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How do tree stand parameters affect young Scots pine biomass? – Allometric equations and biomass conversion and expansion factors



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ABSTRACT

Due to the impact of climate change and rising atmospheric carbon dioxide concentrations, assessment of forest carbon pools becomes a crucial task for forest ecology. One of the scientific gaps in this task is the assessment of young tree stands, not included in forest inventories, due to lack of merchantable volume. We aimed to provide a comprehensive set of allometric equations (AEs) and biomass conversion and expansion factors (BCEFs) for young Scots pine tree stands and to develop models of tree stand biomass based on stand features easy-measurable by remote sensing: height and density. We used data collected in 77 tree stands of Scots pine ranging in age from 3 to 20 years in Western and Central Poland, covering forest, post-agricultural and post-industrial sites. Our dataset included 423 sample trees. Our study resulted in collection of 256 site-specific AEs, 12 generalized AEs and equations allowing for dynamic BCEF calculation. Due to lack of BCEF applicability for young trees, we also provided age- and height-dependent functions allowing for precise biomass estimation at the tree-stand level. It was found that tree-stand biomass increased with tree-stand age, height and volume, and decreased with increasing density in the chronosequence. BCEFs decreased with tree-stand age, height and volume and increased with increasing density. Using these relationships we provided stand-level equations based on BCEFs and on tree height - the stand characteristic which is easily obtained from airborne data. These two models did not show a big difference in accuracy. Thus, height-based models are expected to be useful for extensive assessments of young tree stand biomass and carbon sequestration, allowing for better estimation of forest carbon pools. Moreover, our models, in comparison with IPCC guidelines, give more precise values of carbon pools and biomass of young Scots pine tree stands.

1. Introduction

Forest ecosystems act as sustainable carbon reservoirs. A number of recent studies have focused on the role of forests in mitigation of climatic change and its effects (e.g. Pan et al., 2011; Fearnside, 2012; Seidl et al., 2014; Naudts et al., 2016; Dyderski et al., 2017). The international pressure to implement comprehensive mechanisms limiting emissions of greenhouse gases to the atmosphere, also involves heightened attention to look for potential carbon sinks. Forest ecosystems are the main terrestrial carbon stock, accumulating globally ca. $2.4 \pm 0.4 \, \mathrm{Pg} \, \mathrm{C} \, \mathrm{year}^{-1}$ (Pan et al., 2011). Enhanced photosynthesis by forests growing under elevated CO₂ can limit processes leading to increasing atmospheric CO₂ concentration (Chmura et al., 2010; Lindner et al., 2014). Consequently, in addition to the modification of some forest management practices aimed at increasing the sequestration of

carbon (Lindner et al., 2014; Sohngen and Tian, 2016), there is a need to include stands formerly omitted from consideration, especially young tree stands, which have not yet produced merchantable wood or tree stands growing on specific sites, e.g. post-industrial or peatlands. Therefore, detailed estimation of tree biomass components of a given species, as well as carbon contents, are high in importance, as generalized data is often used, according to IPCC guidelines (Eggleston et al., 2006). This in turn, could result in underestimation of total carbon sequestered in a stand. For example, IPCC assumes that conferous species root biomass amounts to 20% of aboveground biomass, but Oleksyn et al. (1999) found higher values, depending on tree provenance. The concentration of carbon in different tissues is less variable than biomass of tree stands (Lehtonen et al., 2004; Martin and Thomas, 2011; Jagodziński et al., 2012; Uri et al., 2012). Therefore, we can estimate carbon contents based on biomass assessment. However, the

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accuracy of the method used is crucial for proper estimation.

There are two main approaches for biomass estimation: use of allometric equations (AEs) or biomass conversion and expansion factors (BCEFs) (e.g. Baskerville, 1972; Lehtonen et al., 2004; Montero et al., 2005; Zianis et al., 2005; Teobaldelli et al., 2009; Neumann et al., 2016; Jagodziński et al., 2017). These two methods differ in accuracy and labor requirement, as AEs are applied at the tree level, while BCEFs are at the tree-stand level. AEs are based on relationships between tree biomass and usually common dimensions, i.e. diameter or/and height, and allow tree-level calculations (Baskerville, 1972; Weiner, 2004; Poorter et al., 2015). Despite their relatively high accuracy, AEs have the disadvantage of requiring a high amount of labor and associated costs. In contrast, BCEFs as coefficients of tree stand merchantable volume, allow only tree-stand level calculations. Moreover, due to the lack of tree-level data in forest inventories, BCEFs are rather frequently used for large-scale estimations (Neumann et al., 2016). The largest disadvantage of BCEFs occurs when biomass estimation of young tree stands is required, as young trees have not yet reached the threshold size for merchantable wood. Data on young trees and volume of their wood are usually omitted in forest inventories (Lehtonen et al., 2004; Pajtík et al., 2008; Jagodziński et al., 2017). For example, in Poland there is no information about tree stand volume unless trees reach the merchantable volume threshold of diameter at breast height (D_{1.3}) of 7 cm. Analysis of ca. 550,000 records from the forest data bank revealed that information about tree stand volume appears in 4% of 15 y.o. (years old) tree stands and 65% of 20 y.o. tree stands (Forest Data Bank, 2015). In contrast, information about height is available for 57% of 3 y.o. and 82% of 5 y.o. stands. Another disadvantage is high variability of BCEFs in small individuals, in contrast to larger individuals (e.g. Konôpka et al., 2015; Jagodziński et al., 2017). Therefore, large scale analyses using BCEFs on young forests are impossible.

Zianis et al. (2005) published a comprehensive review of allometric equations for European trees, which was updated by Muukkonen and Mäkipää (2006). In this database there are 205 AEs for Scots pine (*Pinus* sylvestris L.). After review of more recent papers we found 240 AEs potentially applicable for various biomass components of young Scots pines, coming from different countries, and possibly connected with different biomass allocation patterns (Oleksyn et al., 1999). The accuracy of these AEs varied across the wide range of dimensions they covered, therefore obscuring age-dependent patterns of biomass allocation (Jagodziński and Kałucka, 2008; Jagodziński and Oleksyn, 2009a,b; Teobaldelli et al., 2009; Uri et al., 2012; Jagodziński et al., 2014). There are also some AEs for young Scots pine trees (e.g. Oleksyn et al., 1999; Claesson et al., 2001; Jagodziński et al., 2014), and individual tree BCEFs (Pajtík et al., 2011). However, these studies were conducted at limited sites and it is not clear whether they are sitespecific. This is especially important because the accuracy of carbon estimation strongly depends on country-specific methods (Neumann et al., 2016) and differences in biomass production and allocation between different land use forms result in site-specific allometric trajectories (Jagodziński and Kałucka, 2008; McHale et al., 2009; Jagodziński et al., 2014). For that reason there is a need for studies to include both site-specific, as well as generalized allometric equations (Muukkonen, 2007).

Collecting such data is laborious and apparently unprofitable from the point of view of forest management, especially in the youngest woodlands, which being apart from timber production, have no detailed volume information. Measurements acquired by remote sensing could be a compromise between time-consuming fieldwork and generalizations based on data obtained in older stands. Airborne Laser Scanning (ALS) may be an interesting solution, yielding data about species composition, stand height and density of tree stands that is useful for biomass estimations (White et al., 2013; Wulder et al., 2013; Zasada et al., 2013). Among tree stand characteristics, height seems to be the feature estimated with the highest accuracy by ALS (Niemi et al., 2015; Kauranne et al., 2017). As the two most frequently used methods for biomass estimation are BCEFs and AEs, there are few data about relationships between biomass and other tree stand parameters (e.g. Castedo-Dorado et al., 2012; Jagodziński et al., 2017). For that reason we aimed to provide a comprehensive set of allometric equations and biomass conversion and expansion factors for young Scots pine tree stands and to develop models of tree stand biomass based on stand features - height and density - easily measurable by remote sensing. We hypothesized that (1) generalized allometric equations would explain lower amounts of variance than those that are site-specific, but (2) also would be useful for biomass estimation due to relatively low bias, (3) despite the generalizations, generalized equations would generate lower biases and lower heteroscedasticity along a gradient of increasing observed biomass than published equations, (4) tree stand features: height, volume, age and density will influence tree stand biomass and BCEFs, and (5) biomass estimation methods based on tree stand height would not differ in accuracy from BCEF-based methods.

2. Material and methods

2.1. Study species

Scots pine (Pinus sylvestris L.) is a pioneer, coniferous tree species, covering over 28 million ha in Europe, constituting over 20% of total timber productivity (Houston Durrant et al., 2016). Scots pine is able to grow in a wide range of site conditions – from dry and poor arenosols to wet and fertile alluvial soils, however, it is able to reproduce naturally on poor to medium fertile podzols and brunic arenosols (Ellenberg, 1988). According to National Forest Inventory from 2011 to 2015 (Forest Data Bank, 2015), in Poland Scots pine covers an area of 5.4 million ha (58.1% of forest area in Poland) and its merchantable volume is 1519 million m³ (60.8% of total wood resources). Thus, Scots pine stands are important carbon reservoirs, playing one of the key roles in global carbon storage accumulated in the tree components: biomass of needles, branches, stems and roots. Scots pine reaches the largest dimensions and biomass in Central Europe, due to droughtmediated limitation in southern Europe and cold-mediated limitation in the North (Oleksyn et al., 1999). However, Cienciala et al. (2006) argue that despite the high economic importance of Scots pine, little is known on this species allometry and biomass production.

Table 1
Overview of the study plots and tree stand characteristics.

Parameter	Plot area [ha]	$V [m^3 ha^{-1}]$	$G [m^2 ha^{-1}]$	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	0.0080	0.06	0.00	2717.0	3.0	0.33	0.174	0.038	0.128	0.057
Mean	0.0534	31.64	8.57	6907.0	10.4	3.88	21.830	5.557	4.417	11.940
SE	0.0057	3.62	0.94	300.2	0.6	0.26	2.066	0.560	0.300	1.353
Max	0.2151	118.20	29.79	14000.0	20.0	9.10	57.590	23.860	11.870	41.170

Abbreviations: V – stem volume, G – basal area, N – tree stand density, A – tree stand age, H_g – mean height weighted by tree basal area, AB – total aboveground biomass, BR – branch biomass, FL – foliage biomass, ST – stem biomass.

(8)

Table 2Criteria for selecting published allometric equations for comparison with results from this study.

Order	Step
1	Review of published allometric equations for Scots pine
2	Excluding equations from non-natural sites
3	Excluding equations from stands located in mountains, i.e. above 500 m a.s.l.
4	Excluding equations from stands older than 20 years old
5	Excluding equations without age information but with minimal $D_{1.3} > 6$ cm, as in our dataset over 75% of trees had $D_{1.3} < 6$ cm
6	Excluding equations without age and diameter ranges information
7	Selecting from equations calculated on the same samples the best equations, basing on \mathbb{R}^2

2.2. Study sites and material

We established 77 plots in pure Scots pine stands ranging 3–20 years old and on all site types typical for this species, including forest, postagricultural and post-industrial sites (Table 1, Appendix A). Using linear regression modelling we found that the type of habitat (postagricultural, post-industrial and forest) did not influence allometric trajectories of diameter-biomass relationships (p > .05). For that reason we treated all study plots as one dataset. Plot size varied from 0.008 to 0.215 ha. Sample tree stands grew in poor or mesic forest sites, mostly occupying podzols and brunic soils (Appendix A), which are potential sites of coniferous pine forests and poor sites of oak forests, constituting optimal sites for Scots pine (Ellenberg, 1988). All plots were located in lowlands of Western and Central Poland (51.21–52.01°N; 14.34–18.24°E; Appendix A), in a zone of transition between maritime and continental temperate climate.

2.3. Methods

Within all study plots we measured tree heights and diameters. Depending on the tree height, we used one of following diameters: D_{0.0} - root collar diameter, D_{0.5} - diameter at a height of 0.5 m and D_{1.3} diameter at breast height. For all trees on the plot taller than 1.3 m we used $D_{1.3}$; for trees taller than $0.5\,m$ but shorter than $1.3\,m$, we used $D_{0.5}$, and only when trees on a plot were shorter than $0.5 \, \text{m}$ we used $D_{0.0}$. $D_{0.5}$ seems to be more accurate to use for modelling equations than D_{0.0}, due to root collar swelling. Within 66 of the 77 study plots we selected and harvested four to twelve sample trees to determine the fresh weight of the biomass components. For most plots (47), number of sample trees was eight or more; only in two plots were four or five sample trees harvested. In total, 423 sample trees were harvested. All sampled materials were oven-dried to a constant mass (65 °C). Then, plant material was weighed with an accuracy of 1 g. Using proportions of dry and fresh masses of samples and total fresh masses of biomass components obtained on the field, we calculated total dry mass of each biomass component. As biomass of dead branches and cones strongly varies across study sites and growing seasons, we decided to exclude these tree components from analyses, focusing on biomass of needles (FL), branches (BR), stem (ST) and their sum - aboveground biomass (AB). For each plot we determined tree stand density (N), mean height weighted by tree basal area (Hg), tree stand volume (V) and age (A).

2.4. Data analysis

Using measurements of height and site-specific Naslund's models implemented in the lmfor::ImputeHeights() function (Mehtatalo, 2008) we imputed heights for each tree. For trees without measured volume (219 of 423), we applied the random forest model (Breiman, 2001) implemented in the caret::train() function (Kuhn, 2008) with RMSE = 0.002 and R^2 = 0.97 to estimate volume, based on the diameter, height and age of the trees. For each study plot where sample

trees were harvested, we developed site-specific allometric equations for all biomass components and volume. For each equation we calculated ten regression models:

$$W= a \times D^{b}$$

$$W= a+b \times D^{2}$$
(2)

$$W = a + b \times \log(D) \tag{3}$$

$$W= a+ (b/D)$$
 (4)

$$W = a \times (D^2 H)^b \tag{5}$$

$$W= a \times D^b \times H^c$$
 (6)

$$W = a + b \times \log(D^2H) \tag{7}$$

 $W = a + b \times D^2 + c \times H$

$$W= a+ b\times (D^2H)$$
 (9)

$$W = a + b \times D^2 + c \times H^2$$
 (10)

where W – dry mass of the considered biomass component (kg), D – diameter (cm), H – height (m), D^2H – pseudovolume (m³). We chose the best model based on Akaike's Information Criterion (AIC). We prepared a set of site-specific equations, using this diameter type which was available for all trees in particular stands. Moreover, we developed set of generalized equations, using all sample trees representing the considered diameter type, also choosing the best model from Eqs. (1)–(10).

We also reviewed published papers to compile allometric equations for Scots pine. We excluded all equations which did not fulfill the criteria for young tree stands (Table 2). As branch biomass equations considered only a part of the branches, we did not take them into account, to maintain comparability. Therefore, after verification, we used 45 allometric equations for further analyses (Appendix B). We decided to apply the functions to particular plots when the range of dimensions fit into the range from 20% of minimal and 120% of maximal dimension, as extrapolation biases usually increase with distance from the range of the source dataset used for model development. 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] and V - total stem volume of trees [m³ ha-1]. For assessment of relationships between BCEFs and tree stand characteristics we used following model types (see Peichl and Arain, 2007; Lehtonen et al., 2004; Jagodziński et al., 2017; Teobaldelli et al., 2009; Wojtan et al., 2011):

BCEF =
$$a \times z^b$$
 (e. g. Peichl and Arain, 2007) (11)

BCEF =
$$a + b \times e^{-z \times c}$$
 (e. g. Lehtonen et al., 2004;

BCEF = a + b/z (e. g. Teobaldelli et al. ,2009; Wojtan et al. , 2011) (13)

BCEF =
$$a + b/z^c$$
 (e. g. Teobaldelli et al., 2009) (14)

where z – considered tree stand characteristic (tree stand density, height, volume or age), a, b and c – model coefficients and e – base of the natural logarithm. Similarly, we used these models (Eqs. (11)–(14)), with W instead of BCEF to find functions explaining biomass excluding tree stand volume, as this feature is rarely measured using forest inventories. Furthermore, we compared them with volume-based functions and biomass estimations based on BCEFs. The best models were chosen using AIC. For model development we used non-linear, least-squares regression using the stats::nls() function. For comparison of model quality, we presented AIC of BCEFs and stand biomass models and AIC $_0$ – AIC of the null model (intercept only). All analyses were conducted using R software (R Core Team, 2015).

Table 3

Overview of coefficients of determination (R²) of site-specific allometric equations, provided in Appendix C.

Diameter type	Biomass component	Min	Mean	SE	Max
D _{0.0}	AB	0.991	0.994	0.002	0.997
	BR	0.903	0.957	0.028	0.995
	FL	0.968	0.983	0.008	0.997
	ST	0.955	0.984	0.014	0.999
$D_{0.5}$	AB	0.750	0.926	0.012	0.997
	BR	0.437	0.848	0.026	0.988
	FL	0.712	0.877	0.014	0.985
	ST	0.710	0.950	0.014	0.999
D _{1.3}	AB	0.925	0.975	0.004	0.999
	BR	0.866	0.952	0.007	0.999
	FL	0.741	0.930	0.012	0.998
	ST	0.874	0.974	0.006	0.999

Abbreviations: AB – total above ground biomass, BR – branch biomass, FL – foliage biomass, ST – stem biomass.

3. Results

3.1. Allometric equations

Site-specific allometric equations developed for each study plot explained from 75.0 to 99.9% of variation in AB biomass, depending on diameter type (Table 2, Appendix C). An average coefficient of determination for equations based on $D_{0.0}$ was 0.994 \pm 0.002, for equations based on $D_{0.5}$ – 0.926 \pm 0.012 and for equations based on $D_{1,3}$ – 0.975 \pm 0.004. For BR, FL and ST, coefficients of determination varied from 0.437 to 0.999 (with an average of 0.907 \pm 0.014), from 0.712 to 0.998 (0.909 ± 0.009) and from 0.710 to 0.999(0.964 ± 0.007), respectively. Generalized allometric equations developed using all sample trees explained from 79.7% to 97.5% of variation in biomass (Table 3). Equations based on D_{1,3} had the highest coefficients of determination: from 0.898 to 0.975. Stem and total aboveground biomass equations showed better performance than those for branches and foliage (Table 4). Residual distributions showed similar trends (Fig. 1). However, generalized equations based on D_{0.0} and D_{0.5} underestimated biomass for larger trees.

3.2. Comparison of site-specific, generalized and published allometric equations accuracy

Through the literature review, 45 allometric equations were identified that fulfilled our criteria. However, only 25 of them could be used in comparative study, as some of them were not applicable for any of the tree stands studied. Compared with site-specific equations, differences in predicted biomasses ranged from -99.7% to 340.6%. Mean bias of AB equations was 13.7 \pm 2.3%, of BR - 4.0 \pm 7.0%, of FL -

 $-34.1\pm3.0\%$ and of ST $-24.2\pm3.1\%$. However, the range of differences was wide (Fig. 2). Generalized model-based biomass estimates showed lower deviations from site-specific model-based estimates than published European equations. The differences were highest in BR and FL models and lowest in ST models. There were no geographic patterns in differences in biomass estimates between site-specific and published allometric equations, however most of the relative biases ranged \pm 50% of the site-specific biomass equations (Fig. 3).

3.3. Changes in BCEFs during tree stand development

At the tree stand level, Scots pine biomass was strongly positively correlated with tree stand age and height (Fig. 4, Table 5). The correlation with volume was weaker, but also positive. Tree stand biomass was also weakly negatively correlated with tree stand density. BCEFs of young Scots pine tree stands differed across components and tree stand characteristics. BCEFs for AB decreased from 3.3333 to 0.4506 Mg m $^{-3}$, with an average of 1.0100 \pm 0.0658 Mg m $^{-3}$ (Table 6, Appendix A). Regardless of biomass components, BCEFs decreased with increasing tree stand age, height and volume, and increased with increasing tree stand density (Fig. 5, Table 7). Tree stand volume and height were the best predictors of BCEFs. There was a clear breakpoint in the decreasing BCEF trend with tree stand characteristics, after which BCEF values remained constant.

3.4. Accuracy of biomass estimation using BCEFs and height-based models

Comparing biomass estimates using BCEFs and height-based models, as the best models excluding volume as a predictor, we found small differences in predictive potential of these two methods (Fig. 6). Mean biases (differences between observed and predicted biomass) for each component did not differ statistically significantly between methods (t-test, p > .05). In comparison with BCEF-based estimates, models based on H_g had similar accuracy and more even residual distributions along the response variable. The best accuracy of our models was found in the lower range of biomass.

4. Discussion

4.1. Accuracy of the developed models

Our generalized AEs had very good performances, comparable to those provided by Muukkonen (2007). In the case of AEs based on $D_{0.5}$ and $D_{0.0}$ coefficients of determination were lower than those based on $D_{1.3}$. This was probably caused by higher variability of the youngest trees, which have not reached canopy closure yet. Comparison of generalized and other published AEs with site-specific models showed that our generalized models performed better. The highest variability and the lowest coefficients of determination were found for models of

Table 4 Allometric equations for biomass components developed using all possible sample trees (for $D_{0.0}$ n = 201, for $D_{0.5}$ n = 323 and for $D_{1.3}$ n = 375 trees).

Diameter type	Biomass component	Model type (Eq. no.)	a	SE	ь	SE	c	SE	AIC	RMSE	ME	\mathbb{R}^2
D _{0.0}	AB	(6)	0.04257	0.00578	1.89614	0.09589	0.54529	0.08437	585.890	0.5680	-0.0398	0.942
$D_{0.0}$	BR	(6)	0.00188	0.00047	3.90711	0.19546	-1.08858	0.14653	146.642	0.0314	0.0022	0.861
$D_{0.0}$	FL	(6)	0.01153	0.00224	2.62717	0.16298	-0.66901	0.11716	-16.319	0.0027	-0.0002	0.829
$D_{0.0}$	ST	(6)	0.02702	0.00365	1.23088	0.08121	1.34495	0.08201	400.542	0.7191	-0.0503	0.953
$D_{0.5}$	AB	(6)	0.10279	0.00909	1.75282	0.07705	0.38734	0.06462	879.649	0.0559	-0.0031	0.930
$D_{0.5}$	BR	(10)	-0.01697	0.02392	0.03815	0.00156	-0.01898	0.00216	224.002	< 0.0001	< 0.0001	0.810
$D_{0.5}$	FL	(6)	0.04170	0.00472	2.32106	0.11171	-0.79185	0.08536	-36.148	0.2643	0.0146	0.797
$D_{0.5}$	ST	(6)	0.04830	0.00426	1.13176	0.06536	1.24315	0.06391	543.494	0.6278	-0.0348	0.948
$D_{1.3}$	AB	(6)	0.14037	0.00918	2.49351	0.04418	-0.38540	0.05346	1378.315	4.4231	0.2275	0.970
$D_{1.3}$	BR	(6)	0.02248	0.00242	3.66530	0.07855	-1.48507	0.08409	741.499	2.1629	0.1112	0.939
D _{1.3}	FL	(6)	0.07325	0.00700	3.06724	0.07975	-1.64488	0.08875	428.175	1.5890	0.0817	0.898
D _{1.3}	ST	(6)	0.06104	0.00390	1.80749	0.03760	0.53169	0.05030	899.760	0.5643	0.0290	0.975

Abbreviations: AB - total aboveground biomass, BR - branch biomass, FL - foliage biomass, ST - stem biomass.

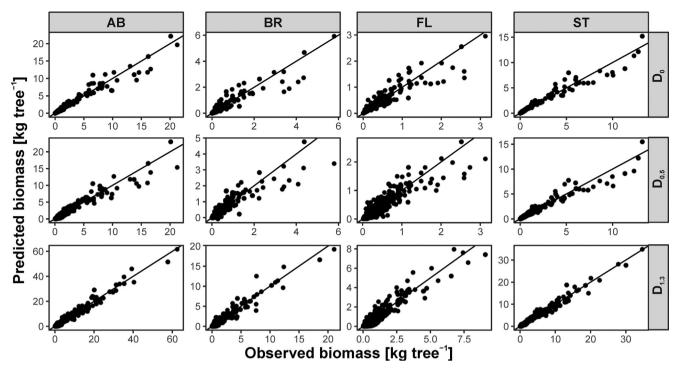


Fig. 1. Goodness of fit of allometric equations for biomass components developed using all possible sample trees (Table 4). Line indicates 1:1 proportion – lack of difference between observed and predicted biomass. Biomass components: AB – total aboveground biomass, BR – branch biomass, FL – foliage biomass, ST – stem biomass.

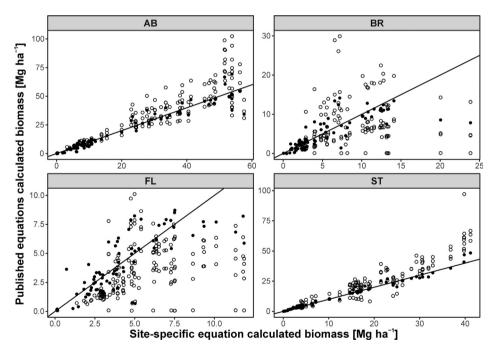


Fig. 2. Biomasses calculated by generalized (black dots) and published (open dots) allometric equations, compared with biomasses obtained using site-specific equations. Biomasses were assessed for total aboveground part (AB), branches (BR), foliage (FL) and stem (ST) of trees. Line indicates 1:1 proportion.

foliage and branch biomass. This trend has been noticed in other studies that developed AEs (e.g. Zianis et al., 2005; Repola et al., 2007; Jagodziński et al., 2014). Other AEs reported high variability of biases compared to ours, indicating usability of our generalized models.

Similar to Jagodziński et al. (2017), studying young birch (*Betula pendula*) tree stands, we found that the BCEFs quickly reached constant values between the fifth and tenth years of life (Fig. 5). In comparison with studies providing BCEFs for whole chronosequences (e.g. Lehtonen et al., 2004; Teobaldelli et al., 2009), our BCEF models based on tree stand age were found to have higher coefficients of determination and lower RMSE than those proposed by Lehtonen et al. (2004). For both of the above-mentioned studies dramatic decreases of BCEF values in first

years of life were not evident (Wojtan et al., 2011). For that reason biomass of young tree stands cannot be calculated using BCEFs derived for older tree stands (Wirth et al., 2004; Jagodziński et al., 2017). BCEFs and biomass decreased with increases of all tree stand parameters studied, except for density. This resulted from high initial densities and self-thinning of the tree stands during growth. During the first years of tree stand development, there are numerous trees with small dimensions and as growth and development proceed, dimensions increase at higher rates than decreasing density. This pattern also depends on the initial tree stand density (Jagodziński and Oleksyn, 2009a,b). Comparing our results with those obtained for young birches (Jagodziński et al., 2017), BCEF model quality was higher for our Scots

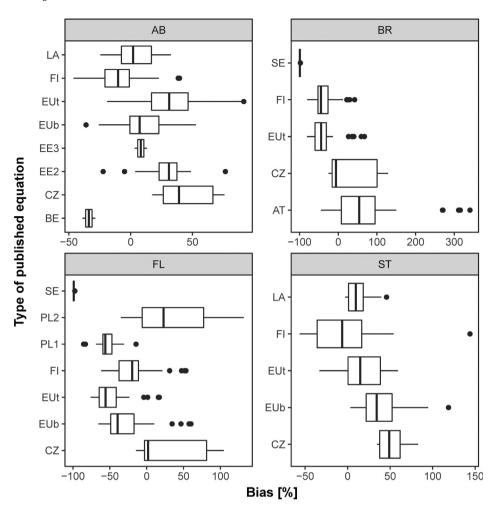


Fig. 3. Distributions of relative biases of published European allometric equations [%], compared with biomasses calculated by site-specific equations. Sources of equations: AT – Austria (Ledermann and Neumann, 2006; Zianis et al., 2005), BE – Belgium (Geudens et al., 2004), CZ – Czech Republic (Chroust, 1985; Zianis et al., 2005), EE – Estonia – two age classes: EE2 – 7 y.o. trees, EE3 – 4 y.o. trees (Kuznetsova et al., 2011), EU – Europe – generalized equations for two biomes: EUt – temperate and EUb – boreal (Muukkonen, 2007), FI – Finland (Repola and Ahnlund Ulvcrona, 2014), LA – Latvia (Lazdins et al., 2011) PL – Poland, PL1 (Barcikowski and Loro, 1995b) and SE – Sweden (Claesson et al., 2001). For details see Appendix B.

pine models. This may be a result of higher light requirements of Scots pine in young tree stands (Ellenberg, 1988; Niinemets and Valladares, 2006), which increases intra-specific competition, with more even height growth as a consequence.

Although our generalized AEs showed very good performances for the Scots pine chronosequence studied, it should be noted that biometrical features and biomass allocation patterns of trees change over stand development, and that these changes might result not only from increasing tree dimensions over age, but also from changes in tree stand density. Moreover, tree stand density may clearly influence both stand growth and development, as well as biomass production and allocation, the variables studied in this paper. In our previous surveys on ecological consequences of silviculture at variable stand densities (Jagodziński and Oleksyn, 2009a,b, and literature cited therein) we showed that stand density and competition among trees clearly modified vertical and horizontal stand structure through changes of tree biometrical traits (e.g. diameter, height, crown width, crown length, crown ratio, tree slenderness, branch diameters and length). Increasing stand density noticeably results in rising competition among trees, leading to increased intra- and inter-specific competition in their above- and belowground parts, thus modifying biomass partitioning. Trees growing at wider spacing compete less intensely for limited resources than those growing at higher density. Thus, in more dense stands total tree biomass accumulation (standing biomass) is usually higher than in less dense stands, but in less dense stands more biomass is allocated to coarse roots. We also noticed that stand density may alter foliage distribution within the crowns (Jagodziński and Oleksyn, 2009a,b). This was clearly shown in the present study, where the highest variability and the lowest coefficients of determination were found for models of foliage and branch biomass. We may assume that tree biometrical features and biomass partitioning are influenced by stand density to a higher extent than local habitat properties. Unfortunately, this kind of research is still lacking, especially for belowground parts of trees (and as a consequence for root to shoot ratio), therefore, biomass allocation patterns and allometric equations in relation to changes in stand density are required to improve biomass models, and should be developed in the near future.

4.2. Sources of variation in biomass

We found the highest variability in biomass of those components which exhibited decreasing contributions to whole tree biomass with tree growth, namely branches and foliage (Mikšys et al., 2007; Uri et al., 2012; Jagodziński et al., 2014, 2017). Therefore, lower coefficients of determination and higher RMSE at young ages are not considered to be an error, but an effect of variation. According to the earlier studies describing impacts of habitat type on allometric trajectories (e.g. Uri et al., 2007; Kuznetsova et al., 2011; Jagodziński et al., 2014, 2017), we could expect differences between post-agricultural, post-industrial and forest sites. Lack of this pattern indicates that site-specific variability within each of these habitat groups is higher than between them. This also confirms the importance of the age trend described above.

4.3. Applicability of height-based models

Due to the high effort connected with on-the-ground inventories of young tree stand biomass, using height-based models may increase the

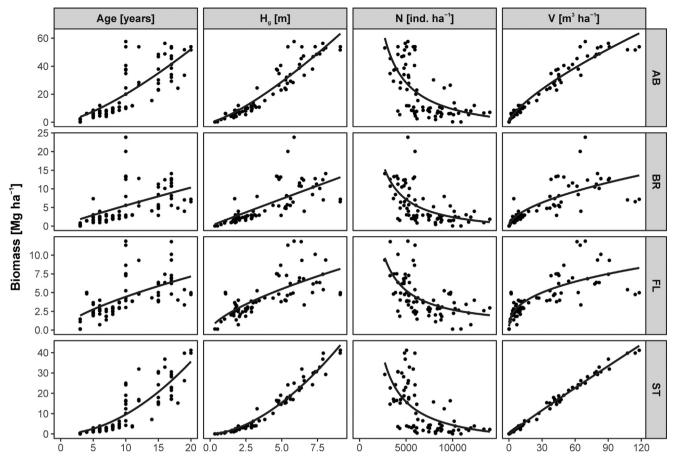


Fig. 4. Relationships between tree stand characteristics and tree stand biomass components: total aboveground (AB), branches (BR), foliage (FL) and stem (ST). Parameters of non-linear regression models are presented in Table 5.

 Table 5

 Relationships between tree stand characteristics (predictors) and tree stand biomass components $[Mg ha^{-1}]$.

Biomass component	Predictor	Model type (Eq. no.)	a	SE	b	SE	RMSE	R^2	AIC	AIC ₀
AB	A	(11)	2.01199	0.24730	0.72326	0.02942	1.4075	0.947	437.313	658.081
	H_g	(11)	3.48757	0.49823	1.31241	0.07650	2.9268	0.887	494.652	_
	N	(13)	-9.61311	4.59095	189562.78019	25970.82589	0.0000	0.419	618.866	_
	V	(11)	0.83596	0.35781	1.37901	0.15793	3.2310	0.648	580.731	-
BR	A	(11)	0.93214	0.28270	0.56196	0.07460	0.7816	0.599	392.090	459.608
	H_g	(11)	1.50801	0.39872	0.97941	0.14737	1.0525	0.516	406.475	_
	N	(13)	-2.36351	1.30356	47741.55897	7374.21360	0.0000	0.362	427.501	-
	V	(13)	10.25636	0.96136	-37.52427	6.68693	0.0000	0.299	434.663	-
FL	A	(11)	1.42747	0.23874	0.36886	0.04335	0.0369	0.594	298.346	364.763
	H_g	(11)	1.86225	0.27884	0.67007	0.08828	0.1746	0.526	310.076	-
	N	(13)	0.13700	0.69506	25798.21309	3931.93847	0.0000	0.368	331.915	-
	V	(11)	0.91161	0.29197	0.68786	0.12549	0.2036	0.353	333.722	-
ST	A	(11)	0.44350	0.03096	0.96047	0.01627	0.7217	0.992	232.258	593.782
	H_{g}	(11)	0.94002	0.11183	1.73903	0.06160	1.9394	0.960	350.419	_
	N	(13)	-7.09258	3.16225	114702.96604	17888.72825	0.0007	0.357	562.200	_
	V	(11)	0.12416	0.06500	1.88887	0.18866	1.9666	0.745	491.893	-

Abbreviations: AB – total aboveground biomass, BR – branch biomass, FL – foliage biomass, ST – stem biomass; A – tree stand age [years], H_g – mean height weighted by tree basal area [m], N – tree stand density [ind. ha $^{-1}$], V – total stem volume [m 3 ha $^{-1}$].

accuracy of biomass estimation. In the case of ALS, accuracy of height measurements in mature tree stands was relatively high, in contrast to tree stand density (Niemi et al., 2015; Kauranne et al., 2017). Our results found that tree stand height can be a good predictor of biomass, and enough to be applicable for estimation of biomass for young tree stands. Because merchantable volume is usually calculated from a given threshold, e.g. 7 cm $D_{1.3}$ over bark, the approach proposed in our study may significantly increase the accuracy of carbon reporting. According

to the guidelines of the IPCC (Eggleston et al., 2006), BCEFs should be used for biomass estimation. IPCC proposes a mean BCEF of 1.8 (reporting a range of 0.6–2.4) for pines, while our study reports BCEFs ranging from 0.45 to 3.33 (Table 6). As our BCEFs are based on whole stem volume, in contrast to those provided by IPCC (based on the merchantable volume), they cannot be directly compared. However, due to the lack of data on merchantable volume, we had to apply the recommended values of 25–30 t ha⁻¹ (value for AB in forest plantations

Table 6Overview of BCEF values for biomass components. Particular BCEF values are presented in Appendix A.

Biomass component	Min	Mean	SE	Max
AB	0.4506	1.0100	0.0658	3.3333
BR	0.0573	0.2892	0.0267	1.6890
FL	0.0415	0.3811	0.0582	2.6920
ST	0.2135	0.3933	0.0102	0.9992

of coniferous tree stands < 20 v.o. in temperate continental forests) or $20 \, \text{t ha}^{-1}$ (for forests < $20 \, \text{y.o.}$). Applying the value of $20 \, \text{t ha}^{-1}$ to our results and calculating RMSE, we obtained 15.72, which is 72.0% of mean AB. Using the medium value of those reported for plantations $(27.5 \, \text{t ha}^{-1})$, we obtained RMSE of 17.10, which is 78.5% of mean AB. Using data from the Polish forest inventory (Forest Data Bank, 2015) we calculated AB for all young tree stands with Scots pine (< 20 y.o.) where our models are applicable (i.e. with tree height < 10 m) of 8.25 Mt, an equivalent of 4.21 Mt C, using a coefficient 0.51 t C per t dry mass, suggested by IPCC (Eggleston et al., 2006). This value constitutes ca. 14% of total biomass of Scots pine in Poland reported by Jabłoński and Budniak (2014). Using values provided by IPCC we obtained 11.55 Mt, an equivalent of 5.89 Mt C ha⁻¹, which is 40% higher. Therefore, models based on height may be an important improvement in evaluation of carbon sequestration of young tree stands, as well as during large-scale inventories, similar to models provided for silver birch (Jagodziński et al., 2017).

5. Conclusions

Our study provided a comprehensive overview of the tree- and stand-level assessments of aboveground biomass estimation for young Scots pine. We developed a set of site-specific allometric equations which may be used where the high accuracy is required and high specificity of the model assumptions does not limit applications. For wide-scale tree-level analyses we developed generalized allometric equations, covering the whole chronosequence of 3-20 year old trees, which performed better than other European allometric relationships. Tree stand biomass increased with tree stand age, height and volume and decreased with increasing density. Using these relationships we provided stand-level equations based on BCEFs and on tree height – the stand characteristic which is easily obtained from airborne data sources. These two models did not show large differences in accuracy. Thus, height-based models may be useful for extensive assessments of biomass and carbon sequestration for young tree stands, allowing for better estimation of forest carbon pool sizes.

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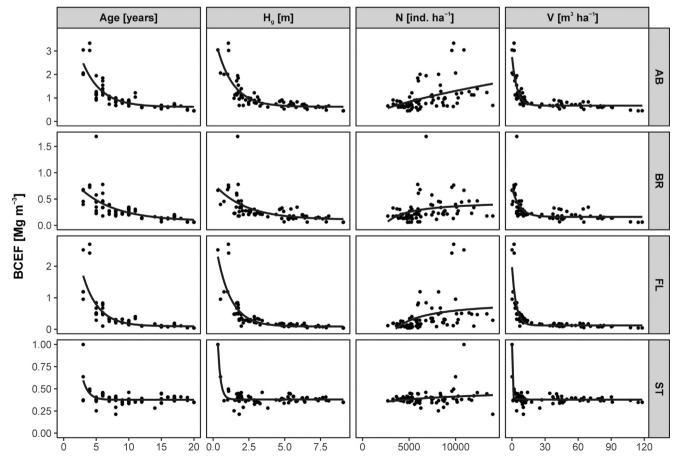


Fig. 5. Relationships between tree stand characteristics and BCEFs for biomass components: total aboveground (AB), branches (BR), foliage (FL) and stem (ST). Parameters of non-linear regression models are presented in Table 7.

Table 7Relationships between tree stand characteristics (predictors) and BCEFs for particular biomass components [Mg m⁻³].

Biomass component	Predictor	Model type (Eq. no.)	a	SE	Ъ	SE	c	SE	RMSE	R^2	AIC	AIC ₀
AB	A	(12)	0.61691	0.06542	5.33448	1.03961	0.35147	0.05317	< 0.0001	0.709	44.473	134.220
	H_g	(12)	0.62412	0.05746	3.26428	0.35316	0.87235	0.10597	< 0.0001	0.729	39.084	_
	N	(11)	0.00376	0.00537	0.63451	0.15950	-	-	0.0119	0.186	120.599	_
	V	(12)	0.67209	0.04559	2.09454	0.15847	0.22621	0.02754	< 0.0001	0.764	28.410	-
BR	Α	(12)	0.07917	0.07343	0.99264	0.22166	0.18209	0.06920	< 0.0001	0.438	- 42.693	-2.843
	H_g	(12)	0.10830	0.06310	0.69410	0.13060	0.45800	0.18110	< 0.0001	0.378	-34.930	-
	N	(13)	0.46840	0.07462	-1080.0	422.1	-	-	< 0.0001	0.081	-7.283	_
	V	(12)	0.16099	0.03062	0.55175	0.08779	0.14350	0.03963	< 0.0001	0.428	-41.339	-
FL	A	(12)	0.09562	0.05773	5.67080	1.45618	0.42193	0.07180	< 0.0001	0.637	42.380	115.452
	H_g	(12)	0.08925	0.05133	3.09855	0.38049	1.01347	0.13006	< 0.0001	0.682	31.089	_
	N	(13)	0.91070	0.15630	-3192.17130	884.35630	-	-	< 0.0001	0.150	32.470	_
	V	(12)	0.12295	0.04423	1.86903	0.16629	0.26766	0.03813	< 0.0001	0.700	27.958	-
ST	Α	(12)	0.37645	0.01009	6.30763	9.27127	1.11956	0.48019	< 0.0001	0.316	-174.461	-149.642
	H_g	(12)	0.38054	0.00548	3.65437	1.24671	5.30087	0.92841	< 0.0001	0.736	-246.734	-
	N	(11)	0.14574	0.08838	0.11308	0.06883	-	-	< 0.0001	0.035	-150.317	-
	V	(13)	0.37748	0.00526	0.03547	0.00240	-	-	< 0.0001	0.747	-252.212	-

Abbreviations: AB – total aboveground biomass, BR – branch biomass, FL – foliage biomass, ST – stem biomass; A – tree stand age [years], H_g – mean height weighted by tree basal area [m], N – tree stand density [ind. ha $^{-1}$], V – total stem volume [m 3 ha $^{-1}$].

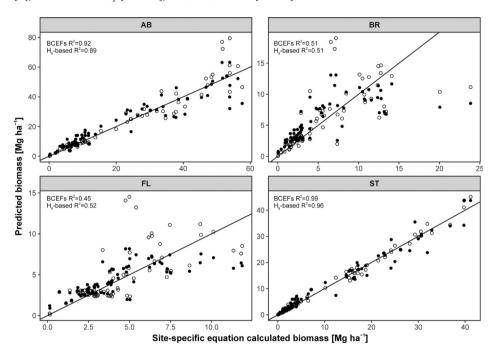


Fig. 6. Distributions of deviations between biomasses calculated applying H_g -based models (black dots) and BCEFs (open dots) for total aboveground biomass (AB), branches (BR), foliage (FL) and stem (ST) biomass. Line indicates 1:1 proportion. R^2 values consider relationships between observed and predicted biomasses.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.11.001.

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