Biomass functions applicable to oak trees grown in Central-European forestry

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ABSTRACT: This study describes the parameterization of biomass functions applicable to oak (Quercus robur, Quercus petraea) trees grown in the conditions of Central-European forestry. It is based on destructive measurements of 51 grown trees sampled from 6 sites in different regions of the Czech Republic important for oak forest management. The samples covered trees of breast height diameter (D) ranging from 6 to 59 cm, tree height (H) from 6 to 32 m and age between 12 and 152 years. The parameterization was performed for total aboveground biomass and its individual components. The two basic levels of biomass functions utilized D either as a single independent variable or in combination with H. The functions of the third level represented the best function for each biomass component with the optimal combination of available independent variables, which included D, H, crown length (CL), crown width (CW), crown ratio (CR = CL/H), tree age and site altitude. D was found to be a particularly strong predictor for total tree aboveground biomass. H was found to always improve the fit, particularly for the individual components of aboveground biomass. The contribution of CW was minor, but significant for all biomass components, whereas CL and CR were found useful for the components of stem and living branches, respectively. Finally, the remaining variables tree age and altitude were each justified only for one component function, namely living branch biomass and stem bark, respectively. The study also compares the fitted functions with other available references applicable to oak trees.

Keywords: Quercus robur; Quercus petraea; biomass components; carbon; forest; temperate region

Tree biomass equations are tools to express biomass components in terms of dry mass on the basis of easily measurable variables. These are generally tree diameter at breast height (D) and tree height (H). Other variables such as crown length, crown width or tree age are sometimes estimated in ecosystem studies and specific inventories of forest ecosystem and may additionally improve the tree biomass assessment. The information on tree biomass is required to assess the amount of carbon held in trees, which in turn represents the basis of the assessment of carbon stock held in forests. This leads to the estimation of forest carbon stock changes, which belongs to reporting requirements of the parties to the United Nations Framework Convention on Climate Change and its Kyoto Protocol. As these policies require transparent and verifiable reporting of emissions by sources and sinks related to carbon stock changes in forests, countries develop suitable methodological approaches to do so. The fundamental methodological advice on the carbon reporting from the sector Land Use, Land Use Change and Forestry (LULUCF) is given in the Good Practice Guidance (GPG) for the LULUCF sector (IPCC 2003). GPG encourages using and/or developing suitable region- and species-specific tree biomass functions. Tree biomass equations may be used directly at tree level or as a component of biomass expansion factors, which may be also designed to be applicable to aggregated stand level data (e.g. Lehtonen et al. 2004; Somogyi et al. 2007).

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The most important tree species in the Czech Republic are European beech, English and sessile oak, Scots pine and Norway spruce. Recently, several studies on allometry of these species of temperate Europe were conducted, including beech (Joosten et al. 2004; Cienciala et al. 2005), pine (Cienciala et al. 2006) and spruce (Wirth et al. 2004). The species that has not been in the focus is oak and suitable allometric equations applicable to oak are still missing. The reported studies on oak species include Hochbichler (2002), who provided equations for bulk aboveground biomass applicable to oak, but this study did not include individual components. Very recently, Austrian scientists reported branch biomass equations for oak grown in admixtures together with other species (Gschwantner, Schadauer 2006; Ledermann, Neumann 2006). Outside Europe, a pooled function for aboveground biomass of broad-leaves including oak species is available (Schroeder et al. 1997). A rigorous quantification of total tree biomass for a certain region requires locally parameterized allometric equations, optimally based on representative and large sampling. In practice, however, sampling is limited since biomass studies are generally very laborious and costly.

Here, we parameterize allometric equations based on destructively measured components of 51 grown oak trees from 6 selected regions. The aim of this paper was to determine and parameterize allometric equations for oak trees (Quercus robur L. and Quercus petraea (Matt.) Liebl.) grown in classically managed oak-dominated stands in the conditions of Central-European temperate forestry. These functions could be used for the quantification of total aboveground biomass and individual tree components, i.e. stem (over and under bark), living branches, dead branches and stem bark.

**MATERIAL AND METHODS**

Generally, the study is based on tree sampling that was aimed at covering the most important regions for oak forest management in the Czech Republic. At each site, 8–9 trees were measured in standing position and thereafter measured again after felling and destructively sampled to estimate biomass and wood density. The site description and sampling are given below.

**Site description and tree sampling**

Altogether six locations (Nymburk, Křivoklát, Lanžhot, Bučovice, Buchlovice and Slapy) were identified for destructive biomass sampling including

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**Fig. 1.** The map of six locations selected for destructive sampling and measurement of oak trees. The labels indicate the forest site type (FST) according to the local typological classification (see Material and Methods)
51 trees. The sites represented the most important regions for the growing of oak in this country (Fig. 1). The sites represented typical growth conditions with site index 1 to 5 (Table 1) of the possible range (1 to 9). The forest site types according to the local forest typological system represented a range of conditions from fertile (1L, 2H, 3B), medium fertile (1O, 3S) to a poorer site class (2K). The typical altitude for oak management in this country includes mostly lowlands, which is reflected in the range of sample site altitudes between 150 and 430 m a.s.l. At each site, oak was a dominant species with a proportion between 40 and 100%. Altogether 8 to 9 trees per site were selected for destructive sampling so as to cover the full range of dimensions. The trees were selected subjectively to represent typical trees of the main canopy layer for selected sites, site class and stands. The diameter height relationship for all sample trees (n = 51) classified by site locations is shown in Fig. 2.

Sampling of trees at all sites was conducted in early spring before bud break. All selected trees were measured both standing and lying on the ground after felling. All basic measurable information was recorded, including tree diameter along the stem axis in 1-m intervals, tree height, crown base and stem diameter at the point of the crown base, height of the green crown and bark thickness.

The biomass components were assessed either from direct measurements or from in situ weighing and later oven-drying of biomass samples. Stem and stem bark volume was assessed using diameter and bark thickness measurements in 1-m intervals. These components in volume units were converted to biomass using the conventional density of 580 kg/m$^3$ for stem wood and 300 kg/m$^3$ for bark, respectively (IPCC 2003). Living branch biomass was assessed on the basis of fresh to oven-dry weight ratio, which was estimated from selected branches from three segments of the tree crown of each sample tree. Oven-drying of segments was performed at a temperature of 90°C for a period of about 8 days. The total aboveground biomass was represented by the sum of stem-wood over bark and living branches. The component of dead branches was treated separately (and biomass equations estimated specifically, see below) due to the mostly insignificant quantity (see Results) and it was not included in the aboveground biomass. As the sampling was conducted in a leafless stage prior to bud break, no leaf biomass was considered in this study.

**Biomass functions**

The pooled dataset of all trees and their components was used for the parameterization of biomass equations. The analyzed biomass components included total aboveground biomass, stem over bark,
stem under bark, living and dead branches and stem bark.

The most common form of biomass functions (e.g. Zianis, Mecuccini 2004) used to estimate tree aboveground tree biomass ($Y$) and its components is the power form

$$Y = p_0 \times D^{p_1}$$

(1)

where: $D$ – diameter at breast height, representing the independent variable,

$p_0, p_1$ – parameters to be fitted.

Other fundamental information on trees is tree height ($H$), which is often used to differentiate growth conditions at different sites and commonly serves as a basis for expressing the site index for the purpose of forest management planning. Hence, the inclusion of tree height is crucial for merging data sets from different sites. The most commonly used functional dependence of the biomass components on the two basic measurable independent variables, i.e. $D$ and $H$, has the form as follows:

$$Y = p_0 \times D^{p_1} \times H^{p_2}$$

(2)

where: $p_0, p_1, p_2$ – three parameters of the equation.

However, it is to note that in allometric studies the nonlinear regression analysis is often avoided using the logarithmic linearization of the power functions, which can be exemplified as below:

$$\ln Y = p_0 + p_1 \times \ln X_1 + p_2 \times \ln X_2 + p_3 \times \ln X_3 \ldots$$

$$\ldots + p_n \times \ln X_n + \varepsilon$$

(3)

Eq. (3) contains the independent variables $X_1$ to $X_n$ and a corresponding set of parameters $p_0$ to $p_n$, while $\varepsilon$ represents an additive error term. While the linearization permits a common linear regression procedure to be applied and stabilizes variance across the observed tree dimensions, this transformation produces a bias and must be statistically treated (e.g. Sprugel 1983; Zar 1996). This is commonly done by setting a correction component estimated as a half of the standard error of the estimate of parameterized Eq. (3) (e.g. Zianis et al. 2005), which is added to the linearized equation for the exponential back-transformation, although no standard correction has been proposed yet. Instead, Marklund (1987) calculated a model specific correction factor $\lambda$ from the data as

$$\lambda = \frac{\sum_{i=1}^{n} Y_i}{\sum_{i=1}^{n} \ln \hat{Y}_i}$$

(4)

where: $n$ – number of sample trees,

$Y_i, \hat{Y}_i$ – represent the observed and fitted values.

This method ensures that the mean predicted value is equal to the mean observed value. Hence, an unbiased estimate of $Y$ is given as

$$\hat{Y} = \lambda \times \exp( p_0 + p_1 \times \ln X_1 + p_2 \times \ln X_2 + p_3 \times \ln X_3 \ldots$$

$$\ldots + p_n \times \ln X_n )$$

(5)

The approach of linearization and general linear model were used for the parameterization of biomass functions for aboveground biomass and all other components besides dead branches. For each of these components three functions were determined using the linearized model (Eq. 3), namely (i) that utilizing solely $D$, (ii) that combining $D$ and $H$, and (iii) the best function detected by a step-wise regression procedure that tested the combination of the available independent predictors, namely $D, H$, altitude ($Z$), tree age ($A$), crown length ($CL$), crown width ($CW$) and crown ratio ($CR$) defined as $CL/H$.

As for the component of dead branches with several zero values involved, the non-linear regression procedure with Eqs. (1) and (2) was applied to determine a suitable biomass function and its parameters.

The mean relative prediction error ($MPE; \%$) was calculated as follows (see e.g. Nelson et al. 1999):

$$MPE = \frac{100}{n} \sum_{i=1}^{n} \left| \frac{Y_i - \hat{Y}_i}{Y_i} \right|$$

(6)

When calculating $MPE$ for dead branches, only the trees with non-zero observed values were taken into account.

The test of equality of regression equations obtained from different sample sites was performed for the optimal equations for aboveground biomass and living branch biomass using the Chow criterion as it was described in our earlier study (Cieńciala et al. 2006). The criterion calculated for each pair of sites is compared with table values of $F$-distribution taking into account the amount of parameters and standard deviations of residuals of the tested sites.

Reference stand

For a quantitative analysis of the parameterized allometric equations of this study and available equations published elsewhere, a fictitious oak stand of young (25 years), medium (50 years) and old (100 years) age was generated. This was done on the basis of Czech growth and yield tables (Cerny et al. 1996) and its software derivative, growth and yield
model SILVISIM (e.g. Černý 2005). The prescribed stand characteristics corresponded to a typically managed oak stand of site index 3 (slightly above-average conditions) with a management regime set to full stocking. Stand characteristics for the exemplified stand age phases (young, medium and old) are given in Table 2 and the frequency distribution of trees in this example stand at 25, 50 and 100 years of age is shown in Fig. 3.

Table 2. Stand characteristics of a generated test stand exemplifying the typical management of oak; mean stand height, basal area and stocking density (N) are shown for each stand age

<table>
<thead>
<tr>
<th>Stand</th>
<th>Age (years)</th>
<th>Mean stand height (m)</th>
<th>Basal area (m²/ha)</th>
<th>N (trees/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Young</td>
<td>25</td>
<td>11.1</td>
<td>20.7</td>
<td>3,626</td>
</tr>
<tr>
<td>Medium</td>
<td>50</td>
<td>19.3</td>
<td>26.5</td>
<td>1,004</td>
</tr>
<tr>
<td>Old</td>
<td>100</td>
<td>26.0</td>
<td>32.9</td>
<td>323</td>
</tr>
</tbody>
</table>

RESULTS

Biomass equations and contribution of independent variables

The dependence of the observed values of aboveground biomass (AB) on the independent variables breast height diameter (D), tree height (H), crown length (CL), crown width (CW) and age is shown in Fig. 4. This relation was typically exponential for all independent variables. As expected, D produces the clearly strongest relationship, while the dependence of AB on other variables produces larger scatter.

The regression analysis performed for all biomass components reflected the above observations. The estimated biomass equations for all biomass components except dead branches are listed in Table 3, while Table 4 shows the results for the component of dead branches. It can be observed that the generally best fit was obtained for the component of aboveground biomass and stem biomass over and under bark, explaining most of the total variation in the observed data on a logarithmic scale (Table 3). Only the slightly weaker match was found for the component of bark (about 97%). Somewhat weaker was the fit for the component of living branches, which ranged between 90 and 93% for the set of applied equations. These observations for logarithmically transformed variables were magnified in terms of the mean prediction error (MPE) using the real values. For the optimal models, MPE reached about 5–6% for the components of aboveground biomass and stem, while it increased to 15.5 and 29% for bark biomass and living branches, respectively (Table 3).

Generally, the inclusion of tree height (H) and other independent variables in equations always improved the fit for biomass components relative to the equation including only a single independent variable D. H usually helped to explain the variation of logarithmically transformed variable by additional 0.5 to 1% (Table 3). In terms of the mean prediction error (MPE), however, the inclusion of tree height always meant a notable MPE reduction (Table 3). As for information on the tree crown, it helped to improve the regression estimates for all tested biomass components. The optimal combination of independent variables for each component always included crown width (CW), whereas other variables worked differently for individual biomass components. The optimal equation for stem biomass (under or over bark) included, besides D and H, both CW and crown length (CL). However, the effect of these additional variables was rather small relative to the function combining just D and H: the improvement in the explained variability on a logarithmic scale was barely significant, although MPE was further

Fig. 3. Frequency histogram of tree diameters (D) for a fictitious managed stand of oak at 25, 50 and 100 years of age, site class 3. The corresponding stand characteristics are shown in Table 1. Note that for clarity the y-axis is shown on a power-transformed (0.5) scale.
reduced by about one half percent (Table 3). The component of living branch biomass was best approximated with the function combining $D$, crown ratio ($CR$) and altitude ($Z$). Finally, bark biomass was best approximated using the combination of $D$, $H$, $CW$ and age ($A$). Including $CW$ and $A$ helped to reduce $MPE$ to 15.5%, which was an improvement by over 2% relative to the Level 2 equation combining $D$ and $H$ only (Table 3).

The results of nonlinear fitting performed for the biomass of dead branches (Table 4) revealed that $H$ was important for estimation of this component. It improved the fit by about 33% relative to the basic estimation using only $D$. Note, however, that $MPE$ did not correspondingly improve for the equation combining $D$ and $H$, which is due to the fact that zero-values were omitted in the $MPE$ calculation. The contribution of other variables to dead biomass
Table 3. Estimated parameters ($p_0$ to $p_7$) of biomass equations for individual tree components using the form of Eq. (3) with one independent variable ($D$; Level 1), two independent variables ($D, H$; Level 2) and the best combination detected from the available set of independent variables, namely $D, H, CL, CW, CR, A$ and $Z$ (Level 3). The adjusted coefficient of determination ($R^2_{adj}$), mean square error (SE; in log units), correction factor ($\lambda$) and mean prediction error (MPE; %) are also listed for the fit of each equation.

<table>
<thead>
<tr>
<th>Component</th>
<th>Level</th>
<th>$p_0$</th>
<th>$p_1$</th>
<th>$p_2$</th>
<th>$p_3$</th>
<th>$p_4$</th>
<th>$p_5$</th>
<th>$p_6$</th>
<th>$p_7$</th>
<th>$R^2_{adj}$</th>
<th>SE</th>
<th>$\lambda$</th>
<th>MPE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aboveground biomass</td>
<td>1</td>
<td>-2.380</td>
<td>2.549</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.991</td>
<td>0.122</td>
<td>0.974</td>
<td>9.7</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>-3.069</td>
<td>2.137</td>
<td>0.661</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.996</td>
<td>0.084</td>
<td>0.999</td>
<td>6.9</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>-2.944</td>
<td>1.935</td>
<td>0.738</td>
<td>0.193</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.997</td>
<td>0.076</td>
<td>0.994</td>
<td>6.0</td>
</tr>
<tr>
<td>Stem biomass over bark</td>
<td>1</td>
<td>-2.652</td>
<td>2.578</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.987</td>
<td>0.154</td>
<td>0.962</td>
<td>12.5</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>-3.731</td>
<td>1.933</td>
<td>1.036</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.998</td>
<td>0.063</td>
<td>0.999</td>
<td>5.3</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>-3.629</td>
<td>1.861</td>
<td>1.097</td>
<td>-0.098</td>
<td>0.101</td>
<td></td>
<td></td>
<td></td>
<td>0.998</td>
<td>0.059</td>
<td>0.996</td>
<td>4.9</td>
</tr>
<tr>
<td>Stem biomass under bark</td>
<td>1</td>
<td>-2.828</td>
<td>2.599</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.985</td>
<td>0.166</td>
<td>0.962</td>
<td>13.4</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>-3.964</td>
<td>1.920</td>
<td>1.089</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.997</td>
<td>0.077</td>
<td>1.000</td>
<td>6.3</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>-3.827</td>
<td>1.794</td>
<td>1.172</td>
<td>-0.100</td>
<td>0.153</td>
<td></td>
<td></td>
<td></td>
<td>0.997</td>
<td>0.071</td>
<td>0.997</td>
<td>5.6</td>
</tr>
<tr>
<td>Branch biomass</td>
<td>1</td>
<td>-3.687</td>
<td>2.363</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.898</td>
<td>0.407</td>
<td>1.149</td>
<td>40.4</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>-2.707</td>
<td>2.949</td>
<td>-0.940</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.906</td>
<td>0.391</td>
<td>1.097</td>
<td>36.7</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>-4.131</td>
<td>2.014</td>
<td>0.625</td>
<td>0.957</td>
<td>0.260</td>
<td></td>
<td></td>
<td></td>
<td>0.928</td>
<td>0.343</td>
<td>1.072</td>
<td>29.5</td>
</tr>
<tr>
<td>Bark biomass</td>
<td>1</td>
<td>-4.426</td>
<td>2.419</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.967</td>
<td>0.230</td>
<td>0.987</td>
<td>18.2</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>-5.027</td>
<td>2.059</td>
<td>0.577</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.970</td>
<td>0.218</td>
<td>1.007</td>
<td>17.7</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>-5.206</td>
<td>1.961</td>
<td>0.403</td>
<td>-0.252</td>
<td>0.340</td>
<td></td>
<td></td>
<td></td>
<td>0.975</td>
<td>0.200</td>
<td>1.019</td>
<td>15.5</td>
</tr>
</tbody>
</table>

Biomass component = $\lambda \times \exp(p_0 + p_1 \times \ln D + p_2 \times \ln H + p_3 \times \ln CL + p_4 \times \ln CW + p_5 \times \ln CR + p_6 \times \ln A + p_7 \times \ln Z)$
Table 4. The component of dead branches – the results of non-linear regression analysis applied to Eqs. (1) and (2), showing parameter values, asymptotic standard error (A.S.E.), Wald confidence intervals, adjusted coefficient of determination ($R^2_{adj}$) of the fit and prediction error (MPE; %; calculated with non-zero values only)

<table>
<thead>
<tr>
<th>Equation</th>
<th>Parameter</th>
<th>Value</th>
<th>A.S.E.</th>
<th>95% confidence interval</th>
<th>$R^2_{adj}$</th>
<th>MPE</th>
</tr>
</thead>
<tbody>
<tr>
<td>$Y = p_0 \times D^{p_1}$</td>
<td>$p_0$</td>
<td>0.4E–5</td>
<td>0.9E–5</td>
<td>–1.4E–5 – 2.2E–5</td>
<td>0.61</td>
<td>48.6</td>
</tr>
<tr>
<td></td>
<td>$p_1$</td>
<td>3.932</td>
<td>0.570</td>
<td>2.787 – 5.077</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$Y = p_0 \times D^{p_1} \times H^{p_2}$</td>
<td>$p_0$</td>
<td>0.004</td>
<td>0.005</td>
<td>–0.006 – 0.014</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$p_1$</td>
<td>5.712</td>
<td>0.305</td>
<td>5.100 – 6.324</td>
<td>0.94</td>
<td>54.9</td>
</tr>
<tr>
<td></td>
<td>$p_2$</td>
<td>–4.186</td>
<td>0.270</td>
<td>–4.728 – 3.644</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Prediction was also tested, but it did not further improve the results obtained for the fit of Eq. (2) combining solely $D$ and $H$.

Since the data on tree biomass used in this study were collected from different locations (Fig. 1), it was important to analyze the effect of different locations on the parameterized regression functions. The Chow test showed no significant differences between the regression equations obtained for different plots at 5% confidence level. Although insignificant, a somewhat higher test criterion relative to other pairs of sites was observed for $AB$ between the site Nymburk and other sites. Similarly, a somewhat higher criterion was observed for branch biomass between the site Slapy and other sites.

**Components of aboveground biomass**

The mean observed aboveground biomass ($AB$) of the tree sample set analyzed here ($n = 51$) was 536.0 kg, with the corresponding mean $D$ of 26.3 cm and $H$ of 21.3 m. It was dominated by stem biomass (75%), while the biomass of living branches, stem-bark, and dead branches constituted on average 16.2, 8.1 and 0.7%, respectively. Using the fictitious, typically managed oak stand at different age (Table 2, Fig. 3), the parameterized biomass equations showed that stem biomass already dominates (71% proportion of $AB$) once the stand is 25 years old, but its relative proportion remains about constant between 50 and 100 years reaching about 76% of $AB$ (Fig. 5). Similarly, the proportion of living branch biomass decreased from 20% in the young stand to about 15–16% for 50 and 100 years old managed stand of oak. The proportion of stem bark remained relatively constant for different stands stages, declining slightly from about 9 to 8%. Note, however, that for the above fictitious stand-level comparison, the selection of an applicable biomass equation was limited to Level 2 models, i.e. using independent variables limited to tree diameter, height and age. This was determined by model-generated stand data. The match of the absolute values for stand $AB$ estimated either from the single function or as the sum of component

![Fig. 5. The relative proportions of biomass components for examples of young (25 yrs), medium (50 yrs) and old (100 yrs) stand of oak that is managed according to common forestry practice](image-url)
functions for stem biomass under bark, bark, living branches and dead branches was also explored on the above fictitious oak stand managed in a classical way at 25, 50 and 100 years of age (Table 2, Fig. 3). The estimated aboveground biomass from a single equation reached 83.2, 168.2 and 275.4 Mg/ha, while the estimation from the summed biomass components was 83.8, 168.8 and 274.9 Mg/ha for the young, medium and old stand, respectively. This means that for the young and medium stand the additive estimation of $AB$ from biomass component equations was higher by 0.7 and 0.4%, respectively, as related to the single-equation estimate, whereas the above difference in the single and composed biomass estimation was –0.2% for the old stand.

**DISCUSSION**

**Optimal equations**

The selection of appropriate biomass functions is driven by the intention to find the best prediction using the available set of independent variables. Although the biomass functions may use many independent variables to reduce the prediction bias, it is always desirable to keep the set of predictors as small as possible to reduce the variability of predictions (Wirth et al. 2004). Generally, the most easily measurable and also the absolutely fundamental variable is $D$, while the measured $H$ and other tree variables such as crown length and width are less frequent. To save costs, forest inventories commonly use a subset of $H$ measurements and estimate $H$ for the remaining trees by regression approaches or other statistical methods, such as the method of $k$-nearest neighbours (e.g. Sironen et al. 2001). Crown parameters are mostly measured in specific ecosystem studies, while they are often omitted when biomass or tree volume is to be inventoried on larger scales. Hence, it was important to note that single variable Eq. (1) utilizing solely $D$ was able to explain as much as 99% of the variability in the observed aboveground biomass of oak: this applies to both logarithmically transformed values (results reported in Table 3) and direct observations once estimated by non-linear regression with Eq. (1) (results not shown here). This was more than reported for pine (Cienciala et al. 2006), which was sampled in a similar manner to oak in this study. On the other hand, $D$ explained just over 70% of the variability in the observed branch biomass (untransformed values, not shown here) or 90% of log-transformed values. This is basically identical to the values reported for oak branch biomass by Ledermann and Neumann (2006).

The importance of additional independent variables increased for the estimation of individual tree components. Their contribution can be best seen on improving the error of prediction (MPE, Table 3). For example, stem biomass predicted with both $D$ and $H$ as independent variables decreased MPE by more than 50% relative to the prediction using $D$ only. As for additional information on the tree crown ($CL$, $CW$ or $CR$), it proved to be useful mainly for the component of living branches and aboveground biomass that include living branches. This is in line with the other independent studies, which proved the importance of crown variables for the prediction of branch biomass either for oak or other tree species (e.g. Wirth et al. 2004; Ledermann, Neumann 2006; Gschwantner, Schadauer 2006). The use of the independent variable crown ratio (CR) combining the information on tree height and crown length was found optimal for the prediction of branch biomass, but not for other components. This also applies to altitude ($Z$), which did not have any pronounced effect except branch biomass. Obviously, $Z$ as a good proxy of climatic conditions is pronounced in tree allometry mainly for those species that are grown in a substantially larger elevation range. Hence, $Z$ was found to be an important predictor for aboveground biomass of beech (Joosten et al. 2004), stem and aboveground biomass of pine (Cienciala et al. 2006). The small importance of $Z$ reflects the fact that oak forestry in this country is located at the lower elevations with a rather small range to be pronounced in the sample set analyzed here. A similar reasoning could be given for the independent variable of tree age ($A$). The managed forests of oak sampled in our study suppressed the effect of age in tree allometry, and a significant contribution of $A$ was detected only in the equation applicable to bark biomass (Table 3). On the other hand, accurate estimation of bark biomass for oak is needed, as this species is known to have the largest proportion of bark in aboveground biomass among the forest tree species grown in Central Europe. Therefore, the optimal equation (Level 3 in Table 3) should be prioritized over the other alternatives for the assessment of bark biomass once the required independent variables are available. Interestingly, the relative proportion of bark biomass was shown not to be increasing with age (Fig. 5). The estimation performed on the fictitious oak stand suggested a relatively constant proportion of 8–9% on the total aboveground biomass. It should be noted that this proportion is not identical to the volume proportion because different densities (see the methods) were applied to stem bark and stem wood. It implies that
on a volume basis, the proportion of oak bark would reach about 15% of the aboveground biomass.

The obtained mean prediction errors (MPE) for the optimal equations applicable to individual biomass components (Level 3 in Table 3) were compared with the errors estimated in the same way for Scots pine based on the results of our earlier study (Cienciala et al. 2006). The comparison showed a marginally better prediction for oak compared to pine for all components except bark biomass. Thus, the errors for pine, calculated according to Eq. (6), would reach 7.4, 7.3, 11.0, 32.3 and 56.5% for aboveground biomass, stem under bark, bark, living branches and dead branches, respectively. This is to be compared with the current estimates for oak, which reached 6.0, 5.6, 15.0, 31.0, 54.9 and 6.0% for the respective biomass components of oak (Tables 3 and 4). These results are promising and suggest that the biomass estimation of broadleaved species grown in managed stands may not be associated with larger prediction errors as compared to coniferous species. Note, however, that in our study, variability in wood density was basically neglected by assuming single density values for stem and bark components. Hence, natural variation in stem-wood and bark density was not considered and this would have resulted in additional uncertainty that was not included in our estimates.

In this study, we showed that composed biomass functions matched the single equation for aboveground biomass well in terms of the absolute values. However, as follows also from the assessed MPE for individual biomass components, in order to reduce the prediction error, it is always advisable to develop and/or apply a single biomass equation instead of combining the component functions for the estimation of aboveground biomass.

The literature presenting biomass equations for oak grown in the conditions of temperate European forestry is very scarce. We may compare a published equation applicable to aboveground biomass for oak in the coppice-with-standards type of forest grown in Austria (Hochbichler 2002) and another widely used reference for aboveground biomass for broadleaves suggested by IPCC (2003), namely that of Schroeder et al. (1997). The latter study gives a robust function parameterized on several hundreds of broadleaved trees (including oak species) from NE of USA. Both equations include only one independent variable, namely D. It is surprising to note that these equations matched the observed oak biomass used in this study fairly well (Fig. 6). Although the function of Hochbichler (2002) systematically overestimates AB for the diameter range up to 40 cm, which contributes to a relatively large MPE (33.5%) estimated for this function relative to the observed data. However, it fits the large-diameter trees fairly well considering the fact that the function was estimated on limited material from a specifically man-
aged oak stands in Austria. Even better match was found with the general function for broadleaves of Schröder et al. (1997). It corresponds well to our observations across the whole diameter range (Fig. 6) and hence the estimated MPE was as low as 10.6%. Although the Level 3 function estimated by us is still considerably better in terms of MPE, Schröder et al. (1997) should rather be compared with our Level 1 function deploying solely $D$, which gave only a marginally better MPE (Table 3). When comparing these functions on the absolute values to detect systematic errors, the function of Hochbichler (2002) indicated overestimation by 10.5%, whereas that of Schröder et al. (1997) gave smaller values by 9.6% relative to the mean tree aboveground biomass of our oak sample set.

A similar comparison of component functions applicable to oak remains limited to the functions applicable to branch biomass (BB) from by the recently published studies of Ledermann and Neumann (2006) and Gschwantner and Schadauer (2006). Of these, the latter study considers branches with a minimum diameter threshold of 5 cm, which makes it not directly comparable with our material. The comparison of the oak branch biomass functions determined by Ledermann and Neumann (2006) with the observed data and functions from this study is shown in Fig. 7. It can be seen that the function using solely $D$ (Austria 1) matches data fairly well up to $D$ of 35–40 cm, while the more complex function deploying both $D$ and $CR$ (Austria 3) works generally better for larger trees. To evaluate these different functions, one may apply relative or absolute measures. For example, $MPE$ estimated for the two selected functions of Ledermann and Neumann (2006) relative to our observed data reached 37 and 61%, respectively. At the same time, the quantitative comparison on our oak sample set indicated that the simple equation (Austria 1 in Fig. 7) would systematically underestimate the observed values by 30%, whereas the more complex function (Austria 3 in Fig. 7) reached 95.9% of the mean observed branch biomass. This is practically as much as observed with our optimal equation (Level 3; Table 3), although $MPE$ (indicating random error) was naturally much higher as compared to our function. This good correspondence of two independently estimated equations gives confidence in branch biomass estimation for oak grown in temperate Europe.

**CONCLUSIONS**

This study provides a set of parameterized equations applicable to total aboveground biomass and individual components for oak ($Q. robur$ and $Q. petraea$) species as grown in Central-European forestry. Tree diameter at breast height was shown to be a very strong predictor of aboveground biomass, although considering other independent variables such as tree height and information in the equation on crown naturally improved the fit. The contribution of additional variables was more significant for individual biomass components, always notably reducing the estimation uncertainty. The variables describing crown were specifically crucial for the estimation of living branches. Altitude was not shown to be a useful predictor for any biomass component except bark. Similarly, tree age was found to facilitate only the prediction of branch biomass. Although the study demonstrated a very good match between the single estimate of aboveground biomass and its composition by individual parameterized component functions, it is always recommended to prioritize the single equation for total aboveground biomass in order to minimize the assessment error.

**References**


Stanovení alometrických rovnic pro biomassu stromů dubu pěstovaného v podmínkách středoevropského lesnictví

ABSTRAKT: Studie předkládá parametrizaci alometrických vztahů použitelných pro dub (Quercus robur, Quercus petraea) rostoucí v podmínkách středoevropského lesnictví. Je založena na destruktivním měření 51 vzorníků rostoucích na šesti lokalitách významných pro dubové hospodářství v České republice. Měřené stromy zahrnovaly rozpětí výčetní tloušťky (D) 6 až 59 cm, výšky (H) od 6 do 32 m a věku od 12 do 152 let. Byly parametrizovány vzta- hy pro celkovou nadzemní biomassu a její jednotlivé složky. Dvě základní úrovně alometrických funkcí využívají D jako jedinou nezávislou proměnnou, nebo v kombinaci s H. Funkce třetí úrovně reprezentovaly nejúspěšnější funkci a optimální kombinaci dostupných nezvislých proměnných, které zahrnovaly D, H, délku koruny (CL), šířku koruny (CW), poměr dimenzí koruny (CR = CL/H), věk vzorníků a nadmořskou výšku stanoviště. K predikci celkové nadzemní biomassy byla zvláště významná proměnná D. Zahrnutí H zvýšilo přesnost fit funkcí, a to především pro jed- notlivé položky nadzemní biomassy. Příspěvek CW byl slabý, ale signifikantní pro všechny položky biomassy. CL byla významná pro biomassu kmene a CR pro biomassu živých větví. Ostatní proměnné byly významné pouze pro jednu z funkcí, konkrétně věk stromu pro predikci biomassy živých větví a nadmořská výška stanoviště pro kůru kmene. Práce rovněž porovnává parametrizované funkce pro dub z této studie s funkcemi jiných publikovaných prací.

Klíčová slova: Quercus robur; Quercus petraea; složky biomassy; uhlík; les; mírné pásmo