A New Set of Biomass Functions for *Quercus petraea* in Western Pomerania

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Abstract

The study covers the development and calibration of a set of functions to estimate volume, dry matter, and nutrient contents for a regional database of Sessile oak (*Quercus petraea* [Matt.] Liebl.) in northeast Germany. We applied regression analyses to biomass samples from a total of 22 trees using methods of Randomized Branch Sampling and Importance Sampling. Coarse wood volume and dry matter content in coarse wood were available for all sample trees. A subsample of ten trees was used for separate estimations for the components foliage, twigs, branches, and coarse wood. Subsequent analyses focused on the respective contents of carbon, nitrogen, potassium, calcium, magnesium, phosphorus, and sulphur. The determined allometric functions use diameter and/or tree height to estimate individual volume, dry matter, and nutrient contents. Stand values for mean basal area diameter, mean height, and stem number per hectare were applied to calculate biomass data for whole stands. Analyses of the different components show that trees during growth accumulate coarse wood dry matter to an increasing degree. Dry matter of the other components is growing much slower. The amounts stay almost constant for twigs and foliage above a certain age. Nutrient contents over time follow an analogue course except for branches where – similarly to coarse wood – the share of nutrients in the respective totals per trees is continuously increasing. The established models are restricted to trees in the diameter range of 8–40 cm. Within this range tree height is statistically insignificant as explanatory variable in 81% of all cases. Further research is needed to extend the range of reliable model predictions especially for larger trees.

Key words: Biomass functions, Nutrient contents, *Quercus petraea,* Randomized Branch Sampling.

Introduction

In recent years, the strategic shift from fossil fuels towards renewable resources has been a central strategy in energy and production politics in Germany (BMWi 2015). Reliable knowledge of the biomass and dry matter quantities of forest trees at stand, enterprise, and regional scale is of increasing relevance for sustainable production purposes. Correct information on the amount of carbon stored in trees and forests is particularly important in the framework of emission trade according to the Kyoto protocol. The utilization of biomass also affects nutrient cycles and balances in the forest ecosystems. To counteract the negative impacts of biomass extraction and to sustain soil productivity it is necessary to know exactly which amounts of which elements are stored in the different components (or fractions) of forest trees.

The required levels of detailed information on forest productivity in terms of biomass and its chemical composition cannot be provided by conventional forest inventories. These surveys focus on stand-level averages and sums of heights, diameters, species diversity, and timber volumes that can be scaled up to cover whole enterprises or regions. Reliable estimations of biomass and element dynamics can only be derived by combining the “traditional” forest inventory data with statistical models relating to single trees and their components. Biomass models of this type are available for a wide range of forest tree species in Europe (Zianis et al. 2005), most of them producing at least estimates of dry matter contents (DMC) as the basic level of biomass prediction.

Statistical models tend to get developed and calibrated on a foundation of regionally acquired data. Their “off-range” application – to other regions with different growing conditions or management practices – will in most cases not deliver reliable estimates (Mencuccini and Grace 1994, Schröder et al. 2007, Zell 2008). For this reason regional biomass estimations should employ species-specific models and functions that are based on samples and data representative for the area under investigation.

This paper describes methods and outcomes of investigations into biomass of whole trees and of their components in the lowlands of northeastern Germany (Figure 1). Together with the north-western parts of Poland, the region is also known as “Western Pomerania” in a broader sense (GTS 2010). Site conditions in this area are dominated by glacially formed sandy soils and a climate ranging from sub-maritime in the West to sub-continental in the East. The forest tree species distribution is dominated by Scots pine (*Pinus sylvestris* L.) (Müller and Luthardt 2009). Other relevant species include European beech (*Fagus sylvatica* L.), Sandy birch (*Betula pendula* L.), Sessile oak (*Quercus petraea* [Matt.] Liebl.), and European oak (*Quercus robur* L.) (Oehmichen et al. 2011).

The availability of biomass functions reflects the economic importance of the various species. Scots pine for instance is well covered by the models of Heinsdorf and Krauß (1990) which estimate DMC and nutrient contents of various tree components from tree height and diameter at breast height (dbh). Węgiel et al. (see Bembenek et al. 2014, LFB 2014) have created a new set of Scots pine biomass functions based on 60 trial plots in stands at the age of 41–100. Although these plots are located in western Poland, the resulting models can be recommended for application in northeastern Germany as well because site conditions of the two regions are very similar. Regional biomass models for European beech have been developed by Krauß and Heinsdorf (2008) similar to those for Scots pine. The situation is different for *Betula pendula*, which is also abundant in northeastern Germany but possesses comparably lower silvicultural and economic relevance. Biomass functions for this species are very scarce throughout Europe (Zianis et al. 2005).

The share of oak species (*Quercus robur* L. and *Quercus petraea* [Matt.] Liebl.) in the region has currently reached a level of 8.2% (MLUL 2015). This proportion is still rising due to the ongoing activities of converting conifer monocultures into mixed stands (MLUV 2006, Stähr and Oldorff 2013). The species has great economic value and is considered a key element for close-to-nature forest management as well as for conservation goals (Ziesche et al. 2014). There are, however, even fewer biomass models available for oak in the region than for birch (Zianis et al. 2005). In this context, the goals of our study were:

- to establish a set of regionally adapted biomass functions to estimate individual-tree biomass and nutrient contents for oak,
- to evaluate the performance of the developed models by comparing their results to those of other regionally relevant biomass functions,
- to propose a geographic range where the new functions may be applied to produce reliable predictions.

Material and Methods

Data and variables

In accordance with the beech models created by Krauß and Heinsdorf (2008) the investigations focused on whole tree biomass and on the following basic components:

- coarse wood including bark (all dendromass or wood with a diameter [d] larger than 7 cm),
- branches including bark (d = 2–7 cm),
- twigs including bark (d < 2 cm),
- foliage.

For each component, separate functions predict the respective contents (mass in kg) of dry matter and of the major nutrients: carbon (C), nitrogen (N), calcium (Ca), potassium (K), magnesium (Mg), phosphorus (P), and sulphur (S). For total above-ground biomass, coarse wood, and branches the respective volumes are estimated by additional models. All calculations based on 22 sample Sessile oak trees that were cut in the forests of Maienpfuhl (district Barnim) and Zerpenschleuse (district Oberhavel) in the state of Brandenburg (Figure 1).

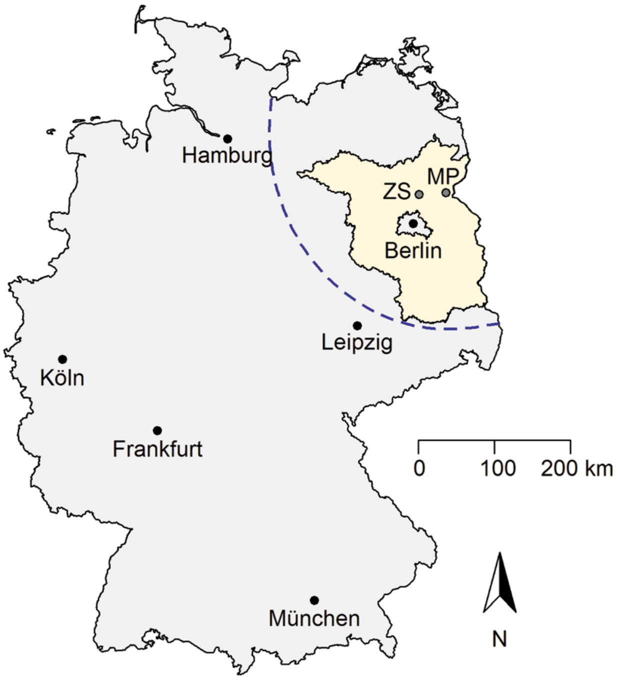

Figure 1. The state of Brandenburg (yellow) with the two plots where sample trees were cut (MP = Maienpfuhl, ZS = Zerpenschleuse). The northeastern German lowlands are delineated by the dashed blue line

The species *Quercus petraea* was chosen because of its greater relevance on the widespread sandy and dry sites in the project area as compared to *Quercus robur*. Sample trees were selected to cover a range of dbh values from 8 to 40 cm. Their basic properties are presented in Table 1.

Table 1. Characteristics of sample trees

tree no.	dbh [cm]	height [m]	age [a]	site	location	used for modeling
1	8.0	7.1	27	M2	MP	all components
2	10.0	11.7	27	M2	MP	all components
3	15.4	14.1	27	M2	MP	all components
4	18.4	21	50	M2	ZS	coarse wood
5	20.1	21.5	50	M2	ZS	coarse wood
6	20.5	15.2	27	M2	MP	all components
7	22.1	21.3	50	M2	ZS	coarse wood
8	23	24.4	60	M2	ZS	coarse wood
9	23.2	19.8	44	M2	MP	all components
10	23.5	21.5	50	M2	ZS	coarse wood
11	23.8	23.6	50	M2	ZS	coarse wood
12	24.1	19.9	44	M2	MP	all components
13	24.2	22.1	60	M2	ZS	coarse wood
14	24.4	23.4	80	M2	ZS	coarse wood
15	24.6	24.8	50	M2	ZS	coarse wood
16	26.6	21.7	60	M2	ZS	coarse wood
17	30.4	23.9	111	M2	MP	all components
18	30.6	26.3	90	M2	ZS	coarse wood
19	35.0	23.4	111	M2	MP	all components
20	35.6	24.3	110	M2	ZS	coarse wood
21	38.6	30.6	148	K2	MP	all components
22	40.0	30.7	148	K2	MP	all components

The majority of trees come from stands growing on site quality class "M2" which denotes medium nutrient supply and average water availability. The geological conditions are dominated by ground and terminal moraines as well as Pleistocene sands (MUGV and LFE 2006). Ten out of the 22 trees were felled and analyzed in September 2012 (Maienpfuhl), the other twelve (Zerpenschleuse) were part of data collections related to the third German national forest survey BWI^3 (Kändler et al. 2010). Measurements of the latter were provided by the Baden-Wuerttemberg Forest Research Institute (FVA). They complemented the data base for the coarse wood and DMC models. Tree height was calculated as the arithmetic mean of four measurements per tree before felling with a laser clinometer mounted on a tripod.

Field measurements

To reduce measurement efforts in the forest we applied *Randomized Branch Sampling* (RBS, Jessen 1955, Gregoire and Valentine 2007) instead of completely dividing and weighing all trees. RBS is a reliable multi-stage sampling technique that can be subjected to statistical tests (Figure 2). The method is based upon natural branching patterns to determine a sequence of random samples dependent upon the diameter of the respective section. The application in practice uses the branch diameters of subsequent ramifications to select a "path" of internodes in the tree (van Laar and Akça 2007).

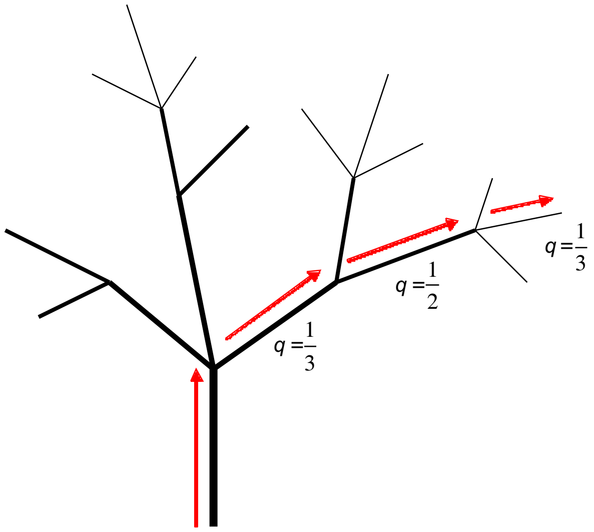

Figure 2. Application of the RBS method to create a "sample path" with the respective conditional sampling probabilities

The path marked by red arrows in Figure 2 shows the conditional sampling probabilities q_1, q_2 and q_3 of its internodes. Each selected internode is measured to obtain the necessary data for calculating the respective volumes. The end of a path is defined by a terminal diameter that can be chosen arbitrarily. Multiplication of all internode volumes by the inverse values of their sampling probabilities yields an estimate of the total tree volume down to the chosen terminal diameter (Cancino 2003, Hepperle 2010). Total volume multiplied by wood density results in the amount of dry matter of the respective tree.

In the case presented here we obtained individual wood density values from stem disks taken from the sample trees. The exact positions of the stem disks (one for coarse wood and one for non-coarse wood per tree) were determined by means of *Importance Sampling* (Sandmann 2004) which ensured a representative choice of samples. Stem disks of 10 cm in height were measured and weighed immediately after felling. A linear wood sample was extracted from each disk covering the whole diameter of the intersection area. Of this sample we determined its fresh weight before subjecting it to kiln-drying and laboratory analyses. The resulting values for DMC and nutrient contents allow the calculation of estimates for the totals of coarse and non-coarse wood per tree.

For all branches and twigs smaller than the chosen limiting diameter we estimated their weight instead of volume: The whole branch at the end of the chosen "path" was cut from the tree, weighed, and prepared for further analyses at the laboratory. Wood and foliage were processed separately to obtain individual values for both compartments. Predictions for the whole tree can then be obtained from the values derived from the estimated volume and nutrient contents of all elements smaller than the limiting diameter.

To evaluate the standard error of the models on the individual-tree level at least two separate estimates are required. In this study we applied the recommend minimum of three RBS paths per tree (Kändler and Bösch 2009, von Wilpert et al. 2011, Chirici et al. 2014) to derive models for volume, DMC, and nutrient contents. In each path, samples were extracted from coarse wood, non-coarse wood (i.e. larger branches), twigs, and foliage. The concentrations of Ca, K, Mg, P, and S were derived from one sample per compartment and per tree. Sample preparation and analyses followed the regulations laid down in the respective guidelines for forest science analytics (GFA 2009).

Techniques like RBS and Importance Sampling require a complex study design and suitable data collection software due to their random elements and the wide range of parameters to be measured. We employed a Microsoft Access data bank developed by Dr. B. Bösch at the Baden-Wurttemberg Forest Research Agency (FVA-BW). Data analyses were supported by a Java program written by Prof. J. Nagel and K. Husmann at the Northwestern Germany Forest Research Agency (NW-FVA).

Modelling

The data obtained on the individual-tree and component level were used in a following step to calibrate models that estimate component volumes and nutrient concentrations as dependent variables from dbh and tree height as independent variables. Analyses involved power functions which are widely applied in biomass modelling (Zianis et al. 2005, Röhle et al. 2006) but focused as well on exponential and linear models. To perform regression analysis on the non-linear functions we calculated natural logarithms of dependent (exponential function) or independent and dependent (power function) variables. After this initial linearization we were able to compute the adjusted coefficient of determination ($R^2_{adj.}$) of the respective regression functions. This coefficient was used as the first selection criterion for the analysed models. The statistical significance of the independent variables was derived from two-sided Student's *t*-Tests with a threshold of $\alpha = 0.05$. If one of the regression coefficients did not show significance against this level, the model was excluded from further investigations and a new model based on the remaining variable(s) was tested. Eventually the model exhibiting the highest $R^2_{adj.}$ among those with significant regression coefficients was chosen for further application.

Due to the results of primary steps in the analyses we eventually focused on functions of the allometric type to model the relations between measured parameters of the sample trees and their DMC and nutrient contents of total aboveground biomass as well as of the separate components. Functions that follow the simple linear form with two predictors have often proved to yield the highest coefficients of determination ($R^2_{adj.}$) (Röhle et al. 2006):

$$Log_{10}(M) = a + b \times Log_{10}(d) + c \times Log_{10}(h)$$

where M represents DMC or contents of the analysed nutrients, d is diameter at breast height, and h is height. If in some cases the explaining power of one of the predictors should be statistically insignificant, the respective coefficient assumes the value of zero.

The precision of the estimations obtained via Randomized Branch Sampling and Importance Sampling was evaluated based on the three chosen paths per sample tree. Estimation errors for nutrient contents are proportional to those of wood volume and DMC because the respective amounts depend directly on the latter two variables. For this reason we will focus in this section on the precision of estimations for wood volume and DMC.

Results

Estimation errors

The precision of the estimations for wood volume and DMC is highlighted by the figures in Table 2. Maximal estimation errors are given for the 80% and 95% confidence levels.

Table 2. Estimation errors for wood volume and DMC of the individual trees

target variable	component	number of sample trees	maximum estimation error μ ± [%]	
			80% confidence level	95% confidence level
volume	aboveground biomass	10	6.6%	10.3%
	coarse wood	22	4.3%	6.6%
	branches	10	89.4%	165.6%
dry matter	aboveground biomass	10	8.4%	13.2%
	coarse wood	22	5.2%	8.0%
	branches	10	45.4%	77.2%
	twigs	10	188.1%	404.4%
	foliage	10	343.7%	876.5%

Different scales of the measured properties (volumes and DMC) result in estimation errors that may be very different in absolute size (Figures 3 and 4). Figure 3 for instance shows rising absolute estimation errors with increasing dbh. To compare estimation errors for different target variables and tree components we computed the geometric coefficient of variation (Bland and Altman 1996a, 1996b). The maximum estimation error in Table 2 represents this coefficient as expressed in percent in relation to the expectation value for a given tree, i.e. the average of the samples or rather paths that would result from unlimited replication. Of all estimations for DMC of above-ground biomass of tree no. 3, for instance, 95% are not further away than ± 13.2% from the expectation value μ for this parameter.

Nutrient contents at the component level

The contents of nutrients in the different tree components are listed in Table 3. Arithmetic mean $\bar{x}$, minimum $x_{\min}$, maximum $x_{\max}$ and standard deviation s_x refer to the share of the respective element in the weight of the total dry matter. The levels of significance at $\alpha = 0.05$ / 0.01 / 0.001 are shown as + / ++ / +++. Three paths were chosen twice due to the stochastic nature of selection; therefore, in the case of carbon and nitrogen calculations based on 27 instead of 30 samples per component. All other analyses draw from 10 samples per component. Average nutrient contents that differ significantly from the general mean of a component were identified by applying an F-Test at $\alpha = 0.05$.

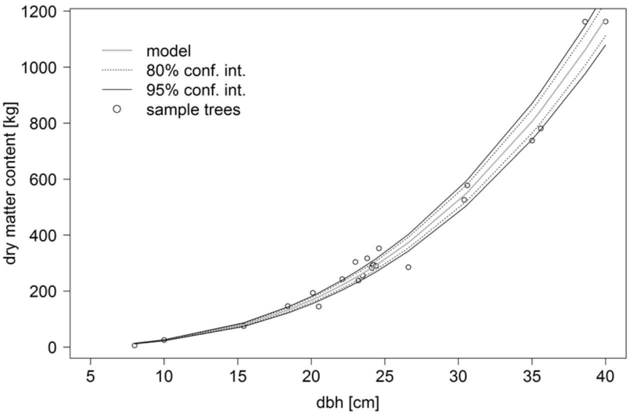

Figure 3. Confidence intervals of estimation errors for coarse wood DMC in relation to dbh

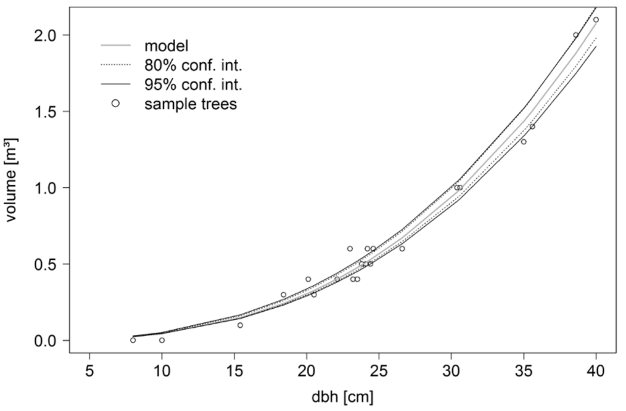

Figure 4. Confidence intervals of estimation errors for coarse wood volume in relation to dbh

Dry matter carbon contents exhibit a mean share of 50% with a small variance. Foliage shows the greatest span of absolute percentages at 47.48 to 52.88%. Nitrogen, however, is significantly increasing its share from coarse wood and branches to twigs. Leaves consist to an extent of roughly 2.34% of nitrogen which is almost 15 times more than the nitrogen contents of coarse wood. A similar yet somewhat less prominent trend can be observed for Calcium which makes up 0.79% in foliage but only 0.28 in coarse wood. While this element shows the smallest variation between the different components next to carbon, variation within the various components, especially in foliage, twigs, and branches assumes its highest levels of all analysed nutrients. Potassium follows the same pattern as nitrogen but increases its percentage from coarse wood to foliage only by slightly less than six times. Sulphur,

Table 3. Nutrient contents in the analyzed tree components

component	nutrient	$\bar{x}$ [%]	$x_{\min}$ [%]	$x_{\max}$ [%]	s_x [%]	sign. (*F*-test)
coarse wood	C	49.95	48.85	51.19	0.62	+++
branches		49.71	48.37	50.71	0.57	
twigs		49.91	47.33	51.34	0.81	
foliage		50.68	47.48	52.88	1.36	
coarse wood	N	0.16	0.09	0.36	0.06	+++
branches		0.33	0.25	0.62	0.09	
twigs		0.66	0.49	0.85	0.08	
foliage		2.34	1.84	2.91	0.29	
coarse wood	Ca	0.28	0.13	0.43	0.10	+++
branches		0.45	0.20	0.70	0.16	
twigs		0.59	0.45	0.79	0.12	
foliage		0.79	0.59	1.37	0.23	
coarse wood	K	0.15	0.10	0.35	0.07	+++
branches		0.24	0.18	0.37	0.05	
twigs		0.34	0.24	0.50	0.07	
foliage		0.86	0.59	1.13	0.16	
coarse wood	Mg	0.02	0.01	0.04	0.01	+
branches		0.05	0.03	0.06	0.01	
twigs		0.08	0.06	0.10	0.01	
foliage		0.15	0.10	0.22	0.03	
coarse wood	P	0.02	0.01	0.04	0.01	+++
branches		0.05	0.03	0.07	0.01	
twigs		0.08	0.06	0.10	0.01	
foliage		0.21	0.13	0.33	0.06	
coarse wood	S	0.02	0.01	0.02	0.00	++
branches		0.03	0.02	0.05	0.01	
twigs		0.05	0.04	0.06	0.01	
foliage		0.15	0.12	0.18	0.02	

magnesium, and phosphorus are the elements with the smallest shares in DMC. Each of them makes up between 0.15 and 0.21% of DMC in leaves but only around 0.02% in coarse wood. Phosphorus shows the widest difference of concentrations between components, second only to nitrogen in this respect.

In general, the highest contents of all analysed nutrients have been found in the foliage. These relative proportions are on average eight times higher than those in coarse wood with carbon and calcium showing the smallest relational differences. Twigs contain roughly thrice as much nutrients as coarse wood, branches twice as much (in relation to DMC).

Nutrient contents at the sample tree level

The absolute amount of nutrients per component results from multiplying the quantity of dry matter of the individual component with the relative contents of the respective element. The total sum of all components then represents the absolute value for the entire tree. The shares of the components in dry matter and in the total amount of nutrients per tree sorted by dbh are shown in Figure 5.

The analysis of the diagrams in Figure 5 reveals that coarse wood makes up from 39 to 93% of the total dry weight of the sample trees. The respective percentage increases with tree dbh. As a consequence, the share of the remaining components decreases from 61% in the smallest to less than 14% in the largest sample tree. Component shares in total carbon contents show a slightly different pattern: While coarse wood, branches, and twigs contain lower percentages, leaves contribute to a higher extent to carbon contents than to DMC. The share of foliage in the total amount of the analysed nutrients is highest for nitrogen at 13.2%. Twigs contain a slightly lower amount of nitrogen while coarse wood and branches make up for the remaining nitrogen at 41% and 37%, respectively. The lowest share of leaves in nutrient contents of the whole tree was observed for calcium at only 4.1% while coarse wood and branches contribute 55% and 34% to total calcium contents. The values for branches vary greatly between the sample trees. An analogical distribution between compartments was shown for potassium with slightly lower shares for coarse wood at an average of 49%.

Magnesium could be found mainly in branches which make up more than 48% on average of the total amount in the trees. The percentages of leaves and twigs in overall magnesium contents steadily decrease with growing sample tree dbh. As in phosphorus, there is no significant correlation for magnesium between dbh and the share of coarse wood in total nutrient contents. The percentage of coarse wood in overall phosphorous is 32% on average, which is the lowest mean value in all analysed nutrients – for all other elements, the share of coarse wood was higher. Branches contain a percentage of phosphorus similar to that of magnesium, while the share of foliage is closest to the value of this component (10%) in total sulphur contents. The share of coarse wood in the overall amount of sulphur per tree is positively correlated to tree diameter. As a consequence, the contribution of twigs and foliage to total sulphur contents decreases with growing tree size, whereas branches do not show any significant trend.

For the relations between measured parameters of the sample trees as independent variables and their DMC and nutrient contents, functions of the allometric type that follow the simple linear form with two predictors proved to yield the highest coefficients of determination ($R^2_{adj.}$). The coefficients of the various functions are listed in Table 4. If coefficients are given at the value of zero, the explaining power of the respective predictors was statistically insignificant. Table 4 also contains the maximal estimation errors for the confidence intervals $\mu \pm \sim 1{,}28\sigma$ and $\mu \pm \sim 1{,}96\sigma$. In relation to all possible estimations, 80% and 95%, respectively, fall within these intervals: The absolute difference of 95% of all estimations to the expected value μ for aboveground biomass volume, for instance, is not greater than 5.5%. All information in Table 4 presumes the integration of diameter at breast height (d) as given in centimetres and of height (h) as given in meters.

The statistical significance of the predicting variables was tested with Student's *t*-test that shows for two independent variables their minimal common level. Tree height exerted a significant influence in the estimation of volume, dry matter, and carbon contents of total aboveground biomass and of the coarse wood component. The models for potassium contents in branches and for magnesium contents in leaves use tree height as the only independent parameter. In all remaining functions, tree dbh is the only statistically significant predictor. Estimations tend to be more precise for components with a relatively high share in aboveground biomass: While estimations for total biomass vary in a 95% confidence interval around 5.5% for volume and around 53.1% for calcium contents, these variations increase in the case of foliage analyses to 132.5% for dry matter contents and 568.4% for the contents of carbon.

Nutrient contents at the stand level

One possible approach to estimate the nutrient contents of forest stands is based upon traditional yield tables. The allometric functions in this case use

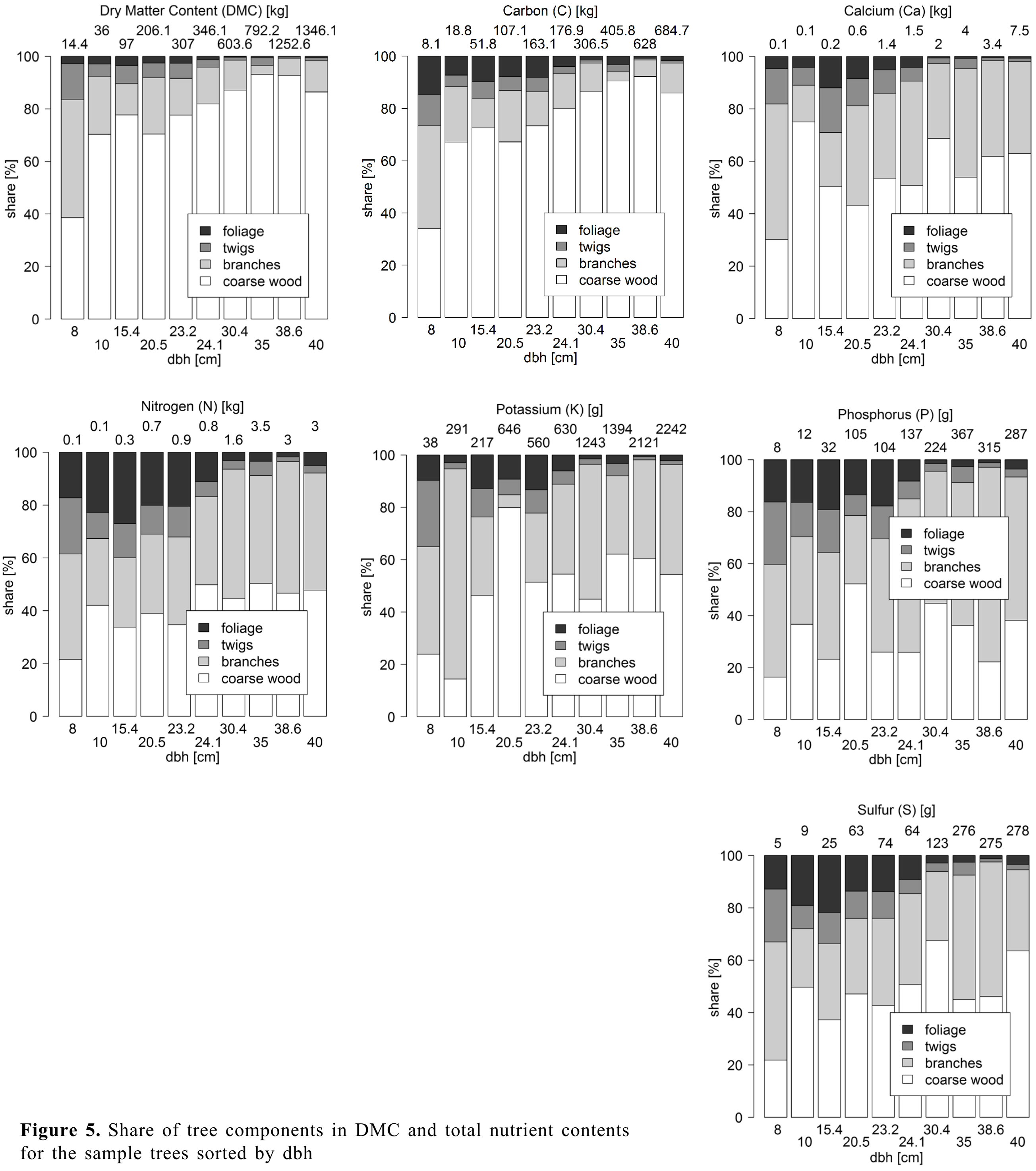

Figure 5. Share of tree components in DMC and total nutrient contents for the sample trees sorted by dbh

mean dbh (d_g, derived from the average basal area per tree in the stand) and mean height (h_g, taken from the height vs. dbh function or “stand height curve”). Predictions for whole stands are obtained by multiplying the values per mean (basal area) tree by the total number of trees per stand or per hectare. We followed this approach and applied the yield table for *Quercus petraea* in northeastern Germany developed by Muchin (2005). To demonstrate the effects of different site quality, the results for the lowest yield class were compared to those of the highest yield class of this table. The stand conditions that can be represented are limited to diameters between 8 and 40 cm due to the diameter range of the sample trees forming the

Table 4. Coefficients and selected statistical parameters of the applied allometric functions

target variable	component	coefficients			$R^2_{adj.}$	sign. (t-Test)	max. est. error μ ± [%]	
		a	*b*	*c*			$\alpha = 0{,}80$	$\alpha = 0{,}95$
volume [m^3]	a.ground total	-4.3331	2.0303	0.9646	0.999	+++	3.5%	5.5%
	coarse wood	-4.8546	2.1084	1.2383	0.993	+++	8.8%	13.8%
	branches	-3.3242	1.3973		0.861	+++	28.5%	46.7%
dry matter [kg]	a.ground total	-1.3860	2.0378	0.8416	0.999	+++	3.2%	4.9%
	coarse wood	-2.1081	2.0695	1.2746	0.992	+++	9.4%	14.8%
	branches	-0.7755	1.7121		0.799	+++	46.5%	79.3%
	twigs	-0.8013	1.2631		0.629	++	52.7%	91.0%
	foliage	-1.1619	1.2237		0.470	+	73.6%	132.5%
carbon [kg]	a.ground total	-1.7029	2.0156	0.8769	0.999	+++	5.8%	9.0%
	coarse wood	-2.5111	1.6887	1.7722	0.995	++	10.2%	16.0%
	branches	-1.0798	1.7100		0.809	+++	44.7%	75.9%
	twigs	-1.1103	1.2684		0.632	++	52.6%	90.8%
	foliage	-1.4436	1.2126		0.457	+	246.3%	568.4%
nitrogen [kg]	a.ground total	-3.4644	2.4994		0.988	+++	13.2%	20.9%
	coarse wood	-4.3417	2.8572		0.980	+++	20.2%	32.5%
	branches	-4.2684	2.7714		0.978	+++	20.4%	32.9%
	twigs	-3.0391	1.2995		0.616	++	56.3%	98.0%
	foliage	-2.6630	1.1281		0.412	+	75.8%	137.0%
calcium [kg]	a.ground total	-3.7305	2.7650		0.952	+++	32.1%	53.1%
	coarse wood	-4.2949	2.9842		0.930	+++	44.3%	75.2%
	branches	-4.4880	2.9613		0.901	+++	55.4%	96.2%
	twigs	-3.2115	1.3942		0.584	++	66.6%	118.4%
	foliage	-3.3115	1.2489		0.370	+	96.1%	180.0%
potassium [kg]	a.ground total	-3.5177	2.6143		0.930	+++	30.3%	50.0%
	coarse wood	-4.3161	2.7935		0.940	+++	37.3%	62.3%
	branches	-4.0452		2.6386	0.721	++	81.4%	148.6%
	twigs	-2.8675	0.9558		0.537	++	46.5%	79.3%
	foliage	-3.0750	1.1054		0.352	+	85.2%	156.6%
magnesium [kg]	a.ground total	-4.1661	2.3310		0.983	+++	14.6%	23.2%
	coarse wood	-4.4600	2.2120		0.919	+++	34.2%	56.9%
	branches	-5.0971	2.7732		0.958	+++	29.6%	48.7%
	twigs	-3.7256	1.1184		0.616	++	46.9%	80.1%
	foliage	-4.1252		1.4021	0.430	+	74.7%	134.8%
phosphorus [kg]	a.ground total	-4.3508	2.4632		0.978	+++	19.2%	30.9%
	coarse wood	-5.1332	2.6717		0.909	+++	45.9%	78.2%
	branches	-5.0592	2.7545		0.969	+++	24.9%	40.4%
	twigs	-3.6792	1.1146		0.549	++	54.6%	94.7%
	foliage	-3.4350	0.9084		0.241	n.s.	86.7%	159.9%
sulfur [kg]	a.ground total	-4.5819	2.5269		0.988	+++	13.4%	21.2%
	coarse wood	-5.4420	2.9135		0.981	+++	19.8%	31.8%
	branches	-5.2272	2.6573		0.942	+++	34.6%	57.5%
	twigs	-4.0751	1.2268		0.567	++	59.0%	103.3%
	foliage	-3.8444	1.1131		0.452	+	67.9%	120.9%

With a.ground total = aboveground total; max. est. error = maximum estimation error

basis of the respective model functions. Because in stands of the highest yield class 20% of trees exceed the diameter at breast height of 40 cm at an age of 70 years, comparisons of the site conditions as mentioned above are restricted to ages up to 65 years. As an example, Figure 6 shows the range of total volume production (sum of all thinnings plus standing volume) as expressed in the respective aboveground nutrient contents of oak stands at the age of 65. The lower bar ends represent the poorest growth in yield class 20 (mean height [m] of dominant trees according to Weise, see Pretzsch 2009, at the age of 100), the upper limits are produced by stands in yield class 32. The absolute quantities of nitrogen, potassium and calcium range from 500 to 1,500 kg per hectare, values for magnesium, phosphorus and sulphur are much lower (40–150 kg per hectare).

The smallest relative difference between the two yield classes can be observed for potassium contents with almost 80% higher values per hectare for yield class 32 than those of yield class 20 while calcium shows the largest difference at 203%. Total volume production in carbon differed from 75 t to 216 t (188%) following the span of DMC from 151 t to 432 t (187%). The latter parameter is the basis for the contents of the investigated nutrients in single trees as well as in stands and shall therefore be analysed in more detail.

The increase in total volume production in DMC over time for the different components is demonstrated in Figure 7. At the age of 65 years, i.e. in the end of the investigated interval, yield class 32 has produced about 275% (i.e. 240 tha^{-1}) more dry matter than yield class 20. The difference for branches is considerably smaller at 42% or 18.9 t×ha^{-1}, for twigs it is only

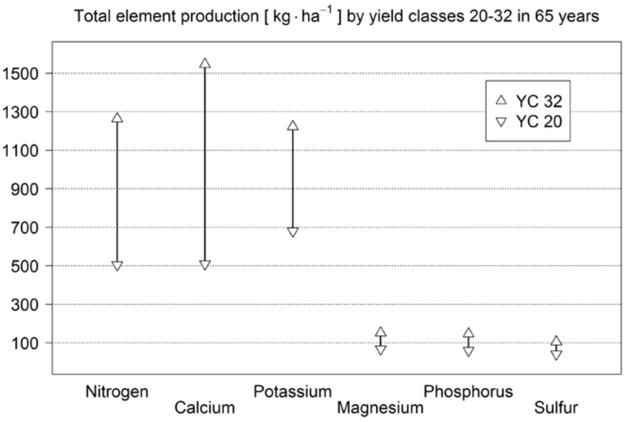

Figure 6. Total volume production of oak stands at the age of 65 for yield classes 20 (lower limits) and 32 (upper limits). Yield classes according to Muchin (2005) are indicating mean height of dominant trees at the age of 100 according to Weise (see Pretzsch 2009)

3% or 0.5 t×ha^{-1}. The two yield classes produce almost equal amounts of dry matter in leaves differing at a minimal 0.1% or 18.9 t×ha^{-1}. Relations between yield class and productivity with regard to the current annual increments follow a similar pattern (Figure 8): While increment in coarse wood dry matter is steadily increasing in amount and in difference between yield classes, this increase is less pronounced in the other components. Twigs and foliage in particular do not show any significant divergence between the exemplary yield classes.

Discussion

Reliability of the predicted initial data

The results of this study are based upon data derived from a specific sampling method (Randomized Branch Sampling, RBS). Their validity depends to a

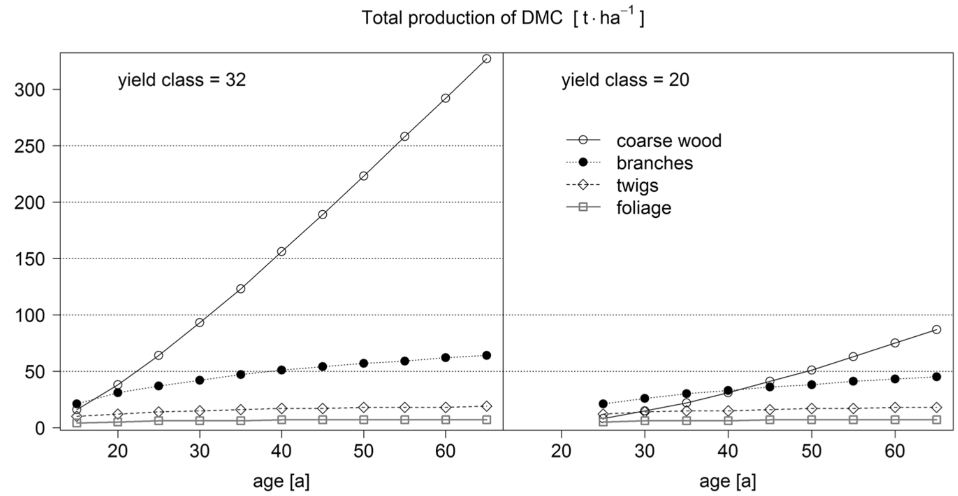

Figure 7. Total volume production of oak stands between ages 15 (25) and 65 for yield classes 32 (left) and 20 (right) according to Muchin (2005)

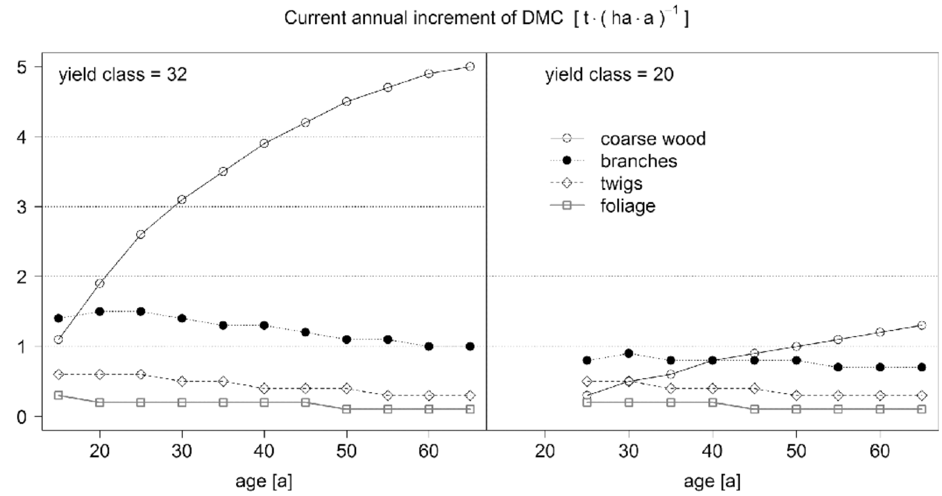

Figure 8. Current annual increment of oak stands between ages 15 (25) and 65 for yield classes 32 (left) and 20 (right) according to Muchin (2005)

large extent on how well these data represent the empiric values of the explanatory parameters. To determine sample data quality we related the number of chosen RBS paths to the expected values of volumes, dry matter, and nutrient contents, because it was impossible to measure the "real" values of these parameters as references. We also assumed constant densities and nutrient contents throughout the various components disregarding the effects of competition or differences in light availability as described by Grote et al. (2003). A more detailed analysis involving additional data like tree ring width and other allometric or size-related parameters would probably yield more precise results (cf. Seifert et al. 2006). To acquire these data a more diversified data basis would have been necessary but was not available.

The relation of the root mean square error (*RMSE*) to the expected value (μ) according to the chosen sample paths per tree in this context is the coefficient of variation (*CV*). It varies for DMC of aboveground wooden biomass between 0.24 and 7.99% for the ten sample trees resulting in a mean error of 3.02%. If we assume that the expected value is close to the "real" DMC, the achieved precision is in the same range as other studies in this field. In their investigation of 14 Corsican pines (*Pinus nigra*) Özçelik and Eraslan (2012) obtained an estimation error for fresh weight of 2.65% (between 2.5 and 22.6% per tree). Fresh weight of aboveground biomass in six deciduous species was determined for eight trees by Valentine et al. (1984) at an error of 4.9% (4.9–14.4%). Williams (1989) analysed five Loblolly pines (*Pinus taeda*) and found fresh weights at errors between 5.3 and 28.9% with an average of 3.3%. Similar estimation errors were found by Schuck (2013) in his study dealing with five European beech trees (*Fagus sylvatica*).

Based on these comparisons the estimation of aboveground biomass may be regarded as reliable with only minor errors. The precision in estimating coarse wood biomass should be on a equivalent level due to the close relationship between coarse wood and total aboveground biomass. It was not possible to evaluate the estimation errors for the remaining compartments in a similar way because we did not encounter comparable results from other studies in this field. We expect, however, a higher level of errors related to the estimation models for branches, twigs, and foliage as a result of the higher sample variance in these compartments. The RBS method can be recommended to efficiently deliver results from field trials that can later be processed statistically. The effects of rationalization achieved by this approach increase with tree size and sample numbers.

Evaluation of the calculated nutrient contents

In all compartments the contents of nitrogen, phosphorus, potassium, calcium and magnesium correspond to those in the studies collected by Jacobsen et al. (2003). These authors did not distinguish between branches and twigs; therefore we compared the respective total values to those obtained for branches in a stricter sense of our sample trees. The most remarkable differences were found for magnesium and calcium: The contents in foliage of the Pomerania sample trees were only 65.6% and 69.1% of the contents for the trees described by Jacobsen et al. (2003).Nitrogen contents in branches, coarse wood, and foliage were also considerably lower than the average amounts ascertained in the mentioned study at 53.5%, 78.3%, and 91.4%, respectively. All the other nutrients show higher concentrations in our sample trees than in those analysed by Jacobsen et al. (2003). This refers in particular to potassium and phosphorus exhibiting contents in coarse wood that were 42.1% and 35.1% higher than the references

Evaluation of the allometric functions

The developed models of the relationships between tree dimensions (dbh and height) and their volume or nutrient contents exhibit coefficients of determination ($R^2_{adj.}$) between 0.93 and 0.99. At 0.91-0.99 this parameter is equally high for the allometric models of the coarse wood component. It decreases, however, for the remaining components: For branches they still show $R^2_{adj.}$ values between 0.72 and 0.98, for twigs the range is 0.54–0.63 and for foliage only 0.35–0.47.

The differences between nutrient contents within the separate components tend to be less significant. Figure 9 compares various functions for modelling aboveground biomass as found in a number of European studies. Bends or breaks in the course of some

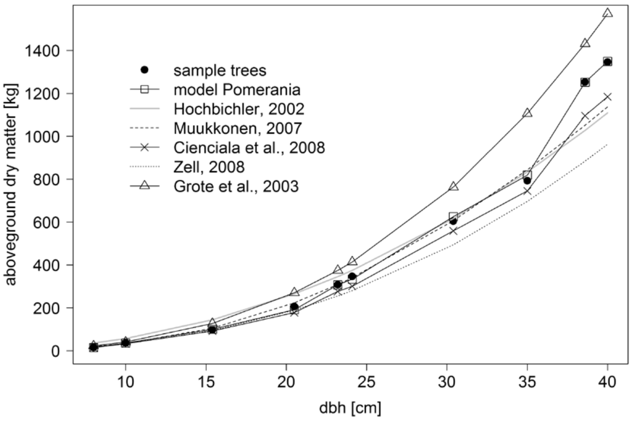

Figure 9. Comparison of allometric models of DMC in aboveground biomass expressed in dry matter content

graphs result from the integration of height as a second predictor variable in the respective function.

The function developed in our investigation delivers for the mayor part of its range values between those obtained by the models of Hochbichler (2002) for Austria and of Cienciala et al. (2008) for the Czech Republic. Its course follows a pattern that is biologically and mathematically plausible. There is, however, a general problem regarding tree height that was statistically significant in only 8 out of 43 models and is not used for predictions in the remaining 35 models. Due to varying stem form allometric functions based solely on dbh can hardly be transferred to other regions or growing conditions (Ledermann and Gschwanter 2006, Seifert et al. 2006). Another source of possible variance in estimations lies in focusing on dbh as the central predictor. By definition this parameter is measured at a constant height of 1.3 meters. This *absolute* height is contradictory to the basic principle of allometric functions to model the relation between *relative* growth rates like those of diameter, height, and biomass. The strict application of this principle would require the use of a relative height for measuring tree diameter, for instance the d_{10} at 10% of a tree's height. As a consequence trees with varying heights would have to be measured for their diameter $d_{1.3}$ at different relative heights. This violation of basic allometric assumptions can lead to significant variance in predictions (Fehrmann 2006). Due to the limited range of samples it is at the moment impossible to solve this methodological problem.

Evaluation of nutrient contents at stand level

The quantities of the nutrients determined in our study do not differ significantly from those found in similar studies by Jacobsen et al. (2003) and Block et al. (2007). Nitrogen, calcium, and potassium are the most prominent elements in absolute mass ($t \times ha^{-1}$) due to their high relative contents in the different tree components. On the other hand the considerably lower concentrations of magnesium, phosphorus, and sulphur lead to much lower absolute quantities per hectare.

DMC development over time in the various components reflects the changes in their shares during the process of tree growth and stand formation. The percentages of foliage, twigs, and branches decline continuously from high initial values, particularly after canopy closure when tree morphology is shaped more and more by competition for resources (cf. Jacobsen et al. 2003). In this phase the growth in DMC over all components assumes an asymptotic course while the share of coarse wood in the stand's total DMC continues to increase drastically. This pattern can be found equally in good and in poor yield classes with slower and less pronounced trends in the latter. These results correspond to findings by Nebe and Herrmann (1987) for *Picea abies* and by Rademacher et al. (1999) for *Pinus sylvestris*. The respective results for nutrient contents are very similar to those for DMC. The older (or larger) the oak trees get, the higher the share of coarse wood and the lower those of twigs and foliage in the total amounts of the investigated elements. Branches, however, behave differently: Their percentages in total nutrient contents rise with age (or size). For magnesium and phosphorus this increase is even more intense than that of coarse wood.

Geographic range of applicability

The map in Figure 1 highlights the northeastern German lowlands, which are seen as the primary region of reference. Due to the more or less homogenous site and climatic conditions the models developed in this study can safely be recommended for application to oak trees growing in this area. Adjacent regions with similar geographic characteristics (e.g. the eastern part of the German state of Lower Saxony and the north-western region of Poland) provide site conditions that result in analogous growth patterns. The presented functions will also reliably predict oak biomass and element contents there. In addition to this, the comparison in Figure 9 shows that they do not differ significantly from those developed by Grote et al. (2003) and Zell (2008) that were applied to a wide range of stand and site conditions throughout Germany. Therefore our models will most certainly deliver representative and reliable estimations for a range of conditions similar to those covered by the established biomass functions. However, this last assumption has to be evaluated in additional field trials based on larger samples from other regions.

Conclusions

The aim of this study was to develop and calibrate a set of functions for estimating volume, dry matter and nutrient contents for a regional database of the tree species *Quercus petraea* [Matt.] Liebl. We applied regression analyses to biomass samples from a total of 22 trees that were subjected to the methods of Randomized Branch Sampling (RBS) and Importance Sampling (IS). For all sample trees data of their coarse wood volume and the dry matter content in coarse wood were available. In a subsample of ten trees the investigations were carried out separately for the components foliage, twigs, branches, and coarse wood. These trees were additionally analysed for their contents of carbon, nitrogen, potassium, calcium, magnesium, phosphorus, and sulphur.

The determined allometric functions use dbh and/or tree height to estimate individual volume, dry matter, and nutrient contents. Analyses of the different components show that the relative share of coarse wood dry matter in total biomass steadily increases with growth of the trees. Dry matter of the other components is growing much slower in relation and even stays almost constant in absolute amount for twigs and foliage above a certain age. Nutrient contents over time follow an analogical course except for branches where – similarly to coarse wood – the share of nutrients in the respective totals per trees is continuously increasing. Finally, we calculated data for whole stands based on stand-related values for mean diameter, mean height, and stem number per hectare to explore the scale of differences between yield classes.

The application of the models developed in this study in practical forest research and management can be accomplished by integrating them into forest growth simulation programs, for instance into BWIN-Pro (Meiwes et al. 2012, Hansen and Nagel 2014). This combination could be used for detailed comparisons of different forest management strategies involving the harvest of whole trees vs. that of only stems, leaving branches and tree crowns in the forest. Investigations into the effects of these strategies on the nutrient balances in the forest ecosystems would require data about the site-specific availability of the respective elements. Due to the given data base our models are at the moment restricted to trees in the dbh range of 8–40 cm. This is particularly relevant for higher yield classes which cross the upper dbh limit at ages of 65–80 years. The important stage of mature stands entering the phase of harvest and regeneration can therefore not be covered. The weak significance of tree height as predictor variable in most functions is another indicator for the narrow data base. Acknowledging these limitations the models presented here can be applied to a wide range of research questions concerning oak in a region from eastern Lower Saxony in Germany to the western lowlands of Poland. Further research is needed to extend the range of reliable model predictions especially for larger trees and in general to base the functions on a higher number of sample trees.

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