregated level. Candidate models differed in their basic form, the description of the variance, and inclusion of various combinations of additional fixed and random effects and were compared by the AIC criterion. Model performance increased most when accounting for between-study-differences in the variability of biomass predictions. Further, performance increased with the inclusion of age, site index, and altitude as predictor variables. We show that neglecting variance partitioning and the fact that prediction errors of trees are not independent with respect to their predictor variables will lead to a significant underestimation of prediction variance.

Keywords inventory, allometric equation, regression, mixed-effects models, upscaling, covariance, stem, branch, timber, foliage, root, brushwood

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Introduction

The estimation of biomass at the tree-level and the subsequent step of scaling up biomass to the stand and eventually the regional level using forest inventory data is an essential component of monitoring carbon storage in forests (Kauppi et al. 1992, Liski et al. 2006, Nabuurs et al. 2003). Advances in the quality and the efficiency of carbon monitoring will affect decisions on climate politics and energy politics (Raupach et al. 2005). Furthermore, accurate forest carbon stocks are important to validate models (Thurig and Schelhaas 2006, Vanclay and Skovsgaard 1997)

List of Symbols

Symbol	Unit	Description
symbols of tree measure and predictors		
m	kg	biomass
d	cm	diameter at breast height (1.3m)
h	m	tree height
age	yr	tree age
si	m	site index (mean height of trees at age 100 years)
alt	m	altitude (height above sea level)
dh		models with predictors diameter and height only
dhc		models with additional covariates age, si, and alt
statistical symbols		
i		group (study)
j,k		individuals (trees)
y_{ij}		target variable (biomass m)
x_{ij}		vector of predictors. (d,h)
v_{ij}		vector of covariates (age,si,alt)
β		vector of fixed effects
b_i		vector of random effects
c_s		coefficients c_0, c_1, and c_2 of the basic model forms
int		intercept (constant)
ε		residual
σ^2		variance or first coefficient of the variance model
δ		second coefficient of the variance model

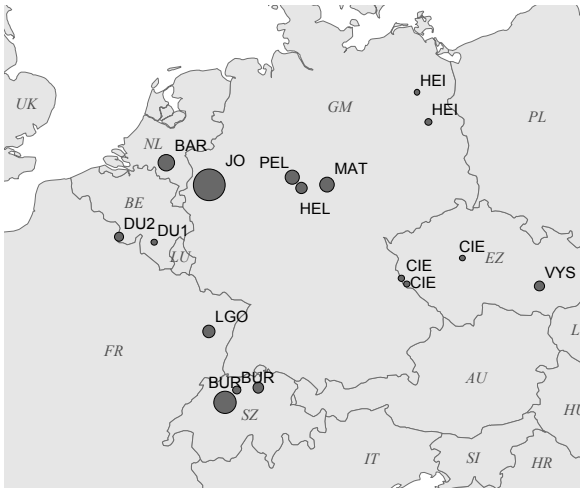

Figure 1: Map showing the location of study sites. The plot labels correspond to the studies listed in Table 1. The size of the symbols increases with the number of trees sampled at the location.

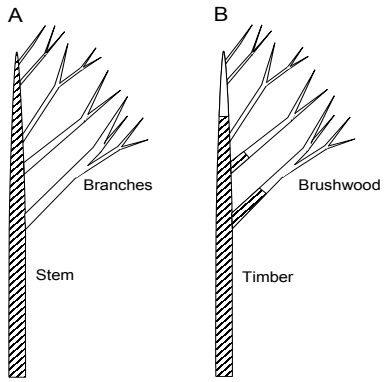

Figure 2: Schemes of different definitions of above ground woody biomass compartments. Scheme A separates between stem and branch wood with the assumption that the main stem can be clearly identified all the way to the top. Scheme B which is less subjective and most commonly applied in forest sciences separates between timber and brushwood based on a fixed diameter threshold (usually 5 or 7 cm).

and for validating spatial extrapolations based on remote sensing (Lu 2006). The basis for the assessment of forest carbon stocks are biomass equations. These equations relate variables that are commonly measured during forest inventories, such as tree diameter at breast height, to dry mass of biomass compartments. They may be applied directly at the tree level, or as a component of biomass expansion factors, which operate on aggregated data at the stand-level (Jalkanen et al. 2005, Wirth et al. 2004a).

There are numerous studies on biomass equations of different species for different regions (Jenkins et al. 2003, Marklund 1987, Zianis et al. 2005) and also several studies for common beech (Table 1) (Hochbichler 2002, Hochbichler et al. 1994, Lebaube et al. 2000, Zianis and Mencuccini 2003, 2005). With the exception of Burger (1949/50) and Joosten et al. (2004) the biomass equations presented in these studies are limited with respect to the number of trees (median 20 trees, minimum 7 and maximum 38 trees), the size range of the sample trees, and the extent of the study area (mostly single stands or catchments). None of these studies is sufficiently representative for a nationwide monitoring of forest carbon stocks and covers a large enough environmental gradients to be applicable to such a large and diverse area as Central Europe. Furthermore, none of the above studies provides the statistical background information to allow a straightforward variance estimation of stand- and regional level biomass (for other species see Phillips et al. 2000, Wirth et al. 2004b). Nor, can this information be provided by meta-analysis-studies that are based on published equations instead of tree measurements (Muukkonen 2007, Zianis and Mencuccini 2003). However, uncertainties of biomass predictions are as important as the predictions themselves (e.g. Raupach et al. 2005). And finally, most studies only report data and equations for a subset of the biomass compartments. Compartments considered usually include the economically relevant above-ground woody compartments (timber, stem), less often branches and leaves and rarely belowground compartments. However, monitoring and modelling changes of carbon stocks requires the estimation of all the biomass compartments.

In our study we compiled available biomass data for Common beech (*Fagus sylvatica* L.) and developed generic biomass equations applicable for a broad range of sites and situations and for all major biomass compartments. In addition, we provide tools for a realistic estimation of uncertainties of biomass predictions that account for the heterogeneity of the underlying data. We used non-linear mixed-effects models in order to make inference on variance components. We outline how functions of biomass and functions of prediction variance were developed and how they can be used to estimate variances and confidence intervals for individual tree predictions as well as for estimates of biomass stocks on aggregated-level, e.g. stands, from forest inventory data. While the aggregation of stand-level predictions and uncertainties to the regional level involves further steps, our generic equations for the wide-spread Common beech – covering 15% of the forest area in Germany – will serve as an important component in an improved national carbon monitoring.

Methods

Data

We collected biomass of tree compartments from sample trees of Common beech originating from 13 studies (Table 1), which cover the extent of Central Europe quite well (Fig. 1). The tree-level entries included biomass *m* of a tree compartment (kg) and as predictor variables the diameter at breast height *d* (cm), the tree height *h* (m), and the

Table 1: Methods used and compartments sampled by 13 studies to determine tree biomass of Common beech.

ID	Study	n_{Treea}	n_{Plot}	Country[b]	Compart-ments[c]	Altitude [m]	Site Index [m]	Vari-ables[d]	Comments
BAR	(Bartelink 1997)	38	6	NL	agr,st,br,l	23	34 - 36	sr,cl,cp	
BUR	(Burger 1949)	91	18	SZ	bw,l	480 - 1360	24.5 - 36	sr	br included thin stem parts and was not considered here
CIE	(Cienciala et al. 2006)	20	4	EZ	agr,st,br	450 - 750	24 - 28	cl,cp	
DU1	(Duvigneaud et al. 1971)	7	1	BE	agr,st,br,t,bw	330	26		reconstructed tree heights
DU2	(Duvigneaud et al. 1977)	13	1	BE	agr,st,br	250 - 250	24	cl	
HEI	(Krauß and Heinsdorf 1996)	14	3	GM	agr,st,br,l	42	28.5 - 30		also quantified bark
HEL	(Heller and Göttsche 1986)	29	3	GM	agr,t,bw,r	500	22.5 - 24	sr	r only for 4 trees
JO	(Joosten et al. 2004)	116	28	GM	agr,t,bw	30 - 500	18 - 45.5		
LGO	(Le Goff et al. 2004)	23	2	FR	agr,st,br,l,r	300	36	sr,cl	r only for a subset
MAS	Masci, A. pers. comm. within project FORCAST (Schulze et al. 2003)	28	1	IT	agr,st,br,l,r	1560	18	sr,cl,cd	r only for a subset
MAT	Matteucci, G. pers. comm. within project FORCAST (Schulze et al. 2003)	30	3	GM	agr,st,br,l	440 - 450	32 - 35		l only for a subset
PEL	(Pellinen 1986)	19	5	GM	agr,t,bw,l,r	420	29 - 30.5	sr	r only for a subset, age uncertain
VYS	(Vyskot 1990)	15	1	EZ	agr,st,br,l,r	505	36	sr,cl,cd,cp	also quantified twigs and stump, provides further data on root
	Total	443	76	7		23 - 1560	18 - 45.5		

[a] n_{Tree} = number of sample trees considered; n_{Plot} = number of plots where trees have been samples;

[b] NL = Netherlands, SZ = Switzerland, EZ = Czech Republik, BE = Belgium, GM = Germany, FR = France, IT = Italy

[c] agr = above ground wood; st = stem including bark; br = branches; t = timber (agr with diameter > 7cm); bw = brushwood (agr with diameter < 7cm); l = leaves, r = roots

[d] in addition to diameter at breast height, tree height, age, site index and altitude: sr = social rank, cl = crown length, cd = crown diameter, cp = crown projection

Table 2: Number of sample trees and range of predictors by tree compartments.

Compartment	nTree	nStudy	Dbh (cm)	Height (m)	Age (yr)	Site Index (m)	Altitude (m)
agr	350	12	1 - 79	2 - 37	8 - 173	18 - 46	23 - 1560
stem	187	9	2 - 79	3 - 37	8 - 165	18 - 36	23 - 1560
branches	175	8	2 - 64	3 - 37	8 - 165	18 - 36	23 - 1560
timber	170	4	1 - 79	2 - 35	18 - 173	18 - 46	30 - 500
brushwood	276	6	1 - 79	2 - 40	14 - 173	18 - 46	30 - 1360
root	48	5	3 - 38	7 - 29	21 - 160	18 - 36	300 - 1560
leaves	247	8	1 - 62	3 - 40	8 - 165	18 - 36	23 - 1560

tree age *age* (yr). Stand-level predictors are the site index *si* (mean height of trees at age 100 years in m) and the altitude *alt* (height above sea level in m).

The biomass compartments considered are foliage (*leaves*), coarse roots (*root*) and above-ground woody biomass (*agr*). Due to the weak apical dominance of Common beech there is a gradual transition between stem and branch wood, which renders the separation into these two compartments ambiguous (Fig. 2). In this study we report functions for both schemes and thus for all four compartments: brushwood, timber, stem, and branches. The number of sample trees and the range of predictor values differed between compartments (Table 2).

Basic model forms

We used three basic model forms as starting points of our model selection. First, the simplest allometric equation for predicting the biomass of a tree compartment *m* is a function of its diameter at breast height *d* (eq. 1). It can be shown that the functional form of a power function arises from the assumption that the ratio of the relative growth rates of mass and diameter (here *m* and *d*) is constant (Wenk et al. 1990). Second, to improve the predictive power this basic allometric equation is often extended to include the tree height *h* as an additional predictor. Eq. 2 still can be viewed as allometric equation that relates biomass to the volume of a cylinder defined by *d* and *h* (Cienciala et al. 2006, Wirth et al. 2004b). Third, a multiple allometric equation for predicting the biomass of a tree compartment as a multiplicative function of *d* and *h* is given by eq. 3 (Widlowski et al. 2003).

[1] $m = c_0 d^{c_1}$ (d2)

[2] $m = c_0 \left(d^2 h\right)^{c_1}$ (dh2)

[3] $m = c_0 d^{c_1} h^{c_2}$ (dh3)

Here m is the biomass of a tree compartment for a sample tree, d is the diameter at breast height (cm), h is the tree height (m), c_s, i.e. $c_0..c_2$, are model coefficients to be estimated. The number at the end of the equation labels (d2, dh2, dh3) indicates the number of parameters.

Rational of using nonlinear mixed-effects models

We used non-linear mixed-effects models (Lindstrom and Bates 1990) to directly fit the candidate models to the data. The main advantage of using mixed-effects models lies in their capability to account for groupings in residual variance due to random effects (Pinheiro and Bates 2000). In our case, the grouping variable is the study from which the data originate. The mere fact that sample trees from one study usually share a common provenance and were collected in the same environment by the same team of scientists with a specific set of methods often causes their residuals to be consistently lower or higher than the mean predictions of a fixed effects model. This violates a fundamental assumption of independent residuals in conventional regression analysis (Crawley 2002), and will lead to an underestimation of variance. Mixed-effect models are one way to adequately address this type of data heterogeneity. Instead of assuming the same fixed effects across all groups (eq. 4a), mixed models allow the coefficients c_s of the model (eq. 1..3) to vary between groups by adding a group dependent random effect (eq. 4b). Additionally, they allow to include covariates that in part explain the deviation from generic coefficient value β_s (eq. 4c).

[4a] $c_s = \beta_s$

[4b] $c_s = \beta_s + b_{s,i}$

[4c] $c_s = \beta_s + b_{s,i} + \beta_{s,age} \cdot age + \beta_{s,si} \cdot si + \beta_{s,alt} \cdot alt + \beta_{s,age.alt} \cdot age \cdot alt + \beta_{s,si.alt} \cdot si \cdot alt$

,where β_s and $\beta_{s,<covar>}$ are fixed effects, $b_{s,i}$ is the study dependent random effect, *age*, site index (*si*), and altitude (*alt*) are covariates.

For a single level of grouping to studies, the tree compartment biomass m_{ij} of the tree j from the i^{th} study can be expressed as the target by a

single level mixed-effects model (eq. 5) (Lindstrom and Bates 1990)

[5] $$m_{ij} = y_{ij} = f\left(x_{ij}, v_{ij}; \beta, b_i\right) + \varepsilon_{ij}$$

$$b_i \sim N(0, \Psi), \text{ and } \varepsilon_{ij} \sim N(0, \sigma^2)$$

where, f is a general, real-valued, differentiable function (one of eq. 1..3, with coefficients expressed as eq. 4c) of a vector of predictors, x_{ij}(*d, h*), a covariate vector v_{ij}(*age, si, alt*), the vector of fixed effects β, and study dependent vector of random effects b_i (Pinheiro and Bates 2000). In this study we used an unconstrained symmetric positive definite covariance matrix Ψ of random effects. We used extended mixed-effects models, where the assumption of the within-group residuals $\varepsilon_i = (\varepsilon_{i1}, \ldots, \varepsilon_{in})$ is relaxed by $\varepsilon_i \sim N(0, \sigma^2 \Lambda_i)$, and where Λ_i are positive-definite matrices parameterized by a set of parameters δ_i. Typically the variance of the residuals ε_j increases with compartment biomass m_j for tree j at the original scale. We thus explicitly modeled the variance of the residuals by a power function (eq. 6).

[6] $$Var(\varepsilon_j) = g\left(\varepsilon_j; \sigma^2, \delta\right) = \sigma^2 \left| m_j \right|^{2\delta}$$

Not only the coefficients but also the residual variance may potentially vary between studies. We accounted for this by modifying the model of residual variance (eq. 6) to eq. 7 by replacing the single exponent δ by the group-dependent exponent δ_i.

[7] $$Var(\varepsilon_{ij}) = g\left(m_{ij}; \sigma^2, \delta_i\right) = \sigma^2 \cdot \left| m_{ij} \right|^{2\delta_i}$$

for the i^{th} study and the j^{th} observation. The parameters σ^2 and δ_i were estimated by iteratively re-weighted sum of squares simultaneously with the other coefficients in the model fitting algorithm.

We used non-linear models (Lindstrom and Bates 1990) for the following reasons. For model fitting the biometric data are often log-transformed to linearize the allometric equation and to homogenize the variance, which otherwise increases with size on the original scale (Baskerville 1972). However, the back-transformation of the predicted value to the original scale introduces biases in the expected values and the uncertainties (Smith 1993). The proper dealing with these biases introduces new assumptions and the simple nonparametric correction using the smearing estimate (Duan 1983, Taylor 1986), as it is frequently employed (e.g. Joosten et al. 2004), is not directly applicable if mixed-effects models are used (Wirth et al. 2004b). In addition, the logarithmic form does not allow to include the covariances between predictions errors at the original scale when calculating the variance of a biomass prediction errors for several trees (eq. A2.1). In Appendix A2 we show how the variance of new predictions can be propagated to aggregated levels.

Fixed effects models partition the variance around the mean prediction into the variance arising from uncertainty in the parameter estimates and into residual variance. In mixed-effects models a further component is added: the variance that is induced by the random effects, which represents groupings in the data (eq. A1.2)

In our case the random effect accounts for all implicit differences between sites, provenances and methods etc. associated with the sample material and sites of different studies that are not represented by any specific predictors. Besides the grouping of variances according to studies there is potentially also a grouping according to stands. In addition to the presented results we tried to fit two-level mixed models to account for this additional grouping level. However, the highly unbalanced design of the data, i.e. several studies include only one stand, and the differences in variances of random effects between the studies caused problems in the numerical algorithm to fit the two-level mixed model and we concluded that the available data was not sufficient to account for groupings at both the stand- and the study-level at the same time. Diagnostic graphs of stand level random effects and study level random effects showed that groupings according to studies were much more pronounced than groupings according to stands. In the presented approach the stand-level differences are partly accounted for by the study random effect. This approach can be seen as a pooling of the comparatively similar stands of each study in order to obtain enough within-group cases.

It shall be noted that the equations for the different compartments are based on different subsets of the whole dataset. Hence, we separately fitted the models for the different biomass compartments and the derived biomass equations are not additive (Lambert et al. 2005, Parresol 2001).

Definition of the candidate model set

In order to find an appropriate model, we compared 246 models for each biomass compartment by the Akaike information criterion (AIC) (Akaike 1987). Figure 3 summarizes the

- d2,dh2,dh3: basic model forms (eqs. 1..3)
- ran: inclusion of study random effects in model coefficients ($b_s = b_{s,\text{int}} + b_{s,i}$)
- c: inclusion of covariates in model coefficients (eq. 4)
- ranres: inclusion of a study effect in the residual model (eq. 7 instead of eq. 6)

Figure 3 Dimensions of the candidate model set.

different dimension of constructing the candidate model set.

First, we tested which coefficients (c_s) differed randomly by study. We fitted the models (eqs. 1..3) with all 8 combinations of random effects (either eq. 4a or eq. 4b) for the model coefficients and compared model performance by AIC. The non-linear fixed or mixed-effects model after this step is called the 'best dh-model'. In some cases with random effects in three or two coefficients the model fitting algorithm did not converge. We excluded these cases from the candidate model set.

Second, we included covariates in the model coefficients (eq. 4c). To reduce the number of possible combinations and to avoid overly complex models we constructed our candidate models according to the following three rules: (1) Higher-order polynomial terms for any of the covariates were avoided because such models are difficult to extrapolate. (2) A covariate effect was added to a coefficient c_s only if the same covariate effect was not already associated with another coefficient. This was done because including covariates on correlated coefficients caused unrealistically high counteracting effects (e.g. c_0 strongly increases with age while c_2 decreases with age). (3) Covariates were added to either c_1 or c_2 , in the dh3 model form (eq. 3) because diameter and height were highly correlated and the AIC hardly changed when the covariate was included in either one of the two coefficients. If the dh-model with random effects in c_0 and c_2 resulted in a better AIC than the dh-model with random effects in c_0 and c_1, we selected c_2 else c_1. In total, this led to 41 combinations of the terms in eq. 4 across the three coefficients. Finally, the resulting best model, which included the random effects from the first step, was compared to the models with covariates but with fewer random effects. We call the resulting best model after this step the 'best dhc-model'.

Third, we assessed if including a study dependent formulation of the residual variance increased model performance by replacing eq. 6 by eq. 7.

The model fitting was done using the nlme and the gnls functions using a general positive-definite variance-covariance matrix using Maximum Likelihood (ML) method for model selection. The resulting best models were refitted using the REML method to improve estimates for the variance components. We used R-nlme library version 3.1-66 (Pinheiro and Bates 2000).

Calculation of Confidence intervals

We computed symmetrical 95% confidence intervals around single tree biomass predictions with width $w_{cf95} = 2 \cdot 1.96 \cdot \sqrt{Var(m_{new})}$. The variances of the predictions were computed by eq. A1.2 and the residual variance component $Var(\varepsilon_{new})$ was determined by eq. A1.5. A numerical example for the tree-level calculation is given in Appendix A3.

At aggregated level the 95% confidence intervals around the biomass predictions were calculated with the same equation as for the tree level. However, the variance of the prediction error of the sum of the biomass of several trees has to include covariances between the single tree-level predictions errors (eq. A2.1 and eq. A2.3). The covariance between predictions errors of two trees explicitly depends on the predictors and covariates of the two trees (eq. A2.2). All calculations were programmed with the statistical software R[1]. The calculation of variance at the stand level was exemplified[2] using data of an inventory of a chronosequence of shelterwood beech forests in Thuringia, Germany (Mund 2004)[3].

Cross validation and comparison to previously published biomass functions

The validity of the presented model and its performance in comparison to published studies is demonstrated using cross validation (Davison and Hinkley 1997). This was done by comparing the predictive performance of a range of published

[1] www.r-project.org. The programmed R-model objects, including variance-covariance matrices, derivative functions, and additional functions to apply prediction and uncertainty calculation at tree and stand level are provided as supplementary material S5

[2] R-code is provided with electronic supplementary material S6.

[3] Details of the inventory are provided with electronic supplementary material S1.

functions with the results of the cross-validation of our generic functions. In the cross validation the observations that were used for validation were not used to fit the model, i.e. the biomass of a tree from a given study was predicted with our generic model, but the parameterization of the respective model was based only on the data of all other published studies. For each model we calculated the root mean squared error (RMSE) with the modification of applying a weighted mean. The weights were the inverse of the square root of the expected variance according to eq. A1.5.

Results

Comparison of the models without additional covariates

The three-parameter model dh3 (eq. 3) fitted the data best for most compartments (see Table 3 for the example of stem biomass[4]). Only for the stem and timber biomass, the dh2-model (eq. 2) and for the root biomass the d2-model (eq. 1) showed similar or better performance. In all cases, the inclusion of parameters that allow the variance to differ between studies (eq. 7) resulted in the largest improvement of model performance. In comparison, the mere inclusion of random components into the model coefficients improved the model performance only slightly for the compartments stem, branches, roots, and leaves. However, it did not improve the model performance at all for the compartments above-ground wood and timber. The coefficients of the best dh-models are listed in Table 4.

Table 3: Comparison of the model forms and inclusion of random components by AIC for stem.

Kind of Model	AIC	degrees of freedom
dh3_c_ran_ranres	1507.3	17
dh2_c_ranres	1509.0	16
dh2_ran_ranres	1512.8	15
dh3_ranres	1538.3	13
dh3_c_ran	1567.2	9
dh3_ran	1571.3	8
dh2_c	1596.5	7
dh2	1623.6	4

dh3,dh2,d2: basic model forms (equations 2..4), c: covariates included, [c] ran: random effects included, ranres: model of residuals includes study dependence. results of the other compartments are given in electronic supplement S2 (Fig. 3)

[4] For other compartments see electronic supplementary material S2

Effect of additional covariates

The inclusion of the additional covariates age, site index, or altitude improved the model performance in all cases (see Table 3 for the example of stem biomass[5]). The highest improvement was achieved for the compartments above ground wood, branches, brushwood, and leaves (Fig 4; compare neighboring graphs). The coefficients of the best dhc-models are listed in Table 5. We will come back to the magnitude and sign of individual coefficients and their interpretation in the Discussion section.

Variance of predictions

The estimated parameters that are needed to calculate the residual variance (eq. A1.5) are listed in Table 6. The standard deviations of the random effects with the dhc-models in Table 6 were smaller compared to the ones of the corresponding dh-models. This indicates that a large part of the variance that was previously accounted for in the random effects component was now accounted for by the covariates.

The 95% confidence intervals of several single tree biomass predictions by the best dh-models (Table 4) and dhc-models (Table 5) are shown in Fig. 4. In all cases, the width of the confidence intervals strongly increased with the size of predicted biomass. This represented the increasing variability in the observed biomass that was modelled with a power model (eq. 6 or 7 respectively). The amount of prediction variance differed considerably between the different compartments. The confidence intervals for above ground wood biomass and timber are comparatively narrow (both have a coefficient of variation cv = 12% for tree age of about 70 years). However, confidence intervals of single tree biomass predictions of branches, root, and leaves are very wide (cv = 59%, 35%, and 49% respectively). The inclusion of additional covariates in the models resulted in narrower confidence intervals in most cases (compare neighbouring graphs in Fig. 4). However, the confidence intervals for branches and leaves were still comparatively wide (cv = 45% and 43%). Inclusion of additional covariates also accounted for a large part of the variance that, before, in the dh-models was attributed to unknown random effects between the studies (see background bars in Fig. 4).

[5] For other compartments see electronic supplementary material S2

The biomass equations were developed at tree level. However many applications make inference at the aggregated level, e.g. stands, by taking the sum of predicted biomass of all trees. At the stand level, the confidence intervals were much narrower (Fig. 5) (cv = 2.5%, 2.9% for above ground wood and timber) compared to the corresponding confidence intervals at the tree

Table 4: Regression coefficients (β_i) and their standard errors in brackets of the best models of diameter and height (dh-models, eq. 1..3, with coefficients as in eq. 4b).

Compartment[a]	Form		β_0	β_1	β_2
agr	dh3	ranres	0.0523 (0.00330)	2.12 (0.0225)	0.655 (0.0394)
stem	dh2	ran_ranres	0.0293 (0.00406)	0.974 (0.0163)	
branches	dh3	ran_ranres	0.123 (0.0296)	3.09 (0.107)	-1.17 (0.175)
timber	dh3	ranres	0.00775 (0.00125)	2.11 (0.0406)	1.21 (0.0841)
brushwood	dh3	ran_ranres	0.466 (0.0862)	1.85 (0.100)	-0.349 (0.150)
root	d2	ran_ranres	0.0282 (0.00263)	2.39 (0.0467)	
leaves	dh3	ran_ranres	0.0377 (0.00686)	2.43 (0.0817)	-0.913 (0.120)

[a] This table is also available with electronic supplementary S2. Empty cells denote the term to be not included

Table 5: Regression coefficients and their standard errors for the models that include additional covariates (dhc-models, eq. 1..3, with coefficients as in eq. 4c).

Compartment	agr	stem	branches	timber	brushwood	root	leaves
Form	dh3 ran_ranres	dh3 ran_ranres	dh3 ran_ranres	dh2 ran_ranres	dh3 ranres	d2 ranres	dh3 ranres
β_0	0.0551 (0.00463)	0.00351 (0.00704)	0.122 (0.0294)	0.0106 (9.43E-04)	0.805 (0.159)	0.0292 (0.00225)	0.0561 (0.00882)
β_1	2.11 (0.0242)	1.84 (0.0333)	3.09 (0.106)	1.08 (0.00795)	1.83 (0.113)	1.70 (0.0792)	2.07 (0.0770)
β_2	0.589 (0.0427)	1.04 (0.0548)	-0.151 (0.304)		-0.560 (0.149)		-1.09 (0.112)
$\beta_{s,age}$	s=2: 4.06E-04 (1.07E-04)	s=0: 3.47E-05 (2.43E-05)			s=1: 0.00134 (3.03E-04)	s=0: 4.36E-05 (1.65E-05)	
$\beta_{s,si}$	s=0: 2.39E-04 (8.15E-05)	s=0: 6.72E-04 (2.38E-04)	s=2: -0.0309 (0.00783)			s=1: 0.0209 (0.00387)	s=1: 0.0137 (0.00192)
$\beta_{s,alt}$	s=0:-4.68E-06 (1.39E-06)	s=0: 8.11E-06 (2.77E-06)	s=2:-9.87E-04 (2.58E-04)	s=0:-1.54E-06 (5.84E-07)	s=1:-1.68E-04 (5.26E-05)	s=1: 7.43E-04 (1.72E-04)	s=0: -3.29E-06 (3.62E-06)
$\beta_{s,si.alt}$			s=2: 3.06E-05 (1.08E-05)			s=1:-2.70E-05 (8.55E-06)	

[a,] see Table 4, see appendix A3 for an example of constructing the full equation.

Table 6: Uncertainty coefficients of the best models.

	Compartment[a]	Form	σ^2 [b]	$Mean(\delta_i)$ [c]	$Var(\delta_i)$	$sd(b_{0,i})$ [d]	$sd(b_{1,i})$	$sd(b_{2,i})$
dh-models	agr	dh3	0.166	0.770	0.00965			
	stem	dh2	0.0708	0.873	0.0177	3.47E-07	0.0176	
	branches	dh3	0.249	0.863	0.0274			0.132
	timber	dh3	1.29	0.614	0.0104			
	brushwood	dh3	0.149	0.979	0.00448		0.0811	
	root	d2	0.0432	0.902	0.118		0.0660	
	leaves	dh3	0.179	0.854	0.117	0.00882		
dhc-models	agr	dh3	0.142	0.782	0.00912			
	stem	dh3	0.0903	0.842	0.0196	0.00316		
	branches	dh3	0.250	0.860	0.0260			0.0690
	timber	dh2	1.29	0.615	0.00779			
	brushwood	dh3	0.191	0.935	0.00434		0.0661	
	root	d2	0.0410	0.874	0.185			
	leaves	dh3	0.174	0.858	0.121			

[a] seeTable 4; The estimated covariance matrices of the fixed and the random effects are provided with electronic supplementary S4 in csv format, [b] σ: base variance [c] δ_i: power of variance for study i, [d] $sd(b_{s,i})$: estimated standard deviation of the random coefficients

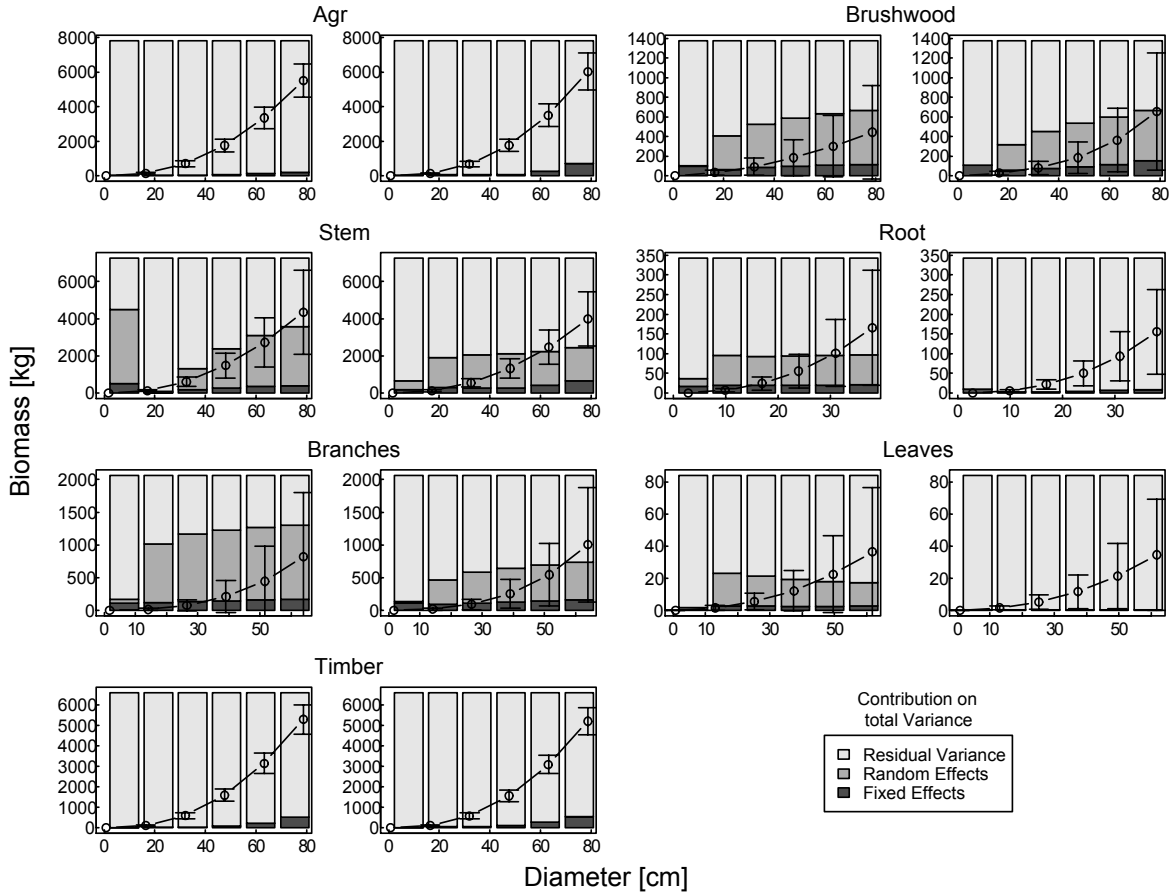

Figure 4 Tree-level predictions and 95% confidence intervals of the best dh-models (left) and dhc-models (right) for each biomass compartment, respectively. The bars in back represent the proportions of the different variance components (residual, random effects and fixed effects variance). The predictors site index and altitude were kept constant (*si* = 30m, *alt* = 470m). The predictors height and age were chosen to be consistent with the site index and the diameter.

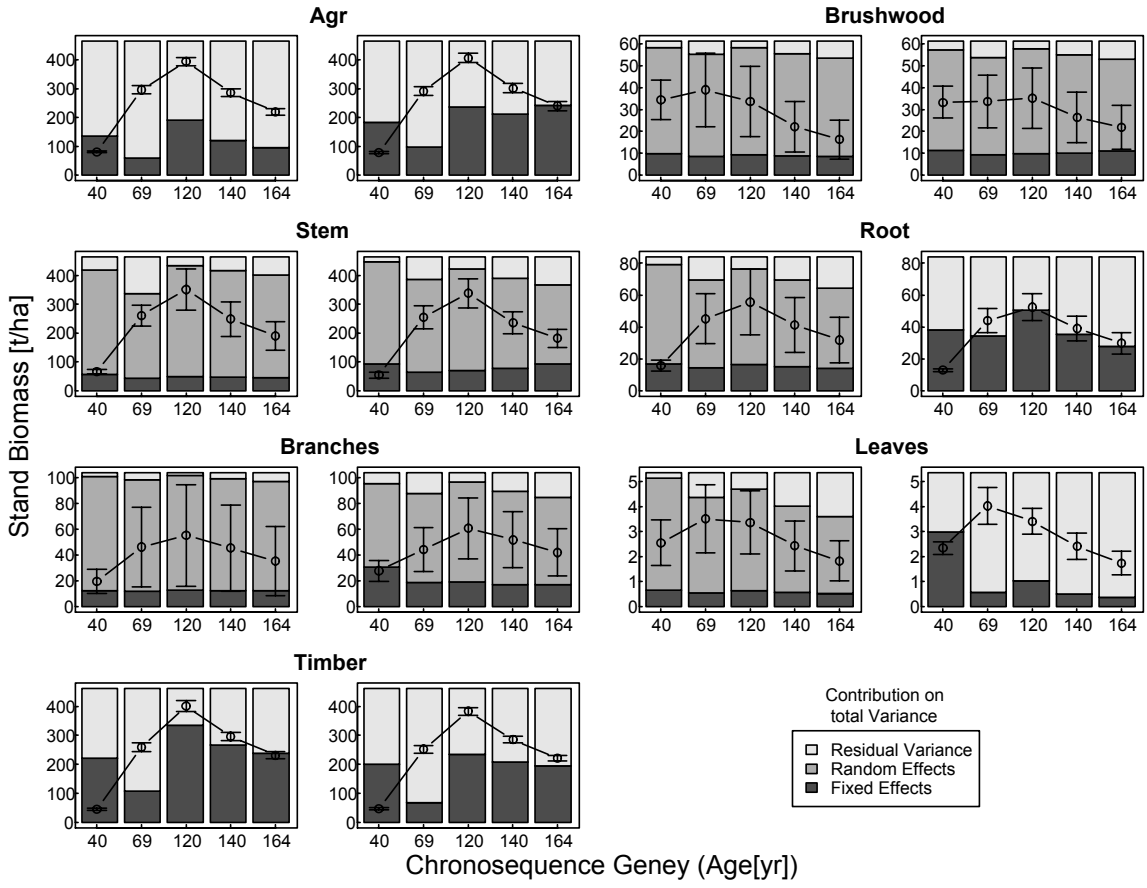

Figure 5: Predictions and 95% confidence intervals of the best dh-models on the left and the best dhc-models on the right for biomass predictions at the stand level for 5 stands of a shelterwood chronosequence. The bars in back represent the proportions of the different variance components as in Fig. 4.

level (Fig.4). The effect of wider confidence intervals for higher biomass predictions was still present, but not as pronounced as with the single tree biomass predictions. The relative contribution of model residuals to total variance was much smaller (background bars in Fig. 5). The decrease in total variance upon inclusion of covariates was much stronger than at the tree-level (cv = 34%→20%, 18%→8%, and 20%→10% for branches, root, and leaves, respectively, at stand age 69 years).

The different model forms are compared exemplarily for stem biomass at tree level in Fig. 6. The predictions were very similar for average covariate values. However, the variability between studies added uncertainty to the biomass prediction. The mixed-effects dh-model accounted for these differences by random effects, which resulted in a wider confidence band. The mixed-effects dhc-model explained these differences in part by additional covariates and the width of the confidence band was smaller than without covariates. The fixed effects model neglected the inter-group variability and underestimated the variance. Hence, the confidence band for the dh-fixed effects model was too narrow. However, this underestimation of variance due to ignoring differences between studies was small compared to ignoring covariances between single tree prediction errors at stand scale (Fig. 7).

Cross Validation

The advantages of generic models of the dh- and dhc-type can be evaluated by comparison with other published beech biomass functions for Central Europe that are based on far smaller data sets. The stem biomass predictions of the cross validation of the dh-models (including only diameter and height as predictors) were very similar to the predictions of the previously published equations by Ciencala et al. (2006) and Bartelink (1997) across the range of sizes (Fig. 8a). For our generic functions, the inclusion of additional covariates in the dhc-model improved the model fit slightly (weighted RMSE decreased from 21 to 18 kg). For foliage biomass, however, the larger dataset and the inclusion of covariates led to a more pronounced improvement of the model fit and a reduction of estimated biomass (Fig. 8b) in comparison to the predictions according to Bartelink (1997) and Le Goff and Ottorini (2001).

Discussion

Our study provides the first comprehensive set of functions for predicting biomass for Common

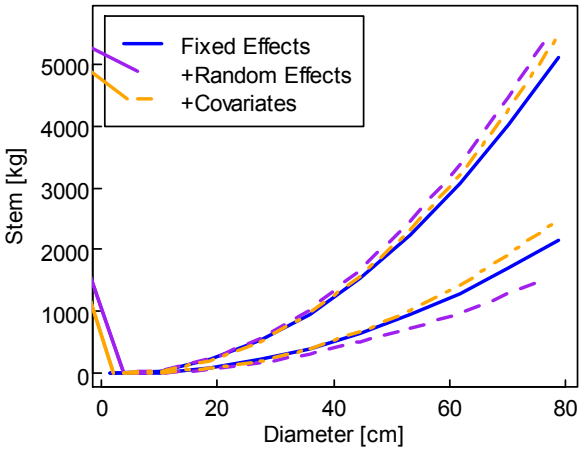

Figure 6: 95% confidence intervals of stem biomass for different forms of modelling variation between groups. Predictors site index and altitude were given intermediate values (*si* = 30m, *alt* = 470m). The predictors age, diameter and height were chosen to represent typical values for these conditions from the dataset of sample trees.

beech in Central Europe for all major tree compartments. Combining original tree biomass data from many sites across Central Europe, which varied in climate and soil characteristics, it was possible to develop generic equations that are representative for the great majority of beech sites in the study region. However, the obvious advantages of combining data from various sources comes at the cost of data heterogeneity, which can only be appropriately dealt with by using non-standard statistical methods (Bates and Watts 1988, Wirth et al. 2004b). We used non-linear mixed-effects models (Pinheiro and Bates 2000) that have been successfully applied in forestry studies for trunk circumference (Lindstrom and Bates 1990), tree height (Calama and Montero 2004, Calegario et al. 2005, Fang and Bailey 2001, Hall and Bailey 2001), stand and bole volume (Fang et al. 2001, Gregoire and Schabenberger 1996, Zhao et al. 2005), yield (Hall

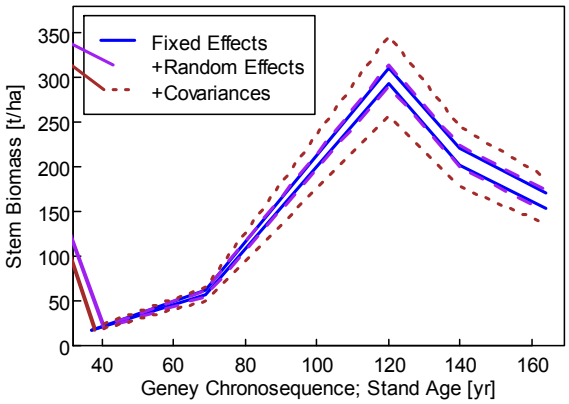

Figure 7 95% confidence bands of stem biomass at stands of the Geney beech forest chronosequence. None of the displayed model results used additional covariates.

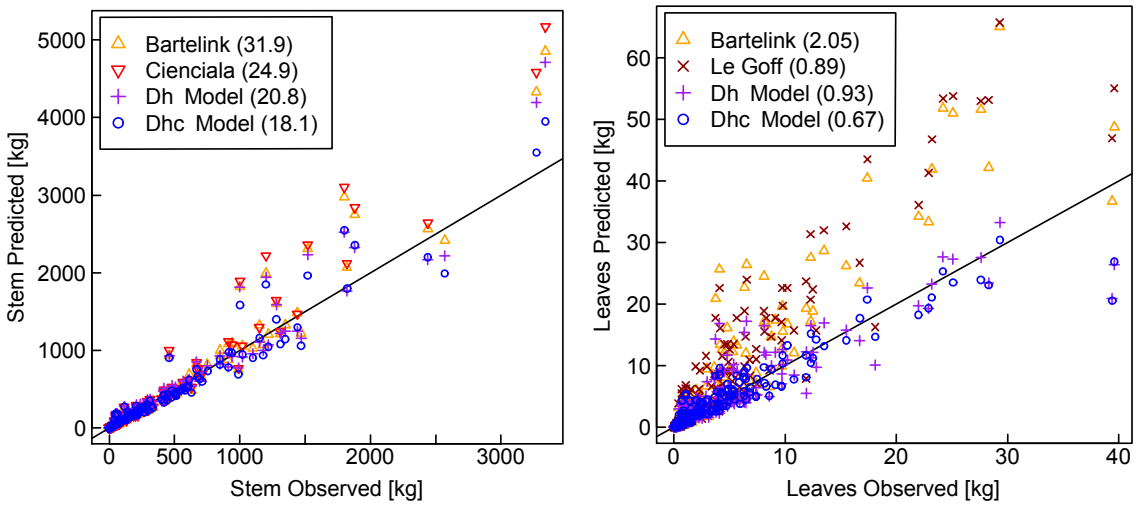

Figure 8 Predictions of the models fitted in the cross validation of a) stem and b) leaves biomass and comparison to previously published biomass functions. $m_{\text{stem}} = 0.0109 \cdot d^{1.951} \cdot h^{1.262}$ (Bartelink 1997) $m_{stem} = 0.014 \cdot d^{2.053} \cdot h^{1.084}$ (Cienciala et al. 2006). $m_{leaves} = 0.0167 \cdot d^{2.951} \cdot h^{-1.101}$ (Bartelink 1997) $m_{leaves} = \exp(-4.8599 + 2.1935 \cdot \ln(d))$ (Le Goff and Ottorini 2001). Values in brackets indicate the variance weighted RMSE.

and Clutter 2004), and biomass (Wirth et al. 2004b). Using non-linear mixed models allowed us to propagate different sources of variance and to analyse the structure of variance when scaling up from tree-level to aggregated level.

Our study illustrates the continuum between **fixed and random effects models.** When we compare models with and without additional covariates (dh and dhc-models), the contribution of the random effects to the total variance was much smaller in the dhc-models than in the dh-models (Figures 4 and 5). The effects of the covariates were formerly accounted for in part by the random effects in the dh-models. This finding corroborates the finding of Fang et al. (2001), where the inclusion of the predictor dominant height accounted for the differences between stands, that were formerly accounted for by random effects. The effect of covariates was less pronounced for the biomass compartments branch, brushwood, and stem biomass (Fig. 4). We hypothesize, that this is in part caused by the subjectivity involved in the separation of the stem and branch compartment and that thus there are inherently large differences between studies that are not due to environmental conditions but unknown differences in sampling protocols of different teams. This is confirmed by the fact that the random effects almost disappear for the sum of the two compartments (above ground woody biomass). In this context it is important to realize that the inclusion of covariates is only possible if – as in our case – data from many stands covering a range of ages and site conditions are pooled.

We generally observed that the random **effect of the variable 'study'** was small for biomass of stem, timber and above ground wood (Tables 4 and 5). This indicates that study-specific effects are relatively small compared to the dominating effect of the predictors diameter and height. Hence, the predictions of stem biomass did not vary much when we compared equations from different studies (Fig. 8a). However, we observed that models accounting for grouping effects in the residual variance performed better (eq. 7, Table 3). This implies that although the mean prediction was similar, the estimated variance of the biomass did vary between studies. The data, which were used in our study, do not allow us to distinguish whether this was an effect of differences in the sampling scheme between the studies, or a real effect of differences in growth variability between the studies. For other tree compartments, the random effects associated with the study were larger. Hence, for a specific new inventory, the biomass predictions will be more strongly biased towards the mean across studies. If a few additional biomass measurements for the new inventory are available it is possible to estimate the specific values of the random effects (e.g. Nothdurft et al. 2006). However, in most applications additional measurements of tree biomass compartments are too expensive. Lappi (1991) provides methods to estimate the values of the random effects of linear mixed-effects models for volume equations by related equations that require only diameter and height measurements. To develop similar related equations for the non-linear tree biomass equations presented here is beyond the scope of this paper and warrants further study.

Applying biomass functions from a single study outside the reference area will inevitable ignore the site influence on biomass allocation patterns (see discussion below) and will also underestimate variance (Fig. 6). This is, because the biomass function does not account for the differences between the studies, neither implicitly by random effects nor explicitly by covariates.

In the statistical analysis we assumed that the **measurement error** of the predictors does not have a profound effect on the estimation of the model coefficients (Table 5). Diameter, height, stand age, and altitude have been measured with high precision at the considered studies. For the covariate site index, which was in some cases estimated by age and height, we performed a Monte Carlo study for the above ground biomass where we varied the site index randomly with a standard deviation of ±1m and re-fitted the best dhc-model. The additional uncertainty introduced in the estimates of the model coefficients ranged only from 3% to 24% of the standard errors in Table 5 for the for coefficients β_1 and $\beta_{0.si}$ respectively. Hence, we conclude that the uncertainty in predictor site index has a sufficiently small effect on the results and does not change our interpretations.

Although certainly not all features of the models can be readily interpreted, some obvious **biologically plausible** patterns emerged that can be related to well-known allocation patterns thus increasing our confidence in the model predictions.

The three parameter model fitted the data of most biomass compartments best (Table 3). The better performance of the dh-models showed that the parameter tree height is an important additional predictor of biomass as observed in other studies for beech (Cienciala et al. 2006, Joosten et al. 2004, Zianis and Mencuccini 2003) as well as in studies of other species (Cienciala et al. 2006, Montagu et al. 2005). However, tree height did not significantly influence root biomass, as indicated by the best performance of the d2 model form (eq. 1). This corresponds to findings for Norway Spruce (Wirth et al. 2004b).

The parameter β_2 associated with the predictor tree height was negative for all crown compartments. This means, that (at a given diameter) higher trees tended to have a lower biomass of crown compartments. We think that this is most likely due to the fact that individuals with a high h/d-ratio tend to be suppressed trees with an elevated allocation to stem growth at the expense of allocation to crown biomass (Nilsson and Albrektson 1993, Vanninen et al. 1996, Wirth et al. 2004b). Negative values of β_2 have also been observed in a similar study on Norway spruce (Wirth et al. 2004b)

At a given diameter and height stem biomass increased with stand age in the best dhc-model. This may be related to a negative correlation between wood density and ring width (Bouriaud et al. 2004). At a given diameter and height older trees have more and thus smaller tree rings. This implies a higher wood density and hence higher biomass. The fact that the best model included also the site index and altitude as covariates with positive coefficients suggests additional environmental modulation of wood density that warrants further investigation.

Biomass equations are usually applied to make inferences at the **aggregated level**. For up-scaling, the sum of the biomass predictions of many single trees, e.g. within one stand, is calculated. When calculating the variance of the sum, prediction errors of the single trees are usually regarded as independent of each other for simplicity sake. Instead, our statistical approach accounts for covariances between prediction errors for several trees. The residuals of different trees are still considered independent. However, biomass predictions based on uncertain model coefficients deviate from the prediction that would result if the true (but unkown) model coefficients were used. The deviations of the predictions have the same direction for similar predictor values and therefore have a positive covariance (for a more formal description see Appendix A2). This issue is independent of using fixed-effects models, single-level random-effects models or multi-level mixed effects models. We showed how much the variance of biomass predictions at the aggregated level is underestimated when covariances between single tree-prediction errors are neglected (Fig. 7). This was already shown by exploring different assumptions about the covariances (Lehtonen et al. 2007, Lehtonen et al. 2004), however we provide the approach to actually quantify the covariances.

Further, we demonstrated that the reduction of variance upon scaling from tree level to aggregated level depends on the **partitioning of variance**. When differences between studies were represented explicitly by additional covariates instead of random effects, the relative contribution of fixed and random effects to total variance on tree level decreased (Fig. 4 background bars). Because of the linear scaling of the residual variance with the number of trees, the coefficient of variation (cv) of the predicted biomass at the stand level decreases with the square root of the number of trees if trees are regarded independent.

However, variance attributed to the uncertainty of fixed and random effects scale in a quadratic manner with the number of trees (Appendix A2), these partitions of variance became much more important at aggregated level. Hence, the decreased contribution of fixed and random variance at tree level with the inclusion of additional covariates led to a large decrease of total variance at aggregated level (Fig. 5 background bars). This finding highlights the importance to factor out variance components at the original, i.e. not log-transformed, scale.

Conclusions

This study presents generic biomass equations of seven biomass compartments for beech trees in Central Europe. A meta-analysis of biomass measurements of 443 trees of 76 sites from 13 studies across Central Europe enabled the assessment of the effect of the covariates age, site index, and altitude on tree biomass. Further, our study illustrates for the first time the importance of separating variance components (residual, fixed, random) in the context of scaling up uncertainties from tree to the aggregated level.

- Leaves and branch biomass prediction varied considerably across Central European studies. Using our large dataset for calibration improved model performance most for these compartments in comparison to previously published functions. Stem and above ground biomass did not vary this much, but still model performance slightly improved.
- In addition to mean predictions, also the variability of tree biomass differed between studies in Central Europe. Biomass functions based on a data set of a single study, did not account for the implicit differences between studies. Hence, using these functions outside the calibration area underestimates the variance of the prediction error for new biomass predictions.
- The covariates age, site index, and altitude modulated the effect of diameter and height. These additional variables accounted for a large part of the differences in biomass predictions between studies, which were otherwise accounted for by the random effects. Hence, the inclusion of these covariates increased model performance for several biomass compartments and reduced prediction variance.
- The predictions errors of trees are correlated, because of uncertain model coefficients. Neglecting these correlations when scaling up biomass to aggregated level underestimates prediction variance significantly. We developed equations and tools to quantify the covariances between single tree prediction errors as well as for up-scaling.

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References

Akaike H (1987) Factor-analysis and AIC. Psychometrika 52:317-332

Bartelink HH (1997) Allometric relationships for biomass and leaf area of beech (Fagus sylvatica L). Annales Des Sciences Forestieres 54:39-50

Baskerville GL (1972) Use of logarithmic regression in the estimation of plant biomass. Canadian Journal of Forestry 2:49-53

Bates DM, Watts DG (1988) Nonlinear regression analysis and its applications. Wiley, New York

Bouriaud O, Breda N, Le Moguedec G, Nepveu G (2004) Modelling variability of wood density in beech as affected by ring age, radial growth and climate. Trees-Structure and Function 18:264-276

Burger H (1949) Holz, Blattmenge und Zuwachs (X): Die Buche. Mitteilungen der Schweizerischen Anstalt für das Forstliche Versuchswesen 26:419-468

Calama R, Montero G (2004) Interregional nonlinear height-diameter model with random coefficients for stone pine in Spain. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 34:150-163

Calegario N, Daniels RE, Maestri R, Neiva R (2005) Modeling dominant height growth based on nonlinear mixed-effects model: a clonal Eucalyptus plantation case study. Forest Ecology and Management 204:11-20

Cienciala E, Cerny M, Tatarinov F, Apltauer J, Exnerova Z (2006) Biomass functions applicable to Scots pine. Trees-Structure and Function 20:483-495

Crawley MJ (2002) Statistical computing - An introduction to data analysis using S-Plus. John Wiley & Sons Ltd., Chichester

Davison AC, Hinkley DV (1997) Bootstrap methods and their application. Cambridge University Press, Cambridge

Duan N (1983) Smearing estimate - a nonparametric retransformation method. Journal of the American Statistical Association 78:605-610

Duvigneaud P, Denaeyer S, Ambroes P, Timperman J (1971) Recherches sur l'ecosysteme foret. Institut royal des sciences naturelles de belgique - Memoires - 164:101

Duvigneaud P, Kestemont P, Timperman J, Moniquet J-C (1977) La hetraie ardennaise a Festuca Altissima a mirwart biomasse et productivite primaire. In: Duvigneaud P, Kestemont P (eds.), Productivite biologique en Belgique, Editions Duculot, Paris-Gembloux, pp 107-154

Fang ZX, Bailey RL (2001) Nonlinear mixed effects modeling for slash pine dominant height growth following

intensive silvicultural treatments. Forest Science 47:287-300

Fang ZX, Bailey RL, Shiver BD (2001) A multivariate simultaneous prediction system for stand growth and yield with fixed and random effects. Forest Science 47:550-562

Gregoire TG, Schabenberger O (1996) Nonlinear mixed-effects modeling of cumulative bole volume with spatially correlated within-tree data. Journal of Agricultural, Biological, and Environmental Statistics 1:107-119

Hall DB, Bailey RL (2001) Modeling and prediction of forest growth variables based on multilevel nonlinear mixed models. Forest Science 47:311-321

Hall DB, Clutter M (2004) Multivariate multilevel nonlinear mixed effects models for timber yield predictions. Biometrics 60:16-24

Heller H, Göttsche D (1986) Biomasse-Messungen an Buche und Fichte. In: H. E (ed.) Ökosystemforschung - Ergebnisse des Solling-Projekts, Eugen Ulmer, Stuttgart, pp 507

Hilborn R, Mangel M (1997) The ecological detective. confronting models with data. Princeton Univesity Press, Princeton, NJ.

Hochbichler E (2002) VorläufigeErgebnissevonBiomasseninventuren in Buchen- und Mittelwaldbeständen. In: Dietrich H-P, Raspe S, Preushlert T (eds.), Inventur von Biomasse- und Nährstoffvorräten in Waldbeständen. Forstliche Forschungsberichte, Heft 186, LWF, München, pp 37-46

Hochbichler E, Putzgruber N, Krapfenbauer A (1994) Biomassen- und Nährstoffuntersuchungen in einem 40 jährigen Buchenbestand (Fagus silvatica L.). Centralblatt für das Gesamte Forstwesen 111:1-22

Jalkanen A, Mäkipää R, Stahl G, Lehtonen A, Petersson H (2005) Estimation of the biomass stock of trees in Sweden: comparison of biomass equations and age-dependent biomass expansion factors. Annals of Forest Science 62:845-851

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

Joosten R, Schumacher J, Wirth C, Schulte A (2004) Evaluating tree carbon predictions for beech (Fagus sylvatica L.) in western Germany. For Ecol Manage 189:87-96

Kauppi PE, Mielikäinen K, Kuusela K (1992) Biomass and carbon budget of European forests, 1971 to 1990. Science 256:70-74

Krauß H-H, Heinsdorf D (1996) Herleitung von Trockenmassen und Nährstoffspeicherung in Buchenbeständen. Forstliche Forschungsanstalt Eberswalde e. V. Abteilung Standort / Umwelt, Eberswalde

Lambert MC, Ung CH, Raulier F (2005) Canadian national tree aboveground biomass equations. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 35:1996-2018

Lappi J (1991) Calibration of height and volume equations with random parameters. Forest Science 37:781-801

Le Goff N, Granier A, Ottorini JM, Peiffer M (2004) Biomass increment and carbon balance of ash (Fraxinus excelsior) trees in an experimental stand in northeastern France. Annals of Forest Science 61:577-588

Le Goff N, Ottorini JM (2001) Root biomass and biomass increment in a beech (Fagus sylvatica L.) stand in North-East France. Annals of Forest Science 58:1-13

Lebaube S, Le Goff N, Ottorini JM, Granier A (2000) Carbon balance and tree growth in a Fagus sylvatica stand. Annals of Forest Science 57:49-61

Lehtonen A, Cienciala E, Tatarinov F, Mäkipää R (2007) Uncertainty estimation of biomass expansion factors for Norway spruce in the Czech Republic. Ann. For. Sci. 64:133-140

Lehtonen A, Mäkipää R, Heikkinen J, Sievänen R, Liski J (2004) Biomass expansion factors (BEFs) for Scots pine, Norway spruce and birch according to stand age for boreal forests. For Ecol Manage 188:211-224

Lindstrom MJ, Bates DM (1990) Nonlinear mixed effects models for repeated measures data. Biometrics 46:673-687

Liski J, Lehtonen A, Palosuo T, Peltoniemi M, Eggers T, Muukkonen P, Mäkipää R (2006) Carbon accumulation in Finland's forests 1922-2004 - an estimate obtained by combination of forest inventory data with modelling of biomass, litter and soil. Annals of Forest Science 63:687-697

Lu DS (2006) The potential and challenge of remote sensing-based biomass estimation. International Journal of Remote Sensing 27:1297-1328

Marklund LG (1987) Biomass functions for Norway spruce (Picea abies (L.) Karst.) in Sweden. Rep. No. 43. Department of Forest Survey - Swedisch University of Agricultural Sciences, Umea

Montagu KD, Duttmer K, Barton CVM, Cowie AL (2005) Developing general allometric relationships for regional estimates of carbon sequestration - an example using Eucalyptus pilularis from seven contrasting sites. For Ecol Manage 204:113-127

Mund M (2004) Carbon pools European beech forests (*Fagus sylvatica*) under different silvicultural management. University Göttingen, Göttingen

Muukkonen P (2007) Generalized allometric volume and biomass equations for some tree species in Europe. European Journal of Forest Research 126:157-166

Nabuurs GJ, Schelhaas MJ, Mohren GMJ, Field CB (2003) Temporal evolution of the European forest sector carbon sink from 1950 to 1999. Global Change Biology 9:152-160

Nilsson U, Albrektson A (1993) Productivity of needles and allocation of growth in young Scots pine trees of different competitive status. Forest Ecology and Management 62:173-187

Nothdurft A, Kublin E, Lappi J (2006) A non-linear hierarchical mixed model to describe tree height growth. European Journal of Forest Research 125:281-289

Parresol BR (2001) Additivity of nonlinear biomass equations. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 31:865-878

Pellinen P (1986) Biomasseuntersuchungen im Kalkbuchenwald. Dissertation. Georg-August-Universität Göttingen, Göttingen

Phillips DL, Brown SL, Schroeder PE, Birdsey RA (2000) Toward error analysis of large-scale forest carbon budgets. Global Ecology and Biogeography 9:305-313

Pinheiro JC, Bates DM (2000) Mixed-Effect Models in S and S-Plus. Springer-Verlag, New York

Raupach MR, Rayner PJ, Barrett DJ, DeFries RS, Heimann M, Ojima DS, Quegan S, Schmullius CC (2005) Model-data synthesis in terrestrial carbon observation: methods, data requirements and data uncertainty specifications. Global Change Biology 11:378-397

Schulze E-D, Zimmermann R, Hofmann Y (2003) ForCast-Projektseite. http://www.bgc-jena.mpg.de/public/carboeur/Forcast/home/index.html.

Smith RJ (1993) Bias in equations used to estimate fossil primate body mass. Journal of Human Evolution 25:31-41

Taylor JMG (1986) The retransformed mean after a fitted power transformation. Journal of the American Statistical Association 81:114-118

Thurig E, Schelhaas MJ (2006) Evaluation of a large-scale forest scenario model in heterogeneous forests: a case study for Switzerland. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 36:671-683

Vanclay JK, Skovsgaard JP (1997) Evaluating forest growth models. Ecological Modelling 98:1-12

Vanninen P, Ylitalo H, Sievanen R, Mäkelä A (1996) Effects of age and site quality on the distribution of biomass in Scots pine (*Pinus sylvestris* L). Trees-Structure and Function 10:231-238

Vyskot M (1990) Juvenile Beech in biomass. In: Academia, Prague, Czech Republic, pp 167

Wenk G, Antanaitis V, Šmelko Š (1990) Waldertragslehre. Deutscher Landwirtschaftsverlag GmbH, Berlin

Widlowski J-L, Verstraete MM, Pinty B, Gobron N (2003) Allometric relationships of selected european tree species. Rep. No. EUR 20855 EN. EC Joint Research Centre, Ispra, Italy

Wirth C, Schulze E-D, Schwalbe G, Tomczyk S, Weber G, Weller E (2004a) Dynamik der Kohlenstoffvorräte in den Wäldern Thüringens- Abschlussbericht zur 1. Phase des BMBF-Projektes "Modelluntersuchung zu Umsetzung des Kyoto-Protokolls". Thüringer Landesanstalt für Jagd, Wald und Fischerei, Jena Gotha

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

Zhao DH, Wilson M, Borders BE (2005) Modeling response curves and testing treatment effects in repeated measures experiments: a multilevel nonlinear mixed-effects model approach. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 35:122-132

Zianis D, Mencuccini M (2003) Aboveground biomass relationships for beech (Fagus moesiaca Cz.) trees in Vermio Mountain, Northern Greece, and generalised equations for Fagus sp. Annals of Forest Science 60:439-448

Zianis D, Mencuccini M (2005) Aboveground net primary productivity of a beech (Fagus moesiaca) forest: a case study of Naousa forest, northern Greece. Tree Physiol 25:713-722

Zianis D, Muukkonen D, Mäkipää R, Mencuccini M (2005) Biomass and stem volume equations for tree species in Europe. METLA, Helsinki, Finland

Appendix A1: Variance of single predictions

The prediction $\hat{y}_{new}$ for a predictor vector x_{new}, covariates ν_{new} and an unknown group was done by applying the model formula to the vector of new predictors assuming zero random effects (expected value) and zero residual term.

In order to estimate the variance of the error of the non-linear prediction, we approximated the non-linear function *f* in equation 1 by its first order Taylor expansion in the parameter space around the estimated parameters $\hat{\beta}$ and $\hat{b}_{new} = 0$ (eq. A1.1) (Gregoire and Schabenberger 1996).

[A1.1] $$f\left(x_{new},\nu_{new};\beta\ ,b_{new}\right) \approx f\left(x_{new},\nu_{new};\hat{\beta},0\right)+u_{new}^{T}\left(\beta-\hat{\beta}\right)+w_{new}^{T}\ \left(b_{new}-0\right)$$

where $u_{new}=\left.\dfrac{\partial f\left(x\ ,\nu\ ;\beta,b\right)}{\partial\beta}\right|_{x_{new},\nu_{new},\hat{\beta},0}$, and $w_{new}=\left.\dfrac{\partial f\left(x\ ,\nu\ ;\beta,b\right)}{\partial b}\right|_{x_{new},\nu_{new},\hat{\beta},0}$ are vectors of partial derivates evaluated at the estimated parameters $\hat{\beta}$, $\hat{b}_{new}=0$, and the values of predictors and covariate for the new observation.

Equation A1.1 describes the prediction that uses the true parameters β, and b_{new} by a prediction that uses the modified parameters $\hat{\beta}$ and $\hat{b}_{new}=0$ plus some deviation depending on the model parameters and the predictors. With this approximation the variance of the error of a non-linear prediction evaluates to eq. A1.2.

$$\begin{aligned}
&Var\left(y_{new}-\hat{y}_{new}\right)\\
&=Var\left(f\left(x_{new},\nu_{new};\beta,b_{new}\right)+\varepsilon_{new}-f\left(x_{new},\nu_{new};\hat{\beta},0\right)\right)\\
&=Var\left(u_{new}^{T}\left(\beta-\hat{\beta}\right)+w_{new}^{T}b_{new}+\varepsilon_{new}\right)\\
&=u_{new}^{T}Var\left(\hat{\beta}\right)u_{new}+w_{new}^{T}Var\left(b_{new}\right)w_{new}+Var\left(\varepsilon_{new}\right)\\
&=u_{new}^{T}Var\left(\hat{\beta}\right)u_{new}+w_{new}^{T}\Psi w_{new}+\sigma^{2}
\end{aligned} \qquad [A1.2]$$

Estimates for the unknown true covariance matrices $Var\left(\hat{\beta}\right)$ and Ψ as well for the residual variance σ^2 are obtained as a by-product of the numerical optimization algorithm used for REML estimation of the unknown parameters. The three terms of eq. A1.2 correspond to three components of variance, first the fixed effects, second the random effects, and third the residual variance.

To account for variance heterogeneity within groups, we modeled the residual variance as a power function of the predicted values (eq. A1.3).

[A1.3] $$Var\left(\varepsilon_{ij}\right)=\sigma^{2}\cdot\left|y_{ij}\right|^{2\delta}$$

If the coefficient δ of the power variance model additionally depended on the particular group ($\delta\rightarrow\delta_i$), the parameter δ_i for a new prediction was unknown because the group of the new prediction was unknown. The best estimate for the new prediction is the mean $\bar{\delta}_i$ of the estimate for parameters δ_i. However, the mean-function appears in a non-linear term and a correction factor has to be applied. The general form of the expected value of a non-linear eq. $y=f\left(x\right)$ obtained by the delta-method is eq. A1.4 (Hilborn and Mangel 1997 p.58).

[A1.4] $$E\left(y\right)=f\left(E\left(x\right)\right)+\frac{1}{2}f''\left(E\left(x\right)\right)\cdot Var\left(x\right)$$

This leads in the case of eq. A1.3 ($f\left(\delta\right)=\sigma^{2}\cdot\left|y\right|^{2\delta}$) to eq. A1.5.

$$\begin{aligned}
\hat{Var}\left(\varepsilon_{new}\right)&=\sigma^{2}\cdot\left|y_{new}\right|^{2\bar{\delta}_i}+2\sigma^{2}\left(\ln\left|y_{new}\right|\right)^{2}\left|y_{new}\right|^{2\bar{\delta}_i}\cdot Var(\hat{\delta}_i)\\
&=\sigma^{2}\cdot\left|y_{new}\right|^{2\bar{\delta}_i}\left(1+2\left(\ln\left|y_{new}\right|\right)^{2}\cdot Var(\hat{\delta}_i)\right)
\end{aligned} \qquad [A1.5]$$

Appendix A2: Variance of the sum of predictions

Many applications of statistical models calculate the sum of several individual predictions that originate from the same group (e.g. sum of biomass of individual trees measured by the same team with the same measurement procedure). The expected value of the sum of *n* predictions is simply the sum of the single expected values, i.e. model predictions. However, the variance of the sum of prediction errors has to account for covariances between the individuals. The variance of the sum of prediction errors is given by eq. A2.1

$$Var\left(\sum_j^n y_j - \sum_j^n \hat{y}_j\right) = Var\left(\sum_j^n \left(y_j - \hat{y}_j\right)\right)$$

$$= \sum_j^n Var\left(y_j - \hat{y}_j\right) + 2\sum_j^n \sum_{k=j+1}^n Cov\left(y_j - \hat{y}_j, y_k - \hat{y}_k\right) \quad \text{[A2.1]}$$

$$= \sum_{j=1}^n \sum_{k=1}^n Cov\left(y_j - \hat{y}_j, y_k - \hat{y}_k\right)$$

where $Cov\left(y_j - \hat{y}_j, y_k - \hat{y}_k\right)$ denotes the covariance between the errors of the individual prediction for the new observations *j* and *k*.

In the following we derive the covariance between two prediction errors for predictions based on model of eq. 5 within the same group *i*. With approximating model eq. 5 by its first order Taylor expansion (eq. A1.1) around $\hat{\beta}$ and $\hat{b}_{new} = 0$ we derive eq. A2.2.

$$Cov\left(y_{new,1} - \hat{y}_{new,1}, y_{new,2} - \hat{y}_{new,2}\right)$$

$$\approx Cov\begin{pmatrix} f\left(x_{new,1}, v_{new,1}, \hat{\beta}, 0\right) + u_{new,1}^T\left(\beta - \hat{\beta}\right) + w_{new,1}^T b_{new} + \varepsilon_{new,1} - f\left(x_{new,1}, v_{new,1}, \hat{\beta}, 0\right) \\ , f\left(x_{new,2}, v_{new,2}, \hat{\beta}, 0\right) + u_{new,2}^T\left(\beta - \hat{\beta}\right) + w_{new,2}^T b_{new} + \varepsilon_{new,2} - f\left(x_{new,2}, v_{new,2}, \hat{\beta}, 0\right) \end{pmatrix}$$

$$= Cov\left(u_{new,1}^T\left(\beta - \hat{\beta}\right) + w_{new,1}^T b_{new} + \varepsilon_{new,1}, u_{new,2}^T\left(\beta - \hat{\beta}\right) + w_{new,2}^T b_{new} + \varepsilon_{new,2}\right) \quad \text{[A2.2]}$$

$$= Cov\left(u_{new,1}^T\left(\beta - \hat{\beta}\right), u_{new,2}^T\left(\beta - \hat{\beta}\right)\right) + Cov\left(w_{new,1}^T b_{new}, w_{new,2}^T b_{new}\right) + Cov\left(\varepsilon_{new,1}, \varepsilon_{new,2}\right)$$

$$= u_{new,1}^T Var\left(\hat{\beta}\right) u_{new,2} + w_{new,1}^T Var\left(b_{new}\right) w_{new,2} + 0$$

$$= u_{new,1}^T Var\left(\hat{\beta}\right) u_{new,2} + w_{new,1}^T \Psi w_{new,2}$$

where $u_{new,1}, u_{new,2}, w_{new,1}$, and $w_{new,2}$ are vectors of partial derivates as explained with eq. A1.1. Estimates for the unknown true covariance matrices $Var\left(\hat{\beta}\right)$ and Ψ are obtained as a by-product of the numerical optimization algorithm.

If the two observations were of different groups, i.e. trees of different regions and measured by different teams, the covariance in prediction errors due to random effect would be zero, i.e. $Cov\left(w_{new,2}^T b_{new,1}, w_{new,2}^T b_{new,2}\right) = 0$.

Now we are ready to calculate and interpret the variance of a sum of prediction errors of model eq. 5. Inserting eq. A2.2 into eq. A2.1 leads to eq. A2.3.

$$Var\left(\sum_j^n \left(y_j - \hat{y}_j\right)\right) = \sum_j^n \sum_k^n \left(u_j^T Var\left(\hat{\beta}\right) u_k + w_j^T \Psi w_k\right) + \sum_j^n Var\left(\varepsilon_j\right) \quad \text{[A2.3]}$$

Similar to the variance of single predictions (eq. A1.2), eq. A2.3 is composed of the three terms of the components of variance (fixed, random, and residuals). However, the residual variance occurs in a simple sum over all individuals, whereas the fixed and random terms occur within a sum of sums. Hence the residual variance increases linearly with the number of individuals, whereas the random and fixed components of variance increase quadratically with the number of individuals.

The covariance terms in eq. A2.3 can be negative. Hence, they potentially cancel out each other. However, individuals of the same group often have similar predictor values and have positive covariances.

Appendix A3: Application example

In the following example, we demonstrate how to use the presented models and equations to calculate a new prediction for stem biomass and its confidence interval for a single tree with diameter (d = 18.8 cm), height (h =16.9 m) age (age = 40 years), site index (si = 30 m), and altitude (alt = 470 m). Consequently, we choose the dhc-model, because all the additional covariates are known. The label dh3 in table 5 indicates that the basic model form is $m_{new} = c_0 d^{c_1} h^{c_2}$ (eq. 3). Site index, age, and altitude affect the coefficient c_0, and table 6 indicates that the model includes also random effect in c_0: $c_0 = \beta_0 + b_{0,i} + \beta_{0,age} \cdot age + \beta_{0,si} \cdot si + \beta_{0,alt} \cdot alt$ (eq. 4c). The other coefficients do neither include covariates nor a random effect. Hence the full equation of above ground biomass for tree j is given by eq. A3.1.

$$[A3.1]\quad m_{New} = f(d,h,age,si,alt,b) = (\beta_0 + b_{0,i} + \beta_{0,age} \cdot age + \beta_{0,si} \cdot si + \beta_{0,alt} \cdot alt) d^{(\beta_1)} h^{(\beta_2)}$$

Hence, with setting the random effect $b_{0,i}$ to its expected value 0 for a general prediction, the stem biomass computes to (0.00351 +0 +3.47E-05*40+6.72E-04*30 +8.11E-06*470) *18.8^1.84 *16.9^1.04 = 121 kg. The variance of the prediction error is estimated according to eq. A1.2 and A1.5 as

$$Var(\hat{m}_{new} - m_{new}) =$$

$$\left[\underbrace{4250.244}_{\frac{\partial f(d,h,age,si,alt,b)}{\partial \beta_0}} \quad \underbrace{127507.3}_{\frac{\partial f}{\partial b_{0,si}}} \quad \underbrace{170009.8}_{\frac{\partial f}{\partial \beta_{0,age}}} \quad \underbrace{1997615}_{\frac{\partial f}{\partial \beta_{0,alt}}} \quad \underbrace{360.0897}_{\frac{\partial f}{\partial \beta_1}} \quad \underbrace{347.013}_{\frac{\partial f}{\partial \beta_2}} \right] Var(\hat{\beta}) \begin{bmatrix} 4250.244 \\ 127507.3 \\ 170009.8 \\ 1997615 \\ 360.0897 \\ 347.013 \end{bmatrix}$$

$$+ \left[\underbrace{4250.244}_{\frac{\partial f(d,h,age,si,alt,b)}{\partial b_{0,i}}} \right] \Psi [4250.244]$$

$$+ \underbrace{\overbrace{0.0903}^{\sigma^2} \cdot \left| \overbrace{122.7360}^{\hat{m}_{new}} \right|^{\overbrace{2 \cdot 0.842}^{Mean(\delta)}} \left(1 + 2 \ln^2 \left(\overbrace{122.7360}^{\hat{m}_{new}} \right) \cdot \overbrace{0.0196}^{Var(\delta)} \right)}_{Var(\varepsilon_{new})}$$

$$= 30.3 + 179.9 + 568.6 = 778.9$$

Where f is given by eq. A3.1, $Var(\hat{\beta})$ is the estimated 6x6 covariance matrix the estimated fixed effects, Ψ is the 1x1 random effects covariance matrix[6]. The values of the coefficients of the third term are given in Table 6. A symmetric 95% confidence interval around the prediction is calculated using the quantile of the standard normal distribution as $\pm 1.96 \cdot \sqrt{Var(\hat{m}_{new})}$. This becomes 54.7 kg and the 95% confidence interval ranges from 68 kg to 177 kg.

We provided R-objects[7] of all the best models together with coefficients, gradient functions, the fixed and random effects covariance matrices and functions to calculate the variance of single tree biomass predictions (nlVar). The results of this example are simply obtained with the R-Command: "`nlVar(dhcme.beech$stem, data.frame(dbh=18.8, height=16.9, age=40, si=30, alt=470), pred=TRUE)`".

Similarly, for a group of trees the predicted biomass and the variance of the prediction error are simply obtained with the provided R-function nlCovar[8].

[6] Both matrices are made available with electronic supplementary material S4

[7] Electronic supplementary material S5

[8] An example of calculating biomass and prediction variance at stand level is in electronic suppl. material S6