



Consistent set of additive biomass functions for eight tree species in Germany fit by nonlinear seemingly unrelated regression

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Abstract

• **Key message** Biomass functions are relevant for an easy and quick estimation of tree biomass. Nevertheless, additive biomass functions for different species and different components have not been published for the area of Germany, yet. Now, we present a set of additive biomass functions for estimating component and total mass for eight species and up to nine components.

• **Context** Biomass functions are relevant for an easy and quick estimation of tree biomass, e.g. for carbon budget calculation. Component-specific functions offer even more detail and can be used to answer questions about, e.g., biomass allocation to different components, (nutrient) element stock and flows or the amount and re-distribution of harvested biomass and its consequences.

• **Aims** Since there exists no published additive biomass functions in the context of Germany, we aimed at providing such equations for different species and different components using a comprehensive data set from different sources.

• **Methods** We collected several data sets for eight relevant tree species (Norway spruce, $n = 1150$ trees; Silver fir, $n = 31$; Douglas fir, $n = 161$; Scots pine, $n = 460$; European beech, $n = 918$; Oak, $n = 313$; Sycamore, $n = 28$ and European ash, $n = 37$) in Germany and adjacent countries, homogenised the component information, imputed missing values and applied nonlinear seemingly unrelated regression to eight (for deciduous trees species) respectively nine (for coniferous species) components simultaneously.

• **Results** The collected data set contains trees from 7 cm diameter in breast height to around 80 cm. From this broad data basis, we established two sets of additive biomass functions: a simple model using the predictors diameter in breast height and tree height as well as a more elaborate model using up to six predictors.

• **Conclusion** Finally, we can present additive models for the eight relevant tree species in Germany. Models for Silver fir, European ash and Sycamore are rather limited in their model range due to their input data; the other models are based on a broad range of predictors and are considered to be broadly applicable.

Keywords Biomass allocation · Component mass · Multiple imputation · SUR regression · Norway spruce–Scots pine–Douglas fir–European beech–Oak

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Contributions of the co-authors CV collected, processed and analysed the data and wrote the paper.

GK initiated and supported the work by acquiring funding, assisting data analysis and co-editing of the paper.

CFD assisted in data analysis and co-edited the paper.

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1 Introduction

Information about volume or biomass of trees can easily be derived through allometric equations, as it is done for example for greenhouse gas reporting (IPCC 2003;

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Oehmichen et al. 2011; de Miguel et al. 2014), for analysis of national forest inventories data (e.g. Riedel and Kaendler 2017) and since many decades in ecological studies (e.g. Marklund 1987). Further applications of biomass functions include research on stem increment, gas-exchange, nutrient and energy flow, forest growth and biomass allocation models (see Wirth et al. 2004; Zianis et al. 2005). Newer applications include the estimation of nutrient export, the amount of available wood for bioenergy and tools for controlling sustainability (Pretzsch et al. 2012; Von Wilpert et al. 2015).

Extensive literature on biomass functions exists (e.g. see Ter-Mikaelian and Korzukhin 1997; Zianis et al. 2005), both on total tree or stem biomass (Joosten et al. 2004; Riedel and Kaendler 2017) as well as on component biomass (Pellinen 1986; Marklund 1987; Heinsdorf and Krauß 1990), Cienciala et al. 2005, 2006, 2008, Parresol 2001; Wirth et al. 2004; Muukkonen 2007; Wutzler et al. 2008; Krauß and Heinsdorf 2008; Pretzsch et al. 2012; Skovsgaard and Nord-Larsen 2012; de Miguel et al. 2014; Zhao et al. 2015). A wide variety of methods has been applied, both on the natural or logarithmic scale of the data, i.e. nonlinear or linear regression. These include fixed-effects models (e.g. Joosten et al. 2004; Riedel and Kaendler 2017), random effects models (e.g. Wirth et al. 2004; Wutzler et al. 2008) and generalised allometric equations (e.g. Muukkonen 2007; de Miguel et al. 2014). Most studies applied these methods to each biomass component separately, although a desirable trait of component functions is additivity, i.e. that estimates of the component masses sum up to the estimate of the total mass.

Methods which ensure additivity include simple component summation (separately fitted component functions which are additively linked, while variances are summed up and additionally include the covariances between the components, see Parresol 2001), expansion of total or stem estimates using predefined or modelled factors such as specific gravities and proportions (e.g. Forest Inventory and Analysis component ratio method: FIA-CRM, in Poudel and Temesgen 2015; Zell 2008) or biomass expansion factors (BEF, e.g. Lehtonen et al. 2004), linear and nonlinear seemingly unrelated regression (Parresol 2001), error-in-variable modelling (Dong et al. 2015) and compositional data analysis (Poudel and Temesgen 2015).

Following Dong et al. (2015), these methods can be divided into aggregative and disaggregative approaches. While most of the procedures work on aggregated data, i.e. the methods start from component functions, where total (or subtotal) mass functions are represented by the sum of the components, compositional data analysis builds on disaggregation, splitting total mass into the respective components via estimated proportions.

In a very recent article of Affleck and Diéguez-Aranda (2016), both approaches have been presented

within the maximum-likelihood framework aiming at ‘valid probabilistic models’. By pointing out the additivity property (total mass adds no further information as it is the sum of the components), they argue that in this context the inclusion of total mass leads to invalid probabilistic models and consequently to singularities during estimation. They use the data of and compare results to the aggregative approach of Parresol (2001), showing that they differ only slightly—indeed Parresol achieved slightly smaller standard errors.

To our knowledge, no best method for additive biomass functions has yet emerged, although it could be shown that multivariate methods incorporating intrinsic correlation between components improve on univariate methods (Parresol 2001; Poudel and Temesgen 2015). Comparisons between ‘seemingly unrelated regression’ (SUR) and compositional data analysis (Poudel and Temesgen 2015) or error-in-variable models (Dong et al. 2015) could not show one method being clearly superior to another. Although Poudel and Temesgen (2015) showed that in most of their examples, compositional data analysis led to the lowest RMSE, followed closely by SUR, they did not include the estimation error of the total tree biomass when calculating RMSE for their compositional data models.

The objective of this study is to develop and present a consistent set of additive biomass functions for the most important tree species in Germany, incorporating the correlation between the different components and taking into account the heterogeneity and potential missingness within different components of the different data sources. The ultimate aim of the superior project is to estimate nutrient export during (simulated) harvest to assess sustainability of harvesting operations. Hence, we do not solely focus on statistical aspects, but also provide insights on more practical considerations.

In the following sections, we describe data collection (Section 2.1.1), data harmonisation (Section 2.1.2) and imputation of missing component information (Section 2.1.3). The fitting of component-specific biomass functions is shown in Section 2.2.1, based on which the random effects are estimated and a data adjustment is conducted (Section 2.2.2). Finally, the nonlinear seemingly unrelated regression is described (Section 2.2.3). The results are given in Section 3 also including a comparison to formerly estimated spruce functions (Wirth et al. 2004) and showing the relation between different components. These results are discussed in Section 4, while conclusions are drawn in Section 5.

2 Material and methods

Data preparation and analysis from the raw input data to the final NSUR parameter estimates is described in the following sections and displayed in Fig. 1.

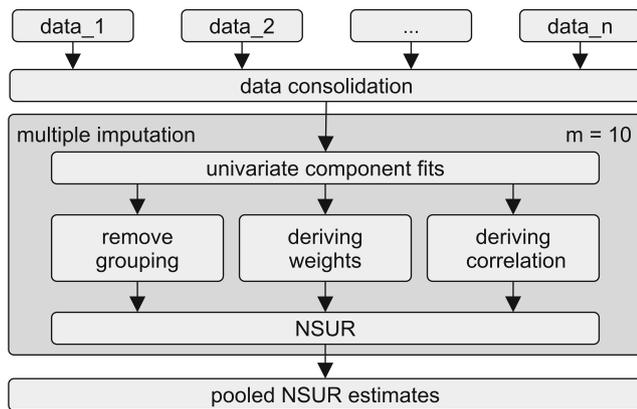


Fig. 1 Flow chart for data preparation and analysis. Different data sources (*data_1* ... *n*) are consolidated, multiply imputed and fitted by univariate and multivariate procedures. Intermediate steps involve removing grouping structure and deriving regression weights and correlations among components. The final results are formed by pooling the NSUR parameter estimates from each of $m = 10$ imputed datasets

2.1 Data preparation

2.1.1 Data acquisition

The goal of our study was to develop broadly applicable, additive component biomass functions, and hence, the aim of data acquisition was to gather data from a broad range of environmental conditions. Data were included if the species were of interest and if the geographic extent was suitable (i.e. ‘central Europe’). We could include 17 studies with data mainly from within Germany, but also from neighbouring countries (see Fig. 2 for spruce and Appendix A for all other species). Studies varied in sample size and intention, and also data from other meta-studies were included (e.g. Wirth et al. 2004; Wutzler et al. 2008). Species include Norway spruce (*Picea abies* (L.) Karst.), Silver fir (*Abies alba* Mill.), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and Scots pine (*Pinus sylvestris* L.) as well as oak (*Quercus robur* L. and *Q. petraea* Liebl.), European beech (*Fagus sylvatica* L.), European ash (*Fraxinus excelsior* L.) and Sycamore (*Acer pseudoplatanus* L.). Although very different component definitions exist, we decided upon a set of additive components commonly recognised in Germany. Firstly, we separated trunk wood and bark. Secondly, coarse wood (i.e. merchantable wood) and bark were split from small wood at 7 cm diameter. For coniferous trees, needles were a separate component. For the final additive biomass models, total aboveground biomass and the summary components ‘trunk including bark’ and ‘coarse wood including bark’ were also included into the models. Abbreviations to these components are given in Table 1. An overview of the collected data is available in Tables 2 and 3.

Norway spruce

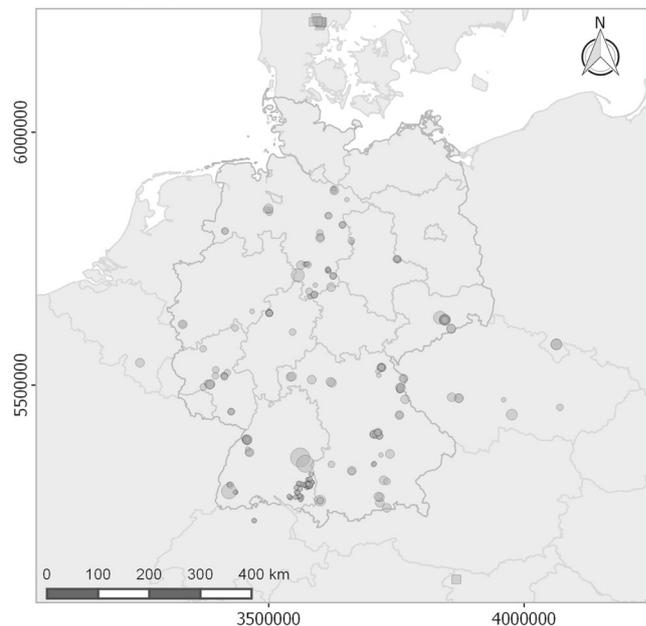


Fig. 2 Geographic distribution of referenced sample data for Norway spruce. The size of the symbols indicate the number of sample trees and scales from 1 to 80. For circles, the sample location is known, whereas squares indicate unknown coordinates which could be approximated by location names

Table 1 Predictor and component abbreviations as used throughout the text

	Abbr.	Description
Predictors	<i>dbh*</i>	Diameter in breast height (1.3 m)
	<i>h*</i>	Tree height
	<i>upd</i>	Upper diameter in 30% of tree height
	<i>a</i>	Tree age
	<i>hsl</i>	Height above sea level
	<i>cl</i>	Crown length
	<i>dh</i>	Product between <i>dbh</i> and <i>h</i>
	<i>sth*</i>	Stump height
Components	<i>stw</i>	Stump wood
	<i>stb</i>	Bark of stump wood
	<i>stwb</i>	Stump wood incl. bark
	<i>cww</i>	Coarse wood (≥ 7 cm in diameter)
	<i>cwb</i>	Bark of coarse wood (≥ 7 cm in diameter)
	<i>cwwb</i>	Coarse wood (≥ 7 cm in diameter) incl. bark
	<i>sw</i>	Small wood (< 7 cm in diameter) incl. bark
	<i>nd</i>	Needles
	<i>agb</i>	Total aboveground biomass

Only asterisk predictors are used in the simple models, while *sth* is only used to model stump components and *cl* only for crown components

Table 2 Summary of acquired and preprocessed data

Species	Data sources	Trees	Components								
			stw	stb	stwb	cww	cwb	cwwb	sw	nd	agb
Norway spruce	8–12, 16	1150	612	610	630	911	910	982	971	1074	976
Silver fir	11, 16	31	28	28	28	31	31	31	31	31	31
Douglas fir	10–12	161	161	161	161	161	161	161	153	153	153
Scots pine	3, 6, 10–13, 16	460	310	310	328	351	351	366	381	431	416
European beech	1, 4, 7, 8, 10–12, 14–17	918	634	634	634	810	810	828	837		903
Oak	2, 5, 10–12	313	253	253	253	253	253	263	263		313
European ash	10	37	37	37	37	37	37	37	37		37
Sycamore	10, 16	28	25	25	25	28	28	28	28		28

For each species and component, the number of observations is given. Only the components finally used are shown, but the intermediate step of imputation and merging is based on the full list of available components. The referenced studies are 1 = Cienciala et al. (2005), 2 = Cienciala et al. (2008), 3 = Cienciala et al. (2006), 4 = Joosten et al. (2004), 5 = Schröder (2014), 6 = Heinsdorf and Krauß (1990), 7 = Krauß and Heinsdorf (2008), 8 = Weis and Göttlein (2012), 9 = Wirth et al. (2004), 10 = Rumpf et al. (2011), 11 = Riedel and Kaendler (2017), 12 = Pretzsch et al. (2012), 13 = data collection of C. Wirth, 14 = Pellinen (1986), 15 = Westermann (2014), 16 = data collection of W. Weis, 17 = Ellenberg et al. (1986). For component definitions see Table 1

2.1.2 Data consolidation

The collected data originate from heterogeneous sources with respect to species, sampling methodology, and component selection and definition (e.g. see Wutzler et al. 2008, for different sampling schemes of deciduous tree species). Consolidation of the different studies with respect to component definitions led to a comprehensive list of different components. For example, some studies sampled their trees by separating into main axis and branches, while others sampled according to a threshold diameter of 7 cm, irrespective of branching. While for most studies, the raw data of the sampling were not available or could not be used to calculate further components beside those already given, this was possible with the data from studies 8, 10, 11, 12 and 17 (see Table 2 for references), which made up most of the trees collected. These studies sampled their data either according to the Randomized Branch

Sampling (RBS) (Saborowski and Gaffrey 1999; Good et al. 2001) procedure or as full main axis measurement with sampled branches. Consequently, we computed the mass of as many components from the comprehensive component list as possible to remove missingness in the original data. These enhanced raw data, including all available component masses, served as base for the subsequently applied imputation.

2.1.3 Multiple imputation

Missing data is often handled by complete-case analysis (e.g. Wirth et al 2004) or single imputation of conditional or unconditional means; these are methods which potentially exhibit bias or do not take into account the uncertainty of the imputation (Rubin 1987). In contrast, multiple imputation, developed by Rubin (1987), has been shown to treat the deficiencies of these methods while the only ‘extra work’

Table 3 Ranges of *dbh*, *h*, *a*, *hsl*, *upd*, *cl* and *agb* based on the raw data of the different species

Species	<i>dbh</i> cm	<i>h</i> m	<i>a</i> years	<i>hsl</i> m	<i>upd</i> cm	<i>cl</i> m	<i>agb</i> kg
Norway spruce	7–81	5–43	15–200	5–1300	7–61	3–29	6–3415
Silver fir	13–84	13–42	25–270	239–1080	11–63	6–22	45–4670
Douglas fir	7–86	10–45	20–100	115–765	6–68	5–24	15–5333
Scots pine	7–70	5–39	14–212	10–1080	7–58	2–18	9–2751
European beech	7–85	8–42	10–200	30–1100	6–63	2–32	10–7803
Oak	8–95	7–38	15–220	40–610	7–79	2–24	14–6517
European ash	9–76	14–38	34–153	270–400	8–60	5–28	33–5824
Sycamore	12–56	15–32	33–185	270–1080	10–42	5–19	50–2162

The predictor *dbh* rarely exceeds 85 cm. For the abbreviations of the predictors, see Table 1

is to perform the analysis ‘*m* times instead of once’ (Little and Rubin 2002, p. 86). This is achieved by producing several complete data sets from draws of a predictive distribution, which are subsequently analysed by the desired methods. The results of these methods are finally *pooled*, e.g. averaged in case of point estimates (see Little and Rubin 2002, for more details).

Missing data methods should be particularly applied when missing data depend on observed variables (confusingly called ‘missing at random’, MAR) or even unobserved, i.e. missing values (‘missing not at random’, MNAR). In contrast, data ‘missing completely at random’ (MCAR) do not lead to biases during estimation. For a more detailed definition, see Little and Rubin (e.g. 2002, p. 11f). At the level of our set of collected data, missingness within each study and components is assumed to be completely at random, but missing components at study level are assumed to be missing by design. This is because at study level it was never intended to record these components. According to Schafer (1997), data missing by design tends to be missing at random and hence should be treated by multiple imputation.

For data preparation and analysis, we used the open source software R (R Core Team 2014). To implement multiple imputation, the *mice*-package (multivariate imputation by chained equations, van Buuren and Groothuis-Oudshoorn 2011) was used. Imputed values were based on dichotomous component ratios instead of absolute component mass to preserve additivity of all components. Because ratios are bounded within the unit interval, the technique of predictive mean matching (pmm) was chosen, being a ‘general purpose semi-parametric imputation method’ (van Buuren and Groothuis-Oudshoorn 2011, p. 18) which draws new values from the observed values only. Actual component mass was computed by multiplying the respective parent component by the imputed ratio. Additionally, missing predictors were also imputed given the other tree characteristics, but *dbh* and *h* were fully observed.

For each tree species, we imputed each missing value ten times ($m = 10$ chains) and used 30 iterations for the default Gibbs-sampler to obtain the multivariate posterior distribution of our data. Convergence was visually assessed by inspecting the development of the chains, densities of the conditional distributions and the distribution of the imputed values.

The result of the imputation is a set of ten complete data sets. Previously missing observations, which made up 0 to 24% (up to 47% in stump components, see further in Table 2 and in Section 3), are now replaced by imputed values, from which the uncertainty of the imputation can be computed at a later stage.

Although the complete set of available components was used during imputation, only the selected set of

components—stated in Table 2—were used during model building. Here, multiple imputation not only served the replacement of missing values but also homogenised studies with different sampling scheme.

The effect of the imputation can be measured by the indicator λ , which gives the proportion of variation attributable to the missing data, i.e. the between-imputation variability divided by the total variability of the parameter estimate. The between-imputation variability is the variance across the m parameter estimates, while the total variability is the sum of the mean of the within-imputation variance (which is usually reported in regression analysis as standard error) and the between-imputation variance. The measure λ is given in the results, jointly with the final parameter estimates and corresponding standard errors.

2.2 Data analysis

The method of seemingly unrelated regression (SUR) was invented by Zellner (1962). Parresol explicitly introduced this methodology for nonlinear forest biomass studies using generalised nonlinear least-squares (GNLS) (Parresol 2001). Technically, the multivariate SUR is a system of stacked univariate equations, allowing for different predictors in each equation (block diagonal design matrix) and correlations among the errors of the different responses. To fit nonlinear SUR (NSUR) models, we used code of the *systemfit*-package (Henningsen and Hamann 2007), extended to allow for regression weights to account for heteroscedasticity. With these extended *systemfit*-package functions (available on request from the first author), we could reproduce the parameter estimates of the data and models, which are exemplarily given in Parresol (2001) to introduce the NSUR methodology.

2.2.1 Component-specific biomass functions

The NSUR system (Eq. 4 in Section 2.2.3) requires prior knowledge on correlation among components and heteroscedasticity of each component. Hence, we fitted component-specific biomass functions to model heteroscedasticity, to estimate the variance-covariance matrix among the errors of different components, but also to specify model equations and to identify significant predictors. These steps were accomplished using the *nlme*-package (Pinheiro and Bates 2000).

For each species and component, we fit an allometric model of the form

$$y = \alpha + \beta_0 x_1^{\beta_1} x_2^{\beta_2} \dots x_n^{\beta_n} \quad (1)$$

to find the best-fitting model given a set of predictors. Evaluation criteria were AIC (Akaike 1974) and visual

inspection of model diagnostics: Q-Q-plots, residual plots and plots comparing fitted and observed values.

Two sets of predictors were considered: firstly, using *dbh* and *h* only (further called ‘simple model’) and, secondly, allowing all significant predictors from the set of *dbh*, *h*, *a*, *hsl*, *upd* and *cl* (henceforth called ‘full model’). Variable *cl* was considered only for crown components (small wood and needles). For models of stump components, we used *sth* instead of *h* as predictor, but included *h* into the full models additionally if necessary. The product of *dbh* and *h*—called *dh*—was tested if the individual predictors were not sufficient.

Initial tests showed that it is reasonable to model residual variance by a power function to account for the heteroscedastic errors ϵ :

$$\text{Var}(\epsilon) = \sigma^2 |v|^\delta \quad (2)$$

where v is a variance covariate and δ is the variance parameter. In all cases, *dbh* was used as variance covariate, while some models required a group-specific modelling of the variance to improve on the normality assumption.

Additionally, to account for the factor ‘study’, random effects were tested for all species with a relevant number of groups and trees (excluding Silver Fir, European Ash and Sycamore). The random effects were assumed to be independent of one another. No correlation of errors was assumed at this stage.

2.2.2 Data adjustment

Previous steps of data preparation aimed at unifying components definition and imputing missing values. Still, as the collected data originated from different sources, it is inherently grouped by the factor ‘study’. The method of choice for such data would be to use mixed effects modelling (Pinheiro and Bates 2000, p. 4ff), as we did when modelling the component-specific biomass functions. But as shown in Affleck and Diéguez-Aranda (2016) and further discussed in Section 4, the use of random effects and summary components within a Maximum Likelihood (ML) setting is mutually exclusive.

To account for the grouping, we adjusted the data by removing the estimated ‘study’-effects caused by differences in methodological and technical aspects of data acquisition. From each observation, we subtracted the amount of the prediction, which is attributed to the random effect:

$$\begin{aligned} y_{\text{adj}} &= y_{\text{obs}} - \hat{y}_{\text{fixed+random}} + \hat{y}_{\text{fixed}} \\ &= y_{\text{obs}} - \underbrace{f(\mathbf{A}\boldsymbol{\beta} + \mathbf{B}\mathbf{b}, v)}_{\text{fixed+random effects}} + \underbrace{f(\mathbf{A}\boldsymbol{\beta}, v)}_{\text{fixed effects}} \end{aligned} \quad (3)$$

The resulting data, y_{adj} , can be considered to contain only the fixed effects of the raw data. We have checked the

difference between the adjusting mixed model on the original data and a structurally identical fixed effect model on the adjusted data by several measures (RMSE = 0.55, MAE = 0.26, BIAS = 0.04, CV = 0.0083, averaged over all models, see Eqs. 5 to 8), and found very small differences only.

2.2.3 Nonlinear seemingly unrelated regression

Seemingly unrelated regression (Zellner 1962) describes a system of regressions, in our case one for each biomass component, whose errors are correlated. Hence, the—in principle independent—regressions become related through their errors’ variance-covariance matrix, making them only ‘seemingly’ unrelated.

Using GNLS, Parresol (2001) showed that in NSUR

$$\begin{aligned} S(\boldsymbol{\beta}) &= \boldsymbol{\epsilon}' \boldsymbol{\Delta}' (\boldsymbol{\Sigma}^{-1} \otimes \mathbf{I}) \boldsymbol{\Delta} \boldsymbol{\epsilon} \\ &= [\mathbf{Y} - \mathbf{f}(\mathbf{X}, \boldsymbol{\beta})]' \boldsymbol{\Delta}' (\boldsymbol{\Sigma}^{-1} \otimes \mathbf{I}) \boldsymbol{\Delta} [\mathbf{Y} - \mathbf{f}(\mathbf{X}, \boldsymbol{\beta})] \end{aligned} \quad (4)$$

minimises the residual sum of squares with respect to the parameter vector $\boldsymbol{\beta}$, where $\boldsymbol{\epsilon}$ are stacked residuals of each equation ($\boldsymbol{\epsilon} = \mathbf{Y} - \mathbf{f}(\mathbf{X}, \boldsymbol{\beta})$), with \mathbf{Y} being y_{adj} from Eq. 3), $\boldsymbol{\Delta}$ is a transformed diagonal weights matrix, $\boldsymbol{\Sigma}$ is the weighted variance-covariance matrix, incorporating the correlation between different components and \mathbf{I} is the unit matrix of dimension n , being the number of observations.

From a theoretical point of view, the advantage of the seemingly unrelated regression is that by using $\boldsymbol{\Sigma}$ a system with correlated errors is transformed into one with uncorrelated errors (Zellner 1962; Rossi et al. 2005), allowing the transformed model to be estimated by Least Squares (LS). In case of heteroscedastic errors, the diagonal matrix $\boldsymbol{\Delta}$ weights each observation, so that more precise observations get more weight during parameter fitting.

The matrix $\boldsymbol{\Delta}$ is the result of an ‘elementwise square root operation on the inverse of the diagonal weights matrix’ ($\boldsymbol{\Delta} = \sqrt{\boldsymbol{\Psi}^{-1}}$, c.f. Parresol 2001, p. 871), which contains the weights of the fitted component functions. Weights for total and subtotal mass were derived by summing the residuals of the respective components and equivalently modelled by the variance functions of Eq. 2.

The variance-covariance matrix $\boldsymbol{\Sigma}$ was estimated according to Parresol (2001) from the weighted residuals of the univariate component models. Again, the total and subtotal component was obtained by analysing the sum of the residuals of the respective components.

The same model equations as in the component models were used in the multivariate NSUR case. Respective component equations were additively linked to form the model equation for the subtotal (stump wood incl. bark and coarse wood incl. bark) and total aboveground mass. If parameters were insignificant within NSUR and subsequent

pooling, they respective predictors were removed from the system of equations, except the scaling parameters and intercepts (if they were necessary for the inclusion of important predictors or proper convergence).

Parameter estimates were obtained by minimising Eq. 4 by means of an optimisation algorithm. Proper convergence was assured by assessing the convergence indicator of the minimisation function (function *nlm* in *stats*-package), graphical output of observed and fitted values and of the residuals.

We averaged the results of the ten imputation runs for all of the imputed data sets to receive the final parameter estimates, significance tests and approximate *p* values according to the pooling rules of Little and Rubin (2002).

2.2.4 Fit statistics

Several fit statistics were calculated for each species and component, subtotal and total mass as the mean of each analysed imputation. These are root mean squared error (*RMSE*, kg), mean error (*BIAS*, kg), mean absolute error (*MAE*, kg) and the coefficient of variation of the RMSE (*CV*, unitless). These quantities were calculated for each imputed data set and subsequently averaged:

$$RMSE = \sqrt{\frac{\sum_{i=1}^n (Y_i - \hat{Y}_i)^2}{n}} \quad (5)$$

$$BIAS = \frac{\sum_{i=1}^n (Y_i - \hat{Y}_i)}{n} \quad (6)$$

$$MAE = \frac{\sum_{i=1}^n |Y_i - \hat{Y}_i|}{n} \quad (7)$$

$$CV = \frac{RMSE}{\bar{Y}} \quad (8)$$

where *n* is the number of observations, *Y_i* is the *i*th observation, \hat{Y}_i is the *i*th fitted value and \bar{Y} is the mean of the observed values.

3 Results

3.1 Additive biomass functions

We included a large number of sample trees for Norway spruce (*n* = 1150), Douglas fir (*n* = 161), Scots pine (*n* = 460), European beech (*n* = 918) and Oak (*n* = 313), while the remaining three species had a more limited number of sample trees (Silver fir: *n* = 31, European ash: *n* = 37 and Sycamore: *n* = 28). Our data collection exhibited missingness besides full observations in variable extend, depending on species and component (see Table 2). Highest missingness occurred in stump components ranging from 10

to 47 %. Missingness was lowest in aboveground biomass (2 to 15 %). Coarse wood components (10 to 24 %) and crown components (5 to 17 %) showed intermediate values.

The overall minimum *dbh* of 7 cm reflects the minimum diameter of merchantable wood in Germany. Maximum *dbh* is at around 80 cm for all species, except for Sycamore with 56 cm and Oak with 95 cm. All but Silver fir, Sycamore and European ash distribute nicely inside a wide range interval for all given variables. For the last three, predictor range and geographical extent are rather limited.

Data adjustment (Section 2.2.2) was conducted for 42 of the 56 univariate mixed effects biomass component models (5 species, 5/6 components, 2 model types). Biggest changes occurred in stump (*n* = 15), bark (*n* = 8) and in crown components (*n* = 9). The adjustment in coarse wood was very small. Notably, Douglas fir exhibited only three adjusted components, all of which were stump components.

The final parameter estimates together with standard error and *p*-value are given in Table 4 for Norway spruce and in Appendix B for all other species. The corresponding equations are given in Tables 5 and 6 for all species. Additionally, in Table 4, the amount of variability due to missingness is indicated by λ . For Norway spruce, λ is high for stump components, as the rate of missingness is high (c. f. Table 2). For the other components, λ often is rather low in the simple models and slightly higher for the full models, especially for crown components. This is because *dbh* and *h* are fully observed and with additional incomplete predictors the variability of the parameter estimates increases.

The variability measured by λ is not only dependent on the predictor and response variables of the respective component, but also on the other components and their predictors and responses because all components are connected through the variance-covariance-matrix of the errors. An example for this behaviour is the Douglas fir data (Table 10 in Appendix B), where missingness exists only in small wood and needle components, but λ is different from zero for all components.

The estimated correlation between different components is high for stem parts and total aboveground biomass as well as for components and their (sub)total aggregates (see Table 7 for Norway spruce, upper triangular matrix). Moderate correlations were found between crown components and between crown and total aboveground biomass. Similar pattern can be seen for all species, with highest correlations between aboveground biomass and total coarse wood. These correlations are accounted for by seemingly unrelated regression. In Appendix C, results for the other tree species are shown.

The full models generally improve over the simple models in terms of *RMSE*, *CV* and *MAE* for all species and components (Tables 5 and 6). *BIAS* is usually small compared to the *RMSE* and \bar{Y} ($=RMSE/CV$), with some

Table 4 Parameter estimates for Norway spruce

Type	comp.	pred	est	se	p	λ
Simple	stw	<i>slope</i>	0.0220	0.0027	0.0000	0.8627
		<i>dbh</i>	2.1212	0.0542	0.0000	0.9587
		<i>sth</i>	0.6056	0.0583	0.0000	0.9816
	stb	<i>intcp</i>	- 0.0128	0.0042	0.0074	0.7055
		<i>slope</i>	0.0067	0.0007	0.0000	0.6419
		<i>dbh</i>	1.7268	0.0550	0.0000	0.9248
	cww	<i>sth</i>	0.5947	0.0676	0.0000	0.9784
		<i>slope</i>	0.0142	0.0005	0.0000	0.4360
		<i>dbh</i>	1.7414	0.0125	0.0000	0.4632
	cwb	<i>h</i>	1.2401	0.0174	0.0000	0.3596
		<i>slope</i>	0.0038	0.0001	0.0000	0.2236
		<i>dbh</i>	1.6076	0.0103	0.0000	0.1058
sw	<i>h</i>	1.0528	0.0181	0.0000	0.1756	
	<i>intcp</i>	1.8472	0.2097	0.0000	0.4647	
	<i>slope</i>	0.0243	0.0028	0.0000	0.3630	
nd	<i>dbh</i>	2.9671	0.0426	0.0000	0.2935	
	<i>h</i>	- 0.8183	0.0446	0.0000	0.1973	
	<i>intcp</i>	- 1.6847	0.2762	0.0000	0.1763	
Full	stw	<i>slope</i>	0.2850	0.0302	0.0000	0.1315
		<i>dbh</i>	2.1173	0.0529	0.0000	0.2751
		<i>h</i>	- 0.8334	0.0419	0.0000	0.2923
		<i>slope</i>	0.0166	0.0021	0.0000	0.8240
	stb	<i>dbh</i>	2.0011	0.0573	0.0000	0.9474
		<i>sth</i>	0.6441	0.0920	0.0001	0.9924
		<i>a</i>	0.1736	0.0141	0.0000	0.4364
		<i>slope</i>	0.0070	0.0008	0.0000	0.7036
	cww	<i>dbh</i>	1.6769	0.0869	0.0000	0.3082
		<i>sth</i>	0.5405	0.0881	0.0002	0.9857
		<i>upd</i>	0.2185	0.0943	0.0227	0.3134
		<i>hsl</i>	- 0.1088	0.0307	0.0064	0.9822
cwb	<i>intcp</i>	- 0.7624	0.2420	0.0042	0.6035	
	<i>slope</i>	0.0123	0.0005	0.0000	0.4899	
	<i>dbh</i>	0.7693	0.0585	0.0000	0.6469	
	<i>h</i>	1.0984	0.0176	0.0000	0.3395	
sw	<i>upd</i>	1.0365	0.0671	0.0000	0.6851	
	<i>a</i>	0.1432	0.0071	0.0000	0.3758	
	<i>slope</i>	0.0034	0.0001	0.0000	0.1299	
	<i>dbh</i>	0.4310	0.0359	0.0000	0.1244	
nd	<i>h</i>	1.0555	0.0134	0.0000	0.0836	
	<i>upd</i>	1.2898	0.0380	0.0000	0.1171	
	<i>slope</i>	0.0439	0.0033	0.0000	0.4533	
	<i>dbh</i>	1.5689	0.1963	0.0000	0.6792	
Full	<i>h</i>	- 0.8835	0.0609	0.0000	0.6452	
	<i>upd</i>	1.0863	0.2274	0.0002	0.7169	
	<i>cl</i>	0.4006	0.0411	0.0000	0.6027	
	<i>intcp</i>	- 1.7874	0.2721	0.0000	0.4703	
Full	<i>slope</i>	0.3045	0.0325	0.0000	0.4905	
	<i>dbh</i>	1.2705	0.1839	0.0000	0.6926	
	<i>h</i>	- 0.8664	0.0443	0.0000	0.4760	

Table 4 (continued)

Type	comp	pred	est	se	p	λ
		<i>upd</i>	0.8402	0.2108	0.0009	0.7121
		<i>a</i>	- 0.1391	0.0166	0.0000	0.2229
		<i>cl</i>	0.3485	0.0374	0.0000	0.6316

Column ‘comp’ refers to the fitted component, column ‘pred’ indicates the associated predictors as well as intercept (*intcp* = α in Eq. 1) and slope parameter (= β_0). Columns ‘est’, ‘se’ and ‘p’ give parameter estimates, standard errors and associated *p* values. λ denotes the increase in variance due to missingness. C.f. Tables 5 and 6

exceptions in stump and crown components. This is more pronounced in deciduous than in conifer species, especially for stump components of European beech and oak. The relative measure *CV* indicates, that *RMSE* is smaller than the mean observation \bar{Y} . Only in one case (simple model of needle component for Scots pine) it reaches a value of 1.00. The components *cww*, *cwb* and *agb* exhibit the smallest values (0.1–0.3), while the more variable stump and crown components tend to reach values between 0.3 and 0.7 (in some cases up to 0.9). The pooled variance parameter δ (see Eq. 2) and the model equations are also included in Tables 5 and 6.

Plotting standardised residuals against the fitted values indicates homoscedasticity and no trend in the residuals (for the full model of Norway spruce see Fig. 3). For bark and stump components (e.g. *stw*, *stb*, *stwb* and *cwwb*), we encountered some deviations from the normality assumption, finding slightly more positive than negative residuals.

The model equations of the simple models rarely changed in the NSUR setting compared to the initial setup from the component-specific functions. Due to their relevance, *dbh* and *h* were usually included into the model. In one case—coarse wood bark of ash—the model was constrained on the product of *dbh* and *h* (= *dh*). In the case of Silver fir, European ash and Sycamore, only *dbh* was used in crown components. Intercepts were necessary in 11 of 44 cases to improve on normality assumptions. Sometimes, estimated values of intercepts were negative, so care has to be taken in applications.

The full models extended the simple models. For all species but Silver fir, *cl* was a significant predictor for the crown components. For all conifer species but Silver fir, *upd* was included for stem and crown components. *Upd* even replaced *dbh* for some species and components.

The predictors *hsl* and *a* were less important and jointly included only four times, with no instance in deciduous species. Also, both predictors could not be linked to specific components or species, besides that Sycamore included neither, and in contrast, Silver fir and Douglas fir functions each included four instances of *hsl* and two of *a*.

Table 5 Summary of the resulting additive biomass functions for coniferous species giving the equation for each species, model type and component, as well as the pooled variance parameter δ and the fit statistics (in kg, unitless for CV)

Species	Type	Comp.	Equation	δ	RMSE	BIAS	MAE	CV	
Norway spruce	Simple	stw	$0.022 \cdot dbh^{2.1212} \cdot sth^{0.6056}$	5.33	7.41	0.28	3.49	0.56	
		stb	$-0.0128 + 0.0067 \cdot dbh^{1.7268} \cdot sth^{0.5947}$	4.46	0.59	0.05	0.28	0.55	
		stwb	stw + stb	5.30	7.81	0.34	3.71	0.55	
		cww	$0.0142 \cdot dbh^{1.7414} \cdot h^{1.2401}$	4.64	60.33	2.81	33.20	0.18	
		cwb	$0.0038 \cdot dbh^{1.6076} \cdot h^{1.0528}$	4.21	6.47	0.19	3.66	0.19	
		cwwb	cww + cwb	4.46	63.78	3.00	35.23	0.17	
		sw	$1.8472 + 0.0243 \cdot dbh^{2.9671} \cdot h^{-0.8183}$	3.96	21.70	0.32	12.03	0.41	
		nd	$-1.6847 + 0.285 \cdot dbh^{2.1173} \cdot h^{-0.8334}$	3.41	10.92	0.41	6.69	0.42	
		agb	Sum of all components	4.41	82.95	4.07	46.70	0.18	
		Full	stw	$0.0166 \cdot dbh^{2.0011} \cdot sth^{0.6441} \cdot a^{0.1736}$	5.32	7.52	0.25	3.49	0.57
	stb		$0.007 \cdot dbh^{1.6769} \cdot sth^{0.5405} \cdot upd^{0.2185} \cdot hsl^{-0.1088}$	4.41	0.58	0.04	0.28	0.54	
	stwb		stw + stb	5.23	7.89	0.30	3.71	0.55	
	cww		$-0.7624 + 0.0123 \cdot dbh^{0.7693} \cdot h^{1.0984} \cdot upd^{1.0365} \cdot a^{0.1432}$	4.70	52.58	0.29	28.10	0.16	
	cwb		$0.0034 \cdot dbh^{0.431} \cdot h^{1.0555} \cdot upd^{1.2898}$	3.99	5.59	0.14	2.92	0.17	
	cwwb		cww + cwb	3.72	54.20	0.43	29.17	0.15	
	sw		$0.0439 \cdot dbh^{1.5689} \cdot h^{-0.8835} \cdot upd^{1.0863} \cdot cl^{0.4006}$	3.57	20.40	0.20	11.37	0.38	
	nd		$-1.7874 + 0.3045 \cdot dbh^{1.2705} \cdot h^{-0.8664} \cdot upd^{0.8402} \cdot a^{-0.1391} \cdot cl^{0.3485}$	3.35	9.36	-0.22	5.63	0.36	
	agb		Sum of all components	3.65	71.07	0.71	40.02	0.15	
	Silver fir		Simple	stw	$0.0121 \cdot dbh^{2.2645} \cdot sth^{0.7596}$	3.30	2.85	0.07	1.82
		stb		$0.0036 \cdot dbh^{2.1225} \cdot sth^{0.7856}$	3.61	0.39	-0.03	0.26	0.13
stwb		stw + stb		3.27	3.39	0.04	2.07	0.16	
cww		$0.0046 \cdot dbh^{1.1917} \cdot h^{2.2103}$		3.24	95.74	17.07	60.48	0.12	
cwb		$0.0019 \cdot dbh^{1.4458} \cdot h^{1.678}$		4.50	19.77	1.76	11.75	0.13	
cwwb		cww + cwb		2.23	118.12	18.83	71.31	0.12	
sw		$0.0273 \cdot dbh^{2.2573}$		5.11	78.24	1.69	44.20	0.47	
nd		$0.1071 \cdot dbh^{1.6952}$		4.11	26.76	-4.20	17.64	0.43	
agb		Sum of all components		2.52	204.65	16.36	86.61	0.17	
Full		stw		$0.0635 \cdot dbh^{2.5304} \cdot sth^{0.8015} \cdot hsl^{-0.4205}$	3.44	2.64	0.07	1.61	0.14
		stb	$0.0091 \cdot dbh^{2.2383} \cdot sth^{0.8168} \cdot hsl^{-0.2111}$	3.88	0.39	-0.00	0.24	0.12	
		stwb	stw + stb	3.43	3.24	0.07	1.83	0.15	
		cww	$0.0542 \cdot dbh^{0.2327} \cdot h^{1.0799} \cdot upd^{1.7805} \cdot a^{0.3421} \cdot hsl^{-0.4926}$	3.98	70.09	1.49	42.17	0.09	
		cwb	$0.005 \cdot h^{0.9923} \cdot upd^{1.851} \cdot a^{0.162} \cdot hsl^{-0.0949}$	4.70	9.70	0.22	5.48	0.07	
		cwwb	cww + cwb	3.90	87.07	1.71	46.59	0.09	
		sw	$0.0254 \cdot dbh^{2.272}$	5.52	78.53	3.55	44.45	0.47	
		nd	$0.1214 \cdot dbh^{1.6556}$	4.11	25.76	-1.68	17.15	0.41	
		agb	Sum of all components	3.85	183.78	3.66	50.87	0.15	
		Douglas fir	Simple	stw	$0.0186 \cdot dbh^{2.185} \cdot sth^{0.7723}$	5.21	8.25	0.06	3.48
stb				$0.0032 \cdot dbh^{2.0357} \cdot sth^{0.7621}$	3.62	0.85	-0.02	0.38	0.51
stwb	stw + stb			5.04	8.69	0.04	3.62	0.40	
cww	$0.0131 \cdot dbh^{1.9299} \cdot h^{1.0715}$			5.77	131.64	3.70	67.46	0.20	
cwb	$0.0018 \cdot dbh^{1.9099} \cdot h^{1.0306}$			4.95	23.04	-2.54	11.74	0.33	
cwwb	cww + cwb			5.16	143.35	1.16	72.78	0.19	
sw	$0.2784 \cdot dbh^{3.1276} \cdot h^{-1.7984}$			3.70	37.67	4.82	21.94	0.52	
nd	$-1.8821 + 0.2749 \cdot dbh^{2.4833} \cdot h^{-1.3051}$			4.39	14.39	2.57	8.47	0.47	
agb	Sum of all components			4.54	190.26	8.58	90.96	0.22	
Full	stw			$0.022 \cdot dbh^{2.1597} \cdot sth^{0.8318}$	5.47	8.44	0.23	3.49	0.43
	stb		$0.0106 \cdot dbh^{1.838} \cdot sth^{0.8417} \cdot h^{0.4136} \cdot hsl^{-0.3138}$	4.87	0.63	-0.03	0.31	0.38	
	stwb		stw + stb	5.20	8.91	0.20	3.64	0.42	

Table 5 (continued)

Species	Type	Comp.	Equation	δ	RMSE	BIAS	MAE	CV
Scots pine	Simple	cww	$0.0084 \cdot dbh^{0.363} \cdot h^{1.1578} \cdot upd^{1.5364} \cdot a^{0.1669}$	5.27	93.45	- 2.87	47.37	0.14
		cwb	$0.002 \cdot h^{1.4131} \cdot upd^{1.7165} \cdot a^{0.1509} \cdot hsl^{-0.1548}$	5.02	15.61	1.35	8.36	0.22
		cwwb	cww + cwb	4.91	97.48	- 1.52	48.61	0.13
		sw	$5.3595 + 0.0446 \cdot h^{-1.6949} \cdot upd^{3.2448} \cdot hsl^{-0.3084} \cdot cl^{1.3312}$	4.34	30.99	2.08	15.93	0.43
		nd	$0.1708 \cdot h^{-1.2492} \cdot upd^{2.5884} \cdot hsl^{-0.2632} \cdot cl^{0.7698}$	4.31	10.97	1.12	6.14	0.36
		agb	Sum of all components	4.35	132.20	1.87	61.15	0.15
		stw	$0.0624 \cdot dbh^{1.9322} \cdot sth^{1.0414}$	4.74	3.18	0.31	1.55	0.34
		stb	$0.0077 \cdot dbh^{1.8127} \cdot sth^{0.8732}$	4.36	0.33	0.01	0.16	0.37
		stwb	stw + stb	4.11	3.35	0.31	1.62	0.33
		cww	$0.0173 \cdot dbh^{2.0072} \cdot h^{0.914}$	4.42	71.22	2.71	36.80	0.20
	Full	cwb	$0.0055 \cdot dbh^{2.0108} \cdot h^{0.5374}$	4.33	8.27	0.00	4.97	0.25
		cwwb	cww + cwb	3.94	74.77	2.72	38.49	0.19
		sw	$0.1316 \cdot dbh^{2.444} \cdot h^{-0.949}$	3.09	21.14	0.45	11.85	0.67
		nd	$0.1484 \cdot dbh^{2.332} \cdot h^{-1.2026}$	3.66	12.31	1.42	4.87	1.00
		agb	Sum of all components	3.90	82.87	4.89	43.04	0.19
		stw	$0.039 \cdot dbh^{1.7956} \cdot sth^{0.9353} \cdot a^{0.1836}$	4.87	2.77	0.06	1.38	0.30
		stb	$0.0078 \cdot dbh^{1.8129} \cdot sth^{0.8788}$	4.36	0.33	0.02	0.16	0.37
		stwb	stw + stb	4.81	2.95	0.08	1.45	0.29
		cww	$0.0159 \cdot dbh^{1.1909} \cdot h^{0.9266} \cdot upd^{0.765} \cdot a^{0.1172} \cdot hsl^{-0.02}$	4.35	55.35	- 3.39	29.95	0.16
		cwb	$0.004 \cdot dbh^{0.8083} \cdot h^{0.7155} \cdot upd^{1.1511} \cdot a^{0.0674}$	4.18	6.87	- 0.03	3.88	0.21
cwwb	cww + cwb	3.99	57.09	- 3.41	30.88	0.15		
sw	$0.2146 \cdot h^{-0.8896} \cdot upd^{2.0322} \cdot cl^{0.6288}$	3.36	20.35	0.06	10.46	0.64		
nd	$0.2135 \cdot h^{-1.4766} \cdot upd^{2.2923} \cdot cl^{0.6001}$	4.06	10.43	0.78	4.34	0.84		
agb	Sum of all components	3.93	62.79	- 2.51	34.86	0.14		

See Table 1 for abbreviations

Table 6 Summary of the resulting additive biomass functions for deciduous species giving the equation for each species, model type and component, as well as the pooled variance parameter δ and the fit statistics (in kg, unitless for CV)

Species	Type	Comp.	Equation	δ	RMSE	BIAS	MAE	CV
European beech	Simple	stw	$0.0315 \cdot dbh^{2.1447} \cdot sth^{0.798}$	5.06	20.04	2.51	6.62	0.83
		stb	$0.004 \cdot dbh^{1.9184} \cdot sth^{0.8076}$	4.39	0.97	0.11	0.29	0.77
		stwb	stw + stb	5.07	20.86	2.62	6.88	0.82
		cww	$- 4.6332 + 0.019 \cdot dbh^{2.0861} \cdot h^{0.9502}$	4.69	179.48	6.01	79.74	0.22
		cwb	$0.0013 \cdot dbh^{1.9596} \cdot h^{1.099}$	4.45	16.14	0.60	7.66	0.27
		cwwb	cww + cwb	3.29	192.78	6.60	84.76	0.22
		sw	$0.4006 \cdot dbh^{2.3211} \cdot h^{-0.7636}$	3.58	85.61	1.20	42.11	0.60
	Full	agb	Sum of all components	3.59	232.42	10.42	102.74	0.22
		stw	$0.0305 \cdot dbh^{2.1514} \cdot sth^{0.7955}$	5.07	20.03	2.53	6.62	0.82
		stb	$0.0039 \cdot dbh^{1.9242} \cdot sth^{0.8081}$	4.35	0.97	0.11	0.29	0.77
		stwb	stw + stb	5.07	20.84	2.64	6.87	0.82
		cww	$- 4.779 + 0.021 \cdot dbh^{1.458} \cdot h^{0.9495} \cdot upd^{0.6351}$	4.69	168.93	5.09	75.30	0.21
		cwb	$0.0014 \cdot dbh^{1.2652} \cdot h^{1.0303} \cdot upd^{0.6633} \cdot a^{0.087}$	4.40	14.98	0.63	7.28	0.25
		cwwb	cww + cwb	4.40	181.29	5.71	80.04	0.21
Oak	Simple	sw	$0.8474 \cdot dbh^{1.6256} \cdot h^{-0.9965} \cdot upd^{0.5037} \cdot hsl^{-0.1014} \cdot cl^{0.5173}$	3.58	84.32	1.14	40.16	0.59
		agb	Sum of all components	4.46	216.52	9.49	96.00	0.21
		stw	$0.0363 \cdot dbh^{2.0657} \cdot sth^{0.7721}$	4.90	11.57	2.92	5.09	0.52
		stb	$0.0158 \cdot dbh^{1.791} \cdot sth^{0.9032}$	4.58	0.91	0.07	0.48	0.35

Table 6 (continued)

Species	Type	Comp.	Equation	δ	RMSE	BIAS	MAE	CV
European ash	Full	stwb	stw + stb	4.71	11.99	3.00	5.38	0.48
		cww	$-3.9731 + 0.0223 \cdot dbh^{2.1012} \cdot h^{0.8647}$	4.74	175.26	-8.70	79.49	0.25
		cwb	$0.0043 \cdot dbh^{1.9437} \cdot h^{0.9576}$	4.93	33.84	0.82	15.01	0.29
		cwwb	cww + cwb	3.73	200.28	-7.89	87.62	0.25
		sw	$0.3028 \cdot dbh^{2.1945} \cdot h^{-0.6882}$	3.70	61.62	-5.77	28.08	0.81
		agb	Sum of all components	3.88	226.77	-10.66	103.60	0.25
		stw	$0.0251 \cdot dbh^{2.077} \cdot sth^{0.7821} \cdot hsl^{0.0623}$	4.96	11.03	2.82	4.96	0.49
		stb	$0.0152 \cdot dbh^{1.8045} \cdot sth^{0.9121}$	4.58	0.91	0.08	0.48	0.35
		stwb	stw + stb	4.66	11.45	2.90	5.28	0.46
		cww	$0.0125 \cdot dbh^{2.0818} \cdot h^{1.0629}$	4.96	170.29	-5.48	74.96	0.24
		cwb	$0.0046 \cdot dbh^{1.922} \cdot h^{0.9592}$	4.93	33.66	2.60	14.86	0.29
		cwwb	cww + cwb	3.83	191.92	-2.88	81.61	0.24
	sw	$0.2854 \cdot dbh^{2.3016} \cdot h^{-0.4922} \cdot a^{-0.4054} \cdot cl^{0.3846}$	3.60	59.66	-8.46	26.26	0.78	
	agb	Sum of all components	3.82	211.70	-8.44	93.89	0.23	
	stw	$1.1307 + 0.0054 \cdot dbh^{2.668} \cdot sth^{0.9223}$	4.05	8.77	-0.45	4.66	0.23	
	stb	$0.0434 \cdot dbh^{1.4611} \cdot sth^{0.9111}$	2.80	1.22	0.06	0.60	0.45	
	stwb	stw + stb	2.38	9.36	-0.39	4.89	0.23	
	cww	$0.0171 \cdot dbh^{2.0198} \cdot h^{1.0356}$	6.21	121.88	7.06	65.43	0.13	
	cwb	$0.0005 \cdot dh^{1.7454}$	4.24	20.08	1.09	10.82	0.18	
	cwwb	cww + cwb	5.19	139.27	8.15	71.30	0.14	
	sw	$0.1024 \cdot dbh^{1.9711}$	4.52	78.92	-12.16	39.44	0.68	
	agb	Sum of all components	4.06	200.61	-4.39	88.62	0.17	
	stw	$0.8108 + 0.0152 \cdot dbh^{2.9503} \cdot sth^{1.0152} \cdot a^{-0.4314}$	4.28	8.32	-1.10	4.03	0.22	
	stb	$-0.5254 + dbh^{1.7942} \cdot sth^{0.544} \cdot h^{-1.3638}$	2.17	0.77	-0.02	0.46	0.29	
stwb	stw + stb	3.10	8.75	-1.12	4.14	0.21		
cww	$0.0159 \cdot dbh^{2.0348} \cdot h^{1.0374}$	6.21	121.76	9.16	65.00	0.13		
cwb	$-1.3879 + dh^{0.3694} \cdot upd^{2.0205} \cdot hsl^{-0.84}$	6.20	33.14	2.99	16.30	0.30		
cwwb	cww + cwb	4.99	134.44	12.15	63.15	0.13		
sw	$0.1394 \cdot dbh^{1.1973} \cdot cl^{0.9249}$	4.81	83.54	-9.89	40.03	0.72		
agb	Sum of all components	5.38	187.73	1.14	78.38	0.16		
Sycamore	Simple	stw	$-0.9368 + 0.0529 \cdot dbh^{1.9653} \cdot sth^{0.664}$	3.91	3.86	-0.07	2.18	0.26
		stb	$-0.1469 + 0.012 \cdot dbh^{1.7668} \cdot sth^{0.6883}$	2.53	0.35	-0.01	0.21	0.23
		stwb	stw + stb	4.19	4.50	-0.07	2.39	0.27
		cww	$0.0171 \cdot dbh^{2.0527} \cdot h^{0.9476}$	5.61	38.03	1.19	23.79	0.10
		cwb	$0.0039 \cdot dbh^{2.0204} \cdot h^{0.7584}$	4.08	4.27	0.19	2.87	0.10
		cwwb	cww + cwb	5.50	44.84	1.38	26.53	0.11
		sw	$0.0416 \cdot dbh^{2.1138}$	5.76	32.18	3.34	18.93	0.55
		agb	sum of all components	4.80	86.06	4.65	36.88	0.17
		stw	$-0.9538 + 0.0682 \cdot dbh^{1.9084} \cdot sth^{0.7021}$	3.91	3.63	-0.11	2.09	0.24
	stb	$-0.1313 + 0.0135 \cdot dbh^{1.7369} \cdot sth^{0.7228}$	2.53	0.34	-0.01	0.21	0.22	
	stwb	stw + stb	4.19	4.24	-0.12	2.29	0.26	
	cww	$0.0162 \cdot dbh^{1.5708} \cdot h^{0.9362} \cdot upd^{0.5447}$	6.08	36.52	-5.07	21.83	0.10	
	cwb	$0.0039 \cdot dbh^{2.0034} \cdot h^{0.7828}$	4.08	4.30	-0.33	2.88	0.10	
	cwwb	cww + cwb	4.07	43.50	-5.41	24.62	0.10	
	sw	$7.8222 + 0.0003 \cdot dbh^{1.6299} \cdot cl^{2.5383}$	6.09	33.62	-2.48	20.22	0.57	
	agb	sum of all components	4.98	73.80	-8.00	28.71	0.15	

See Table 1 for abbreviations

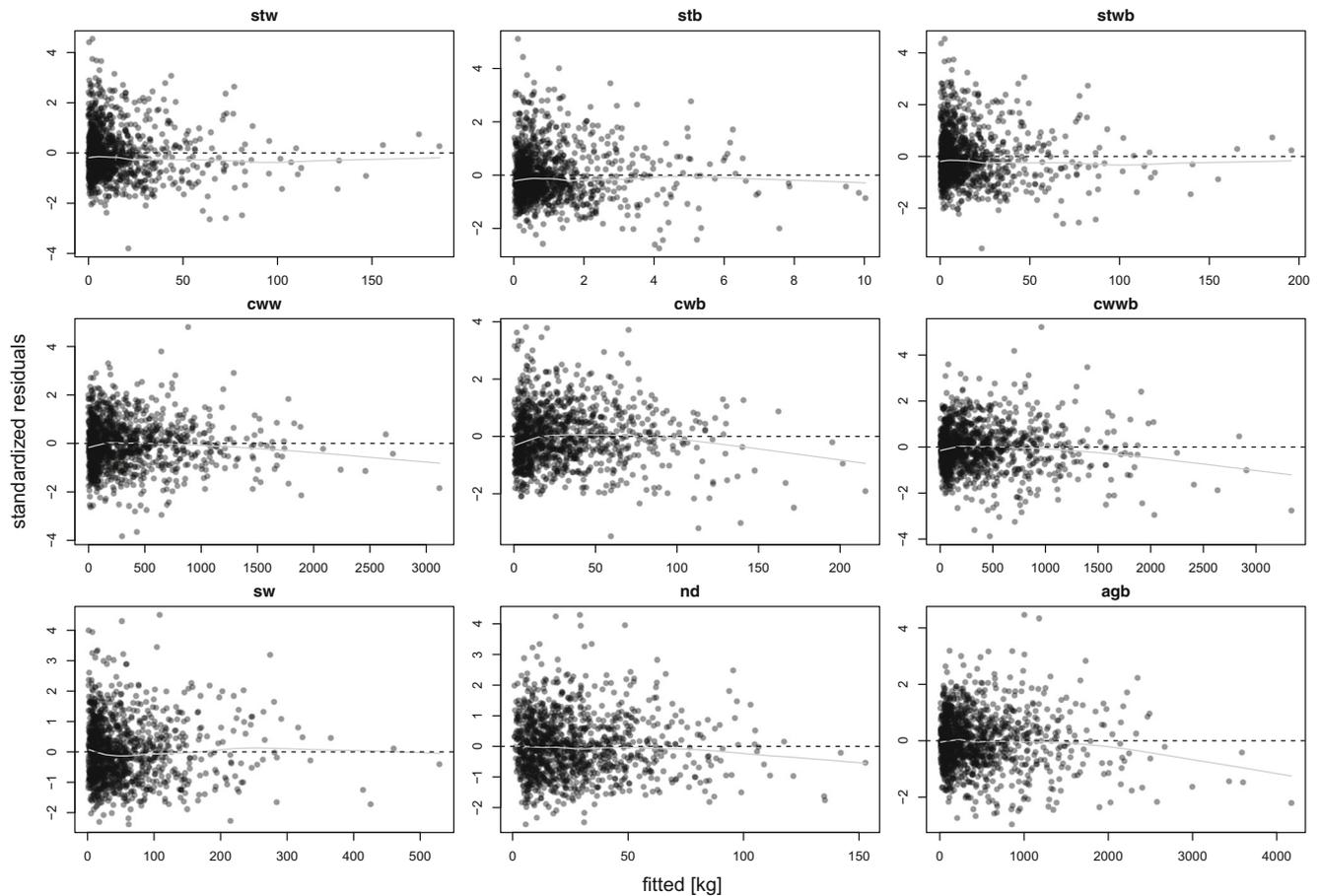


Fig. 3 Residual plot of the Norway spruce first imputed data set. The graph plots the the standardised residuals against fitted values for each component. The model fits the data well and the variance model leads to homoscedastic residuals. Slightly more residuals are positive,

because negative residuals are bounded to the difference between the mean response and zero—a fact which is also visible, e.g. in Zhao et al. (2015)

In summary, additional predictors were more important for coniferous species, which included 1.2 to 1.6 additional predictors (averaged per species over all components) in comparison to the simple model, while deciduous species added only 0.4 to 1.2 additional predictors.

The pooled residual variance σ_{NSUR} (sum of squared errors divided by degrees of freedom) of each system of equations is smaller for the full models compared to the simple models, except for Douglas fir (see Table 8). The highest values of σ_{NSUR} are found for Sycamore, European ash and Silver fir, being double to sixfold increased. This indicates that more observations included to the models lead to less residual variance.

In the case of Douglas fir, the small increase in σ_{NSUR} can be attributed to the moderate decrease in the sum of the squared errors with respect to ten added parameters to the system of equations.

3.2 Biomass allocation

For all species, biomass allocation changes dramatically between components until 20–30 cm dbh (Fig. 4). Small trees ($dbh > 7$ cm) exhibit almost equal proportions of coarse wood and small wood. Two exceptions are Sycamore and Silver fir (but both with few empirical data), the first having a coarse wood proportion of about 70% already for small trees, the latter having only about 30%. Larger trees, i.e. above 30 cm dbh, are rather constant in their proportions, although species-specific differences exist.

Most tree species keep increasing their proportion of coarse wood also beyond 30 cm dbh, mainly drawing from shares of small wood and needles. Sycamore exhibits a rather constant pattern, while European ash keeps changing its proportion with a stronger gradient even for larger trees. In general, coarse wood (including stump mass of about 3–

Table 7 Variance-covariance matrix of the errors for *Norway spruce* (full model)

	stw	stb	stwb	cww	cwb	cwwb	sw	nd	agb
stw	<i>5e-04</i>	0.7948	0.9896	0.3048	0.1789	0.3017	0.1187	0.1283	0.362
stb	<i>7.5e-08</i>	<i>2e-04</i>	0.8233	0.1095	0.3271	0.1399	0.0814	0.0775	0.2002
stwb	<i>2.84e-07</i>	<i>9.4e-08</i>	<i>6e-04</i>	0.2963	0.1949	0.2921	0.117	0.1267	0.3527
cww	<i>1.77e-06</i>	<i>2.54e-07</i>	<i>2.09e-06</i>	<i>0.012</i>	0.4053	0.9531	0.2715	0.3031	0.8534
cwb	<i>3.51e-07</i>	<i>2.55e-07</i>	<i>4.63e-07</i>	<i>1.95e-05</i>	<i>0.004</i>	0.4909	0.1977	0.193	0.4607
cwwb	<i>9.86e-06</i>	<i>1.82e-06</i>	<i>1.16e-05</i>	<i>7.65e-04</i>	<i>1.33e-04</i>	<i>0.0671</i>	0.2779	0.3006	0.8941
sw	<i>1.73e-06</i>	<i>4.72e-07</i>	<i>2.07e-06</i>	<i>9.73e-05</i>	<i>2.38e-05</i>	<i>5.59e-04</i>	<i>0.03</i>	0.7171	0.6224
nd	<i>1.43e-06</i>	<i>3.43e-07</i>	<i>1.71e-06</i>	<i>8.28e-05</i>	<i>1.77e-05</i>	<i>4.61e-04</i>	<i>4.91e-04</i>	<i>0.0229</i>	0.6072
agb	<i>1.77e-05</i>	<i>3.89e-06</i>	<i>2.09e-05</i>	<i>1.02e-03</i>	<i>1.86e-04</i>	<i>6.02e-03</i>	<i>1.87e-03</i>	<i>1.39e-03</i>	<i>0.1003</i>

Values are averaged from each of ten imputation based analyses including the within imputation variance and the between imputation variance. On the diagonal (*italics*), standard deviations of the errors are given; the lower triangular matrix gives the covariances of the errors between the different components and the upper triangular matrix shows the corresponding correlations

5%) claims about 80% of aboveground biomass for trees with $dbh > 30$ cm. Interestingly, Silver fir reaches the least amount of coarse wood with about 70%, while Norway spruce is slightly reducing its coarse wood proportion for large trees. In contrast, small wood of Norway spruce tends to increase its proportions for large trees again, while coarse wood bark and needles reduce their relative amount. In other words, the increase in mass given dbh is steeper for small wood than for the other components. This is rather unexpected and one explanation could be that some

branches, which as a whole are considered as belonging to small wood, surpassing the 7 cm limit and artificially increasing this component. This might be incorrect with respect to the components size limit, but not for the actual possible stem harvesting mass. The same effect occurs using the models of Wirth et al. (2004). Usually, bark makes up about 10% of total mass, slightly more in case of Silver fir and Oak, slightly less for Norway spruce and Scots pine. A noticeable exception is European beech, with a very low proportion of bark.

Table 8 Pooled residual variance of the NSUR system of equations for simple and full models of each species

Species	Type	σ_{NSUR}	N	k
Norway spruce	Simple	0.9823	1150	21
	Full	0.9710	1150	31
Silver fir	Simple	1.8074	31	16
	Full	1.7616	31	23
Douglas fir	Simple	0.8727	161	19
	Full	0.9359	161	29
Scots pine	Simple	0.9636	460	18
	Full	0.9541	460	26
European beech	Simple	0.9301	918	16
	Full	0.9256	918	22
Oak	Simple	0.9669	313	16
	Full	0.9449	313	18
European ash	Simple	3.4007	37	13
	Full	1.8932	37	18
Sycamore	Simple	5.7875	28	14
	Full	1.5619	28	17

Additionally, sample size (N) and number of estimated parameters (k) are given

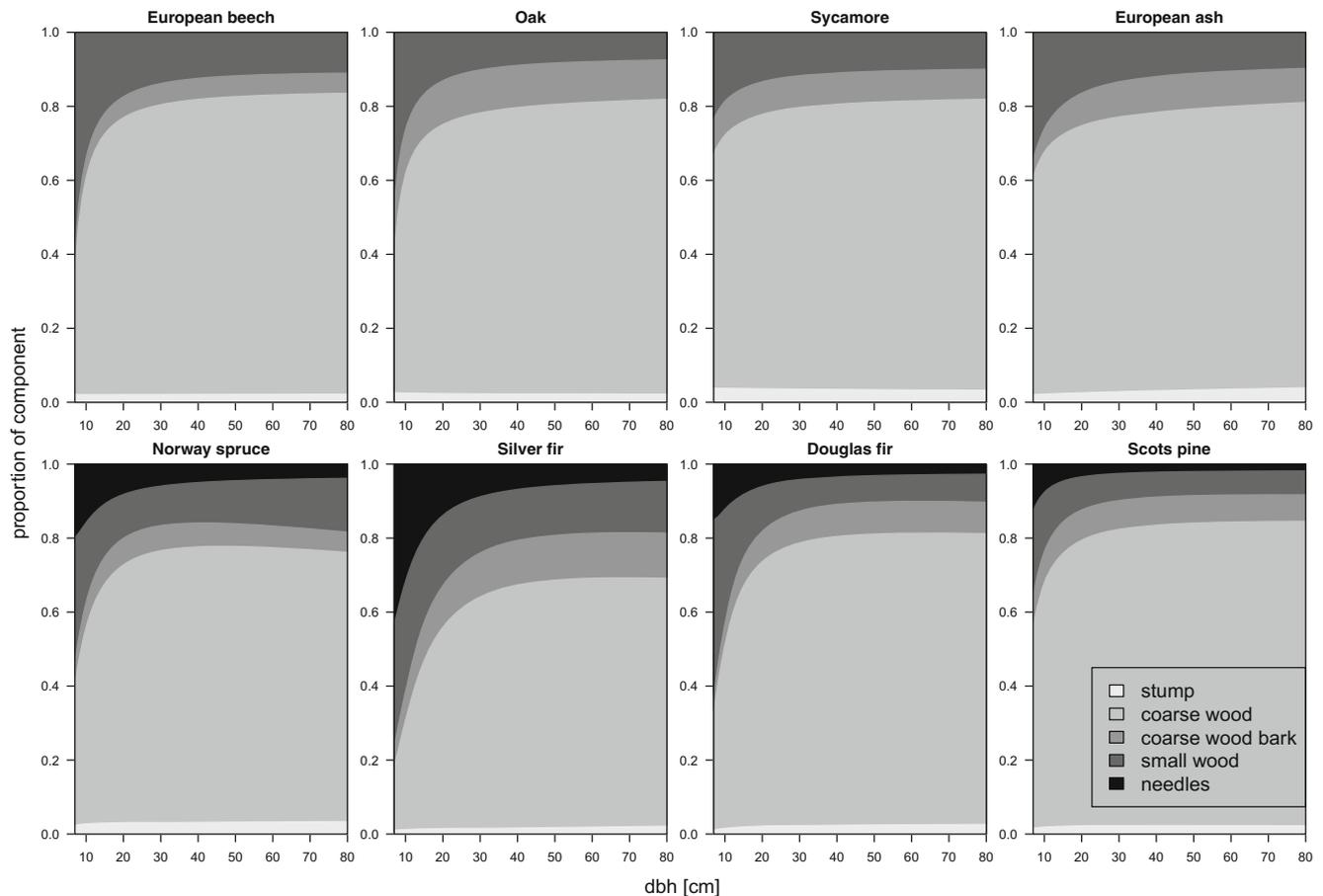


Fig. 4 Biomass allocation to components expressed as proportions of total aboveground biomass for each species based on the simple models. Tree height was assumed to follow a Pettersen model ($h = 1.3 + (a + \frac{b}{dbh})^{-3}$) and fitted by generalised nonlinear regression to the collected observations of each species and stump height was set

to be 1% of tree height. We predicted height for each *dbh* from 7 to 80 cm, calculated stump height and applied our simple model (the full models would have required more input variables). Results for deciduous trees are given in the top row, for coniferous tree species in the bottom row

Biomass allocation is relevant when considering energy wood removal during harvest. Nutrient element concentrations differ between components and are regularly higher in crown and bark than in wood (e.g. Weis et al. 2009). As the harvesting of wood is the main interest in forestry, the additional export of nutrients through the inherently connected components should carefully be weighed against the productivity of the respective soils. With these additive biomass functions and in conjunction with nutrient element concentration very detailed harvesting scenarios and optimisations are possible.

3.3 Comparison to other functions

Wirth et al. (2004) developed univariate biomass component functions for Norway spruce in Central Europe. Their raw data were kindly supplied to be included into the presented study (listed as study 9 in Table 1). Figure 5 plots all data from our study, also indicating the data from Wirth et al

(2004, black squares) for the three common components coarse wood incl. bark, small wood (branches) and needles. The fitted values of the full model of this study and of the best DHA+C-model (using diameter in breast height, tree height, tree age and crown predictors) of Wirth et al. (2004) are given in the form of a solid and dashed line, respectively, to see differences between both models.

For coarse wood incl. bark, the models seem to be approximately equivalent for *dbh* < 70 cm, while above the line is strongly influenced by only five scattered observations. Additionally, these values lie outside the range of Wirth et al. (2004). The models for small wood and needles exhibit stronger deviations already for small to medium trees and the conditional mean response of the model from Wirth et al. (2004) lies above the conditional mean response of our full models. It seems that the data of Wirth et al. (2004) indicates slightly higher component masses for small wood, especially for medium sized trees, compared to our data. Note that Fig. 5 contains our raw

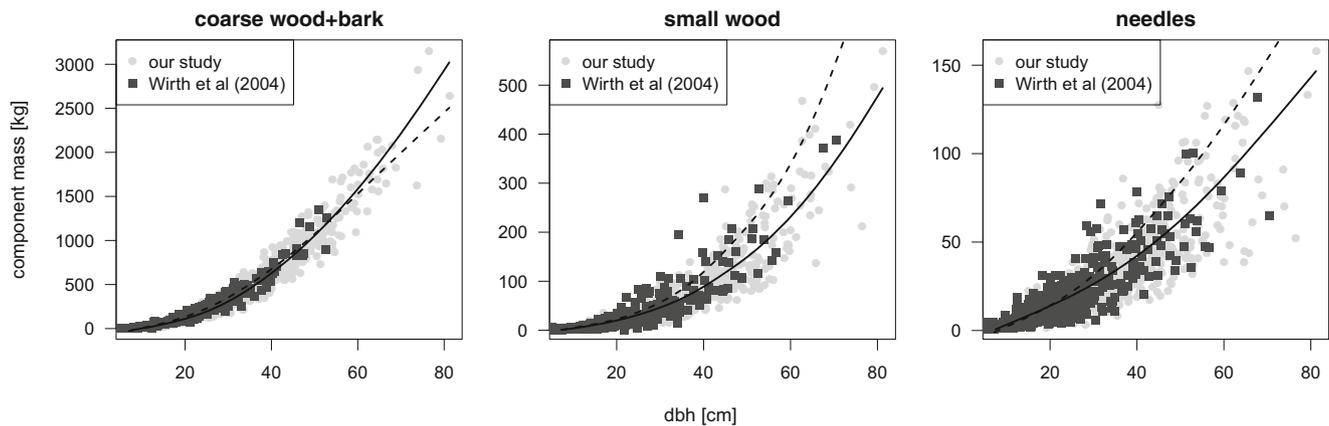


Fig. 5 Comparison of our results against the models of Wirth et al. (2004). They fitted their models to trees with no restrictions on *dbh*, while our data only consists of trees above 7 cm *dbh*. The solid line represents a smoothing curve based on predictions of the presented

NSUR full model, while the dashed smoothing curve is based on the respective best DHA+C-model of Wirth et al. (2004, tab. 4, with published correction factors applied). Predictions are based on our data collection

data, with no imputation or adjustment applied, so that data manipulations can be excluded from being the cause of differences.

Predictions for the crown components using the newly fitted functions should be slightly lower and thus more conservative with respect to expected harvest output.

4 Discussion

With this study, we could develop a consistent set of additive biomass functions for eight tree species and eight to nine components, where each component function is based on the full per-species data set. Models for all species were fit using the same procedure, which accounted for intrinsic correlation between components. Raw data were gathered from different sources so that a general applicability of the equations is given for five of eight species at least for the area of Germany. Although fitted the same way, models for Silver fir, European Ash and Sycamore are less general due to limited data availability and geographic extent of the data. Thickest trees show a *dbh* of more than 80 cm, which is sufficient for most applications. For conservation, where even larger trees are of interest (see e.g. Lutz et al. 2012; Stagoll et al. 2012, and references therein), this high limit might be important.

Consolidation of the heterogeneous data sources was possible because extremely differentiated information was available for some studies and hence component definition of other studies could be mimicked. Remaining missingness in components were handled by multiple imputation. Thereby, we could join studies with different sampling schemes and hence take advantage of the information of as many sample trees as possible.

The model equations are based on allometric theory (Fehrmann and Kleinn 2006), which is well accepted and most commonly applied in literature (c. f. Zianis et al. 2005; Ter-Mikaelian and Korzukhin 1997), but alternative parametrisations exist. Main differences between models occur in large trees, where for example Marklund (1987) is more conservative and deviations can be substantial.

Besides *hsl*, which can be considered tree- or stand-specific, we used only tree-specific predictors to model biomass. *Dbh* was most frequently used as independent variable, followed by tree height. Indeed, *dbh* is the easiest and most relevant measure in tree volume and biomass applications, but from a theoretical viewpoint it would be better to use a diameter in relative height (Fehrmann and Kleinn 2006). To support these assertions, we found that although *upd* and *dbh* are correlated they were often used jointly, while *upd* even replaced *dbh* in some cases. Additional predictors helped to increase accuracy in predictions as could be shown in this study, but also e.g. by Wirth et al. (2004) and Wutzler et al. (2008). Especially crown length (*cl*) was valuable for the modelling of crown components. Because possible applications might differ in their availability of input variables, we developed two sets of biomass functions (simple and full). The more comprehensive full models, taking advantage of more predictors, usually exhibit less residual variance as well as lower *RMSE* and *CV*. Also, *BIAS* is small with some exceptions in stump and crown components, indicating that the allometric model might not be the ideal functional form to model these components. An additional intrinsic systematic bias like in log-linear models (Sprugel 1983) could be avoided by fitting the models on the data scale.

To fit a system of biomass equations simultaneously, several approaches were described and discussed in

literature (e.g. Parresol 2001; Maltamo et al 2012; Dong et al 2015; Poudel and Temesgen 2015; Affleck and Diéguez-Aranda 2016). In this particular case, we had to handle three main difficulties: (i) several studies with different sampling schemes and missing data, (ii) grouping structure of the data, and imperatively and (iii) the inclusion of summary components into the NSUR model. This last requirement excluded models using ML, as described by Affleck and Diéguez-Aranda (2016). On the other hand, random effect structures, usually fit by ML are not available in the LS setting (Fahrmeir et al. 2009, p.263). Hence, we built a data stream from our collected raw data, across enhanced, imputed and adjusted data to pooling of NSUR models fit with GNLS. On that basis, we could include all collected data, incorporate the uncertainty of missing data and treat the grouping of the data. Additionally, through the use of imputation, we avoided potentially biased parameter estimates.

The effect of the data adjustment was a change in variance of the data. We assume that the main effect of the adjustment is in correcting for differences in sampling, since the data adjustment with relevant magnitude mainly occurred in bark and stump components, which are both difficult to sample. Total bark mass can be estimated based on volume or surface area, i.e. interpolated from either measured or modelled bark thickness and assumed shape of the trees. Also, stump components are challenging to measure in the field due to their irregular shape. Hence, larger deviations between different studies are to be expected. Here, the adjustment was used to obtain observations cleared from study specific effects, because the desired response of our models is the conditional mean response of the population average (and not study specific predictions).

By stepping back from the inclusion of summary components, more advanced models such as ML would be possible. ML is able to handle hierarchical data and missingness in the response variable (by allowing unbalanced designs). The question of data harmonisation still applies (c.f. Affleck and Diéguez-Aranda 2016) and fitting parsimonious mixed effect models (Bates et al. 2015) with as many parameters as presented here is not straight forward. In such complex models, the different parts (random effects, correlation and heteroscedasticity) compete with each other (Pinheiro and Bates 2000, p. 204), leading to difficulties in optimisation.

5 Conclusions

Our approach to fit additive biomass functions led to a consistent set of additive nonlinear biomass functions for the most relevant tree species in Germany. We considered a

high number of observations, intrinsic correlations between different components and corrected for study effects. Different studies have been included, of which not all component information was available from the raw data. Some studies did not even sample the same components. With our approach, taking advantage of highly differentiated data and multiple imputation, we could consolidate all studies into one scheme of additive components. For historic data, such measures are necessary to be able to use this data but for future data, projects like ENFIN or Cost E43 help harmonising definitions and methods already during acquisition.

From these multiple sets of complete data, we have developed simple and full allometric models applying nonlinear seemingly unrelated regression (NSUR). These models can now be used to compute component mass for trees of interest. A step further, biomass can be transformed into nutrient element mass of different components using respective elemental concentrations. One can also deduce proportions of the different components and their variation with changing predictors.

Although quite some effort has been put into the development, one could still improve estimates by including even larger trees, to better capture the behaviour and variance of the models. Additional observations could improve the models for some species, while for Norway spruce, Scots pine, Douglas fir, European beech and Oak the number of observations seems to be sufficient for model building.

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Data availability The datasets analysed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix A: Sample tree origin

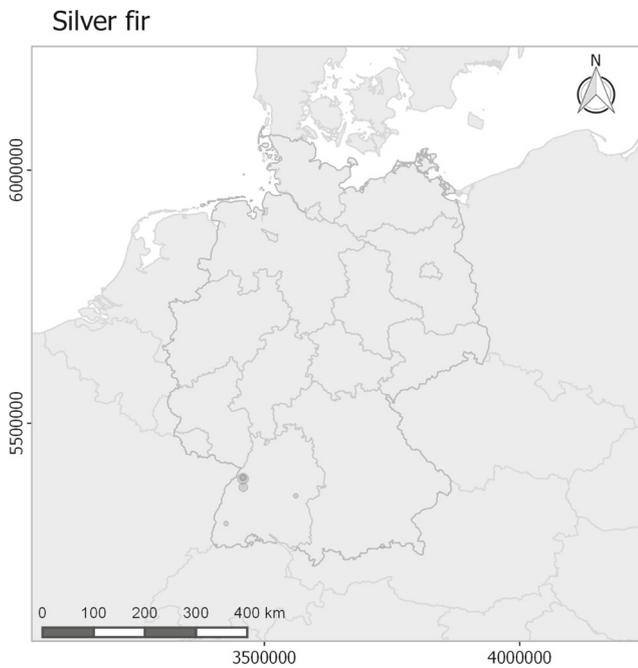


Fig. 6 Geographic distribution of referenced sample data for Silver Fir. The size of the symbols indicate the number of sample trees and scales from 1 to 80. For circles, the sample location is known, whereas squares indicate unknown coordinates which could be approximated by location names

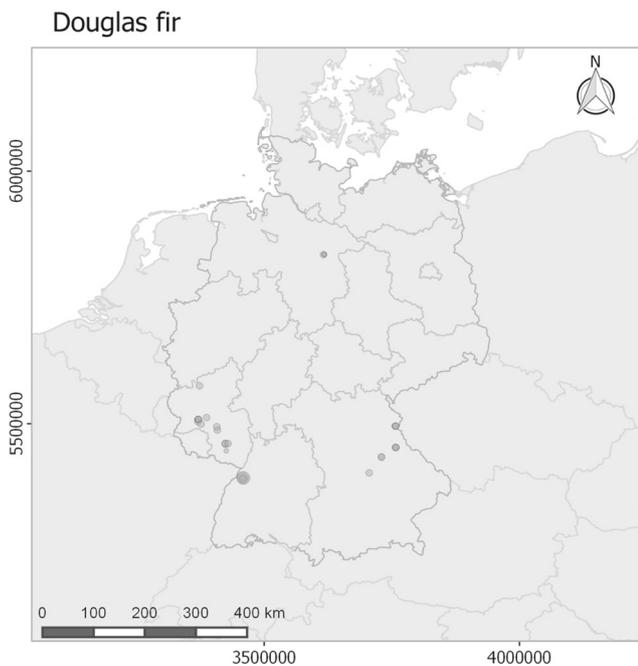


Fig. 7 Geographic distribution of referenced sample data for Douglas Fir. The size of the symbols indicate the number of sample trees and scales from 1 to 80. For circles, the sample location is known, whereas squares indicate unknown coordinates which could be approximated by location names

Scots pine

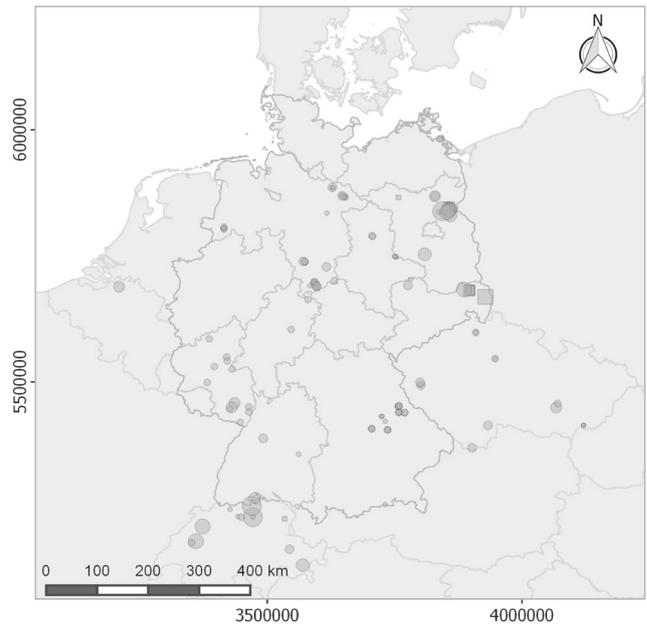


Fig. 8 Geographic distribution of referenced sample data for Scots pine. The size of the symbols indicate the number of sample trees and scales from 1 to 80. For circles, the sample location is known, whereas squares indicate unknown coordinates which could be approximated by location names

European beech

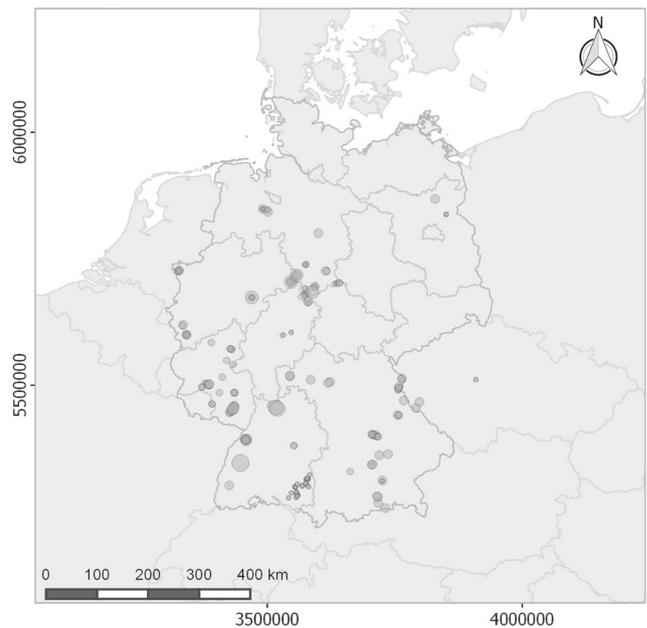


Fig. 9 Geographic distribution of referenced sample data for European beech. The size of the symbols indicate the number of sample trees and scales from 1 to 80. For circles, the sample location is known, whereas squares indicate unknown coordinates which could be approximated by location names

Appendix B: Parameter estimates

In the following, the pooled results of the repeated NSUR model fit for the remaining species are presented.

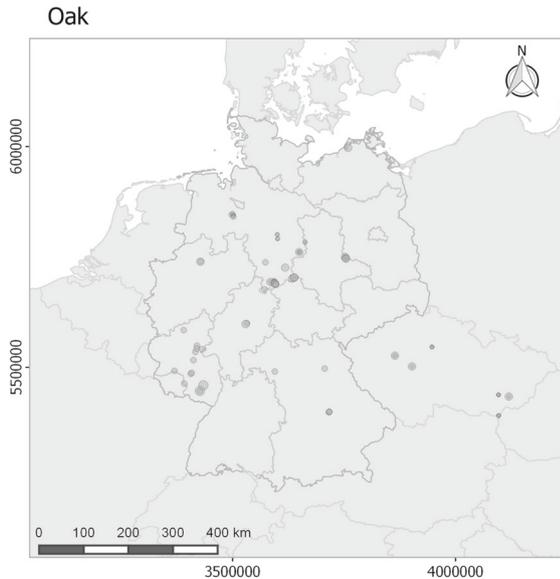


Fig. 10 Geographic distribution of referenced sample data for Oak. The size of the symbols indicate the number of sample trees and scales from 1 to 80. For circles, the sample location is known, whereas squares indicate unknown coordinates which could be approximated by location names

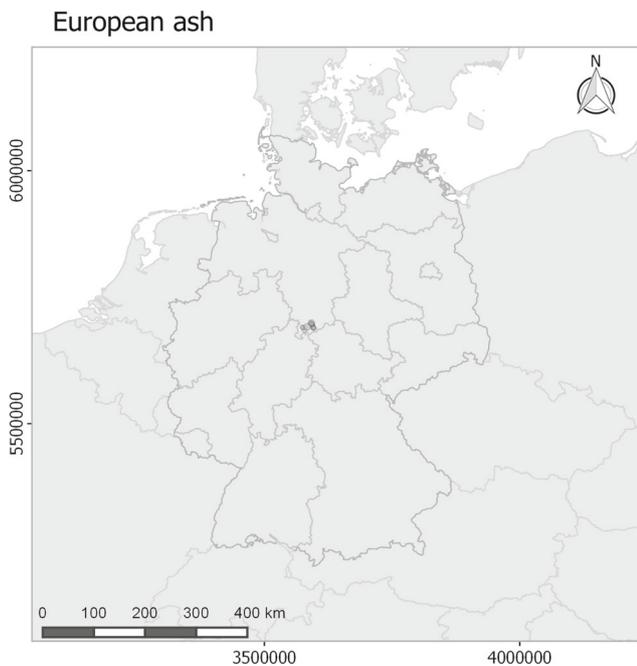


Fig. 11 Geographic distribution of referenced sample data for European ash. The size of the symbols indicate the number of sample trees and scales from 1 to 80. For circles, the sample location is known, whereas squares indicate unknown coordinates which could be approximated by location names

Sycamore

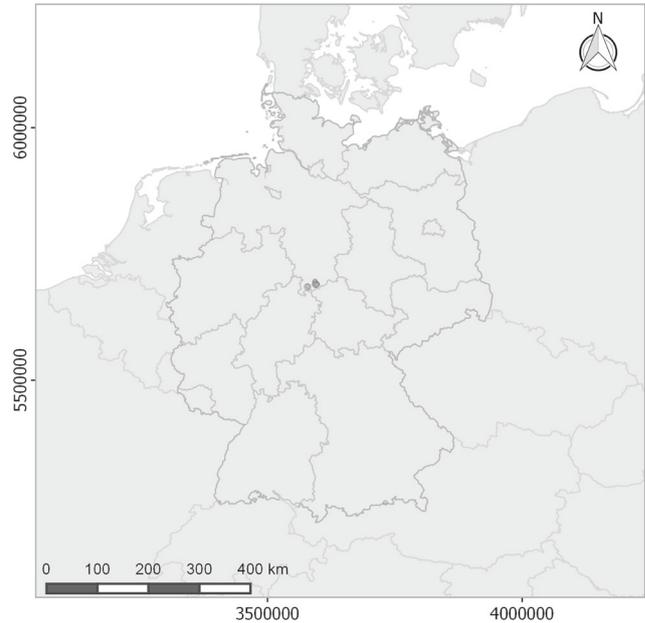


Fig. 12 Geographic distribution of referenced sample data for Sycamore. The size of the symbols indicate the number of sample trees and scales from 1 to 80. For circles, the sample location is known, whereas squares indicate unknown coordinates which could be approximated by location names

Table 9 Parameter estimates for *Silver fir*

Type	comp	pred	est	se	p	λ
Simple	stw	slope	0.0121	0.0077	0.1435	0.7979
		dbh	2.2645	0.1329	0.0000	0.7974
		sth	0.7596	0.0503	0.0000	0.5215
	stb	slope	0.0036	0.0015	0.0310	0.7675
		dbh	2.1225	0.0870	0.0000	0.7667
		sth	0.7856	0.0361	0.0000	0.4085
	cww	slope	0.0046	0.0010	0.0000	0.1895
		dbh	1.1917	0.1062	0.0000	0.0646
		h	2.2103	0.1652	0.0000	0.0620
	cwb	slope	0.0019	0.0003	0.0000	0.0527
		dbh	1.4458	0.0873	0.0000	0.0419
		h	1.6780	0.1404	0.0000	0.0418
sw	slope	0.0273	0.0056	0.0000	0.1022	
	dbh	2.2573	0.0621	0.0000	0.1045	
nd	slope	0.1071	0.0292	0.0003	0.1313	
	dbh	1.6952	0.0807	0.0000	0.1122	
Full	stw	slope	0.0635	0.0283	0.0394	0.6781
		dbh	2.5304	0.1432	0.0000	0.8009
		sth	0.8015	0.0334	0.0000	0.4369
	stb	hsl	- 0.4205	0.1059	0.0013	0.7123
		slope	0.0091	0.0027	0.0020	0.4307
		dbh	2.2383	0.1021	0.0000	0.7011
cww	sth	0.8168	0.0320	0.0000	0.4219	
	hsl	- 0.2111	0.0820	0.0177	0.5896	
	slope	0.0542	0.0134	0.0002	0.3224	

Table 9 (continued)

Type	comp	pred	est	se	p	λ
		<i>dbh</i>	0.2327	0.1569	0.1436	0.3273
		<i>h</i>	1.0799	0.1332	0.0000	0.3041
		<i>upd</i>	1.7805	0.1649	0.0000	0.2462
		<i>a</i>	0.3421	0.0447	0.0000	0.3489
		<i>hsl</i>	- 0.4926	0.0467	0.0000	0.2680
	cwb	<i>slope</i>	0.0050	0.0011	0.0000	0.1202
		<i>h</i>	0.9923	0.1046	0.0000	0.1599
		<i>upd</i>	1.8510	0.0939	0.0000	0.2929
		<i>a</i>	0.1620	0.0413	0.0002	0.1871
		<i>hsl</i>	- 0.0949	0.0448	0.0362	0.1669
	sw	<i>slope</i>	0.0254	0.0045	0.0000	0.2002
		<i>dbh</i>	2.2720	0.0559	0.0000	0.2028
	nd	<i>slope</i>	0.1214	0.0365	0.0013	0.2248
		<i>dbh</i>	1.6556	0.0881	0.0000	0.2293

Column ‘comp’ refers to the fitted component, column ‘pred’ indicates the associated predictors as well as intercept ($intcp = \alpha$ in Eq. 1) and slope parameter ($= \beta_0$). Columns ‘est’, ‘se’ and ‘p’ give parameter estimates, standard errors and associated *p* values. λ denotes the increase in variance due to missingness. C.f. Tables 5 and 6

Table 10 Parameter estimates for *Douglas fir*

Type	comp	pred	est	se	p	λ	
Simple	stw	<i>slope</i>	0.0186	0.0034	0.0000	0.0081	
		<i>dbh</i>	2.1850	0.0373	0.0000	0.0097	
		<i>sth</i>	0.7723	0.0417	0.0000	0.0041	
	stb	<i>slope</i>	0.0032	0.0007	0.0000	0.0092	
		<i>dbh</i>	2.0357	0.0479	0.0000	0.0090	
		<i>sth</i>	0.7621	0.0405	0.0000	0.0057	
	cww	<i>slope</i>	0.0131	0.0007	0.0000	0.0057	
		<i>dbh</i>	1.9299	0.0320	0.0000	0.0283	
		<i>h</i>	1.0715	0.0459	0.0000	0.0221	
	cwb	<i>slope</i>	0.0018	0.0002	0.0000	0.0018	
		<i>dbh</i>	1.9099	0.0511	0.0000	0.0021	
		<i>h</i>	1.0306	0.0720	0.0000	0.0022	
sw	<i>slope</i>	0.2784	0.0577	0.0000	0.0083		
	<i>dbh</i>	3.1276	0.1114	0.0000	0.0618		
	<i>h</i>	- 1.7984	0.1649	0.0000	0.0451		
nd	<i>intcp</i>	- 1.8821	0.1920	0.0000	0.0144		
	<i>slope</i>	0.2749	0.0452	0.0000	0.0123		
	<i>dbh</i>	2.4833	0.0916	0.0000	0.0575		
	<i>h</i>	- 1.3051	0.1114	0.0000	0.0434		
Full	stw	<i>slope</i>	0.0220	0.0028	0.0000	0.0028	
		<i>dbh</i>	2.1597	0.0252	0.0000	0.0040	
		<i>sth</i>	0.8318	0.0298	0.0000	0.0018	
	stb	<i>slope</i>	0.0106	0.0035	0.0026	0.0010	
		<i>dbh</i>	1.8380	0.0937	0.0000	0.0036	
		<i>sth</i>	0.8417	0.0378	0.0000	0.0123	
			<i>h</i>	0.4136	0.1353	0.0023	0.0005
			<i>hsl</i>	- 0.3138	0.0378	0.0000	0.0034
	cww	<i>slope</i>	0.0084	0.0005	0.0000	0.0023	

Table 10 (continued)

Type	Comp	Pred	est	se	p	λ
		<i>dbh</i>	0.3630	0.0980	0.0002	0.0348
		<i>h</i>	1.1578	0.0430	0.0000	0.0030
		<i>upd</i>	1.5364	0.0938	0.0000	0.0341
		<i>a</i>	0.1669	0.0210	0.0000	0.0040
	cwb	<i>slope</i>	0.0020	0.0003	0.0000	0.0123
		<i>h</i>	1.4131	0.0818	0.0000	0.0074
		<i>upd</i>	1.7165	0.0519	0.0000	0.0051
		<i>a</i>	0.1509	0.0410	0.0002	0.0135
		<i>hsl</i>	- 0.1548	0.0232	0.0000	0.0182
	sw	<i>intcp</i>	5.3595	0.2467	0.0000	0.0286
		<i>slope</i>	0.0446	0.0198	0.0272	0.3498
		<i>h</i>	- 1.6949	0.1940	0.0000	0.1984
		<i>upd</i>	3.2448	0.1412	0.0000	0.1411
		<i>hsl</i>	- 0.3084	0.0700	0.0001	0.5485
		<i>cl</i>	1.3312	0.1497	0.0000	0.1000
	nd	<i>slope</i>	0.1708	0.0410	0.0000	0.1789
		<i>h</i>	- 1.2492	0.1191	0.0000	0.1547
		<i>upd</i>	2.5884	0.0976	0.0000	0.1660
		<i>hsl</i>	- 0.2632	0.0360	0.0000	0.2007
		<i>cl</i>	0.7698	0.0930	0.0000	0.1365

Column ‘comp’ refers to the fitted component, column ‘pred’ indicates the associated predictors as well as intercept ($intcp = \alpha$ in Eq. 1) and slope parameter ($= \beta_0$). Columns ‘est’, ‘se’ and ‘p’ give parameter estimates, standard errors and associated *p* values. λ denotes the increase in variance due to missingness. C.f. Tables 5 and 6

Table 11 Parameter estimates for *Scots pine*

Type	Comp	Pred	est	se	p	λ	
Simple	stw	<i>slope</i>	0.0624	0.0074	0.0000	0.6618	
		<i>dbh</i>	1.9322	0.0425	0.0000	0.8715	
		<i>sth</i>	1.0414	0.0222	0.0000	0.5393	
	stb	<i>slope</i>	0.0077	0.0010	0.0000	0.6173	
		<i>dbh</i>	1.8127	0.0244	0.0000	0.5452	
		<i>sth</i>	0.8732	0.0557	0.0000	0.9380	
	cww	<i>slope</i>	0.0173	0.0009	0.0000	0.0554	
		<i>dbh</i>	2.0072	0.0194	0.0000	0.0606	
		<i>h</i>	0.9140	0.0329	0.0000	0.0723	
	cwb	<i>slope</i>	0.0055	0.0006	0.0000	0.1328	
		<i>dbh</i>	2.0108	0.0496	0.0000	0.4079	
		<i>h</i>	0.5374	0.0787	0.0000	0.4376	
sw	<i>slope</i>	0.1316	0.0189	0.0000	0.0735		
	<i>dbh</i>	2.4440	0.0655	0.0000	0.0943		
	<i>h</i>	- 0.9490	0.0880	0.0000	0.0614		
nd	<i>slope</i>	0.1484	0.0137	0.0000	0.0164		
	<i>dbh</i>	2.3320	0.0532	0.0000	0.0573		
	<i>h</i>	- 1.2026	0.0671	0.0000	0.0484		
Full	stw	<i>slope</i>	0.0390	0.0044	0.0000	0.5651	
		<i>dbh</i>	1.7956	0.0279	0.0000	0.3275	
			<i>sth</i>	0.9353	0.0282	0.0000	0.7228
			<i>a</i>	0.1836	0.0206	0.0000	0.3651

Table 11 (continued)

Type	Comp	Pred	est	se	p	λ
	stb	<i>slope</i>	0.0078	0.0009	0.0000	0.6274
		<i>dbh</i>	1.8129	0.0219	0.0000	0.4931
		<i>sth</i>	0.8788	0.0603	0.0000	0.9516
cww	<i>slope</i>	<i>slope</i>	0.0159	0.0011	0.0000	0.4879
		<i>dbh</i>	1.1909	0.1176	0.0000	0.7075
		<i>h</i>	0.9266	0.0317	0.0000	0.3313
		<i>upd</i>	0.7650	0.1216	0.0000	0.7361
		<i>a</i>	0.1172	0.0162	0.0000	0.5468
cwb	<i>slope</i>	<i>hsl</i>	- 0.0200	0.0051	0.0008	0.6885
		<i>slope</i>	0.0040	0.0002	0.0000	0.2542
		<i>dbh</i>	0.8083	0.0702	0.0000	0.2904
		<i>h</i>	0.7155	0.0269	0.0000	0.1660
		<i>upd</i>	1.1511	0.0717	0.0000	0.3368
sw	<i>slope</i>	<i>a</i>	0.0674	0.0156	0.0000	0.1917
		<i>slope</i>	0.2146	0.0405	0.0000	0.4323
		<i>h</i>	- 0.8896	0.1236	0.0000	0.3746
		<i>upd</i>	2.0322	0.0852	0.0000	0.3980
		<i>cl</i>	0.6288	0.0784	0.0000	0.3178
nd	<i>slope</i>	<i>slope</i>	0.2135	0.0381	0.0000	0.4987
		<i>h</i>	- 1.4766	0.1250	0.0000	0.4146
		<i>upd</i>	2.2923	0.1037	0.0000	0.5072
		<i>cl</i>	0.6001	0.1106	0.0000	0.5360

Column ‘comp’ refers to the fitted component, column ‘pred’ indicates the associated predictors as well as intercept ($intcp = \alpha$ in Eq. 1) and slope parameter ($= \beta_0$). Columns ‘est’, ‘se’ and ‘p’ give parameter estimates, standard errors and associated *p* values. λ denotes the increase in variance due to missingness. C.f. Tables 5 and 6

Table 12 Parameter estimates for *European beech*

Type	comp	pred	est	se	p	λ
Simple	stw	<i>slope</i>	0.0315	0.0038	0.0000	0.7811
		<i>dbh</i>	2.1447	0.0257	0.0000	0.7722
		<i>sth</i>	0.7980	0.0202	0.0000	0.6470
	stb	<i>slope</i>	0.0040	0.0006	0.0000	0.7385
		<i>dbh</i>	1.9184	0.0260	0.0000	0.6258
		<i>sth</i>	0.8076	0.0263	0.0000	0.5435
	cww	<i>intcp</i>	- 4.6332	0.4260	0.0000	0.3698
		<i>slope</i>	0.0190	0.0012	0.0000	0.4301
		<i>dbh</i>	2.0861	0.0172	0.0000	0.7011
<i>h</i>		0.9502	0.0352	0.0000	0.6758	
Simple	stw	<i>slope</i>	0.0315	0.0038	0.0000	0.7811
		<i>dbh</i>	2.1447	0.0257	0.0000	0.7722
	cwb	<i>slope</i>	0.0013	0.0001	0.0000	0.1149
		<i>dbh</i>	1.9596	0.0198	0.0000	0.1544
sw	<i>slope</i>	<i>h</i>	1.0990	0.0366	0.0000	0.1346
		<i>dbh</i>	2.3211	0.0456	0.0000	0.3219
	<i>slope</i>	<i>h</i>	- 0.7636	0.0674	0.0000	0.2523
		<i>dbh</i>	2.3211	0.0456	0.0000	0.3219
Full	stw	<i>slope</i>	0.0305	0.0034	0.0000	0.7440
		<i>dbh</i>	2.1514	0.0236	0.0000	0.7255
		<i>sth</i>	0.7955	0.0203	0.0000	0.6465

Table 12 (continued)

Type	comp	pred	est	se	p	λ
	stb	<i>slope</i>	0.0039	0.0005	0.0000	0.5976
		<i>dbh</i>	1.9242	0.0221	0.0000	0.4726
		<i>sth</i>	0.8081	0.0235	0.0000	0.4201
cww	<i>intcp</i>	<i>intcp</i>	- 4.7790	0.4332	0.0000	0.4225
		<i>slope</i>	0.0210	0.0012	0.0000	0.3485
		<i>dbh</i>	1.4580	0.0867	0.0000	0.7247
		<i>h</i>	0.9495	0.0287	0.0000	0.5712
		<i>upd</i>	0.6351	0.0932	0.0000	0.7577
cwb	<i>slope</i>	<i>slope</i>	0.0014	0.0001	0.0000	0.1317
		<i>dbh</i>	1.2652	0.1506	0.0000	0.7111
		<i>h</i>	1.0303	0.0335	0.0000	0.0508
		<i>upd</i>	0.6633	0.1522	0.0004	0.7155
		<i>a</i>	0.0870	0.0184	0.0000	0.3392
sw	<i>slope</i>	<i>slope</i>	0.8474	0.0886	0.0000	0.2381
		<i>dbh</i>	1.6256	0.2339	0.0000	0.7666
		<i>h</i>	- 0.9965	0.0878	0.0000	0.6866
		<i>upd</i>	0.5037	0.2214	0.0376	0.7599
		<i>hsl</i>	- 0.1014	0.0146	0.0000	0.4182
		<i>cl</i>	0.5173	0.0615	0.0000	0.7335

Column ‘comp’ refers to the fitted component, column ‘pred’ indicates the associated predictors as well as intercept ($intcp = \alpha$ in Eq. 1) and slope parameter ($= \beta_0$). Columns ‘est’, ‘se’ and ‘p’ give parameter estimates, standard errors and associated *p* values. λ denotes the increase in variance due to missingness. C.f. Tables 5 and 6

Table 13 Parameter estimates for *Oak*

Type	comp	pred	est	se	p	λ	
Simple	stw	<i>slope</i>	0.0363	0.0047	0.0000	0.1500	
		<i>dbh</i>	2.0657	0.0266	0.0000	0.1119	
		<i>sth</i>	0.7721	0.0305	0.0000	0.2087	
	stb	<i>slope</i>	0.0158	0.0021	0.0000	0.0528	
		<i>dbh</i>	1.7910	0.0292	0.0000	0.0826	
		<i>sth</i>	0.9032	0.0357	0.0000	0.2227	
	cww	<i>intcp</i>	<i>intcp</i>	- 3.9731	0.7048	0.0000	0.3218
			<i>slope</i>	0.0223	0.0035	0.0000	0.7045
			<i>dbh</i>	2.1012	0.0229	0.0000	0.4790
	cwb	<i>h</i>	<i>h</i>	0.8647	0.0692	0.0000	0.7374
			<i>slope</i>	0.0043	0.0005	0.0000	0.1611
			<i>dbh</i>	1.9437	0.0365	0.0000	0.2718
sw	<i>h</i>	<i>h</i>	0.9576	0.0633	0.0000	0.1775	
		<i>slope</i>	0.3028	0.0502	0.0000	0.1441	
		<i>dbh</i>	2.1945	0.0819	0.0000	0.4533	
Full	stw	<i>h</i>	- 0.6882	0.1227	0.0000	0.3586	
		<i>slope</i>	0.0251	0.0037	0.0000	0.1077	
		<i>dbh</i>	2.0770	0.0267	0.0000	0.0733	
	stb	<i>sth</i>	<i>sth</i>	0.7821	0.0301	0.0000	0.1190
			<i>hsl</i>	0.0623	0.0119	0.0000	0.2881
			<i>slope</i>	0.0152	0.0022	0.0000	0.0534
	cwb	<i>dbh</i>	<i>dbh</i>	1.8045	0.0303	0.0000	0.0763
			<i>sth</i>	0.9121	0.0375	0.0000	0.2383
			<i>sth</i>	0.9121	0.0375	0.0000	0.2383

Table 13 (continued)

Type	comp	pred	est	se	p	λ
cww		slope	0.0125	0.0011	0.0000	0.6571
		dbh	2.0818	0.0204	0.0000	0.3782
		h	1.0629	0.0453	0.0000	0.5846
cwb		slope	0.0046	0.0006	0.0000	0.3093
		dbh	1.9220	0.0334	0.0000	0.1068
		h	0.9592	0.0655	0.0000	0.2213
sw		slope	0.2854	0.0598	0.0001	0.6089
		dbh	2.3016	0.1341	0.0000	0.6686
		h	- 0.4922	0.1410	0.0017	0.5725
		a	- 0.4054	0.0871	0.0002	0.7158
		cl	0.3846	0.1498	0.0236	0.8257

Column ‘comp’ refers to the fitted component, column ‘pred’ indicates the associated predictors as well as intercept ($intcp = \alpha$ in Eq. 1) and slope parameter ($= \beta_0$). Columns ‘est’, ‘se’ and ‘p’ give parameter estimates, standard errors and associated *p* values. λ denotes the increase in variance due to missingness. C.f. Tables 5 and 6

Table 14 Parameter estimates for *European ash*

Type	comp	pred	est	se	p	λ
Simple	stw	slope	0.0111	0.0028	0.0001	0.0000
		dbh	2.4593	0.0596	0.0000	0.0000
		sth	0.7579	0.0583	0.0000	0.0000
	stb	slope	0.0367	0.0111	0.0011	0.0000
		dbh	1.4515	0.0759	0.0000	0.0000
		sth	0.7298	0.0579	0.0000	0.0000
	cww	slope	0.0220	0.0012	0.0000	0.0000
		dbh	2.0683	0.0153	0.0000	0.0000
		h	0.9050	0.0291	0.0000	0.0000
cwb	slope	0.0006	0.0001	0.0000	0.0000	
	dh	1.7301	0.0173	0.0000	0.0000	
sw	slope	0.0966	0.0149	0.0000	0.0000	
	dbh	1.9989	0.0504	0.0000	0.0000	
Full	stw	slope	0.0331	0.0106	0.0019	0.0000
		dbh	2.6426	0.0920	0.0000	0.0000
		sth	0.8950	0.0602	0.0000	0.0000
	stb	a	- 0.3668	0.1046	0.0005	0.0000
		slope	0.6414	0.3332	0.0552	0.0000
		dbh	2.6680	0.2008	0.0000	0.0000
	cww	sth	0.7244	0.0841	0.0000	0.0000
		h	- 2.2208	0.3469	0.0000	0.0000
		slope	0.0176	0.0014	0.0000	0.0000
	cwb	dbh	2.0552	0.0247	0.0000	0.0000
		h	0.9872	0.0453	0.0000	0.0000
		slope	- 1.5154	0.3348	0.0000	0.0000
dh	dh	0.4606	0.1297	0.0004	0.0000	

Table 14 (continued)

Type	comp	pred	est	se	p	λ
sw		upd	1.8394	0.2161	0.0000	0.0000
		hsl	- 0.8438	0.0521	0.0000	0.0000
		slope	0.1277	0.0236	0.0000	0.0000
		dbh	1.3032	0.1035	0.0000	0.0000
		cl	0.8110	0.1163	0.0000	0.0000

Column ‘comp’ refers to the fitted component, column ‘pred’ indicates the associated predictors as well as intercept ($intcp = \alpha$ in Eq. 1) and slope parameter ($= \beta_0$). Columns ‘est’, ‘se’ and ‘p’ give parameter estimates, standard errors and associated *p* values. λ denotes the increase in variance due to missingness. C.f. Tables 5 and 6

Table 15 Parameter estimates for *Sycamore maple*

Type	comp	pred	est	se	p	λ
Simple	stw	slope	0.0596	0.0311	0.0928	0.8844
		dbh	1.9934	0.1214	0.0000	0.8741
		sth	0.8314	0.0806	0.0000	0.7270
	stb	slope	0.0121	0.0058	0.0644	0.8102
		dbh	1.8062	0.1332	0.0000	0.8452
		sth	0.8178	0.1266	0.0001	0.8561
	cww	slope	0.0170	0.0025	0.0000	0.8070
		dbh	2.0710	0.0354	0.0000	0.7156
		h	0.9317	0.0607	0.0000	0.6975
	cwb	slope	0.0040	0.0004	0.0000	0.2680
		dbh	2.0287	0.0229	0.0000	0.0975
		h	0.7446	0.0447	0.0000	0.2014
sw	slope	0.0426	0.0127	0.0015	0.3281	
	dbh	2.1166	0.1000	0.0000	0.3504	
Full	stw	slope	0.0488	0.0291	0.1317	0.8721
		dbh	2.0446	0.1245	0.0000	0.8362
		sth	0.8127	0.0780	0.0000	0.6192
	stb	slope	0.0094	0.0039	0.0275	0.6089
		dbh	1.8599	0.1024	0.0000	0.6529
		sth	0.8212	0.0917	0.0000	0.6275
	cww	slope	0.0162	0.0021	0.0000	0.1928
		dbh	1.5643	0.1572	0.0000	0.3514
		h	0.9415	0.0791	0.0000	0.3012
	cwb	upd	0.5472	0.1642	0.0021	0.4400
		slope	0.0041	0.0010	0.0001	0.3677
		dbh	2.0251	0.0546	0.0000	0.1289
sw	h	0.7476	0.1140	0.0000	0.3039	
	intcp	7.1339	0.9300	0.0000	0.1779	
	slope	0.0007	0.0010	0.4819	0.2640	
cl	dbh	1.6367	0.3151	0.0000	0.1643	
	cl	2.2019	0.5073	0.0001	0.2763	

Column ‘comp’ refers to the fitted component, column ‘pred’ indicates the associated predictors as well as intercept ($intcp = \alpha$ in Eq. 1) and slope parameter ($= \beta_0$). Columns ‘est’, ‘se’ and ‘p’ give parameter estimates, standard errors and associated *p*-values. λ denotes the increase in variance due to missingness. C.f. Tables 5 and 6

Appendix C: Estimated variance-covariance matrices

The given matrices in this section are pooled from all repeated analyses including both, the within imputation

variance and the between imputation variance. On the diagonal (in *italics*), standard deviations of the errors are given; the lower triangular matrix gives the covariances of the errors between the different components and the upper triangular matrix shows the respective correlations.

Table 16 Variance-covariance matrix of the errors for *Norway spruce* (simple model)

	stw	stb	stwb	cww	cwb	cwwb	sw	nd	agb
stw	<i>5e-04</i>	0.8124	0.9955	0.3201	0.1696	0.3193	0.1211	0.1007	0.3711
stb	7.07e-08	<i>2e-04</i>	0.839	0.1478	0.3112	0.1811	0.1042	0.0853	0.2459
stwb	2.56e-07	8.12e-08	<i>5e-04</i>	0.3114	0.1848	0.3138	0.1216	0.1013	0.3677
cww	2.28e-06	3.95e-07	2.46e-06	<i>0.0148</i>	0.4997	0.9906	0.3281	0.2602	0.8892
cwb	3.03e-07	2.09e-07	3.67e-07	2.74e-05	<i>0.0037</i>	0.5932	0.2518	0.2126	0.5628
cwwb	3.24e-06	6.91e-07	3.54e-06	3.09e-04	4.64e-05	<i>0.0211</i>	0.3355	0.2661	0.8996
sw	9.36e-07	3.03e-07	1.05e-06	7.79e-05	1.5e-05	1.14e-04	<i>0.0161</i>	0.7125	0.6567
nd	1.18e-06	3.77e-07	1.32e-06	9.39e-05	1.93e-05	1.37e-04	2.79e-04	<i>0.0244</i>	0.5806
agb	5.55e-06	1.38e-06	6.11e-06	4.08e-04	6.49e-05	5.89e-04	3.28e-04	4.4e-04	<i>0.0311</i>

Values are averaged from each of ten imputation based analyses including the within imputation variance and the between imputation variance. On the diagonal (*italics*), standard deviations of the errors are given; the lower triangular matrix gives the covariances of the errors between the different components and the upper triangular matrix shows the corresponding correlations

Table 17 Variance-covariance matrix of the errors for *Silver fir* (simple model)

	stw	stb	stwb	cww	cwb	cwwb	sw	nd	agb
stw	<i>0.0046</i>	0.8275	0.9635	0.0357	- 0.2046	0.0079	- 0.3116	0.4273	- 0.0706
stb	1.37e-06	<i>4e-04</i>	0.8965	- 0.1338	- 0.1351	- 0.1106	- 0.1371	0.4933	- 0.0726
stwb	2.52e-05	1.81e-06	<i>0.0056</i>	0.0216	- 0.1971	- 0.0016	- 0.2964	0.4343	- 0.0754
cww	2.79e-05	- 8.09e-06	2.06e-05	<i>0.1687</i>	0.7047	0.9567	0.0332	- 0.1863	0.7403
cwb	- 2.13e-06	- 1.09e-07	- 2.49e-06	2.67e-04	<i>0.0022</i>	0.7384	0.5022	- 0.038	0.8367
cwwb	4.52e-05	- 4.89e-05	- 1.11e-05	1.99e-01	2.04e-03	<i>1.2335</i>	0.0305	- 0.2074	0.7905
sw	- 3.95e-06	- 1.34e-07	- 4.57e-06	1.53e-05	3.08e-06	1.03e-04	<i>0.0027</i>	0.1652	0.506
nd	1.99e-05	1.78e-06	2.46e-05	- 3.16e-04	- 8.56e-07	- 2.57e-03	4.54e-06	<i>0.01</i>	0.1745
agb	- 3.66e-04	- 2.91e-05	- 4.76e-04	1.4e-01	2.1e-03	1.09e+00	1.55e-03	1.96e-03	<i>1.1193</i>

Table 18 Variance-covariance matrix of the errors for *Silver fir* (full model)

	stw	stb	stwb	cww	cwb	cwwb	sw	nd	agb
stw	<i>0.003</i>	0.8508	0.8643	0.3243	- 0.0383	0.2962	0.0612	0.2276	0.2981
stb	4.9e-07	<i>2e-04</i>	0.8113	0.166	0.0087	0.1639	0.0871	0.3811	0.3011
stwb	1.35e-05	8.03e-07	<i>0.0052</i>	0.3062	- 0.0156	0.3027	0.1153	0.1732	0.3094
cww	2.15e-05	6.96e-07	3.49e-05	<i>0.022</i>	0.2325	0.9602	0.1108	0.0643	0.6408
cwb	- 1.97e-07	2.83e-09	- 1.38e-07	8.71e-06	<i>0.0017</i>	0.2938	- 0.0751	- 0.0146	0.1283
cwwb	2.77e-05	9.71e-07	4.87e-05	6.54e-04	1.55e-05	<i>0.031</i>	0.0992	0.0464	0.6398
sw	2.2e-07	1.98e-08	7.13e-07	2.9e-06	- 1.53e-07	3.67e-06	<i>0.0012</i>	0.1578	0.6619
nd	6.89e-06	7.3e-07	9.02e-06	1.42e-05	- 2.5e-07	1.44e-05	1.89e-06	<i>0.01</i>	0.5045
agb	8.23e-05	5.26e-06	1.47e-04	1.29e-03	2e-05	1.82e-03	7.22e-05	4.64e-04	<i>0.0916</i>

Table 19 Variance-covariance matrix of the errors for *Douglas fir* (simple model)

	stw	stb	stwb	cww	cwb	cwwb	sw	nd	agb
stw	$3e-04$	0.428	0.9858	0.3808	- 0.0264	0.3587	0.1386	0.0872	0.3196
stb	$7.53e-08$	$6e-04$	0.55	0.1672	0.3958	0.227	0.0048	- 0.0165	0.1471
stwb	$1.13e-07$	$1.39e-07$	$4e-04$	0.3687	0.0514	0.3635	0.1256	0.0931	0.3147
cww	$1.94e-07$	$1.88e-07$	$2.7e-07$	0.0018	0.2913	0.9717	0.3067	0.308	0.8381
cwb	- $8.79e-09$	$2.92e-07$	$2.47e-08$	$6.21e-07$	0.0012	0.4471	0.0258	0.2187	0.3684
cwwb	$5.75e-07$	$8.05e-07$	$8.39e-07$	$9.96e-06$	$3e-06$	0.0057	0.3107	0.3528	0.8755
sw	$1.16e-06$	$8.81e-08$	$1.51e-06$	$1.64e-05$	$9.04e-07$	$5.23e-05$	0.0296	0.8124	0.6893
nd	$8.04e-08$	- $3.37e-08$	$1.24e-07$	$1.82e-06$	$8.46e-07$	$6.56e-06$	$7.88e-05$	0.0033	0.6647
agb	$2.2e-06$	$2.24e-06$	$3.11e-06$	$3.68e-05$	$1.06e-05$	$1.21e-04$	$4.98e-04$	$5.3e-05$	0.0244

Table 20 Variance-covariance matrix of the errors for *Douglas fir* (full model)

	stw	stb	stwb	cww	cwb	cwwb	sw	nd	agb
stw	$2e-04$	0.3226	0.991	0.3756	- 0.1977	0.3262	0.1302	0.1112	0.3107
stb	$2.57e-09$	0	0.3956	0.0413	0.5037	0.1536	- 0.0395	- 0.0187	0.1004
stwb	$4.75e-08$	$5.32e-09$	$3e-04$	0.3574	- 0.1443	0.3227	0.1311	0.1136	0.3115
cww	$2.13e-07$	$6.59e-09$	$3.42e-07$	0.0034	0.0265	0.9736	0.2832	0.1774	0.7928
cwb	- $3.24e-08$	$2.32e-08$	- $3.99e-08$	$8.69e-08$	0.001	0.2226	- 0.1615	- 0.0333	0.0852
cwwb	$3.58e-07$	$4.74e-08$	$5.98e-07$	$2.14e-05$	$1.41e-06$	0.0065	0.2504	0.18	0.8094
sw	$1.56e-07$	- $1.33e-08$	$2.65e-07$	$6.79e-06$	- $1.12e-06$	$1.16e-05$	0.0071	0.7679	0.5745
nd	$5.3e-08$	- $2.5e-09$	$9.13e-08$	$1.69e-06$	- $9.16e-08$	$3.32e-06$	$1.54e-05$	0.0028	0.4909
agb	$1.48e-06$	$1.34e-07$	$2.51e-06$	$7.56e-05$	$2.34e-06$	$1.49e-04$	$1.16e-04$	$3.93e-05$	0.0283

Table 21 Variance-covariance matrix of the errors for *Scots pine* (simple model)

	stw	stb	stwb	cww	cwb	cwwb	sw	nd	agb
stw	$6e-04$	0.351	0.8252	0.3296	0.0933	0.3265	- 0.042	0.0308	0.3095
stb	$4.28e-08$	$2e-04$	0.34	0.0268	0.308	0.0728	- 0.0631	- 0.0491	0.0482
stwb	$1.14e-06$	$1.68e-07$	0.0024	0.2775	0.127	0.2861	- 0.0179	0.027	0.287
cww	$4e-06$	$1.16e-07$	$1.37e-05$	0.0208	0.2853	0.9812	- 0.0096	0.121	0.866
cwb	$2.17e-07$	$2.55e-07$	$1.2e-06$	$2.36e-05$	0.004	0.4147	- 0.0316	- 0.0174	0.3613
cwwb	$9.29e-06$	$7.39e-07$	$3.31e-05$	$9.93e-04$	$8.02e-05$	0.0487	0.012	0.116	0.895
sw	- $1.66e-06$	- $8.92e-07$	- $2.89e-06$	- $1.35e-05$	- $8.51e-06$	$3.95e-05$	0.0677	0.3837	0.4014
nd	$1.48e-07$	- $8.4e-08$	$5.26e-07$	$2.07e-05$	- $5.67e-07$	$4.63e-05$	$2.13e-04$	0.0082	0.3674
agb	$1.07e-05$	$5.96e-07$	$4.05e-05$	$1.07e-03$	$8.52e-05$	$2.59e-03$	$1.61e-03$	$1.79e-04$	0.0594

Table 22 Variance-covariance matrix of the errors for *Scots pine* (full model)

	stw	stb	stwb	cww	cwb	cwwb	sw	nd	agb
stw	$4e-04$	0.4034	0.9897	0.2999	0.0079	0.2932	0.0482	0.0717	0.339
stb	$3.73e-08$	$2e-04$	0.5006	0.0139	0.2679	0.0703	- 0.0367	- 0.0055	0.0678
stwb	$2.33e-07$	$5.55e-08$	$5e-04$	0.2816	0.0592	0.2872	0.0402	0.0689	0.3291
cww	$2.57e-06$	$5.58e-08$	$2.89e-06$	0.0193	0.3246	0.965	- 0.0592	0.0571	0.841
cwb	$1.22e-08$	$1.94e-07$	$1.09e-07$	$2.17e-05$	0.0035	0.4663	- 0.1336	- 0.0423	0.3487
cwwb	$4.88e-06$	$5.5e-07$	$5.73e-06$	$7e-04$	$6.06e-05$	0.0375	- 0.0419	0.0634	0.8801
sw	$9.48e-07$	- $3.39e-07$	$9.49e-07$	- $5.08e-05$	- $2.05e-05$	- $6.97e-05$	0.0444	0.2447	0.3915
nd	$2.29e-07$	- $8.32e-09$	$2.64e-07$	$7.95e-06$	- $1.06e-06$	$1.71e-05$	$7.82e-05$	0.0072	0.284
agb	$7.26e-06$	$6.83e-07$	$8.44e-06$	$7.84e-04$	$5.83e-05$	$1.59e-03$	$8.38e-04$	$9.87e-05$	0.0483

Table 23 Variance-covariance matrix of the errors for *European beech* (simple model)

	stw	stb	stwb	cww	cwb	cwwb	sw	agb
stw	$8e-04$	0.682	0.9817	0.1977	0.0894	0.1737	0.0128	0.2232
stb	$8.37e-08$	$2e-04$	0.709	0.072	0.251	0.0915	- 0.0104	0.1226
stwb	$6.8e-07$	$9.19e-08$	$9e-04$	0.1936	0.103	0.1693	0.011	0.2202
cww	$3.4e-06$	$2.32e-07$	$3.51e-06$	0.0212	0.5631	0.908	0.0507	0.793
cwb	$2.36e-07$	$1.24e-07$	$2.87e-07$	$3.89e-05$	0.0033	0.6216	0.0169	0.5259
cwwb	$3.69e-05$	$3.64e-06$	$3.8e-05$	$5.05e-03$	$5.31e-04$	0.2623	0.1033	0.8756
sw	$8.69e-07$	- $1.32e-07$	$7.86e-07$	$8.97e-05$	$4.59e-06$	$2.26e-03$	0.0835	0.5329
agb	$3.4e-05$	$3.49e-06$	$3.54e-05$	$3.16e-03$	$3.22e-04$	$4.32e-02$	$8.36e-03$	0.1879

Table 24 Variance-covariance matrix of the errors for *European beech* (full model)

	stw	stb	stwb	cww	cwb	cwwb	sw	agb
stw	$8e-04$	0.6907	0.9818	0.205	0.0924	0.1955	- 0.0025	0.2308
stb	$9.02e-08$	$2e-04$	0.7247	0.0707	0.2378	0.0884	- 0.0252	0.119
stwb	$6.76e-07$	$1e-07$	$9e-04$	0.1928	0.1029	0.185	- 0.006	0.2245
cww	$3.26e-06$	$2.25e-07$	$3.24e-06$	0.0197	0.5705	0.9655	0.0388	0.8166
cwb	$2.5e-07$	$1.29e-07$	$2.94e-07$	$3.76e-05$	0.0033	0.6317	- 0.0074	0.5064
cwwb	$5.49e-06$	$4.97e-07$	$5.49e-06$	$6.61e-04$	$7.34e-05$	0.0347	0.0455	0.8275
sw	- $1.57e-07$	- $3.15e-07$	- $3.98e-07$	$5.91e-05$	- $1.91e-06$	$1.22e-04$	0.0773	0.5422
agb	$7.03e-06$	$7.26e-07$	$7.23e-06$	$6.07e-04$	$6.39e-05$	$1.09e-03$	$1.58e-03$	0.0377

Table 25 Variance-covariance matrix of the errors for *Oak* (simple model)

	stw	stb	stwb	cww	cwb	cwwb	sw	agb
stw	0.001	0.5677	0.9784	0.4514	0.0524	0.375	0.0594	0.39
stb	$1.04e-07$	$2e-04$	0.557	0.0789	0.2107	0.0834	- 0.0177	0.1117
stwb	$1.53e-06$	$1.52e-07$	0.0015	0.4177	0.0546	0.3519	0.0678	0.3814
cww	$8.01e-06$	$2.46e-07$	$1.11e-05$	0.0174	0.2564	0.8966	0.1843	0.8138
cwb	$1.32e-07$	$9.29e-08$	$2.05e-07$	$1.1e-05$	0.0025	0.4327	0.0642	0.3824
cwwb	$4.03e-05$	$1.57e-06$	$5.66e-05$	$1.64e-03$	$1.12e-04$	0.1053	0.231	0.9268
sw	$2.65e-06$	- $1.38e-07$	$4.52e-06$	$1.4e-04$	$6.9e-06$	$1.06e-03$	0.0437	0.5384
agb	$3.99e-05$	$2e-06$	$5.83e-05$	$1.42e-03$	$9.42e-05$	$9.77e-03$	$2.36e-03$	0.1001

Table 26 Variance-covariance matrix of the errors for *Oak* (full model)

	stw	stb	stwb	cww	cwb	cwwb	sw	agb
stw	$9e-04$	0.5527	0.9544	0.2298	0.0092	0.1722	$9e-04$	0.2283
stb	$9.13e-08$	$2e-04$	0.5446	0.0537	0.2107	0.0749	0.026	0.1156
stwb	$1.46e-06$	$1.61e-07$	0.0017	0.2198	0.0201	0.1728	0.0012	0.243
cww	$2.26e-06$	$1.03e-07$	$3.88e-06$	0.0107	0.3341	0.9349	0.1584	0.8563
cwb	$2.1e-08$	$9.29e-08$	$8.19e-08$	$8.78e-06$	0.0025	0.4685	0.0835	0.4274
cwwb	$1.28e-05$	$1.08e-06$	$2.31e-05$	$8.07e-04$	$9.32e-05$	0.0809	0.1969	0.925
sw	$3.98e-08$	$2.12e-07$	$9.21e-08$	$7.69e-05$	$9.35e-06$	$7.24e-04$	0.0455	0.5052
agb	$2.04e-05$	$2.01e-06$	$3.89e-05$	$8.86e-04$	$1.02e-04$	$7.25e-03$	$2.23e-03$	0.0969

Table 27 Variance-covariance matrix of the errors for *European ash* (simple model)

	stw	stb	stwb	cww	cwb	cwwb	sw	agb
stw	0.0016	- 0.0765	0.9654	- 0.0158	- 0.1363	- 0.0104	0.1968	0.1522
stb	- 5.98e-07	0.0049	0.1384	0.1827	0.638	0.2552	0.0833	0.2327
stwb	3.73e-06	1.62e-06	0.0024	0.0474	0.0113	0.0608	0.2319	0.2097
cww	- 2.64e-08	9.26e-07	1.19e-07	0.001	0.6656	0.9794	0.2515	0.8801
cwb	- 1.26e-06	1.79e-05	1.56e-07	3.99e-06	0.0058	0.765	0.3201	0.7425
cwwb	- 1.15e-07	8.61e-06	1.01e-06	7.05e-06	3.05e-05	0.0069	0.2609	0.9195
sw	3.26e-06	4.19e-06	5.76e-06	2.7e-06	1.9e-05	1.87e-05	0.0103	0.5891
agb	1e-05	4.66e-05	2.07e-05	3.76e-05	1.76e-04	2.62e-04	2.5e-04	0.0411

Table 28 Variance-covariance matrix of the errors for *European ash* (full model)

	stw	stb	stwb	cww	cwb	cwwb	sw	agb
stw	0.0054	- 0.2537	0.9839	- 0.0501	0.0334	0.0136	0.208	0.1418
stb	- 9.32e-06	0.0068	- 0.0879	0.0712	- 0.0558	0.0186	- 0.0864	- 0.0279
stwb	2.57e-05	- 2.85e-06	0.0048	- 0.0311	0.0295	0.0209	0.195	0.1431
cww	- 2.83e-07	5e-07	- 1.55e-07	0.001	0.3128	0.9527	0.1122	0.8597
cwb	3.97e-08	- 8.24e-08	3.09e-08	7.11e-08	2e-04	0.4957	0.1447	0.4836
cwwb	7.54e-07	1.28e-06	1.02e-06	1.01e-05	1.1e-06	0.0102	0.1313	0.9037
sw	6.8e-06	- 3.51e-06	5.63e-06	7.02e-07	1.9e-07	8.04e-06	0.006	0.5344
agb	6.1e-06	- 1.49e-06	5.44e-06	7.07e-06	8.36e-07	7.28e-05	2.54e-05	0.0079

Table 29 Variance-covariance matrix of the errors for *Sycamore maple* (simple model)

	stw	stb	stwb	cww	cwb	cwwb	sw	agb
stw	0.0171	0.4416	0.998	0.0584	0.0213	0.0534	- 0.0061	0.0724
stb	1.66e-05	0.0022	0.4407	0.0776	-0.0187	0.0631	- 0.0785	0.0683
stwb	3.63e-04	2.06e-05	0.0213	0.0542	0.0227	0.0499	0	0.0732
cww	2.25e-06	3.84e-07	2.6e-06	0.0023	0.9308	0.9984	0.2799	0.8609
cwb	1.33e-06	- 1.49e-07	1.76e-06	7.62e-06	0.0036	0.9487	0.4115	0.8941
cwwb	2.96e-06	4.5e-07	3.45e-06	7.31e-06	1.12e-05	0.0032	0.3007	0.8724
sw	- 1.35e-07	- 2.24e-07	3.65e-10	8.21e-07	1.94e-06	1.27e-06	0.0013	0.7
agb	8.45e-06	1.02e-06	1.06e-05	1.32e-05	2.21e-05	1.93e-05	6.21e-06	0.0068

Table 30 Variance-covariance matrix of the errors for *Sycamore maple* (full model)

	stw	stb	stwb	cww	cwb	cwwb	sw	agb
stw	0.0171	0.4416	0.998	0.0661	0.0213	0.0456	- 0.0064	0.0817
stb	1.66e-05	0.0022	0.4407	0.0757	-0.0187	0.0267	- 0.013	0.1447
stwb	3.63e-04	2.06e-05	0.0213	0.0632	0.0227	0.0428	0.0012	0.0854
cww	1.11e-06	1.63e-07	1.32e-06	0.001	0.7821	0.9576	- 0.0926	0.6431
cwb	1.33e-06	- 1.49e-07	1.76e-06	2.79e-06	0.0036	0.8477	- 0.1215	0.6014
cwwb	2.49e-05	1.87e-06	2.91e-05	3e-05	9.82e-05	0.0319	- 0.0934	0.6574
sw	- 7.95e-08	- 2.07e-08	1.8e-08	- 6.59e-08	- 3.19e-07	- 2.16e-06	7e-04	0.4952
agb	1.24e-05	2.82e-06	1.61e-05	5.6e-06	1.94e-05	1.86e-04	3.18e-06	0.0089

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