



Effects of stand features on aboveground biomass and biomass conversion and expansion factors based on a *Pinus sylvestris* L. chronosequence in Western Poland

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Abstract

Although Scots pine (*Pinus sylvestris* L.) is one of the most economically important European timber trees, there is still insufficient data about biomass variability and its relationships with stand features. Therefore, we aimed: (1) to develop biomass models for different aboveground biomass components at tree and stand levels, as well as biomass conversion and expansion factors (BCEFs), (2) to assess the relationships between stand parameters and aboveground biomass and BCEFs and (3) to compare stand biomass obtained using BCEFs with models developed based on stand parameters (age, basal area, stand volume and mean height). Using a chronosequence (3–117 years old) of 120 plots within even-aged pure Scots pine stands and 791 sample trees, we prepared tree- and stand-level allometric equations and BCEFs for aboveground biomass determination. Using stand age, density, stand volume and mean height, we prepared a set of models for biomass and BCEFs. Our study indicated that stand biomass increased with increasing height, volume and age and with decreasing stand density during stand development. Stand-level models provided better accuracy than BCEF-based models. The best predictors of biomass were stand volume and mean height. We also confirmed highly dynamic increases in stand biomass and decreases in BCEFs in the youngest phase of stand growth and relative stabilization in later stages of Scots pine stand development. The models obtained may be used in large-scale forest biomass inventories and increase our knowledge of carbon sequestration in forest biomass.

Keywords Scots pine · Biomass allocation · Allometric equations · Stand age · Volume · Height

Introduction

Stand biomass is one of the most important measures of space and resource utilization in forest ecosystems. As carbon content in plant tissues is relatively constant, in

comparison with the variability of stand biomass (e.g., Lehtonen et al. 2004; Martin and Thomas 2011; Jagodziński et al. 2012), assessment of biomass allows calculation of how much carbon has been sequestered in an ecosystem. This utility of biomass calculation confers its high importance in carbon inventories, allowing estimation of carbon sequestration in forests. In the age of changing climate (Thuiller et al. 2011; Sohngen and Tian 2016) and increasing concentration of CO₂ in the atmosphere (IPCC 2013), increasing accuracy of biomass estimation is an urgent need of science. This is especially important, as forests are one of the most important terrestrial pools of carbon (Pan et al. 2011) and may help to mitigate negative effects of climatic change (Chmura et al. 2010; Lindner et al. 2014; Dyderski et al. 2018).

Usually stand biomass may be assessed using the two main approaches: allometric equations at both tree and stand levels (e.g., Baskerville 1972; Zianis et al. 2005; Zasada et al. 2008; Xie et al. 2016; Forrester et al. 2017) and

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stand-level assessments based on biomass conversion and expansion factors (e.g., Lehtonen et al. 2004; Teobaldelli et al. 2009; Wojtan et al. 2011; Jagodziński et al. 2017). The former is a regression model between two variables expressed in units of different dimensions. The most common are tree-level models, allowing for biomass estimation based on dimensions of single trees. This tool uses general allometric rules of biomass scaling according to the organism's dimensions (Weiner 2004; McCarthy and Enquist 2007; Poorter et al. 2015). Although these models usually have high accuracy (Zianis et al. 2005), their applicability is limited only to datasets containing single tree observations. For that reason usage of tree-level methods of biomass estimation is time and money demanding. BCEFs are coefficients which allow calculation of stand biomass using information on volume (Eggleston et al. 2006; Somogyi et al. 2007). As BCEFs are volume dependent, their application is only possible when this information is available. However, most forest inventories provide this data, as stand volume is the most important parameter from the economical point of view. For that reason, BCEFs are more useful for cases of large-scale analyses (Neumann et al. 2016). Nevertheless, BCEFs are developed using biomass calculated from tree-level inventories; thus, their accuracy is biased at the level of tree-level biomass estimation and development of stand-level models.

Stand biomass, as a function of resource availability, also depends on the other stand features. Allometric trajectories of biomass models are modified by stand age (Wirth et al. 2004; Lehtonen et al. 2004; Jagodziński et al. 2017). Biomass production and allocation also depend on stand density (Jagodziński and Oleksyn 2009a, b). Also, measures of stand density and dimensions, such as volume and basal area, are often used in modeling of stand biomass or BCEFs (Teobaldelli et al. 2009; Castedo-Dorado et al. 2012; Lehtonen et al. 2016; Jagodziński et al. 2017). Biomass allocation patterns (i.e., ratio of stem, branches, root and foliage masses), influencing stand biomass, also differ among habitat types. For example, site-specific allometric models were provided for peatlands (e.g., Laiho and Finér 1996; Hytönen and Aro 2012; Lehtonen et al. 2016), post-agricultural sites (e.g., Uri et al. 2007; Bijak et al. 2013; Jagodziński et al. 2014) or post-industrial sites (e.g., Pietrzykowski and Socha 2011; Kuznetsova et al. 2011; Jagodziński et al. 2014). The differences in growth of trees are also connected with provenances and genotypes, reflecting adaptations to soil and climate (e.g., Oleksyn et al. 1999; Bussotti et al. 2015; Chakraborty et al. 2016). For that reason, for large-scale inventories there is a need to provide generalized models (e.g., Wirth et al. 2004; Muukkonen 2007; Forrester et al. 2017), taking into account stand parameters which are usually available in forest inventory datasets.

Scots pine (*Pinus sylvestris* L.) is the most extensively distributed tree species in Eurasia (Houston Durrant et al. 2016). Its range covers an area from Spain to Eastern Siberia, from boreal to Mediterranean zones. This species typically dominates in poor habitats, connected with sandy soils and harsh climates; however, it has a broad ecological amplitude. Scots pine is able to colonize both extremely dry and extremely wet sites (Ellenberg 1988; Houston Durrant et al. 2016). For that reason, this species has high economic importance in Europe, with a 20% share of timber production (Houston Durrant et al. 2016). Nevertheless, our knowledge about its biomass production is disproportionately low relative to its geographical range and economic usage (Cienciala et al. 2006; Forrester et al. 2017). For Scots pine, Zianis et al. (2005) provided 205 allometric equations for the entirety of Europe. Forrester et al. (2017) found 107 allometric models useful for large-scale analyses, rejecting those not based on diameter at breast height. BCEFs and allometric equations for Scots pine biomass estimation were also reviewed by Neumann et al. (2016) and by Lakida et al. (1996). Numerous raw data of tree- and stand-level biomass are provided in Schepaschenko et al. (2017). Although accounting for large extents within Scots pine geographical range, as well as its variability in ecophysiology and patterns of biomass allocation (e.g., Oleksyn et al. 1999; Lehtonen 2005; Finér et al. 2007; Jagodziński and Oleksyn 2009a; Repola and Ahnlund Ulvcrona 2014; Bronisz and Zasada 2016), this number of biomass estimation models might still be insufficient for proper reporting of carbon sequestration in forest ecosystems. This insufficiency results from local specificities and biogeographic trends. Moreover, despite studies on stand biomass of Scots pine in Poland, at this time there are no published studies covering a whole chronosequence of this species biomass in Poland using both tree- and stand-level approaches. Thus, we aimed: (1) to develop biomass models for different aboveground biomass components at tree and stand levels, as well as biomass conversion and expansion factors (BCEFs) for Scots pine, (2) to assess the relationships between stand parameters and aboveground biomass and biomass conversion and expansion factors (BCEFs) and (3) to compare stand biomass obtained using BCEFs with models developed based on stand parameters (age, basal area, stand volume and mean height).

Methods

Study sites and material

We established 120 plots in pure even-aged Scots pine stands ranging from 3 to 117 years old and on all site types typical for this species, including long-term forest (forest growing on forest sites, in contrast to first-generation forests), post-agricultural and post-industrial sites (Table 1, S1). The plots

Table 1 Overview of the study plots and stand characteristics (n=120)

Parameter	V (m ³ ha ⁻¹)	G (m ² ha ⁻¹)	N (ind. ha ⁻¹)	A (years)	H_g (m)	AB (Mg ha ⁻¹)	BR (Mg ha ⁻¹)	FL (Mg ha ⁻¹)	ST (Mg ha ⁻¹)
Min	0.06	0.00	186.1	3.0	0.3	0.11	0.01	0.05	0.08
Mean	136.97	17.47	5084.5	26.5	9.5	65.65	9.63	5.43	53.40
SD	169.32	14.59	3419.9	29.0	8.9	78.04	7.42	3.49	69.78
Max	600.46	65.79	14,125.0	117.0	31.1	291.25	32.89	17.06	256.10

V —growing stock volume, G —basal area, N —density, A —stand age, H_g —mean height weighted by tree basal area, AB—total aboveground biomass, BR—branch biomass, FL—foliage biomass, ST—stem biomass

were established during different studies; thus, their selection was usually connected with visual estimation as being representative of larger areas of neighborhood forests. Plot sizes varied from 0.008 to 0.6125 ha, to maintain sufficient numbers of trees to analyze stand features (at least 100 trees per plot). Sample stands grew in a wide range of habitats, mostly poor and mesic soils, which are potential sites of pine forests, and poor sites of oak forests, constituting optimal sites for Scots pine (Ellenberg 1988). Within our dataset, we also included stands established in habitats of fertile deciduous forests, where Scots pine was planted to increase its wood production. All plots were located in lowlands of Western and Central Poland, in a zone of transition between maritime and continental temperate climate (51.21–53.92°N; 14.34–18.59°E).

Field and laboratory methods

Diameters of all trees and heights of at least 20% of trees were measured within each study plot. Within study plots, we selected and harvested four to twelve sample trees to obtain weight of the biomass components. We cut off branches of all trees and weighed branches with needles. After that, in the field we weighed subsamples of branches with needles (at least 5% for large trees and usually > 20% for smaller trees). Each subsample was divided into needles and branches in the laboratory and then dried and weighed. Sample trees were selected to be representative of the diameter distribution—one tree from each quantile. Samples of needles (FL), branches (BR) and stems (ST, including wood and bark) were oven-dried to a constant mass (65 °C). Then, plant material was weighed with an accuracy of 1 g. Using the proportion of dry and fresh masses of samples and total fresh masses of biomass components obtained in the field, we calculated total dry mass of each biomass component for a particular model tree. As biomass of dead branches and cones strongly varies among trees, study sites and growing seasons, we decided to exclude these tree components from analyses, focusing on biomass of FL, BR, ST and their sum—aboveground biomass (AB). For each plot, we measured stand density (N), mean height weighted by basal area (H_g), growing stock volume (V) and age (A).

Data analysis

We used site-specific Naslund's models from the *lmfor::ImputeHeights()* function (Mehtatalo 2008) to impute heights for each tree (R Core Team 2017). We also calculated volume of the whole stem. We decided to take into account volume of whole stems instead of merchantable volume, as the youngest trees have no merchantable volume. We also did not account for merchantable branch biomass, as it was present only in 19 of 791 sample trees and constituted a maximum of 3.4% of total stem volume. Volume of each tree stem was calculated using diameter measurements of sections 1 m in length. We assumed the shape of each section as a cylinder and the shape of the last section as a cone. Due to different origins of datasets used, we did not measure volume for 219 young sample trees (<20 years old) and 24 older sample trees (up to 47 years old). To estimate volume of these trees, we used a machine learning technique—the random forest model (Breiman 2001) implemented in the *caret::train()* function (Kuhn 2008) in R software (R Core Team 2017) for obtaining tree volume, based on the diameter, height and age of the trees. We are conscious that joining datasets with measured and predicted volume undermines assumptions of methods identity. However, in our study we did not focus on tree volume estimation, but we calculated it for the purpose of calculating stand volume. Thus, we decided not to remove 54 study plots to decrease uncertainty of our models. This model had RMSE=0.002 and $R^2=0.98$, and RMSE=0.03 and $R^2=0.98$ for younger and older trees, respectively. At the stand level, we calculated H_g , but for the 35 youngest stands we calculated mean height, as diameters at breast height were not available.

In our study, we provided three methods of Scots pine biomass estimation: individual tree biomass models, stand level biomass models and stand level BCEFs. For each biomass component, we calculated nonlinear regression models, using the allometric model, as in previous biomass studies (Zianis et al. 2005; Zasada et al. 2008; Bronisz and Zasada 2016; Bronisz et al. 2016; Jagodziński et al. 2018):

$$W = a \times D^b \text{ (allometric model on } D), \quad (1)$$

$$W = a \times D^b \times H^c \text{ (allometric model on } D \text{ and } H), \quad (2)$$

where W —dry mass of the considered biomass component (kg), D —diameter (cm), H —height (m). For the youngest trees (up to 10 years old), we provided model accounting only for tree height, as the youngest trees may not reach breast height (130 cm):

$$W = a \times H^b \text{ (allometric model on } H\text{)}. \quad (3)$$

Similar models were used to calculate volume of each tree within stands.

We used the provided tree-level biomass models to estimate biomass of each stand studied. In stands with $A < 11$ years old, we used Eq. 3 and for older stands we used Eq. 2. For stand-level biomass analyses, we calculated biomass conversion and expansion factors (BCEFs) as $BCEF = W/V$, where W —dry mass of the considered biomass component (Mg ha^{-1}), obtained as a sum of tree biomass components and V —growing stock volume ($\text{m}^3 \text{ ha}^{-1}$). For assessment of relationships between BCEFs and stand characteristics, we also used power models:

$$BCEF = a \times z^b \text{ (e.g. Peichl and Arain 2007)}, \quad (4)$$

where z —stand characteristic (N , H_g , V or A), a and b —model coefficients. We used Eq. 4, with W instead of BCEF, in stand-level biomass models. To prevent lack of normality of residuals and problems with heteroscedasticity, we used iterative reweighted least squared regression implemented in the *robustbase::nlrob()* function (Myers 1986; Maechler et al. 2018). In this method, the regression curve is refitted in each iteration by weighting observations by the residuals. To check normality of standardized residuals and homoscedasticity, we examined diagnostic plots (standardized residuals versus fitted values). Furthermore, we compared them with volume-based functions and biomass estimations based on BCEFs. Because of variance inflation resulting from inter-correlations between predictors and problems with nonlinear regression convergence, we provided stand-level biomass models for only one independent variable. Although using multiple sample trees from multiple plots would justify application of mixed models (e.g., Repola 2009; Repola and Ahnlund Ulvcróna 2014; Bates et al. 2015), for purposes of model simplicity and applicability by practitioners we chose to use simple linear and nonlinear regression techniques. In all cases, we also calculated other measures of model quality—Akaike's information criterion (AIC), mean error (ME), root mean squared error (RMSE) and modeling efficiency (MEf) using the following formulas:

$$AIC = \frac{2 \log(\hat{\pi})}{n} + \frac{2k}{n} \quad (5)$$

$$ME = \frac{\sum_{i=1}^n (y_i - \hat{y}_i)}{n} \quad (6)$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{n - k}} \quad (7)$$

$$MEf = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2} \quad (8)$$

where \log —natural logarithm, $\hat{\pi}$ —likelihood estimator of model fitness, k —number of model parameters, n —sample size, y_i — i th observed dependent variable value, \hat{y}_i — i th predicted dependent variable value, \bar{y} —mean value of the dependent variable. Although R^2 for nonlinear models is biased and does not provide the proper amount of variance explained by the models, we decided to provide this measure as rough estimations of R^2 of linear models (MEf).

For model development, we used nonlinear, least-square regression using the *stats::nls()* function (R Core Team 2017). For comparison of model quality, we presented AIC of BCEFs and stand biomass models and AIC_0 —AIC of the null model (intercept only), according to Mac Nally et al. (2018). All analyses were conducted using R software (R Core Team 2017).

Results

Biomass of stands

Tree-level biomass models had coefficients of determination (MEf) ranging from 0.836 to 0.990, with an average of 0.922 ± 0.016 (Table 2). The highest values were for total aboveground biomass and stem biomass, and the lowest for branches and foliage biomass. Models based on height only, obtained for young trees (up to 10 years old) had lower accuracy than those for older trees. Total aboveground biomass of the stands studied ranged from 0.11 to $291.25 \text{ Mg ha}^{-1}$, with an average of 65.62 ± 7.12 . Biomass of branches ranged from 0.01 to 32.89 Mg ha^{-1} , with an average of 9.64 ± 0.68 . Biomass of needles ranged from 0.05 to 17.06 Mg ha^{-1} , with an average of 5.43 ± 0.32 . Biomass of stems ranged from 0.08 to $256.10 \text{ Mg ha}^{-1}$, with an average of 53.39 ± 6.37 .

Total aboveground biomass of Scots pine stands increased with increasing stand height, growing stock volume and age, and decreased with increasing stand density (Fig. 1; Table 3). Similar trends were found for particular biomass components; however, increases in foliage and branch biomass quickly reached a plateau, with little to no increase in older stands. For total aboveground biomass and all compartments, the best model was based on stand volume (MEf

Table 2 Final allometric equations for biomass components developed for each age class

Biomass component	Predictors	<i>a</i>	SE	<i>b</i>	SE	<i>c</i>	SE	AIC	RMSE	ME	MEf
AB	H-only	0.1299	0.0115	2.2644	0.0434	–	–	460.300	0.200	0.000	0.931
BR	(trees < 11 years old)	0.0180	0.0023	2.6965	0.0603	–	–	98.069	0.621	0.038	0.917
FL	<i>n</i> = 268	0.0455	0.0056	2.0970	0.0620	–	–	90.059	0.663	0.040	0.836
ST	$a \times H^b$	0.0803	0.0050	2.0618	0.0314	–	–	24.997	1.208	–0.073	0.957
AB	DBH only	0.2076	0.0158	2.2185	0.0203	–	–	5865.693	145.865	–6.214	0.976
BR	(trees > 10 years old)	0.0086	0.0016	2.4422	0.0497	–	–	4211.209	3.511	–0.150	0.885
FL	<i>n</i> = 549	0.0302	0.0048	1.7420	0.0435	–	–	2808.993	1.966	0.084	0.841
ST	$a \times DBH^b$	0.1899	0.0168	2.2082	0.0235	–	–	5889.719	148.756	–6.337	0.967
AB	H + DBH	0.0285	0.0029	1.8166	0.0203	1.0388	0.0418	5425.211	34.769	–1.480	0.989
BR	(trees > 10 years old)	0.0732	0.0178	2.9155	0.0688	–1.1686	0.1150	4124.494	18.723	–0.797	0.902
FL	<i>n</i> = 549	0.1647	0.0288	2.2697	0.0665	–1.0952	0.0992	2712.082	3.746	–0.159	0.867
ST	$a \times DBH^b \times H^c$	0.0138	0.0014	1.6840	0.0192	1.3630	0.0407	5232.995	28.297	–1.204	0.990

^a - abbreviations of biomass components

^b - abbreviations of predictors

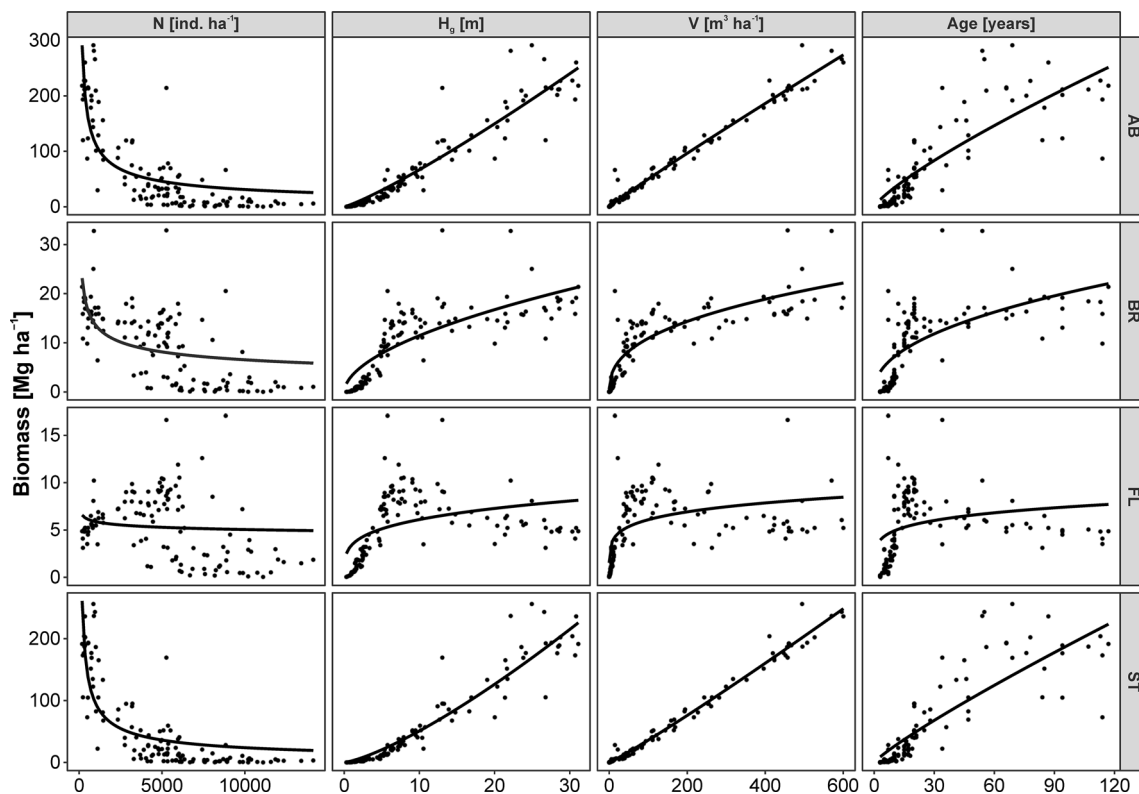


Fig. 1 Relationships between stand characteristics and stand biomass components: total aboveground (AB), branches (BR), foliage (FL) and stem (ST). Parameters of nonlinear regression models are presented in Table 3

from 0.322 in FL to 0.985 in ST). Other biomass components were also strongly correlated with stand height. The weakest predictor of biomass, regardless of the component considered, was stand density (MEf from 0.014 in FL to 0.633 in ST).

Biomass conversion and expansion factors

BCEFs of Scots pine for total aboveground biomass ranged from 0.3173 to 4.5022, with an average of 0.6207 ± 0.0423 , for branch biomass from 0.0287 to 1.3933, with an average of 0.1427 ± 0.0138 , for foliage biomass from 0.0087

Table 3 Relationships between stand characteristics (predictors) and stand biomass components (Mg ha^{-1}), modeled using Eq. 4

Biomass component ^a	Predictor ^b	<i>a</i>	SE	<i>b</i>	SE	RMSE	Mef	AIC	AIC ₀
AB	<i>V</i>	0.6041	0.0382	0.9529	0.0106	22.359	0.979	728.6	1389.3
	<i>H_g</i>	3.5315	0.3258	1.2400	0.0295	13.060	0.896	932.9	–
	<i>N</i>	8041.0766	2344.6831	-0.6244	0.0447	3.142	0.626	1200.6	–
	<i>A</i>	3.5099	0.7243	0.8990	0.0487	17.042	0.722	1134.7	–
BR	<i>V</i>	1.7168	0.3058	0.3955	0.0324	0.072	0.762	616.9	824.7
	<i>H_g</i>	3.0914	0.4615	0.5552	0.0531	0.356	0.662	659.3	–
	<i>N</i>	126.6402	46.4280	-0.3263	0.0503	1.333	0.341	755.7	–
	<i>A</i>	2.3432	0.5358	0.4688	0.0602	0.298	0.503	718.5	–
FL	<i>V</i>	2.4725	0.4758	0.1898	0.0383	0.766	0.322	573.0	643.7
	<i>H_g</i>	3.2928	0.5428	0.2578	0.0664	0.633	0.242	593.1	–
	<i>N</i>	10.0852	4.8999	-0.0797	0.0606	1.556	0.014	627.0	–
	<i>A</i>	3.0516	0.7016	0.1928	0.0691	1.155	0.109	613.6	–
ST	<i>V</i>	0.2260	0.0153	1.0926	0.0112	13.739	0.985	671.2	1362.4
	<i>H_g</i>	1.8131	0.1791	1.4063	0.0313	140.666	0.925	890.1	–
	<i>N</i>	10,213.0317	2859.4499	-0.6885	0.0436	10.268	0.633	1150.2	–
	<i>A</i>	2.0012	0.4310	0.9904	0.0501	23.857	0.722	1087.7	–

^aAB—total aboveground biomass, BR—branch biomass, FL—foliage biomass, ST—stem biomass

^b*A*—stand age (years), *H_g*—mean height weighted by tree basal area (m), *N*—stand density (ind. ha^{-1}), *V*—growing stock volume ($\text{m}^3 \text{ha}^{-1}$)

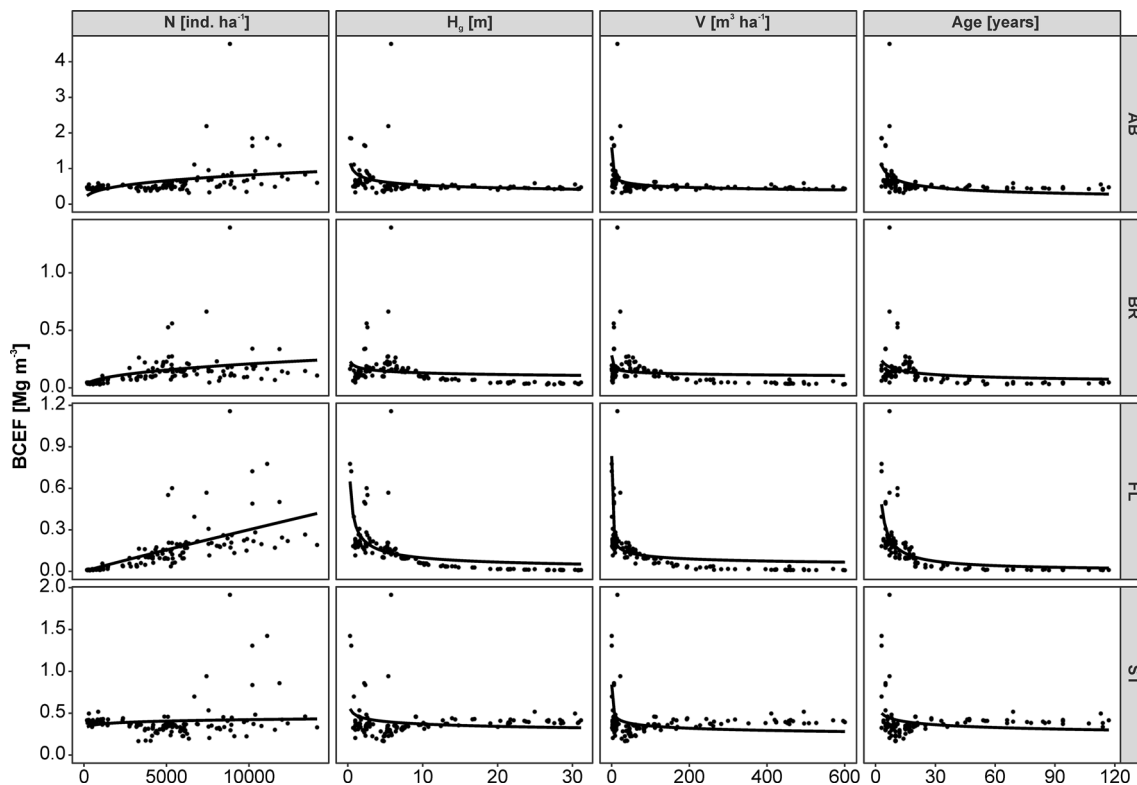
**Fig. 2** Relationships between stand characteristics and BCEFs for biomass components: total aboveground (AB), branches (BR), foliage (FL) and stem (ST). Parameters of nonlinear regression models are presented in Table 4

Table 4 Relationships between stand characteristics (predictors) and BCEFs for particular biomass components (Mg m^{-3}), modeled using Eq. 4

Biomass component ^a	Predictor ^b	<i>a</i>	SE	<i>b</i>	SE	RMSE	Mef	AIC	AIC ₀
AB	<i>V</i>	0.7927	0.0316	−0.1018	0.0103	0.769	0.121	−158.0	159.0
–	<i>H_g</i>	0.6843	0.0232	−0.1403	0.0177	0.880	0.049	−159.2	–
–	<i>N</i>	0.2053	0.0405	0.1172	0.0237	0.923	0.033	−118.4	–
–	<i>A</i>	0.8297	0.0560	−0.1562	0.0240	0.873	0.070	−136.1	–
BR	<i>V</i>	0.1687	0.0163	−0.0932	0.0258	0.243	0.032	−294.5	−110.0
–	<i>H_g</i>	0.1610	0.0136	−0.1773	0.0480	0.249	0.015	−301.0	–
–	<i>N</i>	0.0053	0.0026	0.3725	0.0551	0.263	0.099	−366.9	–
–	<i>A</i>	0.2476	0.0373	−0.2718	0.0593	0.257	0.061	−321.0	–
FL	<i>V</i>	0.3556	0.0137	−0.2939	0.0144	0.147	0.459	−315.7	−81.5
–	<i>H_g</i>	0.3293	0.0116	−0.6336	0.0311	0.178	0.371	−343.5	–
–	<i>N</i>	0.0001	0.0001	0.8659	0.0780	0.284	0.337	−354.8	–
–	<i>A</i>	0.9645	0.1161	−0.7982	0.0580	0.229	0.413	−349.3	–
ST	<i>V</i>	0.3507	0.0187	0.0080	0.0122	0.409	−0.044	−245.0	−19.6
–	<i>H_g</i>	0.3340	0.0134	0.0411	0.0182	0.432	−0.060	−264.1	–
–	<i>N</i>	0.5353	0.0632	−0.0494	0.0148	0.441	−0.057	−278.2	–
–	<i>A</i>	0.3092	0.0189	0.0523	0.0194	0.442	−0.067	−266.5	–

^a - abbreviations of biomass components, AB—total aboveground biomass, BR—branch biomass, FL—foliage biomass, ST—stem biomass

^b - abbreviations of predictors, *A*—stand age (years), *H_g*—mean height weighted by tree basal area (m), *N*—stand density (ind. ha^{-1}), *V*—growing stock volume ($\text{m}^3 \text{ha}^{-1}$)

to 1.1576, with an average of 0.1538 ± 0.0155 , and for stem biomass from 0.1667 to 1.9146, with an average of 0.3984 ± 0.0201 . BCEF values were constant for older stands, but in the youngest stands its values were decreasing with increasing stand age, height and growing stock volume, and increasing with increasing density (Fig. 2; Table 4). However, the rate of these dynamics was distinct only at low values of these parameters and reached a plateau after c.a. 30 years old. The best predictor of BCEFs was stand volume (MEf from −0.044 to 0.459), except for branches where the best was stand density (MEf=0.099). These relationships were weak; however, in most cases RMSE was lower than 0.001 Mg m^{-3} , which was connected with low variability of BCEFs in the higher part of the range of the parameters studied. For that reason, in the older stands (above 10 years old), we may assume mean BCEFs for AB— 0.4767 ± 0.00698 , for BR— 0.1224 ± 0.0116 , for FL— 0.0844 ± 0.0120 and for ST— 0.3648 ± 0.0067 .

Discussion

Effect of stand age

Our results indicated the important role of age in differing relationships between stand features and biomass, as well as BCEFs. The most distinct effect of age was found in the youngest stands, where differentiation of BCEFs and

biomass was the highest. This is similar to the results of Jagodziński et al. (2017) for young stands of *Betula pendula*, where the estimated age breakpoint was c.a. 5 years old. In our study, there was a strong decrease in BCEFs after c.a. 10 years of stand development and after that time BCEFs were more or less constant, similar to a study focused only on young trees (Jagodziński et al. 2018). Also Schepaschenko et al. (2018) revealed this trend using a large dataset from Eurasia. This trend was confirmed for age-class-specific biomass models based on stand parameters (Fig. 3), where strong relationships occurred in the younger stands.

Higher variability of younger stands is connected with different conditions of juvenile growth. This may result from management treatment or site conditions. Moreover, in smaller plants, there are higher proportions of foliage and branches (Mikšys et al. 2007; Uri et al. 2012; Poorter et al. 2015), the biomass of which is less uniform than stem biomass, which constitutes most of the biomass in older trees. Foliage biomass strongly depends on different site-specific factors (Poorter and De Jong 1999; Jagodziński and Kaľucka 2008; Rademacher et al. 2009); thus, its variation affects model accuracy. A similar pattern was found for BCEFs by Lehtonen et al. (2004). However, our previous paper (Jagodziński et al. 2018), where for young stands we used site-specific allometric tree-level models, showed similar patterns. Therefore, this effect is consistent regardless of the accuracy of biomass estimation method.

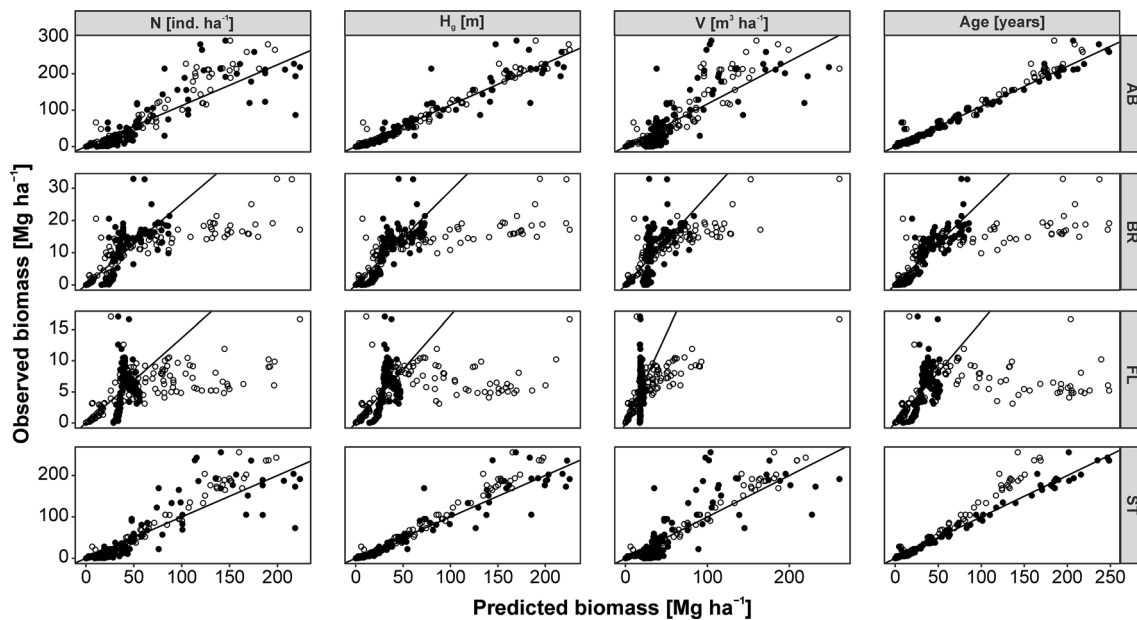


Fig. 3 Distributions of deviations between biomass calculated using stand parameter biomass models (Table 3; black dots) and using BCEF models using different stand parameters (columns) multiplied

by growing stock volume (Table 4; open dots) for total aboveground biomass (AB), branches (BR), foliage (FL) and stem (ST) biomass. Lines indicate 1:1 proportions

Similarly low coefficients of determination for BCEF models were provided by Lehtonen et al. (2004). As older trees are composed mainly of stem biomass, which is strictly related to growing stock volume, this constancy may suggest using constant BCEF values for these trees. Effects of stem mass ratio may be confirmed by higher accuracy of models for BCEFs without leaves than with leaves, provided by Teobaldelli et al. (2009). Constant lines for modeled BCEFs for older Scots pines were also provided by other authors (Lehtonen et al. 2004; Jalkanen et al. 2005; Teobaldelli et al. 2009; Wojtan et al. 2011).

Effect of other stand features

In our study, the most important features influencing biomass and BCEFs were stand height and growing stock volume. These two factors are mostly related to stem biomass, which constitutes the majority of aboveground biomass (Poorter et al. 2015). As these parameters within the same age are site-dependent, we may assume that these models allow predictions to overcome site-specific conditions at the stand level and may also be better than preparing models for different site indices, which are different in particular countries. Other studies revealed high importance of site index in shaping stand biomass (e.g., Shepashenko et al. 1998; Teobaldelli et al. 2009; Schepaschenko et al. 2018). However, when we compare heteroscedasticity of models based on height and growing stock volume, those based on height

seem to be more homoscedastic (Fig. 3). Stand density was the weakest predictor of stand biomass, similar to Castedo-Dorado et al. (2012). Despite its importance in shaping biomass allocation (Jagodziński and Oleksyn 2009b), its primary impact is connected with shaping growth conditions, especially single tree dimensions—at higher density individual trees have lower diameters and higher heights (Jagodziński and Oleksyn 2009a); therefore, this parameter is also included in stand height and growing stock volume.

Accuracy of models and applicability

Our study confirmed higher accuracy of tree-level than stand-level methods. Our study also showed that biomass estimation based on stand-level biomass models and BCEFs gives similar accuracy, when the best models are taken into account. However, for branch and foliage biomass, tree-stand-based models give overestimated results, and BCEFs give underestimated results, compared to biomass calculated using tree-level approaches (Fig. 3). A similar trend, but with lower magnitude of bias, was found for volume-based models. However, due to high randomness, foliage and branch biomass are the most difficult to estimate, both at the levels of trees and stands, similar to other studies (e.g., Zianis et al. 2005; Teobaldelli et al. 2009; Wojtan et al. 2011; Castedo-Dorado et al. 2012).

Regional stand-level biomass models obtained in our study may be applied in large-scale inventories, including those using airborne laser scanning and other remote

sensing techniques. These inventories can easily and quickly provide large amounts of data. However, they provide the highest accuracy for height measurements (Niemi et al. 2015; Kauranne et al. 2017). For that reason, high accuracy of models based on stand height may allow for increasing applicability of these methods. Moreover, it may be used for young stands or when data on stand volume is not available, due to lack of ownership interests or remote localities (Jagodziński et al. 2017, 2018).

Conclusions

Our study provided a comprehensive set of tree- and stand-level biomass models. We also described how stand biomass increases with increasing height, growing stock volume and age, and with decreasing stand density during stand development. Our study indicated highly dynamic increases of biomass and decreases of BCEFs in the youngest phase of stand growth and relative stabilization in later phases. Our models showed that accurate biomass assessment may be conducted using airborne methods, providing data on stand height (Jagodziński et al. 2018).

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