Parameterisation of allometric equations for quantifying aboveground biomass of Norway spruce (*Picea abies* (L.) H. Karst.) in the Czech Republic

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Abstract

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The aim of the present study was to develop allometric equations for predicting aboveground biomass of Norway spruce (*Picea abies* (Linnaeus) H. Karsten) applicable to the typically managed spruce forest on acidic and nutrient-medium sites in the Czech Republic. The models were based on an extensive data set of 139 spruce trees collected in 25 stands on 15 sites. The biomass in dry mass was modelled using linear regression equations with one (diameter at breast height -D), two (D, slenderness ratio -H/D) or three (D, H/D, site index -SI, or tree age -A) predictors. The models were validated using the leave-one-out method. The value of the root mean square error of cross-validation was chosen as the main criterion for the best-model selection. Both the total aboveground biomass and stem biomass were best predicted by three-variable models (D, H/D, SI). For crown and foliage biomass the simple one-variable model (D) is recommended.

Keywords: allometry; biomass model; linear regression; logarithmic transformation

Currently the issue of quantifying forest biomass is a hot topic. Information about the amount of tree biomass in forest ecosystems serves as the primary input variable when predicting the carbon allocated in forests (IPCC 2006; Petersson et al. 2012; Krtková 2016) and for determining the nutrient balance in the aboveground biomass (Augusto et al. 2000; Akselsson et al. 2007; Šrámek et al. 2009), or when estimating the amounts of logging residues (Christoforou, Fokaides 2015) and while quantifying the loss of nutrients during their energy use (Achat et al. 2015; Kaila et al. 2015).

The most frequently used methods of determining the amount of biomass are based on allometric equations and biomass expansion factors (BEF) or biomass expansion and conversion factors. When using allometric equations, biomass is determined at the tree level, while expansion factors enable the quantification of biomass of entire stands. A set of general models for calculating the spruce biomass in the territory of Central Europe was presented by Wirth et al. (2004). However, a wide range of extensive studies that are applicable to larger geographic units can be found both in Europe (Muukkonen 2007; Repola 2009) and worldwide

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(JENKINS et al. 2003; UNG et al. 2008; HENRY et al. 2011; CHOJNACKY et al. 2014). A summary of already published allometric equations for the area of Europe was compiled by ZIANIS et al. (2005).

Expansion factors are applied to the aggregated stand data (mostly stem or timber volume). BEF were primarily developed for estimating biomass at a national level for the purpose of international reporting (Lehtonen et al. 2004; Levy et al. 2004; DI Cosmo et al. 2016). BEF applicable to spruce stands in the Czech Republic were derived by Lehtonen et al. (2007).

The main problems associated with the use of allometric models include the fact that they are often parameterised on a small number of trees and also frequently only from a single location. The use of these models in territories other than those for which they have been developed can cause serious bias in estimates (Somogyi et al. 2007; Čihák et al. 2012). The parameterisation of models for larger scale predictions requires a pooled data set originated from a sufficient number of representative sites.

To date several studies concerned with quantifying the aboveground biomass of Norway spruce have been carried out in the Czech Republic. Some works were only focused on determining the amount of biomass on the basis of destructive analysis (VINŠ, ŠIKA 1975; VYSKOT 1976, 1991), while others used the data obtained for parameterisation of their own models (Chroust, Tesařová 1985; Černý 1990). All these studies can be classified as being local and they cannot be utilised for the biomass prediction on a larger scale.

In recent years, Forestry and Game Management Research Institute (FGMRI) implemented several projects which included a quantification of spruce biomass (Vejpustková et al. 2017). The data obtained were supplemented with data from the studies referred to above that were carried out in the territory of the Czech Republic. It resulted in a data file containing 177 sample trees covering a wide range of dimensions (D 1–52.5 cm; H 1.9–34.6 m) and site conditions (25 stands on 15 different sites, at an altitude between 300 and 950 m a.s.l., site index 20–38).

The goal of the present study is the parameterisation of allometric equations for the estimation of main biomass compartments of Norway spruce applicable to the typically managed spruce forest on acidic and nutrient-medium sites in the Czech Republic. The work also includes the validation of derived models using the leave-one-out method.

MATERIAL AND METHODS

The data used in the present study originates from two sources: (*i*) previously published data (VINŠ, ŠIKA 1975; CHROUST, TESAŘOVÁ 1985; ČERNÝ 1990; VYSKOT 1991), (*ii*) experimental data obtained from recent research projects of FGMRI. The pooled data set contains information from 25 plots on 15 sites in the Czech Republic (Table 1, Fig. 1).

In the data set there was a high proportion (42%) of trees up to 20 years of age. To reduce the number of the youngest trees we generated a random sample of specified percentage (48%) of cases. Hence

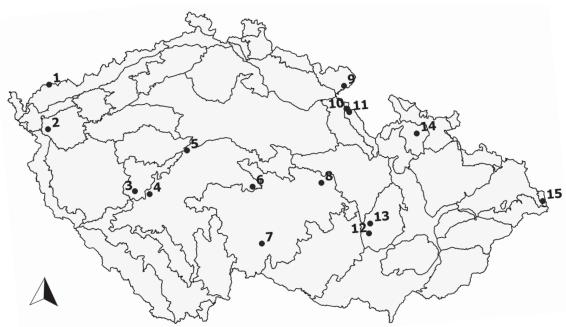


Fig. 1. Location of the study sites on the background of the map of natural forest areas in the Czech Republic (for details see Table 1)

Table 1. A list of sites and sample plots and the basic characteristics of sample trees

| Site | Plot | Author* | N | D (cm) | H(m) | Age (yr) | Site index** |
|------|--------------|---------|----|-------------|-------------|-----------|--------------|
| 1 | Přebuz | 1 | 3 | 37.9-45.2 | 25.6-26.6 | 149-156 | 24 |
| 2 | Horní Lazy 1 | 1 | 3 | 14.5 - 14.8 | 11-12.1 | 26 | 30 |
| 2 | Horní Lazy 2 | 1 | 3 | 23.9-24.8 | 20.1-21.8 | 50 | 30 |
| 2 | Horní Lazy 3 | 1 | 3 | 39.5-41 | 28.5-31.5 | 113 | 28 |
| 3 | Zbiroh | 2 | 8 | 20.9 - 47.2 | 22.9 - 33.4 | 106 | 30 |
| 4 | Obecnice 1 | 2 | 9 | 18.5-44.5 | 22.6-33.4 | 78 | 32 |
| 4 | Obecnice 2 | 2 | 9 | 10.5-32.8 | 13.6 - 27.2 | 57 | 30 |
| 5 | Strnady | 3 | 1 | 19.5 | 21.5 | 61 | 28 |
| 6 | Želivka | 3 | 1 | 20.4 | 23.3 | 88 | 24 |
| 7 | Mrákotín | 5 | 15 | 5.1 - 18.8 | 5.9-13.6 | 15-22 | 32 |
| 8 | Čachnov | 1 | 3 | 49-50.8 | 30.1-34.6 | 110-125 | 30 |
| 9 | Broumov | 4 | 55 | 1-10.7 | 1.85-8.57 | 20 | 26 |
| 10 | Šerlich 1 | 3 | 2 | 29.2-33.4 | 17.2 - 20.4 | 82-96 | 20 |
| 11 | Deštné 1 | 1 | 3 | 17.5-20.8 | 10.6-12.5 | 24 | 30 |
| 11 | Deštné 2 | 1 | 3 | 25.4 - 26.2 | 17.2-17.6 | 82 | 20 |
| 11 | Deštné 3 | 1 | 3 | 41.3-49.5 | 24.5 - 29.1 | 142 | 26 |
| 12 | Olomučany | 5 | 5 | 45.7-52.5 | 30.5-32.4 | 120 - 124 | 30 |
| 13 | Rajec 1 | 5 | 15 | 12.9-31.6 | 16.1-26.1 | 55-74 | 38 |
| 13 | Rajec 2 | 5 | 15 | 11.5-31.7 | 15-28 | 48-56 | 32 |
| 14 | Jeseníky 1 | 1 | 3 | 8.5-10.5 | 5.6-5.9 | 20 | 26 |
| 14 | Jeseníky 2 | 1 | 3 | 25.9-27.7 | 22.2-24 | 46 | 34 |
| 14 | Jeseníky 3 | 1 | 3 | 36.6-37 | 24.1-26.9 | 110 | 24 |
| 15 | Jablunkov 1 | 1 | 3 | 7.7-8.7 | 7-7.8 | 15 | 32 |
| 15 | Jablunkov 2 | 1 | 3 | 19.1-19.7 | 16-19.7 | 35 | 34 |
| 15 | Jablunkov 3 | 1 | 3 | 32.4-39.3 | 27.4-29.5 | 61 | 36 |

^{*1 –} experimental data of Forestry and Game Management Research Institute, 2 – Černý (1990), 3 – Vinš and Šіка (1975),

the age distribution of input data fits better the real distribution of age classes of the spruce stands in the Czech Republic according to the results of National Forest Inventory (NFI 2016). New data set contains 139 sample trees. The distribution of age classes is depicted in Fig. S1 (in electronic supplementary material (ESM), for the supplementary material see electronic version).

The biomass data were used to evaluate the changes in the proportions of individual biomass compartments depending on tree age. The changes in the ratios of stem, crown and foliage biomass in relation to the total aboveground biomass were assessed.

The allometric models were developed for the calculation of dry weight in kg of total aboveground biomass and its basic compartments – stem, crown and foliage. The stump was not included in stem biomass. The crown biomass comprises biomass of branches and assimilation organs. The method of linear regression was used for parameterisation of allometric equations. To meet the basic requirements for the application of this method the variables were linearized by logarithmic transformation. This approach was successfully used in previous studies (WIRTH et al. 2004; PAJTÍK et al. 2008; Čіна́к et al. 2014). The general form of an allometric model is provided by Eq. 1:

$$\ln\left(\widehat{Y}_{i}\right) = \ln\left(b_{0}\right) + b_{1}\ln\left(X_{1}\right) + b_{2}\ln\left(X_{2}\right) + \dots + b_{n}\ln\left(X_{n}\right) + \varepsilon \tag{1}$$

where:

– predicted biomass of i^{th} sample tree,

 b_0 , b_1 , b_n - regression parameters, X_1 , X_2 , X_n - predictors,

- random error.

The back-transformation of predictions is carried out using Eq. 2:

$$\widehat{Y}_i = e^{(b_0 + b_1 \ln(X_1) + \dots + b_n \ln(X_n))} \lambda \tag{2}$$

where:

 λ – correction factor.

⁴ – Chroust and Tesařová (1985), 5 – Vyskot (1991); N – number of trees, D – diameter at breast height, H – tree height,

^{**} mean height at the age of 100 years (ČERNÝ et al. 1996)

The factor λ according to Marklund (1987) (Eq. 3) is used for the correction of bias caused by the back-transformation of logarithmic values (Baskerville 1972):

$$\lambda = \frac{\sum_{i=1}^{n} Y_{i}}{\sum_{i=1}^{n} e^{\ln \hat{Y}_{i}}}$$
(3)

where:

 Y_i – observed biomass of i^{th} sample tree.

The biomass in dry mass was modelled using linear regression equations with one (diameter at breast height – D), two (D, slenderness ratio – H/D) or three (D, H/D, site index - SI, or tree age - A)explanatory variables. The significance of regression coefficients was evaluated based on the values of their standard deviations. Further it was tested using Student's t-test. The normality and homoscedasticity of residuals were assessed using Tukey-Anscombe plots and Q-Q plots. We also tested residuals using Jarque-Bera test of normality, Cook-Weisberg test of heteroscedasticity and sign test of the trend in residuals. For each model the coefficient of determination (R^2), the Akaike information criterion and the root mean square error were calculated on an original scale.

As no explicit validation data set was available, cross-validation was used to predict the model fit to a hypothetical validation set. The leave-one-out method of cross-validation was employed (ARLOT, CELISSE 2010). 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. 4):

RMECV =
$$\frac{100}{n} \sum_{i=1}^{n} \frac{|Y_i - \hat{Y}_i|}{Y_i} (\%)$$
 (4)

Final selection of the best model was based on the value of RMSECV.

The additivity of biomass (PARRESOL 1999) was also analysed. For the entire parameterisation data set (139 trees) the deviation of total aboveground biomass, computed by a single equation, from the sum of stem and crown biomass was calculated.

The biomass predicted by our *D*-models was compared with the estimates by other available spruce biomass functions that refer to the area of Central Europe. The local *D*-models of Černý (1990) and regional *D*-models of Wirth et al. (2004) were selected for this purpose. The ratios of predicted to observed biomass were calculated using data of all 139 trees from the parameterisation

data set. The ratios were plotted against diameter at breast height. The graphical comparison was carried out for aboveground biomass and its individual compartments.

All statistical analyses were performed in STA-TISTICA (Version 12, 2013) and QC EXPERT software (Version 2.7, 2004).

RESULTS

Observed spruce biomass

The total above ground biomass and the biomass of compartments strongly depend on D (Fig. 2). For all compartments the variance increases with tree diameter. It indicates potential heteroscedasticity of residuals in case of the application of nonlinear regression function. Hence the log-log transformation was used to linearize the variables (Fig. 2) and stabilise the variance (Figs S2–5 in ESM).

The percentage of stem biomass increases rapidly up to 40 years of age and then it fluctuates around 80% (Fig. 3). At young age, the proportion of stem biomass shows a high variability, which subsequently decreases in older trees and then gradually stabilises at a constant value. The proportion of crown biomass declines with age and, from 40 years of age onwards, it oscillates around the value of 17%. A different situation occurs in regard to the ratio of foliage biomass, whereby we encounter the greatest variability with trees up to 20 years of age. The percentage of needle biomass has a downward trend and, at adult age, it is usually only ca. 5%.

Allometric equations

Diameter at breast height D, slenderness ratio H/D and site index SI were significant predictors in multi-variable models for total aboveground biomass and stem biomass. Crown biomass was successfully predicted by single- and two-variable models with D and H/D. In case of needle biomass besides D and H/D also tree age A was found as a significant predictor. The slenderness ratio was prioritised over tree height in order to eliminate multicollinearity between explanatory variables.

The inspection of Tukey-Anscombe plots and Q-Q plots of derived models confirms homoscedasticity and normality of residuals (Figs S2–5 in ESM). The same results were obtained from statistical tests except for a single-variable model for stem biomass (Fig. S3a in ESM). For this model a sign test

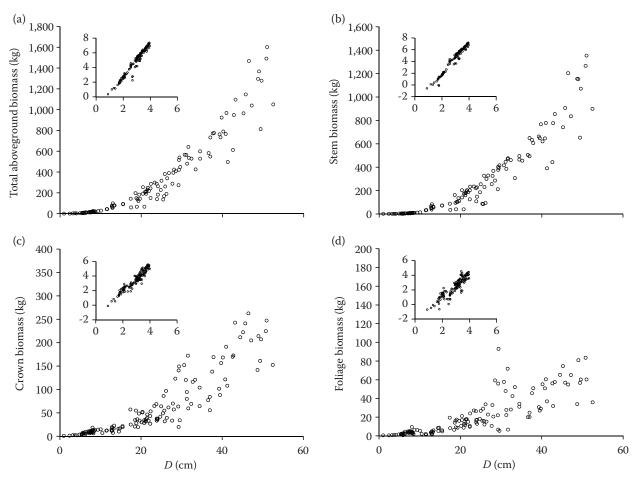


Fig. 2. Observed total above ground biomass (a) and its individual components: stem (b), crown (branches + foliage) (c), foliage (d) biomass for 139 sample trees plotted against diameter at breast height (D) on an original scale. Insets show log-log plots

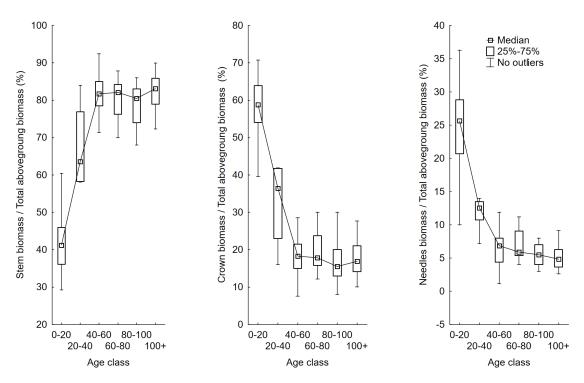


Fig. 3. Changes in the proportions of individual biomass compartments whiskers – interval of no outliers [LV – $1.5 \times$ (UV – LV); UV + $1.5 \times$ (UV – LV)], UV – 75% percentile, LV – 25% percentile

indicated the trend in residuals. In this one case, the nonlinear regression appears to be a more appropriate method. However, we decided to keep the uniform approach for all biomass compartments.

The models for total aboveground biomass and stem biomass reached a large share of explained variability $R^2 = 92-96\%$ (Table 2). The models with single predictor (D) reached the weaker fit than two- or three-variable models. Based on the value of RMSECV the three-variable model (D, H/D, SI) is the best for prediction of both total aboveground and stem biomass.

In general a weaker fit was recorded for crown and needle biomass models. Interestingly, the simple D-model achieved the best fit. The inclusion of tree height, site index or tree age did not improve the model performance. The crown biomass and biomass of needles are best described by one-variable model (*D*) for which the lowest values of RMSECV were recorded. The best models for crown and needle biomass explained 84 and 82% of the variability, respectively.

Biomass additivity and model validation

The biomass additivity was tested using an entire parameterisation data set (139 trees). The median of differences between total aboveground biomass and the sum of stem and crown biomass for singlevariable models is -5.6% and the standard deviation (SD) is 12.51%. The median of differences for two-variable models is -1.07%, with SD of 7.7%, while for three-variable models it is -1.86% with SD of 8.12%. Larger differences were found for trees with D < 7 cm. None of the models considered can therefore be recommended for biomass approximation of the youngest trees.

The RMECV ranged between 0.14 and 0.37% for all aboveground biomass models (Table 2). RMECV of stem biomass estimates was less than 1% apart for the simple D-model with a mean error of approximately 6%. For crown RMECV increased to 14–16%. Similarly the relative mean error of needle biomass prediction ranged between 10 and 16%.

We compared predictions by our single-variable models with those presented by ČERNÝ (1990) and WIRTH et al. (2004) (Fig. 4). Although WIRTH's et al. (2004) model accurately predicted aboveground biomass over the whole range of diameters (ratio close to 1), it slightly overestimated stem biomass for small trees. ČERNÝ's (1990) model overestimated considerably aboveground and stem biomass for trees with diameter up to 20 cm. The models

| - | 714 | , c | 101 | 1000 | RMECV | | Para | Parameter (standard error) | ır) | | - |
|--|---------------------------|--------------------------|---------|-------|--------|--|-------------------|----------------------------|-------------------|--------------------------|-------|
| Model | AIC K^2 KMSE KMSECV (%) | <i>K</i> ² K. | MSE KN | ASECV | (%) | b_0 | $b_1 \ln(D)$ | $b_2 \ln(H/D)$ | $b_3 \ln(SI)$ | $b_4 \ln(A)$ | < |
| $AGB = \exp(b_0 + b_1 \ln(D))\lambda$ | 1,039.220 0.95 87.43 | 3.95 8 | | 88.87 | -0.37 | -1.95298 (0.07127) 2.35768 (0.02398) | 2.35768 (0.02398) | | | | 0.986 |
| $AGB = \exp(b_0 + b_1 \ln(D) + b_2 \ln(H/D))\lambda$ | 1,012.955 0.96 | 7.96.7 | 77.74 8 | 80.51 | 0.21 | $-2.03230 \ (0.06075) 2.40781 \ (0.02131) 0.48803 \ (0.06938)$ | 2.40781 (0.02131) | 0.48803 (0.06938) | | | 1.020 |
| AGB = $\exp(b_0 + b_1 \ln(D) + b_2 \ln(H/D) + b_3 \ln(SI))\lambda$ 1,012.105 | 1,012.105 (| 0.96 | 77.14 7 | 77.49 | 0.14 | $-3.63269 \; (0.38359) 2.36073 \; (0.02280) 0.27645 \; (0.08190) 0.50396 \; (0.11947)$ | 2.36073 (0.02280) | $0.27645 \ (0.08190)$ | 0.50396 (0.11947) | | 1.018 |
| $ST = \exp(b_0 + b_1 \ln(D))\lambda$ | 987.117 0.92 | 9.92 | 91.74 7 | 70.89 | 6.27 | -3.53369 (0.10535) 2.76427 (0.03513) | 2.76427 (0.03513) | | | | 0.915 |
| $ST = \exp(b_0 + b_1 \ln(D) + b_2 \ln(H/D))\lambda$ | 907.650 | 96.0 | 63.43 6 | 68.07 | -0.87 | $-3.62155 \ (0.05227) 2.84648 \ (0.01793) 1.08860 \ (0.05971)$ | 2.84648 (0.01793) | 1.08860 (0.05971) | | | 1.002 |
| $ST = \exp(b_0 + b_1 \ln(D) + b_2 \ln(H/D) + b_3 \ln(SI))\lambda$ | 910.165 0 | 96.0 | 63.88 6 | 65.93 | 0.00 | $-4.54277 \ (0.36111) \textbf{2.81955} \ (0.02036) \textbf{0.97831} \ (0.07223) \textbf{0.28967} \ (0.11241)$ | 2.81955 (0.02036) | 0.97831 (0.07223) | 0.28967 (0.11241) | | 0.993 |
| $CR = \exp(b_0 + b_1 \ln(D))\lambda$ | 886.121 0.84 27.09 | 3.84 | | 27.41 | -16.16 | -1.39874 (0.12291) 1.69000 (0.041111) | 1.69000 (0.04111) | | | | 1.094 |
| $CR = \exp(b_0 + b_1 \ln(D) + b_2 \ln(H/D))\lambda$ | 887.636 | 0.84 27 | 27.14 2 | 27.68 | -13.83 | -1.32840 (0.12263) 1.64827 (0.04288) -0.36054 (0.13075) | 1.64827 (0.04288) | -0.36054 (0.13075) | | | 1.074 |
| $CR = \exp(b_0 + b_1 \ln(D) + b_2 \ln(H/D) + b_3 \ln(SI))\lambda$ | 886.836 0.84 | | 26.96 2 | 27.80 | -13.94 | $-2.33105 \ (0.78995) 1.62051 \ (0.04792) \ -0.48419 \ (0.16209) \ \ 0.31460 \ (0.24487)$ | 1.62051 (0.04792) | -0.48419 (0.16209) | 0.31460 (0.24487) | | 1.075 |
| $FL = \exp(b_0 + b_1 \ln(D))\lambda$ | 530.649 0 | 0.82 | 8.73 | 8.89 | -15.47 | -2.11217 (0.13818) 1.57569 (0.04631) | 1.57569 (0.04631) | | | | 1.075 |
| $FL = \exp(b_0 + b_1 \ln(D) + b_2 \ln(H/D))\lambda$ | 546.547 0 | 0.79 | 9.28 | 9.54 | -9.53 | -1.98720 (0.12753) $1.49555 (0.04471)$ $-0.72780 (0.13989)$ | 1.49555 (0.04471) | -0.72780 (0.13989) | | | 1.032 |
| $FL = \exp(b_o + b_1 \ln(D) + b_2 \ln(H/D) + b_3 \ln(A))\lambda$ | 538.176 0.81 |).81 | 8.93 | 9.76 | -10.77 | 9.26 -10.77 - 1.62797 (0.18847) 1.72229 (0.09933) - 0.60283 (0.14535) | 1.72229 (0.09933) | -0.60283 (0.14535) | | -0.25513 (0.10036) 1.045 | 1.045 |

SI – site index, ST – stem biomass, CR – crown biomass (branches + foliage), FL – foliage biomass, A – tree age, AIC – Akaike information criterion, R² – coefficient of determination, RMSE – root AGB-total aboveground biomass, b_0 , b_1 , b_2 , b_3 , b_4 parameters, D-diameter at breast height (cm), $\lambda-correction$ factor, H/D-slenderness ratio: tree height (m)/diameter at breast height (cm), mean square error of the model, RMSECV – root mean square error of cross-validation, RMECV – relative mean error of cross-validation, statistically significant parameters (α = 0.05) in bold

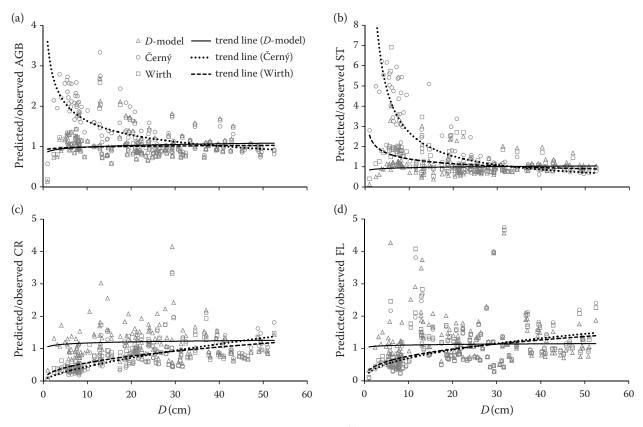


Fig. 4. Comparison of biomass predicted by our *D*-model with ČERNÝ (1990) and WIRTH et al. (2004) estimates: total aboveground – AGB (a), stem – ST (b), crown – CR (branches + foliage) (c), foliage – FL (d). The points represent the ratios of predicted to observed biomass of all 139 trees from the parameterisation data set plotted against diameter at breast height (*D*). Trend lines result from the application of power function

of both Černý (1990) and Wirth et al. (2004) underestimated crown biomass within the whole diameter range. Needle biomass was underestimated for small trees and overestimated for larger trees by both models compared.

DISCUSSION

The allometric models for a large-scale prediction of spruce biomass have not yet been parameterised in the Czech Republic. All previously published studies can be considered as being local (Chroust, Tesařová 1985; Černý 1990). The models derived in this study are applicable to classically managed spruce forests growing on acidic and nutrient-medium sites in the Czech Republic. An accurate estimate cannot be expected for trees growing at extreme sites or for trees growing as solitaires.

There are studies focused on biomass prediction at a national level in Europe, most of which come from Scandinavia (Marklund 1987; Repola 2009). However, their applicability to the conditions of the Czech Republic is limited (Světlík et al. 2016). Zianis et al. (2005) presented a sum-

mary of 152 models for estimation of spruce biomass in the area of Europe. Some of the published models are parameterised on data sets from hundreds of trees (e.g. MARKLUND 1987; WIRTH et al. 2004; Eckmüllner 2006; Ledermann, Neumann 2006), however more frequently they are local studies focused only on selected compartments of biomass. Světlík et al. (2016) carried out a destructive analysis of 9 spruce trees from 106-yearold stand in the Drahanská vrchovina (Czech Republic). Subsequently he compared the measured biomass with the results of biomass calculation using 104 allometric equations. The models of Wirth et al. (2004) were evaluated as the best for estimation of needle and root biomass, the equations of MARKLUND (1987) worked best for stem biomass, whereas branches were best predicted by the model of Hochbichler et al. (2006).

The prediction by our *D*-models was compared with the estimates by published models of Černý (1990) and Wirth et al. (2004). The Wirth et al. (2004) models give reliable estimates of the total aboveground and stem biomass for our data set. Therefore they can be considered suitable for prediction in the conditions of the Czech Republic.

On the other hand, the Černý (1990) models give biased estimates of total aboveground and stem biomass especially for the smallest trees. It is likely due to the insufficient number of small trees in their parameterisation data set. Hence their use is limited within the diameter range of 20 to 50 cm. The lower agreement between the model predictions with crown and needle biomass is generally given by the high variance of these values. In regard to the comparison with the model of Wirth et al. (2004), which was parameterised on data originating mainly from the German and the Swiss areas, the distinctions in forest management may cause the differences in biomass allocation.

A comparison of available biomass functions for spruce in the Czech Republic suggests the underlying problems associated with the utilisation of local models. The equation of Chroust and Tesařová (1985) was developed for a narrowly defined area both geographically and in terms of age and site. When used in the conditions in which it was created, the model attains good results. Its use in other areas, however, can introduce serious errors into the estimate. The model of Černý (1990) is more differentiated, both in terms of age and in terms of the range of dendrometric characteristics, and thereby provides a broader area for its application. Due to the low number of sample trees and regional limitation, neither can this model be recommended for biomass prediction on a large scale.

Changes in the proportion of biomass compartments are the most intensive up to 40 years of tree age. Then the values of ratios are stabilised and they remain almost unchanged up to the age of tree felling. The spruce crown increases rapidly until the age of 40 and then the growth rate decreases in connection with natural pruning, i.e. dropping off of branches towards the lower part of tree trunk. In other words, at the age of forty, the spruce crown is fully developed and it is almost free from any changes. For the assimilation apparatus, this process is even faster and a pronounced decrease in the amount of needles is already evident for 20 year-old trees. Based on these findings we can only confirm the importance of timely and professionally conducted silvicultural operations in young stands (Novák et al. 2015). In the stands up to the small-pole stage the crown biomass is often greater than the biomass of stem. The allometry of the youngest trees is different, that is why we do not recommend the application of regression models presented above to trees with D < 7 cm. Only a few studies were targeted toward the estimation of spruce biomass in young plantations and/or in the small-pole stage (Chroust, Tesařová 1985; Pajtík et al. 2008). The development of reliable models for these age groups would require a separate project involving the destructive analysis of a sufficient number of sample trees.

CONCLUSIONS

A set of allometric equations was parameterised based on a data set comprising 139 spruce trees from 15 different sites in the Czech Republic in order to calculate the total aboveground biomass and the biomass of stem, crown and assimilation organs. The models were verified using leave-one-out cross-validation. The derived equations enable the large-scale prediction of spruce biomass and allocated carbon for the purpose of forest monitoring programme and/or national forest inventory. The models are applicable on a local scale as well. However, an accurate estimate cannot be expected for trees growing at extreme sites or for trees growing as solitaires.

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