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# Models for predicting aboveground biomass of European beech (*Fagus sylvatica* L.) in the Czech Republic

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**ABSTRACT**: We developed optimal models for predicting the aboveground biomass of European beech (*Fagus sylvatica* L.) applicable to the national forest inventory data of the Czech Republic. The models were based on a data set of 81 beech trees collected in 19 stands that represent a wide range of stand and site conditions. The relationship between biomass and tree dimensions (diameter *D*, height *H*) was modelled using non-linear regression equations with one (*D*) or two (*D, H*) independent variables and two or three parameters (D2, DH2, DH3 models). Subsequently additional predictor variables, i.e. tree age, site index and altitude, were added to the basic models. The inclusion of tree age (*T*) and altitude (*A*) in the basic DH2 model resulted in the best model for aboveground biomass (DH2AT model). The altitude (*A*) and site index (*S*) were important predictors for stem biomass estimate (DH3AS model). Similarly, branch biomass was predicted in the best way by four-variable model DH2AS.

**Keywords**: biomass function; temperate forests; tree allometry; wood density

The need to quantify the carbon stock in tree biomass in accordance with the requirements of the UNFCCC and its Kyoto protocol (e.g. Teoballdelli et al. 2009; Petersson et al. 2012), the focus on precise information concerning the availability of nutrients in the biomass of forest trees (Augusto et al. 2000; Aksellson et al. 2007; Šrámek et al. 2009) and finally, the pressure for the use of tree biomass as a renewable energy source (Freppaz et al. 2004; Lambert et al. 2005) are main factors that create a greater demand for the accuracy of tree biomass estimate.

The oldest, and at the same time the most accurate, method for the biomass assessment is destructive analysis (Droste 1970; Vinš, Šika 1977; Vyskot 1980). However, the destructive character, labour-intensity and high cost restrict its application on a large scale. It remains, nevertheless, a highly valued source of empirical data that constitute the basis for parameterization of biomass functions. The most common procedures for a non-destructive biomass estimate consist of the application of (1) biomass factors or (2) biomass functions.

Biomass expansion factors (BEF) and biomass expansion and conversion factors (BECF) were developed primarily for a biomass estimate on a national scale to meet the requirement for national greenhouse gas inventories (Lehtonen et al. 2004; Levy et al. 2004; Cienciala et al. 2006). According to Good Practice Guidance for the Land Use, Land Use Change and Forestry Sector of the Intergovernmental Panel on Climate Change (IPCC 2003) the BEF is expressed as the ratio between aboveground and merchantable biomass, while the BECF is the ratio between merchantable volume and aboveground biomass. However, a unified definition of BEF and BECF has not yet been established (Somogyi et al. 2006; Tobin, Nieuwenhuis 2007; Teobaldelli et al. 2009). The unknown uncertainty of the biomass estimate represents a serious drawback of the BEF method (Somogyi et al. 2006; Lehtonen et al.

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2007). Some studies have proved a high degree of imprecision (Wirth et al. 2003; Jalkanen et al. 2005).

The development of species-specific biomass functions employs various approaches: (*i*) the construction of local models for specific sites (Albaugh et al. 2009; Bollandsås et al. 2009), or for specific age classes (Neumann, Jandl 2005; Pajtík et al. 2008, 2011), (*ii*) the development of generalized models based on extensive data sets collected over a large area and representing a wide range of stand and site conditions (Pretzsch 2000; Joosten et al. 2004; Wirth et al. 2004; Wutzler et al. 2008) or based on pseudo-data generated by existing biomass functions (Jenkins et al. 2003; Zianis et al. 2003; Muukkonen 2007).

In most countries the forest biomass estimate on a national level is exclusively based on forest inventory data. Various biomass factors are routinely applied to volume data (Somogyi et al. 2006). Only countries with a high precision forest inventory may rely on the use of tree-level biomass equations. In such a case generalized models enable reliable large-scale biomass prediction (Wirth et al. 2003). If site-specific biomass models are applied, it might introduce a serious bias into the estimate (Jenkins et al. 2003).

To date two studies dealing with beech biomass in the conditions of the Czech Republic have been published (Vyskot 1990; Cienciala et al. 2005). Only the latter study aimed at parameterization of allometric equations. A limited number of trees and sites sampled, however, restricts its applicability on a national scale.

The objective of the present study was to develop optimal models for aboveground, stem and branch biomass of European beech (*Fagus sylvatica* L.) applicable to the National forest inventory (NFI) data in the Czech Republic. The influence of principal tree and site variables on the models performance was investigated.

## MATERIAL AND METHODS

**Study sites and characteristics of sample trees**. Study material comprised newly sampled trees (hereinafter denoted as Šrámek 2012) and previously published data (Vyskot 1990; Cienciala et al. 2005) (Table 1). A recent sampling campaign (2008–2012) completed previously documented data so that most regions with a significant occurrence of beech forests in the Czech Republic were covered (Fig. 1).

Newly selected stands represented site conditions of the given region. At each study site stands of different age were selected: up to 60 years, 60 to 100 years, more than 100 years old. The even-aged, preferably pure beech stands representative of common production forests were sampled. Sample trees (3–5 trees per stand) with dimensions of the mean stem were selected subjectively from the main canopy layer. No damaged trees were included in the sample. Basic measurable information was recorded both before and after felling.

The pooled data set comprised a wide range of DBH 5.7–62.1 cm and of tree heights 7.5–33.9 m (Fig. 2). The number of trees in specific diameter classes was representative with the exception of the largest trees with diameter at breast height (DBH) above 50 cm for which less than 3 trees per diameter class were at disposal.

**Biomass measurements**. Trees were sampled without leaves, during a dormancy period. After felling the main stem was determined and its volume in 2 m or 4 m sections was calculated, depending on the size of the tree. The first stem disc was taken at breast height, the others from the ends of each section. Discs were weighed immediately and their circumference and two orthogonal diameters were measured. At the same time we took a photo of each cross-section to determine its surface area precisely. The upper parts of stems with a diameter of less than

Table 1. Overview of study sites and the characteristics of sample trees

| Author, year | ID | Study site | *n* | Age | DBH (cm) | Height (m) | Altitude (m a.s.l.) | Site index* |
|---|---|---|---|---|---|---|---|---|
|  | ŠRA1 | Deštné v Orl. h. | 9 | 30–140 | 7.4–34.0 | 7.5–26.4 | 770–880 | 20–28 |
|  | ŠRA2 | Melechov | 9 | 25–115 | 12.1–56.5 | 13.2–32.2 | 615–710 | 18–24 |
| Šrámek, 2012 | ŠRA3 | Jablunkov | 9 | 28–83 | 11.2–31.8 | 14.4–32.5 | 550–590 | 30–32 |
|  | ŠRA4 | Bělá pod Prad. | 11 | 17–150 | 8.1–41.2 | 10–29.9 | 770–890 | 24–30 |
|  | ŠRA5 | Kladská | 8 | 32–56 | 11.4–18.5 | 12.3–21.9 | 768–788 | 24–26 |
|  | CIE1 | Jílové u Prahy | 6 | 40–112 | 5.7–40.3 | 9.2–24.1 | 350 | 24–26 |
| Cienciala, 2005 | CIE2 | Trhanov | 7 | 106 | 26.2–39.4 | 29.6–33.9 | 700 | 28 |
|  | CIE3 | Horšovský Týn | 7 | 114 | 30.9–62.1 | 25.2–29.1 | 750 | 28 |
| Vyskot, 1990 | VYS | Babice | 15 | 33–48 | 7.3–22 | 11.7–21.2 | 510 | 32 |

*used to measure the productivity of the site and reports the mean height of a stand at the standard age of 100 years

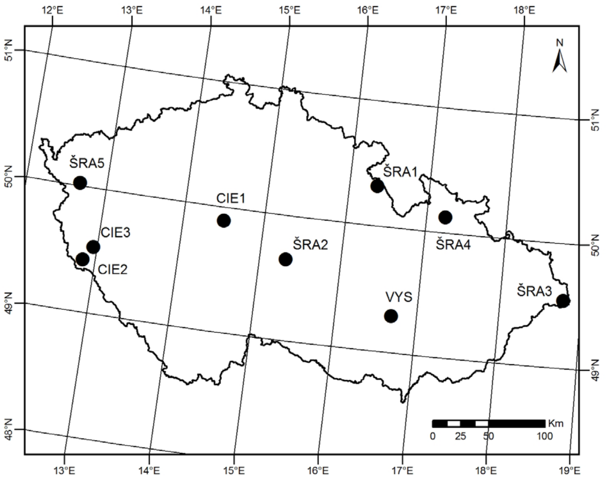

Fig. 1. Locations of study sites

7 cm (measured over bark) were included in the medium-branches category (see below). For the precise assessment of wood density extra stem discs were cut at the lower, middle and upper parts of the stem. The discs were weighed and their volume was determined xylometrically (Vejpustková et al. 2013).

Branches were divided into 4 diameter classes: (1) very small branches with a diameter up to 1.5 cm, (2) small 1.5–3 cm, (3) medium 3–7 cm, (4) large > 7 cm (considered as timber). We selected three sample branches per diameter class and the sorted branches were weighed directly in the field. The following parameters were measured: length, diameter, bark thickness and fresh weight. Sample branches and stem discs were transported to the laboratory where they were dried to a constant weight (dry weight).

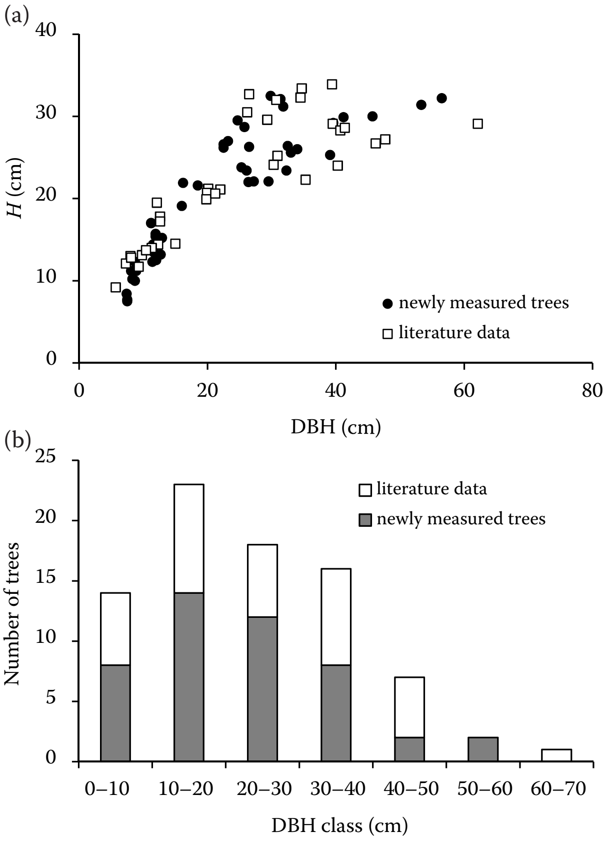

Fig. 2. DBH-height relationship of sample trees (a), distribution of sample trees in DBH classes (b)

Dry weight of specific discs for density assessment was used to assess the conventional wood density (Eq. 1). The mean value of wood density of a given sample tree was applied for converting the stem volume to its biomass. Branch biomass was calculated using the ratio between fresh weight and dry weight of sample branches.

$$\rho = \frac{m_o}{V_{\max}} \qquad (1)$$

where:

$\rho$ – conventional wood density,

$m_o$ – dry weight of wood,

$V_{\max}$ – fresh volume of wood.

**Parameterization of biomass functions**. In the present study the aboveground biomass is defined as the total aboveground biomass of stem and branches excluding the stump. Parameterization of regression equations was based on a pooled data set of 81 beech trees. The same data set was used to develop functions for aboveground, stem and branch biomass. We used the basic set of continuous predictor variables: DBH ($D$), height ($H$), age ($T$), altitude ($A$), site index ($S$).

The relation between biomass and predictors was described by the widely used biomass functions (Zianis et al. 2005) in a non-linear form (Eqs. 2– 4).

$$y(D) = p_1 D^{p_2} \qquad (2)$$

$$y(D,H) = p_1 \left(D^2 H\right)^{p_2} \qquad (3)$$

$$y(D,H) = p_1 D^{p_2} H^{p_3} \qquad (4)$$

where:

$y$ – component biomass,

$D$ – diameter,

H – height,

$p_1$–$p_3$ – parameters.

Subsequently, different combinations of additional variables tree age, altitude and site index were introduced into the basic models. Additive (Eq. 5) and multiplicative forms of functions (Eq. 6) were verified. These additional predictors and corresponding parameters are denoted as $f_i$, and $p_i$, respectively.

$$y(D, H, f) = y(D, H) + \sum_i p_i f_i \qquad (5)$$

$$y(D, H, f) = y(D, H) + \prod_i f_i^{p_i} \qquad (6)$$

In total we tested 45 different models for each component. Parameters were estimated by means of nls function using the R statistical software package (R Core Team 2012). Selection of the best model was based on Akaike Information Criterion *AIC* (Sakamoto et al. 1986) (Eq. 7), other criteria were root mean square error *RMSE* (Eq. 8) and coefficient of determination $R^2$ (Eq. 9).

$$AIC = n\left(1 + \ln\left(2\pi\, MSE\right)\right) + 2(k+1) \tag{7}$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{n-k}} \tag{8}$$

$$R^2 = 1 - \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{\sum_{i=1}^{n}(y_i - \bar{y})^2} \tag{9}$$

where:

$y_i$ – is component biomass of $i^{\text{th}}$ sample,

$\hat{y}_i$ – predicted component biomass,

$n$ – number of samples,

$k$ – number of estimated parameters, mean square error *MSE*.

$$MSE = \sum_{i=1}^{n}(y_i - \hat{y}_i)^2 \Big/ (n-k) \tag{10}$$

**Model validation**. As no explicit validation data set was available, cross-validation was used to predict the model fit to a hypothetical validation set. Leave-one-out method of cross-validation (LOOCV) was employed (Arlot, Celisse 2010). LOOCV involves using a single observation from the original sample as the validation data, and the remaining observations as the training data. This is repeated so that each observation in the sample is used once as the validation data. In our study the root mean square error of cross-validation (*RMSECV*) was calculated as a measure of the anticipated level of model fit. An expected prediction error was expressed as a relative mean error of cross-validation RMECV (Eq. 11).

$$RMECV = \frac{100}{n}\sum_{i=1}^{n}\frac{\left|y_i - \hat{y}_i\right|}{y_i} \quad (\%) \tag{11}$$

The model performance was compared with the other published beech biomass functions that refer to the area of Central Europe. Altogether four studies applying different approaches to the model development were selected. Based on an extensive data set (443 sample trees) Wutzler et al. (2008) developed generic functions using non-linear mixed-effects models. For comparison the best models, including additional covariates, were chosen. Joosten et al. (2004) employed the linear regression method to establish the functions for predicting aboveground biomass carbon. These equations are based on a data set of 116 sample beech trees from North Rhine-Westphalia. For the purpose of comparison the carbon content was recalculated to the aboveground biomass by dividing by 0.5. Muukkonen (2007) derived generalized biomass equations for the temperate zone. Instead of tree measurements already published equations were used for the meta-analysis. Cienciala et al. (2005) analysed the data of 20 trees originating from 3 localities in the Czech Republic and parameterised the local allometric equations.

To explore biomass additivity (Parresol 1999), i.e. the equalness of the sum of branch and of stem biomass estimates with the directly estimated aboveground biomass, a test data set was created using data from four permanent monitoring plots located in different regions in the Czech Republic and covering an altitude range of 350–940 m a.s.l. with a site index of 24–30. Each plot was represented by 40 randomly selected beech trees, i.e. a total of 160 trees. The diameters of trees ranged from 5.4 to 82.7 cm and the tree heights between 4.9 and 42.2 m. The aboveground biomass predicted by the single best equation (DH2AT) was compared with the sum of branch and stem biomass estimated using the best models, DH3AS and DH2AS, respectively.

## RESULTS

### Observed data

Total aboveground biomass and its components showed a strong relationship to DBH (Fig. 3a–c). However, the dependence on tree height was weaker (Fig. 3d–f). The total aboveground, stem and branch biomass observed at particular sites exhibited a similar exponential relationship to DBH, which made it possible to approximate it by means of a simple exponential function with DBH as an independent variable (Fig. 3a–c). The ratio of stem biomass to aboveground biomass amounted to 72% for beech trees up to 80 years of age; for mature trees it increased to 82% (Fig. 4). Conventional wood density ranged between 529 and 621 kg·m$^{-3}$with the mean value of 585 kg·m$^{-3.}$

### Biomass functions

The results of model parameterization are presented in Table 2. For each component the parameters of the five best models are listed. The first three equa-

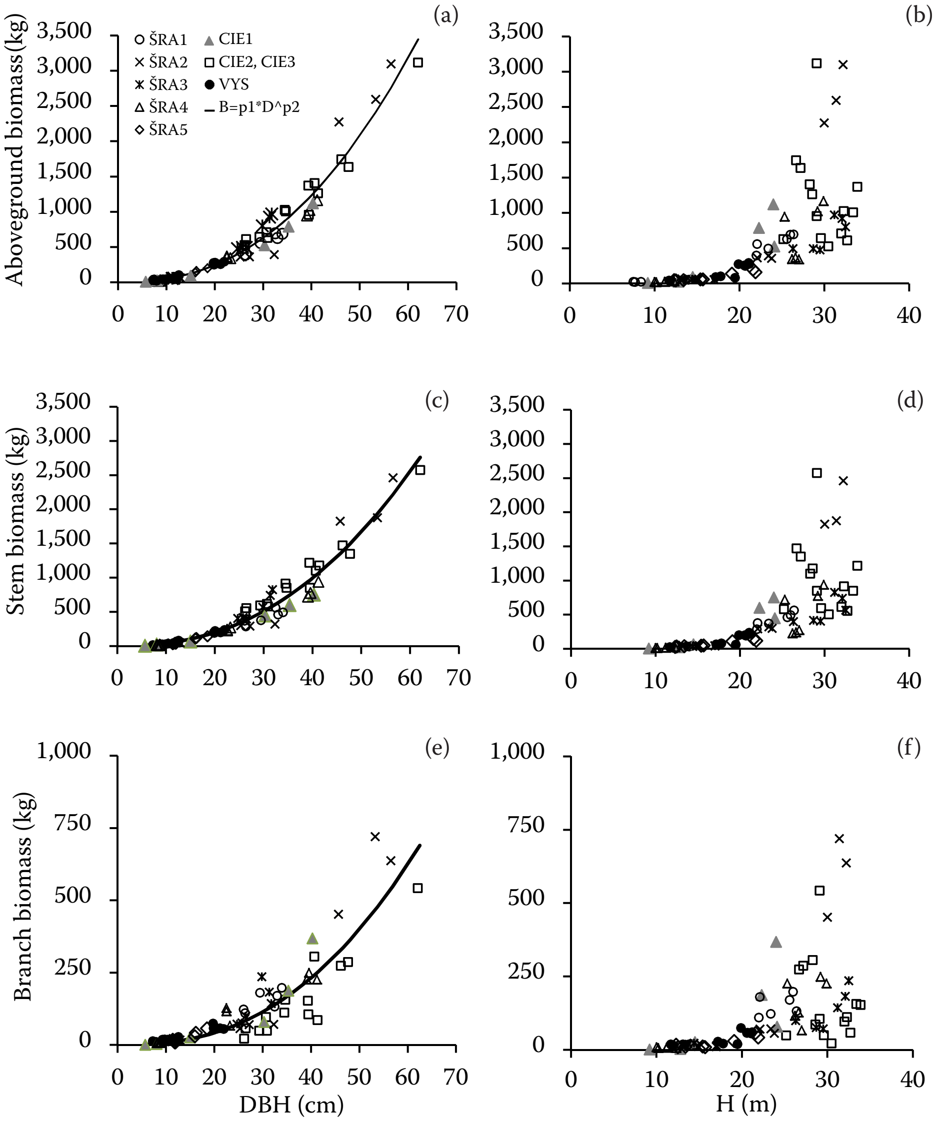

Fig. 3. Observed biomass at particular sites plotted against diameter at breast height (a–c) and tree height (d–f). Derived biomass data according to Eq. 2 are plotted as a line (a–c)

tions represent the basic biomass functions in a nonlinear form (Eq. 2–4) in which tree dimensions (*D*, *H*) act as independent variables. The next two equations are the best models that comprise additional predictors (*T*, *A*, *S*). It was revealed that the multiplicative form of the function (Eq. 6) matched the empirical data better than did the additive form.

In regard to aboveground biomass the basic DH2 and DH3 models (two predictors *D*, *H* and two or three parameters) explained identically 97.8% of empirical data variability. The fit of simple D2 model was weaker ($R^2$ = 96.1%). The incorporation of altitude in DH2 model significantly decreased *AIC* and *RMSE* values (DH2A model). Including tree age (*T*) as a next predictor improved the model fit slightly (DH2AT model), whereas adding the fifth predictor, site index (*S*), had no impact on model performance (not mentioned in Table 2).

The fit of regression models for stem biomass was comparable with the fit of models for aboveground biomass. The basic allometric functions DH3 and DH2 explained 97.6% and 97.5% of stem biomass data variability, respectively. Adding altitude and site index variables into the models had a low effect on the share of explained variability ($R^2$ = 97.9%), however it improved the values of *AIC* and *RMSE*. Thus DH3AS model is considered as the best.

In general, a weaker fit was recorded for branch biomass models. Interestingly, the simple D2 model achieved a fit comparable with that of DH2 and DH3 models. The inclusion of altitude and site index significantly improved the model performance. DH2AS and DH3AS models are regarded as being the most suitable for the branch biomass estimate.

The regression coefficients of the models listed were statistically significant (α = 0.05) with the exception of tree age in DH2AT model for aboveground biomass and tree height in DH3 model for branch biomass (Table 2). Increasing altitude had a significant negative effect on the biomass of all

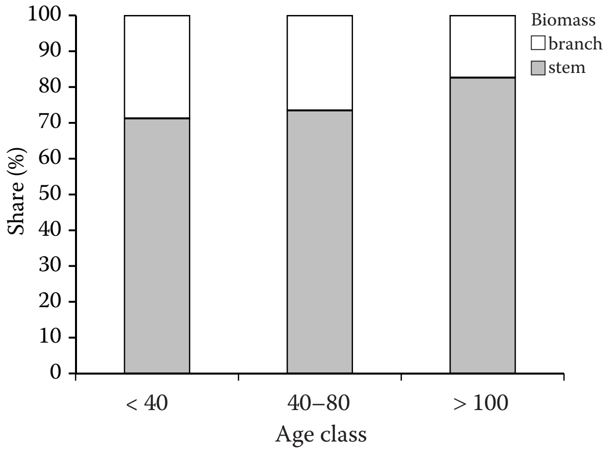

Fig. 4. Proportions of stem and branch biomass for different age classes: up to 40 years, 40–80 years, more than 100 years

components. The increasing quality of site expressed in the values of site index resulted in higher stem biomass; on the other hand, on better sites branch biomass decreased.

### Model validation

The relative mean error of cross-validation (*RMECV*) ranged between 15% and 21% for aboveground biomass for which the lowest value was reached by DH2AT model (Table 2). The error of stem biomass estimates was 14–17% apart from the simple D2 model with a mean error of approximately 30%. For branches *RMECV* increased to 48%; there were no significant differences between specific models.

The selected published models fitted the observed aboveground biomass well. There were no significant differences in the model performance across the whole range of tree dimensions (Fig. 5a). The same is true in regard to the stem biomass with the exception of the largest trees DBH > 45 cm. The DH3ATS and D3 models of Wutzler and Muukkonen, respectively, slightly underestimated the stem biomass of larger trees (Fig. 5b). The branch biomass was overestimated by Wutzler DH3AS and Muukkonen D2 models for trees of medium and large dimensions while the Cienciala DH3 model underestimated it. Branch biomass prediction varied considerably between all studies examined (Fig. 5c).

Biomass additivity was investigated for the entire test data set in a total of 160 trees. Using the best single equation, the estimated aboveground biomass reached a total of 213.1 t; the result of individual biomass component prediction was 173.6 t and 39.4 t for stem and branches, respectively. The relative difference between single-equation and additive estimate of aboveground biomass amounted to 5.06%.

## DISCUSSION

The models were derived for a relatively small area of the Czech Republic but an extensive data set (81 sample trees) representing a wide range of tree ages and site conditions was collected. This enabled to employ, apart from mensurational data, additional predictor variables such as age, altitude and site index. Hence developed functions are not limited only to the Czech NFI data and may be applied to any other data from the Central European region.

Observed conventional wood density ranged between 529 and 621 kg·m$^{-3}$ with the average value of 585 kg·m$^{-3}$. It corresponds well to the density value of 580 kg.m$^{-3}$ recommended by Good Practice Guidance (IPCC 2003). For beech in the Czech Republic Cienciala et al. (2005) reported the stem wood density of 575.5 kg·m$^{-3}$, which is slightly lower compared to our results.

The total aboveground and component biomass was modelled by biomass functions in a non-linear form. The parameterization of non-linear functions requires more demanding computational methods, nevertheless it works with original values and no back-transformation is needed like in the logarithmic linearization of data. Furthermore, logarithmic transformation deforms the original data and the bias has to be corrected statistically through the process of back-transformation (Sprugel 1983; Snowdon 1991). No universal method of bias correction has been established yet and different authors have employed a variety of approaches (Joosten et al. 2004; Repola 2009; Skovsgaard, Nord-Larsen 2012). Cienciala et al. (2006) compared the results of non-linear approach and of linear regression applied to the log-transformed values of pine biomass and it was shown that the non-linear regression procedure always resulted in a closer match in comparison with the procedure involving linearization and bias correction.

Simple allometric functions with a single independent variable, *D*, matched the observed data well explaining 96% of variation in the aboveground biomass and 95% in the stem biomass. The variability of branch biomass was higher and even the incorporation of tree height *H* did not improve the model fit. For beech a weaker fit of branch biomass models was widely identified in previous studies (Cienciala et al. 2005; Gschwantner, Schadauer 2006; Hochbichler et al. 2006; Wutzler et al. 2008; Skovsgaard, Nord-Larsen 2012).

In general, biomass models with additional site predictors showed a better fit to empirical data than simple allometric functions. The inclusion of altitude

Table 2. The results of parameterization of the models for aboveground, stem and branch biomass, including the results of model cross-validation

| Biomass component | Model type | Model form | *AIC* | *RMSE* | $R^2$ | *RMSECV* | *RMECV* (%) | Parameters (standard error) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | $p_1$ | $p_{2\,(\mathrm{D,DH})}$ | $p_{3\,(\mathrm{H})}$ | $p_{4\,(\mathrm{A})}$ | $p_{5\,(\mathrm{T})}$ | $p_{6\,(\mathrm{S})}$ |
| Aboveground | DH2 | $\mathrm{AGB} = p_1 \times (D^2 \times H)^{p_2}$ | 920.8 | 100.8 | 0.978 | 103.8 | 20.0 | **0.01118**<br>(0.00294) | **1.08250**<br>(0.02378) | – | – | – | – |
| | DH3 | $\mathrm{AGB} = p_1 \times D^{p_2} \times H^{p_3}$ | 922.6 | 101.4 | 0.978 | 106.2 | 21.0 | **0.00962**<br>(0.00454) | **2.15540**<br>(0.05466) | **1.13788**<br>(0.14728) | – | – | – |
| | D2 | $\mathrm{AGB} = p_1 \times D^{p_2}$ | 966.5 | 136.1 | 0.961 | 150.9 | 20.5 | **0.22062**<br>(0.05732) | **2.33865**<br>(0.06776) | – | – | – | – |
| | DH2A | $\mathrm{AGB} = p_1 \times (D^2 \times H)^{p_2} \times \mathrm{A}^{p_4}$ | 905.4 | 90.5 | 0.983 | 93.4 | 19.1 | **0.06340**<br>(0.02876) | **1.08859**<br>(0.02133) | – | **–0.27628**<br>(0.06340) | – | – |
| | DH2AT | $\mathrm{AGB} = p_1 \times (D^2 \times H)^{p_2} \times A^{p_4} \times T^{p_5}$ | 904.0 | 89.1 | 0.984 | 93.7 | 15.8 | **0.08275**<br>(0.03885) | **1.10816**<br>(0.02393) | – | **–0.25465**<br>(0.06468) | –0.13227<br>(0.07296) | – |
| Stem | DH3 | $\mathrm{STB} = p_1 \times D^{p_2} \times H^{p_3}$ | 865.5 | 87.8 | 0.976 | 89.0 | 17.6 | 0.00560<br>(0.00286) | **2.10425**<br>(0.05825) | **1.29184**<br>(0.15830) | – | – | – |
| | DH2 | $\mathrm{STB} = p_1 \times (D^2 \times H)^{p_2}$ | 865.5 | 88.4 | 0.975 | 89.1 | 14.8 | **0.01009**<br>(0.00287) | **1.07222**<br>(0.02578) | – | – | – | – |
| | D2 | $\mathrm{STB} = p_1 \times D^{p_2}$ | 913.2 | 122.6 | 0.952 | 127.4 | 30.8 | **0.18819**<br>(0.05455) | **2.32336**<br>(0.07564) | – | – | – | – |
| | DH3AS | $\mathrm{STB} = p_1 \times D^{p_2} \times H^{p_3} \times A^{p_4} \times S^{p_6}$ | 859.7 | 83.3 | 0.979 | 94.8 | 17.2 | **0.00727**<br>(0.00532) | **2.14156**<br>(0.05661) | **1.29066**<br>(0.14753) | **–0.19377**<br>(0.07973) | – | **0.26754**<br>(0.11158) |
| | DH2AS | $\mathrm{STB} = p_1 \times (D^2 \times H)^{p_2} \times A^{p_4} \times S^{p_6}$ | 859.8 | 83.9 | 0.978 | 95.5 | 14.4 | **0.01203**<br>(0.00738) | **1.08814**<br>(0.02542) | – | **–0.18891**<br>(0.07882) | – | **0.27264**<br>(0.11201) |
| Branches | D2 | $\mathrm{BRB} = p_1 \times \mathrm{D}^{\mathrm{p}2}$ | 806.5 | 59.0 | 0.836 | 68.1 | 48.0 | 0.03089<br>(0.01826) | **2.42536**<br>(0.15374) | – | – | – | – |
| | DH2 | $\mathrm{BRB} = p_1 \times (D^{p_2} \times H)^{p_2}$ | 806.6 | 59.0 | 0.836 | 63.2 | 48.8 | 0.00116<br>(0.00095) | **1.13944**<br>(0.07381) | – | – | – | – |
| | DH3 | $\mathrm{BRB} = p_1 \times \mathrm{D}^{p_2} \times \mathrm{H}^{p_3}$ | 806.9 | 58.8 | 0.840 | 69.5 | 46.2 | 0.00611<br>(0.00843) | **2.35509**<br>(0.16939) | 0.56104<br>(0.44366) | – | – | – |
| | DH2AS | $\mathrm{BRB} = p_1 \times (\mathrm{D}^2 \times \mathrm{H})^{p_2} \times \mathrm{A}^{p_4} \times \mathrm{S}^{p_6}$ | 778.1 | 48.0 | 0.895 | 52.2 | 48.6 | 1.99771<br>(2.60454) | **1.13113**<br>(0.06093) | – | **–0.66132**<br>(0.15889) | – | **–0.94862**<br>(0.25881) |
| | DH3AS | $\mathrm{BRB} = p_1 \times \mathrm{D}^{p_2} \times \mathrm{H}^{p_3} \times \mathrm{A}^{p_4} \times \mathrm{S}^{p_6}$ | 778.8 | 47.9 | 0.897 | 53.7 | 47.3 | 3.84929<br>(5.41275) | **2.36756**<br>(0.15529) | **0.72637**<br>(0.36152) | **–0.60928**<br>(0.15906) | – | **–0.95752**<br>(0.25659) |

*D* – diameter at breast height (cm), *H* – tree height (m), *A* – altitude, *T* – tree age, *S* – site index, *AIC* – Akaike information criterion, *RMSE* – root mean square error, $R^2$ – coefficient of determination, *RMSECV* – root mean square error of cross validation, *RMECV* – relative mean error of cross validation, $p_1$–$p_6$ – parameters; in bold – statistically significant parameters (α = 0.05)

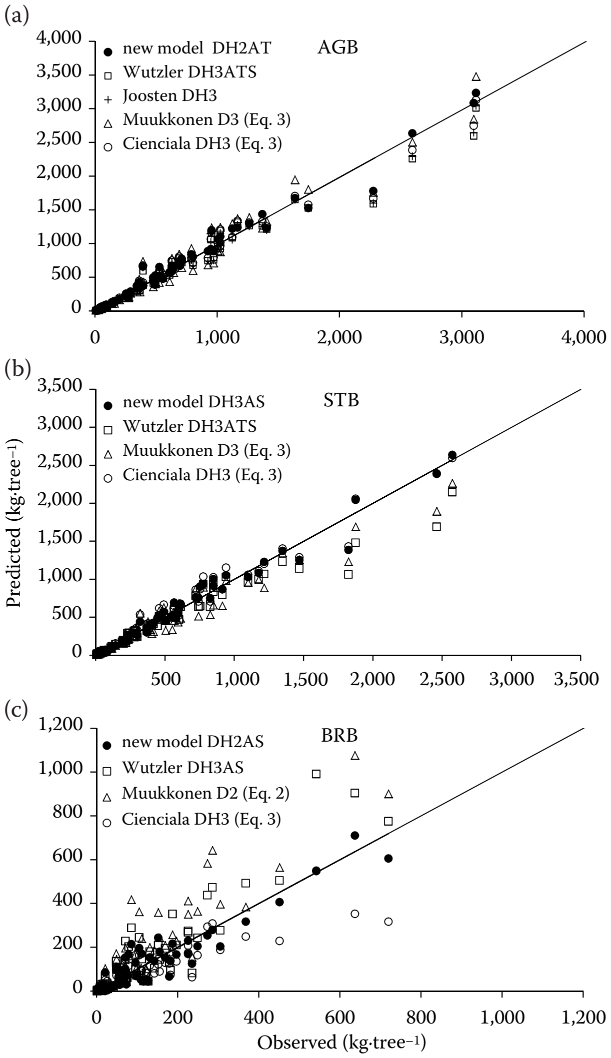

Fig. 5. Biomass predicted by the models of different authors plotted against the values of observed biomass: (a) aboveground biomass (AGB), (b) stem biomass (STB), (c) branch biomass (BRB)

improved our model for total aboveground biomass. Similarly, Joosten et al. (2004) in regard to beech and Cienciala et al. (2006) in regard to pine found that DHA models had a higher predictive power than did DH models. Altitude, in combination with site index, were important predictors for stem and branch biomass. In our study A and S served as reliable proxies for different site conditions. The negative relationship between S and branch biomass reflects the fact that productive sites are characterized by closed canopy stands with shorter crowns. The A and S were included in the biomass models for beech developed by Wutzler et al. (2008). On the other hand, in the study of Joosten et al. (2004) the site index did not help to improve the model. The slight importance given to tree age in our models indicates that beech biomass is strongly influenced by site conditions and competitive status of the individual trees.

LOOCV is the most conventional and exhaustive cross-validation procedure. Each data point is successively "left out" from the sample and used for validation. This is an effective way how to use an available data set to measure the predictive performance of a model (Arlot, Celisse 2010). The prediction error for the best models, both total aboveground and stem biomass, was about 15%. A higher level of error was obtained for branch biomass (RMECV 46–49%). It suggests that available predictors are not able to explain the variability of beech branch biomass. Cienciala et al. (2006, 2008) reported a significant improvement of the model fit by introducing independent variables such as crown length or crown ratio into the models for live branches of pine and oak. We developed other models, including crown length as an additional predictor, for a subset of 38 beech trees for which crown data was available (not presented here). Surprisingly the new models did not perform better than did DH2AS and DH3AS models parameterized on the same subset. Hence we decided to omit the crown length and to retain the original models based on the entire data set of 81 trees representing a wide range of stand and site conditions.

The predictions of aboveground biomass by our best DH2AT model were very similar to the predictions based on previously published functions (Joosten et al. 2004; Cienciala et al. 2005; Muukkonen 2007; Wutzler et al. 2008). In regard to stem biomass the best DH3AS model improved the predictions for large trees in comparison with the generic functions of Muukkonen (2007) and Wutzler et al. (2008). The differences in the prediction may be a result of divergent site conditions and/or stand treatment. The best DH2AS model considerably enhanced the quality of the estimate of branch biomass in comparison with predictions made according to the previously published functions (Cienciala et al. 2005; Muukkonen 2007; Wutzler et al. 2008). We assumed similar results from our models to those from the models of Cienciala et al. (2005) since he had analysed trees originating from the most similar conditions. It was revealed that these were the case for aboveground and stem biomass but Cienciala's DH3 model failed to predict branch biomass. The generic models of Muukkonen (2007) and Wutzler et al. (2008) based on extensive data sets, also provided biased estimates. This suggests that neither DH models nor the models including site covariates fit the branch biomass adequately. The architecture of European beech trees and mainly of branch biomass is strongly influenced by the stand structure. Unlike the stem biomass the variability in the size and number of branches is not connected with a respective change in DBH (Schütz 2002). To improve the performance of branch biomass models, the inclusion of other independent variables related to inter-tree competition (social status, stand basal area) appears to be essential.

The testing of biomass additivity showed a good match between the single-equation and the additive estimate of aboveground biomass. We recommend, however, giving preference to a single-equation estimate whenever a prediction of total aboveground biomass is required. The advantage of single equation is primarily the reduction of estimation uncertainty (Cienciala et al. 2006).

## CONCLUSIONS

The extensive data set of 81 sample trees representing a wide range of stand and site conditions enabled to develop biomass functions that describe, with a high level of precision, both aboveground and stem biomass of European beech in the conditions of the Czech Republic.

The total aboveground and component biomass was modelled by biomass functions in a non-linear form. Simple allometric functions with a single independent variable, D, matched the observed data of total aboveground and stem biomass well. The variability of branch biomass was higher and even the incorporation of tree height H did not improve the model fit. The additional predictor variables (age, site index and altitude) enhanced the fit of models for total aboveground and both component biomass. The inclusion of altitude improved our model for total aboveground biomass. Altitude, in combination with site index, were important predictors for stem and branch biomass.

The results of cross-validation showed a higher level of error for branch biomass. It suggests that available predictors are not able to explain the variability of beech branch biomass adequately. To improve the performance of branch biomass models, the inclusion of other independent variables related to inter-tree competition (social status, stand basal area) appears to be essential.

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