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Stand density sensitive biomass functions for young oak trees at four different European sites

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Abstract

Key message Relative biomass of tree compartments is dependent on plant size and stand density, with stand density being an important predictor, especially for belowground biomass and at high stand densities.

Abstract Estimation of biomass production is an important issue against the background of climate change and carbon storage. Even though many studies investigated the biomass productivity of trees or single compartments, only few considered the belowground biomass. Further, there is a lack of studies focusing on young trees and considering further influencing factors such as the prevailing stand density. In the present study, young *Quercus robur* trees were sampled on Nelder trials, which comprise different stand densities, on four European sites differing in climatic conditions. Besides the estimation of logarithmically transformed power equations, Dirichlet regressions were applied for deriving biomass functions for the single compartments leaves, branches, stem and roots. Thereby, the dependence of total and compartment biomass allocation on diameter at root collar (d_0), tree height and stand density is tested. The results show that besides d_0, the local Stand Density Index (SDI_l) is an important predictor for biomass. Especially, the belowground biomass shows a significant relation to the SDI_l, which is less the case for the aboveground biomass. Not considering the SDI_l leads to an overestimation of the biomass productivity, especially when the stand density is high. Furthermore, the results show that the belowground biomass is lower than the aboveground biomass, but with 50–80% of the aboveground biomass still of considerable size. This indicates the importance of including stand characteristics when estimating above- and belowground tree biomass in future studies.

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Introduction

The amount of stored carbon in biomass is very important for various issues concerning the global climate circle and the carbon cycle. Over the last decades, the quantification of carbon stocks within forests is of rising interest, in line with different attempts at modeling the global climate (Wirth et al. 2004; Cienciala et al. 2008; Vejpustková et al. 2015). This in turn requires appropriate and well adapted biomass functions for the estimation of tree and stand biomass.

While there are plenty of studies dealing with tree biomass, only few actually weigh the trees to quantify the biomass, whereas most studies only use allometric equations (Poudel and Temesgen 2016). The reason is that the attributes inserted into the allometric equations are easily measurable, while harvesting and weighing the trees is time consuming and expensive. As a consequence, the majority of studies are limited to aboveground biomass and neglect the belowground biomass, which would require excavating the trees' roots. The application of generic allometric equations in turn might not be appropriate, due to the fact that biomass productivity is species specific (Chojnacky et al. 2014) and likely to be dependent on several other factors. Besides tree species, Poudel and Temesgen (2016) name tree age, stand density and site productivity, including soil characteristics such as texture and moisture content as the main factors influencing the amount of biomass.

Especially, the maximum stocking density of young trees is scarcely investigated (Wirth et al. 2004; Annighöfer et al. 2016; Cotillas et al. 2016). Some studies include young trees, but work with samples having a broad age range and neglect to differentiate between age classes in the estimation. These trees and their services, however, play a key role in reforestation and afforestation and should be investigated separately. Therefore, the few known studies dealing with biomass productivity of young trees are outlined in the following. Annighöfer et al. (2016) investigated the biomass of seedlings and saplings from different tree species in Central Europe. Their data set refers to 27 explorative or experimental studies covering a wide range of growth conditions (e.g., in situ, ex situ, different light availability). As a result, they report that in juvenile stands site conditions (e.g., light availability, soil properties, resource competition) can be assumed to be the most important factors determining growth in terms of tree height and diameter. Cotillas et al. (2016) have studied the biomass allocation of young *Quercus ilex* and young *Quercus cerrioides*. Looking at aboveground

and belowground biomass they report that overall belowground biomass amounts for 62%. They also report species-specific differences. In difference, Kuznetsova et al. (2011) do not find significant differences in the aboveground biomass allocation between species when studying 8-year-old Scots pine and lodgepole pine. Pajtík et al. (2008) investigated single spruce trees up to ten years at different forest sites in Slovakia. In their study they divided into needles, stem, branches and roots. As a result, they state that the diameter at root collar (d_0) is the most important variable predicting biomass of each compartment. Tree height (h) did not show a detectable added value for the predictions, as this parameter was highly correlated with tree diameter. Further, they mention that wood density might increase with age, which has to be taken into account when projecting biomass. Finally, they found that their young stands amount for 3–10% of a fully grown stand's biomass storage, wherefore young or mixed aged forest stands should not be undervalued. Wirth et al. (2004) estimate biomass functions for Norway spruce in central Europe. They state that the biomass should be recorded for the different compartments, to be able to develop additive biomass functions. Further, they point out the lack of biomass data for trees younger than 10 years, which often limits the applicability of the derived functions.

Besides the neglect of young trees, other possible influence factors such as site characteristics have been poorly researched, e.g., climatic conditions or resource availability such as water and nutrient supply. The availability of resources in turn is influenced by forest management decision, e.g., stand density, leading to different levels of competition. Competition between plants in turn depends on several factors and should be distinguished between aboveground and belowground competition. For root competition, the amount of neighbors and available resources, such as water and several essential mineral nutrients, is of highest importance, whereas for aboveground competition especially light availability is a key factor (Kawaletz et al. 2013). In forestry, a broad range of local stand densities were established and thus different individual levels of competition exist. For an investigation of the productivity under different competition levels, the Nelder design, which consists of concentric circles and radial spokes, is particularly appropriate. Using this Nelder design, Kuehne et al. (2013) could show that the competition level, in terms of stand density, has an enormous influence on tree growth which is ultimately related to productivity. Belowground competition has been found to play an important role concerning tree growth. However, compared to aboveground biomass there are way less studies, and thus need to further investigate belowground biomass (Zianis et al. 2005).

Pretzsch and Biber (2010) analyzed the influence of size-symmetric and size-asymmetric competition along an ecological gradient for three tree species (Norway

spruce, Scots pine, and Sessile oak). Their results reveal that under the same competition index diameter growth is more strongly reduced on light-limited fertile sites than on poor sites. Thus, they conclude that the competition effect is stronger on good compared to poor sites. This shows that biomass investigations are likely to be dependent on the competition level, as well as on site characteristics. Looking also into site characteristics, the investigation of Cienciala et al. (2008) parameterize total aboveground biomass functions in forests of the Czech Republic. They sampled oak trees (*Quercus robur*, *Q. petraea*) from six different sites, representing important regions of oak forest management. In their study, diameter at breast height (dbh) was found to be the strongest predictor for aboveground biomass, tree height and crown parameters could improve the model fits for the biomass estimation of single compartments. Site characteristics in the form of the altitude as an additional predictor did not show an improvement of the fitted models. Further studies support the finding that the inclusion of height parameters, conveying information about the competitive status of the tree, can improve the accuracy of biomass estimations (Wirth et al. 2004; Ruiz-Peinado et al. 2011). Another study (Vejpustková et al. 2015) also conducted in Czech Republic, but covering a broader range of site and stand conditions showed in some points different results. For beech trees, they also found tree diameter to be the main predictor for aboveground biomass. However, in their study tree height could not significantly improve the model fit. Further, they found a better fit for total aboveground biomass by including the altitude. The inclusion of altitude and site index, representing the site productivity and tree height by the age of 100 years, improved the results for stem and branch biomass.

Furthermore, several studies have shown that tree growth is influenced by climatic conditions (Lu et al. 2002; Lindner et al. 2010). In this context, Lindner et al. (2010) report for the Mediterranean zone that biomass growth is expected to decline in future due to droughts caused by rising temperatures and decreasing precipitation. If, however, the climatic conditions have an influence on the biomass productivity, it might be misleading to apply existing biomass equations to tree data due to climate differences between the sample sites.

Addressing the above mentioned research gap, in the present study, 64 juvenile oak trees (dbh <5 cm), grown on Nelder trials in pure stands on four different sites in central Europe, were sampled. Biomass of four tree compartments (leaves, branches, stem, and roots) was quantified and biomass equations for these compartments were derived. In addition, different competition levels were considered and taken into account for the analysis of

biomass productivity. Last but not least, the same tree species was sampled at four climatically different sampling sites, which allows us to analyze the climatic influence on biomass productivity. Doing so we address the following research questions:

1. Which variables (diameter, height, stand density) determine total biomass production and compartment biomass production (leaves, branches, stem and roots) of juvenile oak trees?
2. How does above- and belowground biomass depend on diameter, height and stand density?
3. Is the wood density dependent on plant size and stand density?
4. How much is the total biomass productivity per hectare of juvenile oak trees depending on stand density and climatic conditions?

Summing up, this study addresses the research gap of an investigation focusing on young oak trees and the impact of stand density and environmental conditions on biomass production. Further, this study uses a holistic approach, by considering not only aboveground biomass, like most studies do, but also belowground biomass.

Materials and methods

Experimental design

This study is designed as a comparison of trees grown on four different pedunculate oak (*Q. robur* L.) pure stand sites. The sites were established between 2008 and 2010 as Nelder trials and are located close to the following cities in central Europe: Ingolstadt, Germany (ING650); Györ, Hungary (GYO651); Neckarsulm, Germany (NEC652) and Sant'Agata Bolognese, Italy (SAN653). Table 1 shows information about the sample sites, their locations are visualized in Fig. 1. A detailed description of the sites can be found in Uhl et al. (2015).

As shown in Table 1 the four sites differ in their climate conditions. The climate ranges from subcontinental (GYO651) to sub Mediterranean (SAN653). The long-term mean annual temperatures vary from 8.2 °C (ING650) to 13.2 °C (SAN653), while the highest mean annual precipitation amounts 760 mm (NEC652) and the lowest 537 mm (GYO651). Based on these climate data, the aridity index after De Martonne (DMI) was calculated as follows (de Martonne 1926):

$$\text{DMI} = \frac{P}{T + 10}, \tag{1}$$

with P being the annual precipitation sum of the observation period and T being the mean air temperature for the

Table 1 Site description including location, longitude (long), latitude (lat), altitude (alt), long-term mean annual temperature (MAT), long-term mean annual precipitation (MAP), De Martonne Aridity Index (DMI), planting year (plant year) and tree age in the year 2016 (age)

Site	Location	Long (°E)	Lat (°N)	Alt (m)	MAT (°C)	MAP (°C)	DMI	Plant year	Age (years)
ING650	Ingolstadt (GER)	11.49	48.86	460	8.2	670	36.8	2008	10
GYO651	Györ (HUN)	17.60	47.79	110	11.1	537	25.5	2009	10
NEC652	Neckarsulm (GER)	9.35	49.05	380	9.1	760	39.8	2010	7
SAN653	Sant'Agata (ITA)	11.10	44.46	25	13.2	660	28.4	2010	8

Fig. 1 Map of the sampling locations of this study
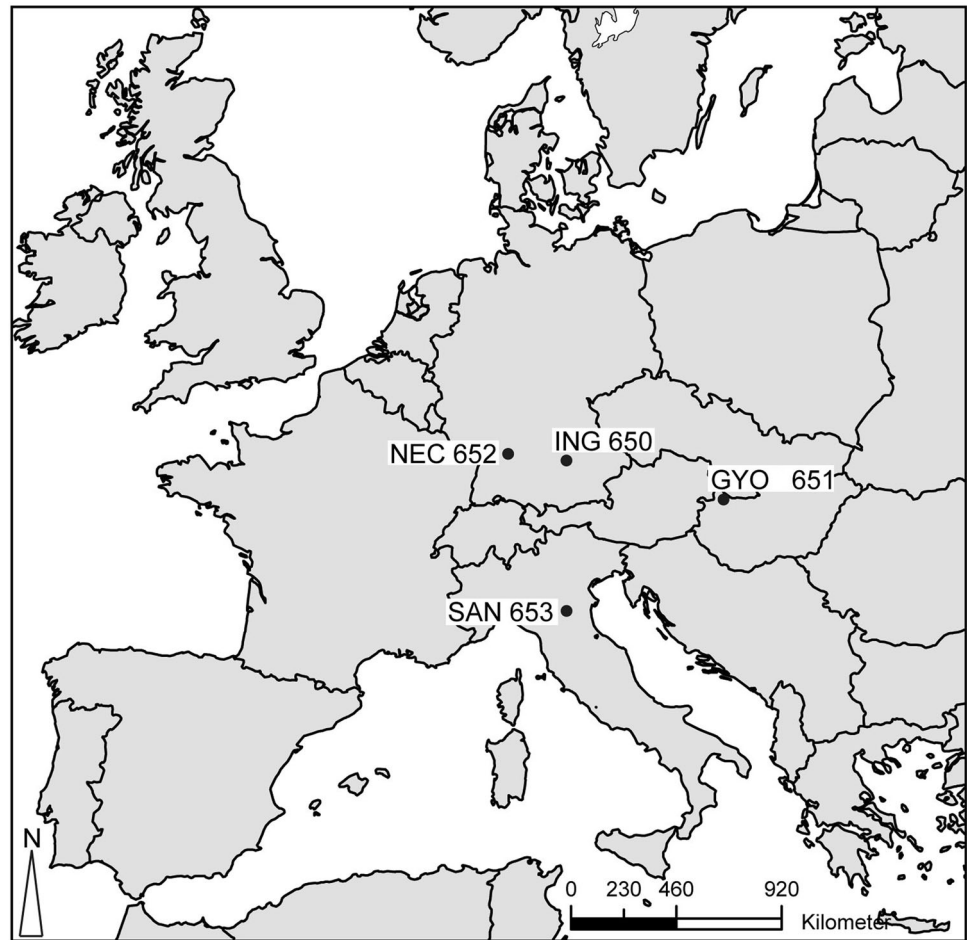
observation period. The DMI (Table 1) shows the highest value for NEC652 and the lowest for GYO651. As lower values represent higher aridity, this indicates that GYO651 is the most arid site, followed by SAN653. In comparison, the two German sites ING650 and NEC652 are more humid.

On all sites local provenances were used, and plant ages at establishment were between 1 and 3 years with heights between 30 and 70 cm. The site ING650 was established 2008 on clear-cuts within forests. In difference, the sites NEC652 (planted in 2010), GYO651 (planted in 2009) and SAN653 (planted in 2010) were established on former agriculturally used areas, within forests (NEC652 and GYO651) or outside forests (SAN653). At all sites long-term yield trials using a Nelder design were established (Uhl et al. 2015). The spacing trial design by Nelder (1962) can be described as an arrangement of concentric circles and radial spokes in a constant angle distance, which is in the case of our experimental sites 20° (Fig. 2). Thus, the trees in the Nelder design differ in their surrounding stand density, with high density in the center and decreasing density to the outer areas. With this planting design the competitive and facilitative effects, which occur simultaneously, can be analyzed and separated. In particular, the transition level of density, where the negative and positive effects are in balance can be identified (Uhl et al. 2015). Each of the investigated sites
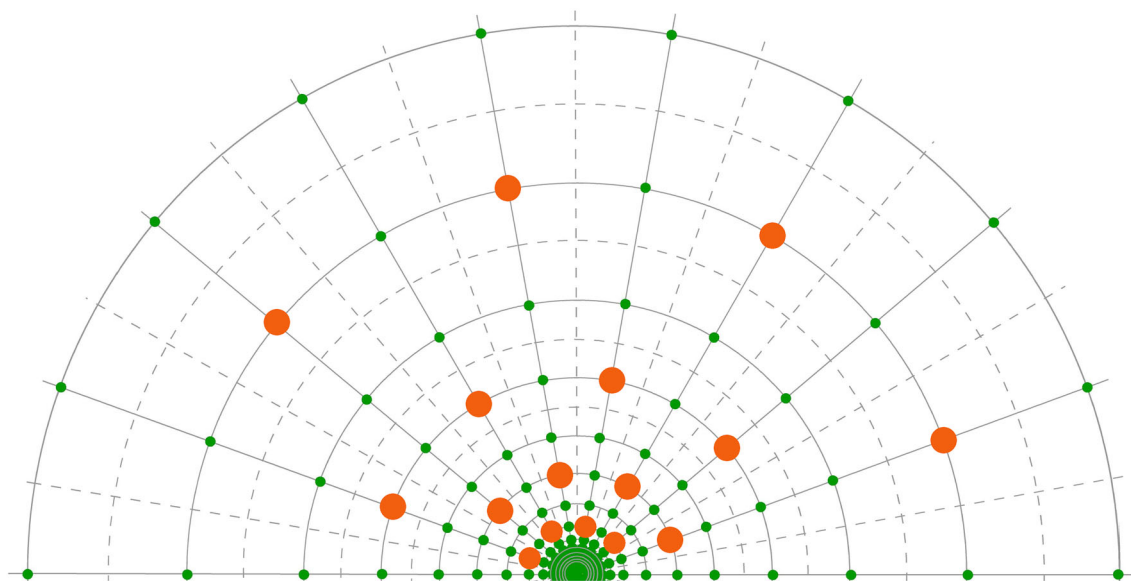
Fig. 2 Schematic representation of half Nelder wheel (Nelder 1962). Plant positions (*green dots*) are defined by intersection points of concentric circles and radial spokes. The *orange dots* show the concept of the tree selection for sampling

comprises two full Nelder wheels reflecting an initial stand density range from 100.000 to 50 trees per hectare. At most sites (GYO651, NEC652 and SAN653), additional semi and even smaller wheels following the same design were established. For this study, we collected only plants from surrounding half and quarter wheels, which were established for this purpose at the same time as the full wheels. These half and quarter wheels follow the same structure as the full wheels. Thereby the quarter wheels consist of 4 (SAN653) or 5 (GYO651, NEC 652) spokes and 11 circles. The half wheels have 9 spokes and 11 circles (SAN635). This results in a total amount of 55 plants per quarter wheel in GYO651 and NEC652 and 44 plants per quarter wheel for SAN653 plus 99 plants per half wheel. In the case of ING650, the trees were also planted in quarter wheels but not strictly following the Nelder concept with its constant angle distances.

Tree sampling

Samples were taken during June and July 2016 at the four different sites. At each investigation site, 16 trees of the species pedunculate oak (*Quercus robur* L.) were sampled. For the selection of trees in the Nelder design, the following criteria were applied: (1) no borderline trees for avoiding edge effects, (2) no neighboring trees and (3) only trees having all eight direct neighbors. Figure 2 visualizes a possible selection of sample trees in the case of a Nelder half wheel.

Before excavating a sample tree, the following variables were measured: stem diameter at root collar (d_0), diameter at breast height (dbh, at a height of 1.3 m, if already achieved), diameter at crown base (dcb), tree height (h), height to crown base (hcb) and the crown radius (cr) in the eight cardinal

directions. After carefully excavating the trees, including all coarse and fine roots, the tree was dissected into four compartments: leaves, stem, branches and roots. All compartments per tree were not only directly weighed in the field, but also later in the laboratory after oven-drying for at least 24 h. The wood density of each tree was determined by the hydrostatic weighing method. To this end, a piece of the stem at a height of 1 m was cut out and freed from bark. The range of the density values for each site is shown in Table 2, together with other tree parameters.

A local stand density index (SDI_l) was chosen for comparing the competition levels between the four sites. Following Uhl et al. (2015), the SDI_l was calculated by applying a search radius around the position of the tree of interest, whose extension was defined by the mean height of all trees in the quarter or half wheel multiplied by the factor 1.25. The number of trees inside the search radius was then considered as the number of competitors for the tree of interest. According to the following formula, the SDI_l normalizes the stem number per hectare to a mean tree size of 25 cm. Equation (2) gives the formula for calculating the SDI_l, with N representing the stem number per hectare (excluding the tree of interest) derived from the stem number in the search radius and dg representing the quadratic mean diameter of all trees within the search radius. The value of the exponent -1.605 was used according to the generic stand density rule (Reineke 1933).

$$SDI_l = N \left(\frac{25}{dg} \right)^{-1.605}. \tag{2}$$

In ING650 (and partly in GYO651) trees were sampled, which were planted at the same time as the Nelder wheel,

Table 2 Tree characteristics (mean values) for each sampling site; minimum and maximum values are given in parenthesis

Site	n	d_0 (mm)	dbh (mm)	Tree height (m)	Density (g/cm³)	SDI_l
ING650	16	44.4 (27–63)	20.4 (12–39)	2.8 (2.0–4.1)	0.82 (0.73–0.92)	211 (155.4–280.3)
GYO651	16	30.9 (16–46)	12.6 (2–29)	1.9 (0.9–3.5)	0.76 (0.68–0.88)	150 (20.9–383.0)
NEC652	16	34.3 (20–53)	14.7 (5–30)	2.1 (1.3–2.9)	0.87 (0.76–0.94)	168 (4.8–688.4)
SAN653	16	44.9 (17–90)	13.7 (4–27)	2.4 (1.6–4.8)	0.79 (0.66–0.94)	266 (8.5–534.1)
All sites	64	38.6 (16–90)	15.5 (2–39)	2.3 (0.9–4.8)	0.81 (0.66–0.94)	199 (4.8–688.5)

using same planting material, but which were not planted with the constant angle distance which is characteristic for Nelder trials. In these cases, for each of the sample trees the competition status was similarly evaluated as for trees from Nelder design. Precisely, the SDI_l for each of those trees was determined by taking the 14 surrounding trees and its distance to the sampling tree as well as its dimensions into account.

Results of the SDI_l calculation shown in Table 2 indicate on average the highest stand density in SAN653 and by far the lowest stand density in GYO651. The very narrow value range for ING650 can be explained by the before mentioned planting design, which is different compared to the other three sites.

Biomass equations

Commonly, biomass is predicted using Snell's (1892) power equation $y = \beta_1 x^{\beta_2}$ (Annighöfer et al. 2016), where y denotes biomass and x denotes the predictors. Due to heteroscedasticity, this equation is often logarithmically transformed before fitting into $\ln y = \ln \beta_1 + \beta_2 \ln x$. Doing so a linear regression can be applied to the data (Pilli et al. 2006). For the biomass estimations in the present study, we follow the described procedure, using the logarithmically transformed data. As shown in Eqs. (3)–(6), we estimate four models for biomass weight, differing in the predictor variables (d_0, h, SDI_l). While the dbh is commonly used for biomass estimations of larger trees, the diameter at root collar has been found to be more appropriate for young trees (Wirth et al. 2004; Pajtík et al. 2008; Annighöfer et al. 2016; Cotillas et al. 2016) (and for trees $h < 1.3$ m there is evidently no choice at all). For all trees with a minimum height of 1.3 m, we fitted all models shown below alternatively with dbh and with d_0 as predictor variable. Thereby d_0 consistently yielded better model fits. Thus, only the results considering d_0 are presented in the further text. The following models were fitted:

$$\ln W = \beta_1 + \beta_2 \ln(d_0) \tag{3}$$

$$\ln W = \beta_1 + \beta_2 \ln(d_0) + \beta_3 \ln(h) \tag{4}$$

$$\ln W = \beta_1 + \beta_2 \ln(d_0) + \beta_4 \ln(SDI_l) \tag{5}$$

$$\ln W = \beta_1 + \beta_2 \ln(d_0) + \beta_3 \ln(h) + \beta_4 \ln(SDI_l). \tag{6}$$

Thereby, W refers to the estimated total biomass weight of a tree. The four models are fitted for total biomass, comprising the single compartments roots, stem, branches and leaves. This single equation estimate of total biomass (in contrast to summing up separate compartment-wise estimates) has been recommended by previous studies, due to reduced assessment errors and better fitting results (Cienciala et al. 2008; Vejpustková et al. 2015). The normality of the residuals was tested with Q–Q plots.

In addition, however, also the compartments biomass shall be estimated as the proportions of total biomass in a way that they can be applied to a previously estimated total biomass, adding always up to 1. To do so, we used a Dirichlet regression. This type of regression is useful for modeling data representing components as percentage of the total (Poudel and Temesgen 2016). In other words, for each component $c = 1…C$ the compartment proportion y_c is given by the compartment biomass divided by the total biomass. These compartment proportions $y = (y_1,…, y_C)$ have to fulfill the following constraints: $y \in (0, 1)$ and $\sum_{c=1}^{C} y_c = 1$.

We then assume that the compartments follow the Dirichlet distribution, which is a multivariate generalization of the beta distribution, where $\alpha_c > 0$, $\forall c$ are the shape parameters for each compartment.

$$D(y|\alpha) = \frac{1}{B(\alpha)} \prod_{c=1}^{C} y_c^{(\alpha_c - 1)}. \tag{7}$$

The Dirichlet regression model can be formulated as follows:

$$\log(\alpha_c) = \eta_c = X^{[c]} \beta^{[c]}. \tag{8}$$

Thereby, $X^{[c]}$ represents a matrix of predictors, where the superscript indicates that the model allows for separate predictors in each compartment. This in turn potentially leads to different numbers of regression coefficients per compartment, which are captured in the column vector $\beta^{[c]}$.

In the study at hand, however, we assume that all compartments are influenced by common covariates [d_0 (mm), h (cm)]. Concretely, in line with the single equation models, the following Eqs. (9)–(12) were fitted for the four compartments roots, stem, branches, leaves ($c = 1, …, 4$):

$$\ln(\alpha_c) = \alpha_{1c} + \alpha_{2c} \ln(d_0) \qquad (9)$$

$$\ln(\alpha_c) = \alpha_{1c} + \alpha_{2c} \ln(d_0) + \alpha_{3c} \ln(h) \qquad (10)$$

$$\ln(\alpha_c) = \alpha_{1c} + \alpha_{2c} \ln(d_0) + \alpha_{4c} \ln(\mathrm{SDI_l}) \qquad (11)$$

$$\ln(\alpha_c) = \alpha_{1c} + \alpha_{2c} \ln(d_0) + \alpha_{3c} \ln(h) + \alpha_{4c} \ln(\mathrm{SDI_l}). \qquad (12)$$

With the common parametrization, the expected values are then defined as $E[y_c] = \alpha_c / \alpha_0$, where α_0 is the sum of all α_c (see Maier 2014 for more information).

In a last step, the biomass productivity of the whole Nelder wheels at each site was projected. To do so, linear regression models with total biomass (kg) and aboveground biomass as the dependent variable were estimated. In accordance with before estimated linear regression models 4 and 6, once d_0 and height, and once d_0, height and $\mathrm{SDI_l}$ were chosen as the independent variables. For each of the four investigation sites, data from inventory measurements (d_0, height, $\mathrm{SDI_l}$) of all trees in the two full wheels was then inserted into the allometric equations. The estimated biomass was than extrapolated to Mg per hectare. To be able to compare the different locations, the projection calculation was based on data by the tree age of 6 years for each site.

The models for the total biomass were fitted using the software R 3.2.2 (R Core Team 2015) with the function "lm" of the R package "stats" (R Core Team 2015) and the compartments biomass was fitted using the R package "DirichReg" (Maier 2014).

Results

The sampled trees showed a dbh between 2 and 39 mm and a height between 0.9 to 4.8 m. $\mathrm{SDI_l}$ values vary between 4.8 and 688.4 reflecting different competition status of single plants (see Table 2). Although, in general, diameter-height relationship is in a narrow range, site-specific variations are observable. Competition status of single plants seems to effect allometric behavior. Plants from ING650 show minimum variation in $\mathrm{SDI_l}$ values as they were sampled from nearly constant spacing areas. Considering trees from all sample sites, the relationship between height and dbh remains within a narrow range (Fig. 3).

On all four sites, most trees have a dbh between 10 and 30 mm with a tree height between 170 and 350 cm. While on the other sites dbh values below 10 mm can be found, all trees in ING650 have a dbh greater than 10 mm. This might be due to the fact that ING650 is the oldest site, or due to the narrow $\mathrm{SDI_l}$ range in ING650. The climate
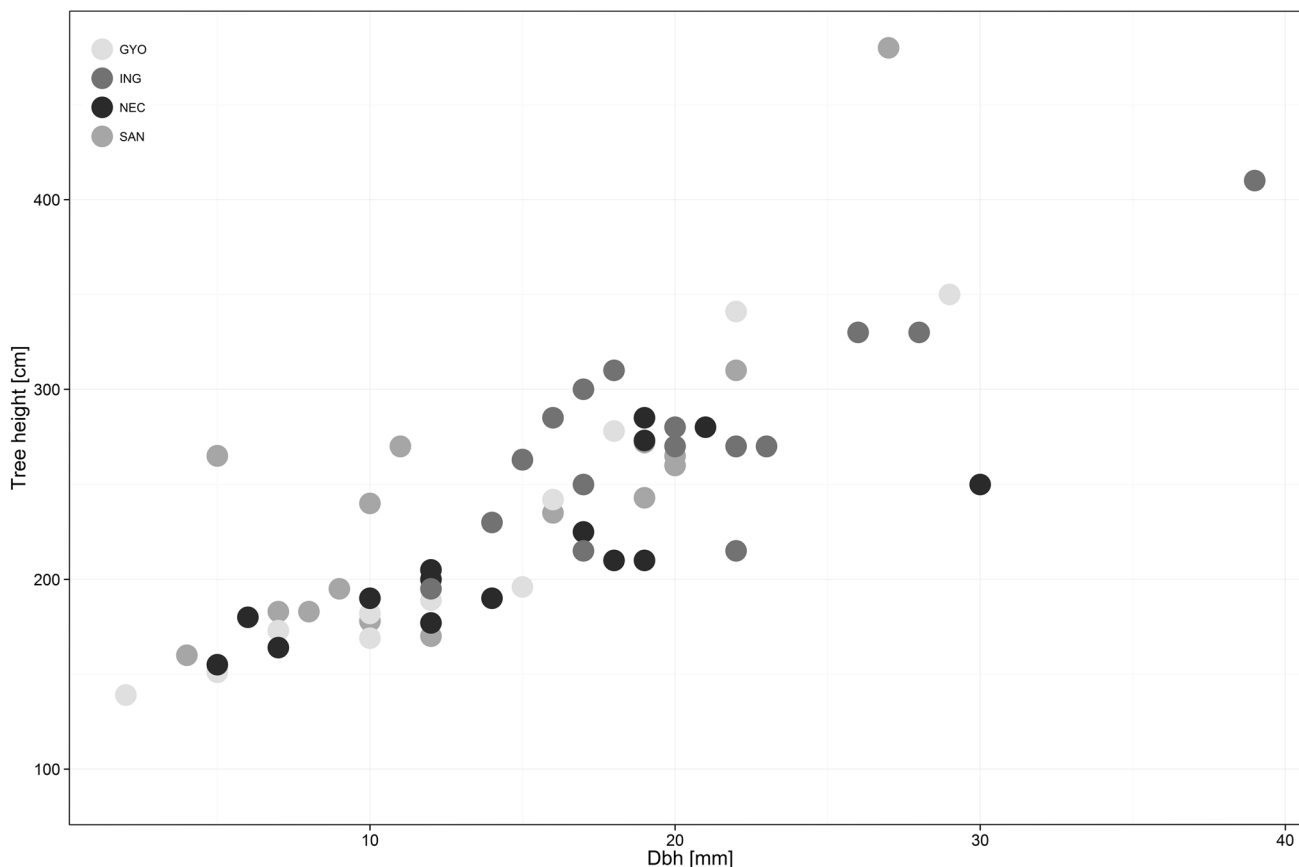
Fig. 3 Tree diameter at breast height (dbh) in relation to tree height ($n = 59$) classified by site characteristics, with *dark color* indicating humidity to *bright color* indicating aridity
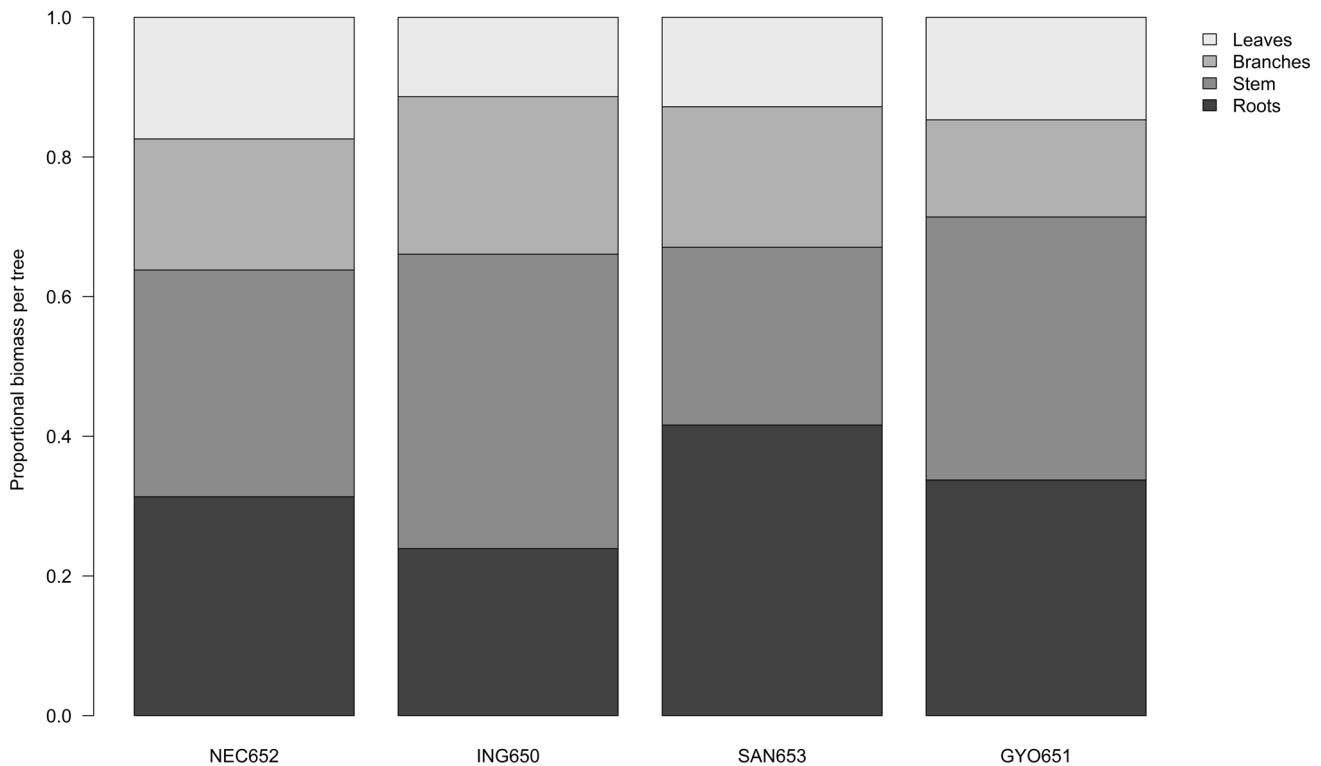
Fig. 4 Relative compartment biomass composition per site based on dry weight

Table 3 Average absolute compartment biomass and total biomass per tree

Site	Root biomass (kg)	Stem biomass (kg)	Branch biomass (kg)	Leaf biomass (kg)	Total biomass (kg)
ING650	0.52 (0.13–1.03)	0.92 (0.21–3.00)	0.49 (0.11–1.07)	0.25 (0.07–0.57)	2.18 (0.52–5.66)
GYO651	0.28 (0.08–0.63)	0.32 (0.07–1.01)	0.12 (0.01–0.33)	0.12 (0.02–0.27)	0.84 (0.18–2.22)
NEC652	0.34 (0.07–0.90)	0.36 (0.08–0.98)	0.21 (0.02–0.91)	0.19 (0.03–0.63)	1.10 (0.26–3.41)
SAN653	0.61 (0.05–2.26)	0.37 (0.07–1.20)	0.29 (0.01–0.88)	0.19 (0.01–0.61)	1.46 (0.14–4.45)

conditions of the sites, indicated by a bright (arid) versus dark (humid) color in Fig. 3, seem to have no influence on the relation between dbh and height.

Differentiating plants' total biomass into the compartments leaves, branches, stem and roots, mean values of site-specific sample trees reveal substantial differences between the relative compartments' amounts (Fig. 4). Leave and branch biomass show for all four sites the smallest and second smallest relative compartment amount. But relative stem and root biomass, respectively, vary between the sites. Moreover, the second highest absolute mean plant stem biomass is found in SAN653 (Table 3); the relative mean stem biomass is smallest on this site.

It is remarkable that although at same age, plants in GYO651 indicate a higher relative root biomass than in ING650. One possible explanation might be climatic differences between the sites, with GYO651 showing higher long-term mean annual temperature and lower long-term mean annual precipitation

values (see Table 1). The same pattern is valid for the nearly same aged tress at NEC652 having moister soil conditions and SAN653 being dryer. Comparing relative above- and below-ground biomass, plants from SAN653 and GYO651 show a share of 40% of aboveground biomass, plants from NEC652 have 50% and plants from ING650 have 60% (Fig. 5).

Relating the biomass of the different compartments to the SDI_l, as depicted in Fig. 6, differences between the sites can be observed.

For the sites NEC652 and SAN653, the biomass of all four compartments decreases with increasing SDI_l. For the site GYO651, a similar trend can be observed. However, the relation is not as clear, due to a high variation in biomass at low SDI_l values. For the site ING650, no trend in the relation can be found, which might be due to a small SDI_l range. Despite this small SDI_l range, high variation regarding the biomass can be found for the trees in ING650.
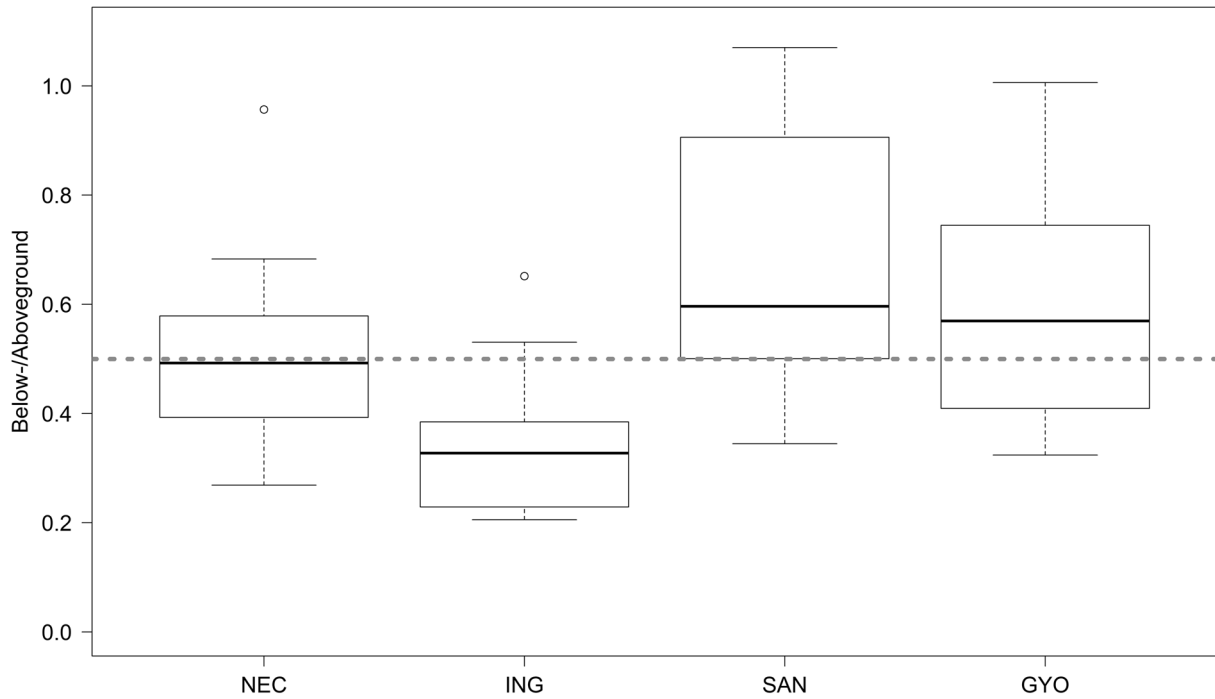
Fig. 5 Below-/aboveground biomass relation of the four sites ordered from humid location (NEC652) to more arid location (GYO651)
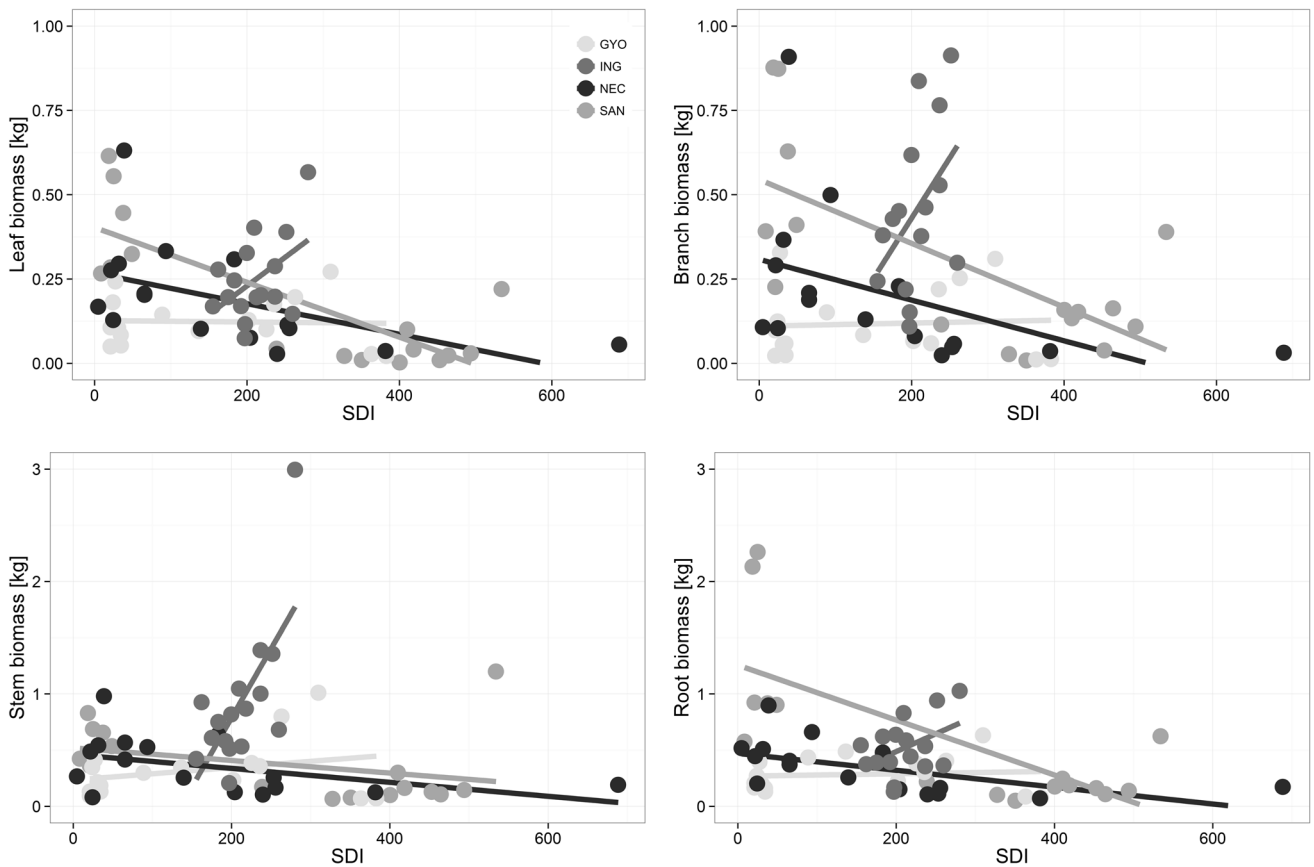
Fig. 6 Relation of biomass to stand density index (SDI$_l$), shown for all four compartments (leaf, branch, stem, root). *Darker* points indicate the more humid sites; *solid lines* symbolize the linear trendline

Table 4 Linear regression models for total (W_{total}), below (W_{below}), above (W_{above}) and the ratio of below to aboveground ($W_{below/above}$) biomass weight (Eqs. 3–6)

Model	β_1	β_2	β_3	β_4	SE	R^2_{adj}	RMSE
W_{total}	−0.9858*	2.2526***			0.3605	0.8298	0.3549
	−2.6591***	1.9543***	0.5096**		0.342	0.8468	0.3339
	−0.7405	2.2286***		−0.0330	0.3615	0.8289	0.3529
	−2.6963***	1.7132***	0.7791***	−0.1139**	0.3251	0.8616	0.3147
W_{below}	−1.4297**	2.0600***			0.3527	0.8098	0.3471
	−1.4898	2.0492***	0.0183		0.3555	0.8067	0.3471
	−0.48714	1.96741***		−0.12660***	0.3242	0.8393	0.3165
	−1.54540*	1.68858***	0.42154*	−0.17038***	0.3144	0.8488	0.3045
W_{above}	−1.673**	2.329***			0.4326	0.7832	0.4258
	−4.1390***	1.8889***	0.7509***		0.3966	0.8178	0.3872
	−1.77941**	2.33901***		0.01426	0.4359	0.78	0.4255
	−4.16654***	1.71006***	0.95087***	−0.08451	0.3907	0.8232	0.3783
$W_{below/above}$	0.2435	−0.2686			0.408	0.037	0.4016
	2.6492**	0.1603	−0.7326***		0.3713	0.2026	0.3625
	1.29226*	−0.37160**		−0.14086**	0.3779	0.174	0.3689
	2.62114**	−0.02148	−0.52933*	−0.08588	0.3641	0.2329	0.3526

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Biomass equations

We tested the dependencies of total above- and belowground plant biomass, as well as of the ratio of below- to aboveground biomass, from plant size parameters (d_0, h) and competition situation (SDI_l) (Eqs. 3–6). The results of the linear regression models are summarized in Table 4. For estimating total biomass, Eq. (6) provides the best fitting indicated by the level of significance of the parameters and adjusted R^2. This is also valid for belowground biomass. In case of aboveground biomass, sufficient fitting quality seems to be achieved using diameter at root collar and height as predictors, only. The relation between below- and aboveground biomass appears to be assessable by the parameters d_0 and SDI_l.

In a second step, the Dirichlet regression was used for analyzing the impact of the independent variables (d_0, h, SDI_l) on the relative biomass of the single compartments. The results of the four estimated models (Eqs. 9–12) are given in Table 5.

While plant height shows no significant effect on the relative compartments' biomass at all, tree diameter and competitive situation modify biomass allocation between compartments. Equation (11) presents best fitting results. Running the model without the variable tree diameter, which is not significant for the compartment branches, does not reveal a better model fit. This means, dropping d_0, lowers the explanatory power of the SDI_l for at least one of the other compartments. Therefore, we continue with the results of Eq. (11). Based on the α coefficients, the expected values of the biomass proportions (E(compartment)) can be estimated as follows:

$$\alpha_0 = 28.789 d_0^{-0.0211} SDI_l^{-0.0042} + 11.254 d_0^{-0.0015} SDI_l^{-0.0021}$$
$$+ 46.433 d_0^{-0.0214} SDI_l^{-0.0018} + 61.596 d_0^{-0.0240} SDI_l^{-0.0030}$$

$$E(\text{leaves}) = 28.789 d_0^{-0.0211} SDI_l^{-0.0042} / \alpha_0$$

$$E(\text{branches}) = 11.254 d_0^{-0.0015} SDI_l^{-0.0021} / \alpha_0$$

$$E(\text{stem}) = 46.433 d_0^{-0.0214} SDI_l^{-0.0018} / \alpha_0$$

$$E(\text{roots}) = 61.596 d_0^{-0.0240} SDI_l^{-0.0030} / \alpha_0.$$

A visualization of the estimates of Eq. (11) is captured in Fig. 7. Proportional compartments' biomass is plotted against d_0. To consider the effect of stand density, the curves' progression is illustrated for two different SDI_l values. SDI_l 650 (dashed lines in Fig. 7) is used to reflect dense stand situations and SDI_l 200 (solid lines in Fig. 7) to represent low competition.

In general, with increasing plant size the relative biomass of stem, roots and leaves is decreasing. Conversely, relative branch biomass is increasing during plant's development. At high stand densities, relative root biomass and relative leaf biomass are substantially smaller than at low densities. Concerning relative stem biomass and relative branch biomass, the opposite pattern is true, having higher relative biomass at higher stand densities, indicating stronger biomass allocation into stem and branches.

Besides the analysis regarding the total and the compartment biomass, it was also tested whether the wood density is dependent on plant size, SDI_l or climatic conditions. In difference to the before shown results, however, no significant influences of these variables on wood density could be found. A possible explanation for this might be little variation in wood density, due to the small age variation within the sample.

Biomass productivity projection for the Nelder wheels

Inserting the tree data of the Nelder full wheels into different allometric equations, Fig. 8a illustrates the projected

Table 5 Alpha coefficients for different variables from Dirichlet regression of the models referring to Eqs. 9–12 for estimating relative biomass weight per compartment

Model (Eq.)	Compartment	α_{1c}	α_{2c}	α_{3c}	α_{4c}
(9)	Leaves	1.9256***	−0.0114		
	Branches	1.6099***	0.0029		
	Stem	3.0992***	−0.0172*		
	Roots	3.1055***	−0.0192		
(10)	Leaves	0.7599	0.0236	−0.0001	
	Branches	0.4781	0.0291*	0.0014	
	Stem	1.4185**	0.0080	0.0039	
	Roots	1.8122***	0.0289	−0.0017	
(11)	Leaves	3.3600***	−0.0211*		−0.0042***
	Branches	2.4207***	−0.0015		−0.0021**
	Stem	3.8380***	−0.0214*		−0.0018*
	Roots	4.1206***	−0.0240*		−0.0030***
(12)	Leaves	1.9813***	0.0138	0.0005	−0.0039***
	Branches	1.2295**	0.0269*	0.0010	−0.0020*
	Stem	2.2364***	0.0075	0.0027	−0.0017*
	Roots	2.6885***	0.0261	−0.0021	−0.0024**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$
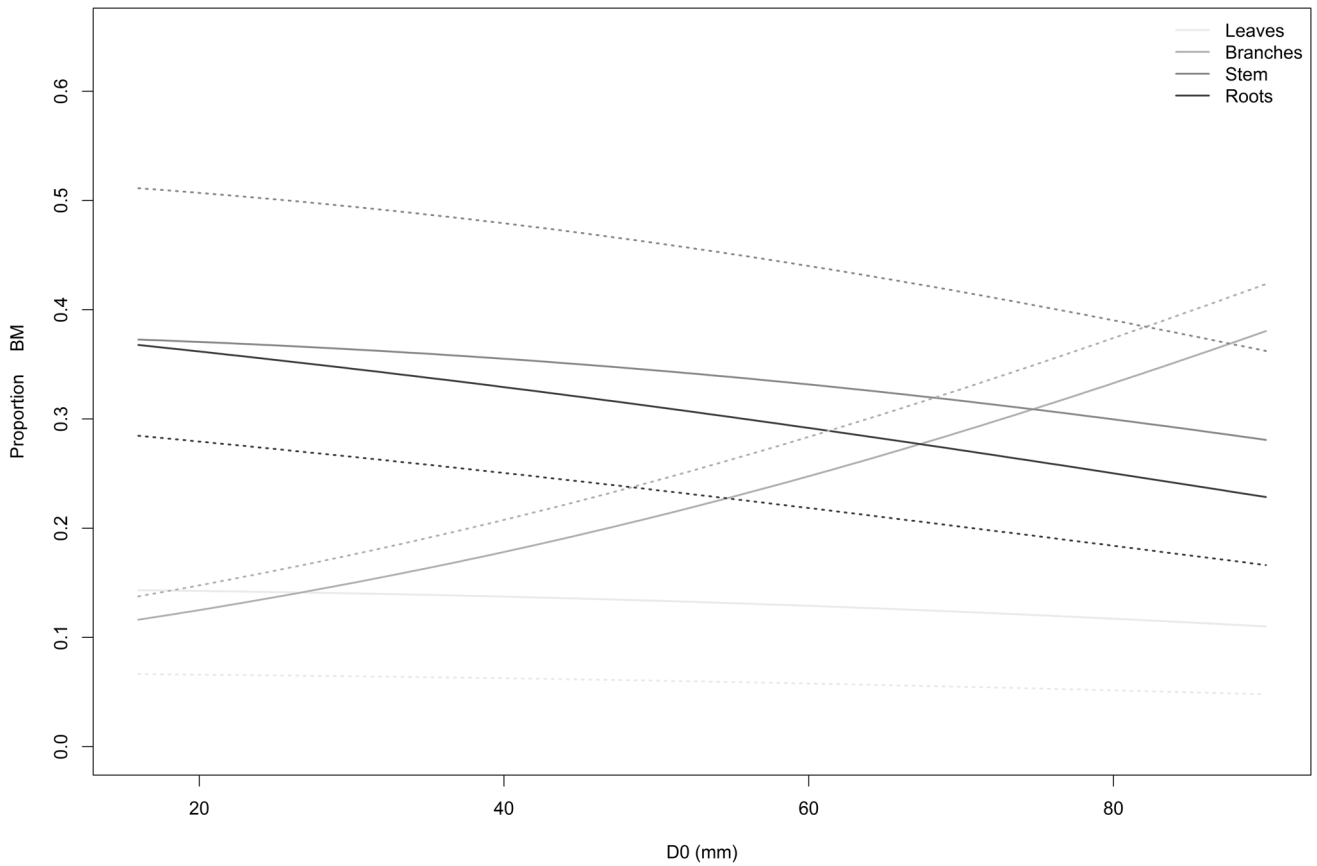
Fig. 7 Fitted values of the Dirichlet regression model (Eq. 11) considering the single biomass compartments. *Dashed line* SDI_1 value fixed at 650, *solid line* SDI_1 value fixed at 200
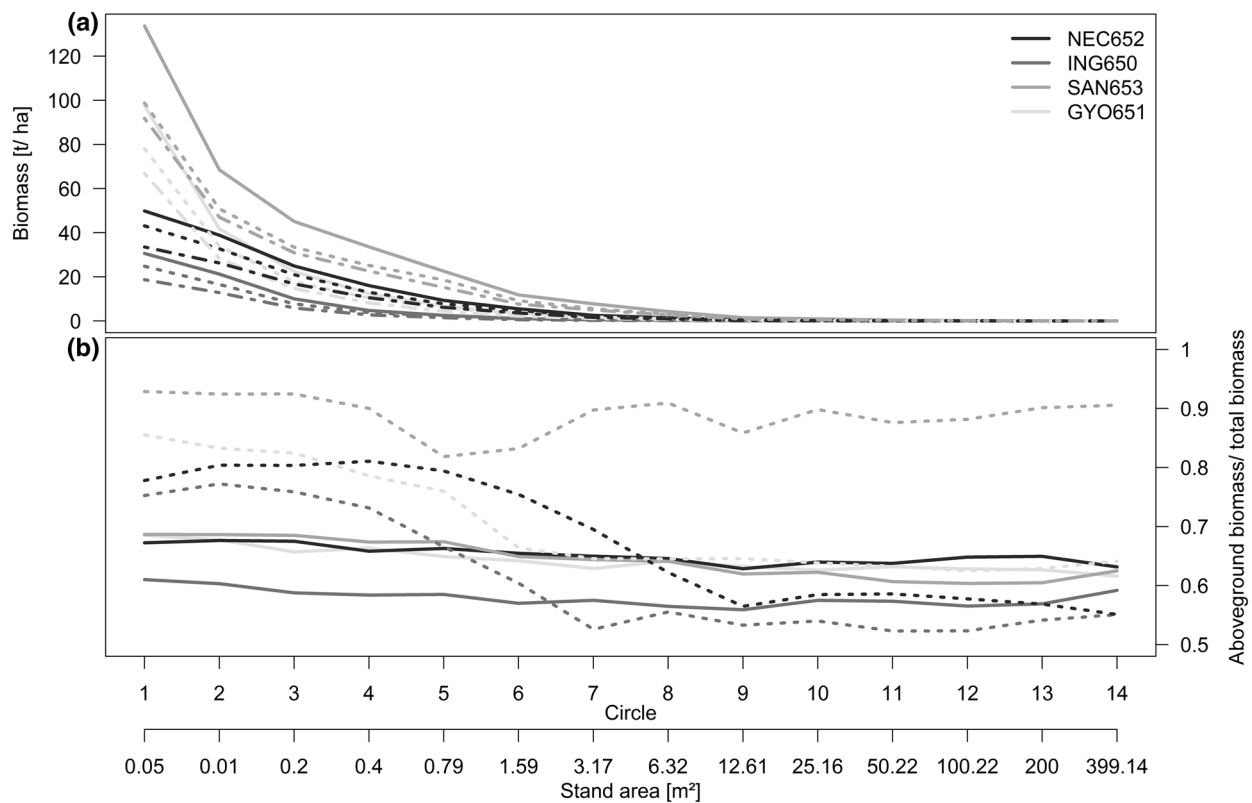
Fig. 8 Projected biomass productivity per site (**a**) and relation of aboveground to total biomass (**b**). *Solid lines* represent biomass productivity estimations using d_0 and height as predictors (model 4), *dashed lines* represent total biomass productivity estimations using d_0, height, and SDI_l as predictors (model 6) *dash-dotted lines* represent aboveground biomass productivity estimations using d_0 and height as predictors (model 4)

biomass productivity per site. The *x*-axis follows a stand density gradient using both circle number and stand area per plant as units. The most productive site is SAN652, followed by GYO651, NEC653 and finally ING650. This order indicates a trend related to the site conditions, as SAN652 and GYO651 represent the more arid sites. However, at stand densities realized from circle eight (=1582 N/ha) upwards productivity related to area is almost neglectable. Focusing on the estimation with the SDI_l, it is remarkable that for all sites the projected biomass productivity is on a lower level compared to the estimation without SDI_l. Again, the differences between the two models decrease with decreasing plant density. This might indicate an overestimation of biomass for sites with high plant density, when not considering the factor stand density. Looking at the aboveground biomass, the graph is logically on a lower level then the graphs visualizing the projected total biomass. Thereby, all three graphs seem to have a parallel course.

In more detail, the ratio of aboveground biomass to total biomass, as well as to SDI_l dependent total biomass, is depicted in Fig. 8b. Looking first at the model with d_0 and tree height, the aboveground biomass, accounts for 50–70%

of total biomass. and respectively, belowground biomass accounts for 30–50% of total biomass independent of the different stand areas. This relativizes the finding of Fig. 8a, where differences in biomass decreased with decreasing plant density. While total biomass decreases with decreasing plant density, the ratio of aboveground and belowground biomass remains constant. Considering also the SDI_l as an additional predictor for biomass, for three sites (NEC652, ING 650, GYO651) a decline can be observed after circle 4. While with little stand area per tree the belowground biomass accounts only for 10–30% of total biomass, it increases to 30–50% when the stand area per tree enlarges. Only for the site SAN653 the ratio remains constantly between 10 and 20% independent of the stand area. A visualization of the proportion of total biomass to aboveground biomass is added in the appendix (Fig. 9). Like Fig. 8b it shows that especially at low stand densities the consideration of belowground biomass is important.

Summing up, these results highlight that (1) the consideration of the root compartment is important, as it accounts for a considerable amount of total biomass, and that (2) the consideration of the plant density is important when projecting biomass productivity, as it shows a strong influence.

Discussion

Biomass equations are essential for inventory, analysis, and modeling of forest trees and stands. They allow the prediction of total plant biomass or various fractions of it (leaves, branches, roots) depending on easy-to-measure tree variables such as stem diameter or height. They mostly assume species specific but age and competition invariant allometric relationships between latter stem attributes and biomass. However, many recently published studies show that beyond species identity (Zianis et al. 2005; Pretzsch 2014) allometry can be determined by age (Genet et al. 2011), and by the spatial constellation of a tree within the stand (Bayer et al. 2013; Pretzsch 2014).

The introduced biomass equations for common oak in the early tree development phase and their derivation for a broad range of spatial constellations consider both, the dependency of intra-individual growth partitioning on size and the competitive status of trees. Our equations represent very well the age of 7–10 years. They are based on a wide range of competition status, from solitary growth (growing space of 399.14 m^2 per tree) to extremely dense stocking (0.05 m^2 per tree). To our knowledge, no existing biomass equations cover such a broad range of competitive constellations. So, their applicability goes beyond so far available equations by Zianis et al. (2005) which are mainly based on older trees and neglect the effect of neighborhood on tree allometry, which is particularly strong in case of common oak due to its phenotypic plasticity (Pretzsch 2014).

The share of the root biomass of the total tree biomass continuously decreases with increasing tree size (Pretzsch 2010). So, any constant ratios or expansion factors as applied by Burschel et al. (1993) for scaling from the aboveground to total biomass will be flawed. According to the optimal partitioning theory (McCarthy and Enquist 2007), the shape of the tree crown, root system, and the relationship between these depends highly on the resource supply of the plant (Pretzsch et al. 2012a, b). Part of the large variation in the root–shoot relationship of plants can be explained by this theory. It predicts that the limitation of a resource leads to the promotion of growth of the plant organ responsible for supplying that critical resource (Keyes and Grier 1981; Comeau and Kimmins 1989).

Our biomass functions consider these dependencies as they estimate total plant and root biomass as a function of size, growing space, and site conditions. And the statistical characteristics when deriving these relationships showed that all factors have a significant effect on the relationship between root biomass and shoot biomass even in the early phase of tree and stand development.

Predictors for biomass functions

As indicated above, most studies chose dbh and tree height as predictors for biomass. Doing so, Pajtík et al. (2008) investigated biomass estimations of young Norway spruce trees and found stem diameter as the main independent variable. The additional variable height did not show an improvement on the overall scale. We find tree height to have a significant influence on total biomass and aboveground biomass, but not on the relative compartment biomass. Regarding the dbh, Annighöfer et al. (2016) proposed to use d_0 instead of dbh in the case of young trees. In the present article, both variables were tested and it can be confirmed that d_0 is the better predictor in the case of young trees. In their study, on seedlings and saplings of European tree species, Annighöfer et al. (2016) found the best model fit for a combination of d_0 and tree height as independent variables.

In addition to these commonly chosen predictors, our approach considered the stand density and found that neglecting this factor leads to an overestimation of biomass. The results show that the SDI_l has a negative influence on biomass. This result holds for total biomass and belowground biomass, as well as for the single compartments. The finding can be confirmed by Xue et al. (2012), who also found for aboveground biomass a decrease with increasing stand density. This result is in accordance with the optimal partitioning theory, as the higher the plant density, the higher the competition for resources. Anyhow, most studies neglect this factor.

The finding that wood density is not dependent on d_0, tree height or SDI_l, can be confirmed by Bergès et al. (2000). In their study on oak trees, they came to a similar finding, concluding that wood density has only a marginal effect on biomass production change, whereas ring widths shows a strong effect. In difference, Zhao et al. (2016) reported for Loblolly pine trees an increase of wood density by raising dbh. We conclude that the small and similar-aged sampling set underlying the present article might not be useful for detecting a tendency. A greater variation in ages and sizes would be needed to accurately test the dependency of wood density on size and competition.

Dirichlet regression

Recently, several studies have used Dirichlet regression models for estimating compartment biomass (Zhao et al. 2016; Poudel and Temesgen 2016). However, these studies primarily have a methodological focus, comparing different methods for biomass estimation, while this article represents an application. Nonetheless, the usability of this method shall shortly be discussed. In general, it can be stated that for compositional data, like in the case of biomass compartments, Dirichlet regressions are superior to usual multivariate statistical methods. The main reason for this is the fact that Dirichlet regression allows simultaneous fitting of the compartment proportions, wherefore the predicted proportions add to 1 (Hijazi and Jernigan 2009; Maier 2014; Zhao et al. 2016; Poudel and Temesgen 2016). Poudel and Temesgen (2016) assume the capability to capture

the variance in proportions that sum to a constant, exhibiting skewness and heteroscedasticity, to be the reason why Dirichlet regression models outperform other methods. In their study on estimating aboveground biomass for Douglas-fir and lodgepole pine trees, they found that Dirichlet and beta regressions are the superior methods for modeling compartment biomass, compared to multinomial log-linear regressions. Zhao et al. (2016) also compared different methods which guarantee the unit sum. Using Dirichlet regression, fractional multinomial logit and log ratio regressions to model aboveground compartment biomass for loblolly pine trees, they found the Dirichlet regression to be the most adequate method. These results confirm earlier works which found that Dirichlet modeling was as successful as log ratio methods, when components have common predictors (Hijazi and Jernigan 2009). This is certainly the case for biomass estimations, where most studies assume all compartments to be primarily influenced by dbh and tree height. The results presented in this study confirm the assumption of common predictors, in our case d_0 and SDI_l. However, the main advantage of the Dirichlet regression is that, through the simultaneous fitting of the compartment proportions, it also reveals how these predictors influence the proportions of the compartments' biomass.

Compliance with ethical standards

Appendix

See Figs. 9, 10.
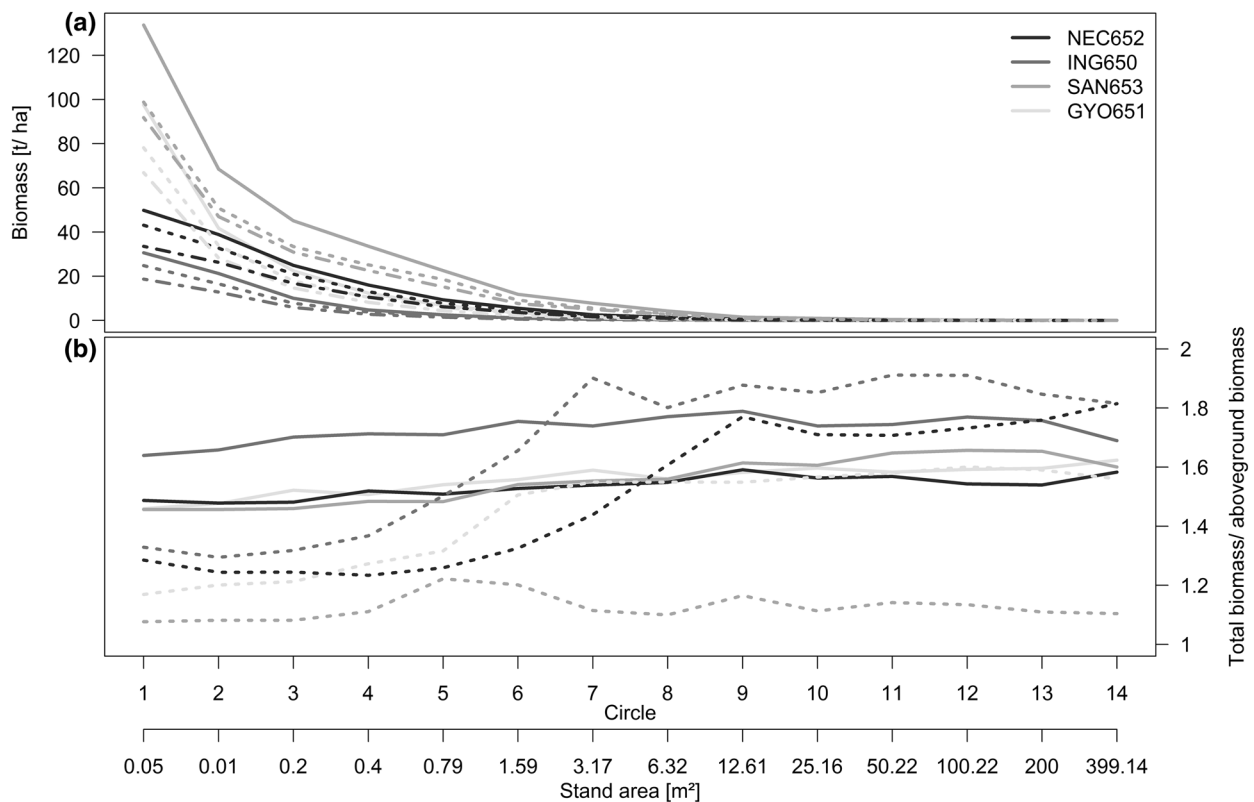
Fig. 9 Projected biomass productivity per site (**a**) and relation of total to aboveground biomass (**b**). *Solid lines* represent biomass productivity estimations using d_0 and height as predictors (model 4), *dashed lines* represent total biomass productivity estimations using d_0, height, and SDI_l as predictors (model 6) *dash-dotted lines* represent aboveground biomass productivity estimations using d_0 and height as predictors (model 4)
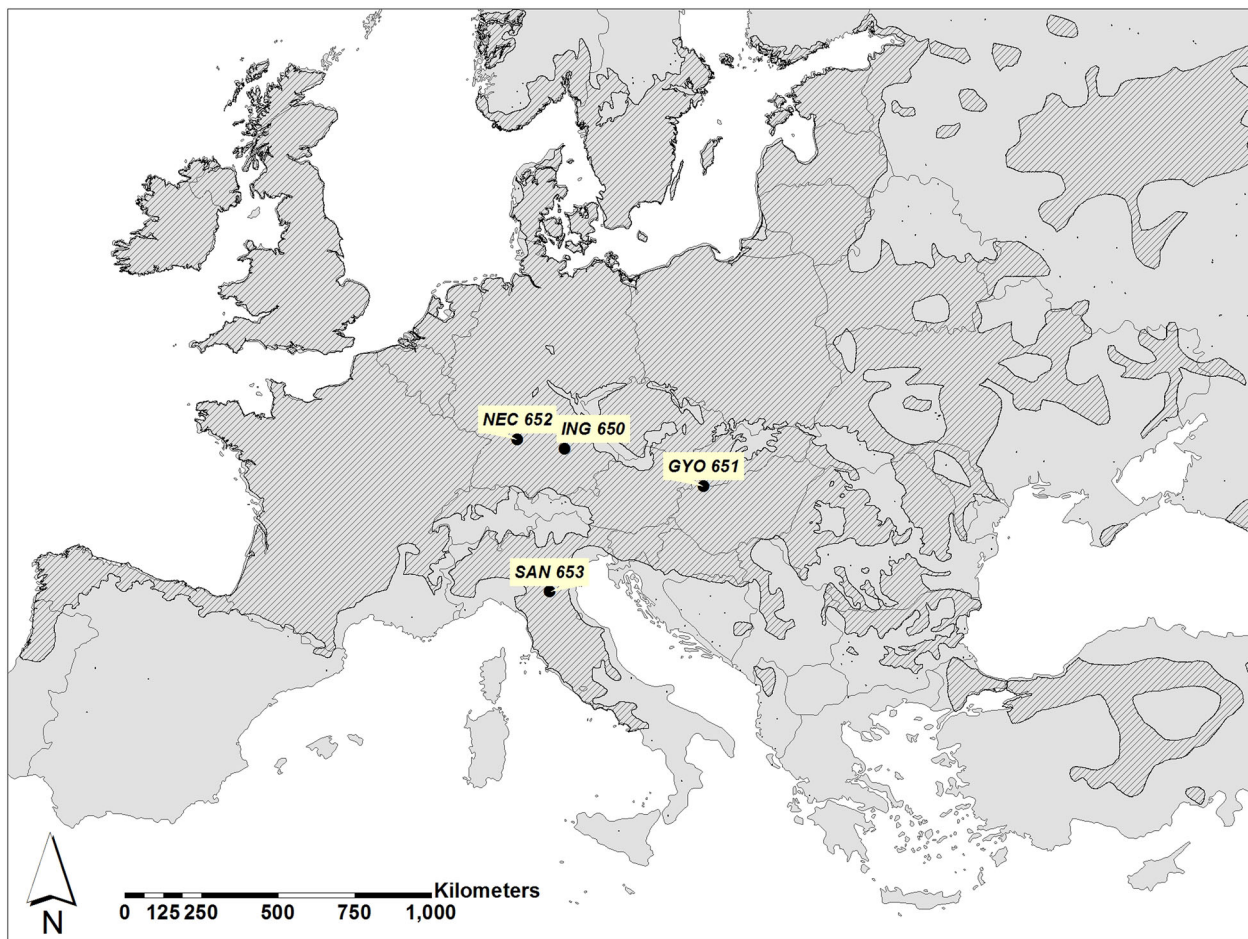
Fig. 10 Distribution of the study locations across Europe and distribution of *Q. robur* according EUFORGEN (http://www.euforgen.org)

References

Annighöfer P, Ameztegui A, Ammer C et al (2016) Species-specific and generic biomass equations for seedlings and saplings of European tree species. Eur J For Res 135:313–329. doi:10.1007/s10342-016-0937-z

Bayer D, Seifert S, Pretzsch H (2013) Structural crown properties of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in mixed versus pure stands revealed by terrestrial laser scanning. Trees 27:1035–1047. doi:10.1007/s00468-013-0854-4

Bergès L, Dupouey J-L, Franc A (2000) Long-term changes in wood density and radial growth of *Quercus petraea* Liebl. in northern France since the middle of the nineteenth century. Trees 14:398–408. doi:10.1007/s004680000055

Burschel P, Kürsten E, Larson BC (1993) Die Rolle von Wald und Forstwirtschaft im Kohlenstoffhaushalt. Eine Betrachtung fuer die Bundesrepublik Deutschland

Chojnacky DC, Heath LS, Jenkins JC (2014) Updated generalized biomass equations for North American tree species. Forestry 87:129–151. doi:10.1093/forestry/cpt053

Cienciala E, Apltauer J, Exnerová Z, Tatarinov F (2008) Biomass functions applicable to oak trees grown in Central-European forestry. J For Sci 54:109–120

Comeau PG, Kimmins JP (1989) Above-and below-ground biomass and production of lodgepole pine on sites with differing soil moisture regimes. Can J For Res 19:447–454

Core Team R (2015) A language and environment for statistical computing; 2013. R Foundation for Statistical Computing, Vienna

Cotillas M, Espelta JM, Sánchez-Costa E, Sabaté S (2016) Above-ground and belowground biomass allocation patterns in two Mediterranean oaks with contrasting leaf habit: an insight into carbon stock in young oak coppices. Eur J For Res 135:243–252. doi:10.1007/s10342-015-0932-9

de Martonne E (1926) L'indice d'aridité. Bull Assoc Géographes Fr 3:3–5. doi:10.3406/bagf.1926.6321

Genet A, Wernsdörfer H, Jonard M et al (2011) Ontogeny partly explains the apparent heterogeneity of published biomass equations for *Fagus sylvatica* in central Europe. For Ecol Manag 261:1188–1202. doi:10.1016/j.foreco.2010.12.034

Hijazi RH, Jernigan RW (2009) Modelling compositional data using Dirichlet regression models. J Appl Probab Stat 4:77–91

Kawaletz H, Molder I, Zerbe S et al (2013) Exotic tree seedlings are much more competitive than natives but show underyielding when growing together. J Plant Ecol 6:305–315. doi:10.1093/jpe/rts044

Keyes MR, Grier CC (1981) Above-and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Can J For Res 11:599–605

Kuehne C, Kublin E, Pyttel P, Bauhus J (2013) Growth and form of *Quercus robur* and *Fraxinus excelsior* respond distinctly different to initial growing space: results from 24-year-old Nelder experiments. J For Res 24:1–14. doi:10.1007/s11676-013-0320-6

Kuznetsova T, Tilk M, Pärn H et al (2011) Growth, aboveground biomass, and nutrient concentration of young Scots pine and lodgepole pine in oil shale post-mining landscapes in Estonia. Environ Monit Assess 183:341–350. doi:10.1007/s10661-011-1925-x

Lindner M, Maroschek M, Netherer S et al (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For Ecol Manag 259:698–709. doi:10.1016/j.foreco.2009.09.023

Lu D, Mausel P, Brondizio E, Moran E (2002) Above-ground biomass estimation of successional and mature forests using TM images in the amazon basin. In: Richardson DE, van Oosterom P (eds) Advances in spatial data handling: 10th international symposium on spatial data handling. Springer, Berlin, Heidelberg, pp 183–196

Maier M (2014) DirichletReg: Dirichlet regression for compositional data in R. Department of Statistics and Mathematics, WU Vienna University of Economics and Business, Vienna

McCarthy MC, Enquist BJ (2007) Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. Funct Ecol 21:713–720. doi:10.1111/j.1365-2435.2007.01276.x

Nelder JA (1962) New kinds of systematic designs for spacing experiments. Biometrics 18:283. doi:10.2307/2527473

Pajtík J, Konôpka B, Lukac M (2008) Biomass functions and expansion factors in young Norway spruce (*Picea abies* [L.] Karst) trees. For Ecol Manag 256:1096–1103. doi:10.1016/j.foreco.2008.06.013

Pilli R, Anfodillo T, Carrer M (2006) Towards a functional and simplified allometry for estimating forest biomass. For Ecol Manag 237:583–593. doi:10.1016/j.foreco.2006.10.004

Poudel KP, Temesgen H (2016) Methods for estimating aboveground biomass and its components for Douglas-fir and lodgepole pine trees. Can J For Res 46:77–87. doi:10.1139/cjfr-2015-0256

Pretzsch H (2010) Re-evaluation of allometry: state-of-the-art and perspective regarding individuals and stands of woody plants. In: Lüttge U, Beyschlag W, Büdel B, Francis D (eds) Progress in botany 71. Springer, Berlin, Heidelberg, pp 339–369

Pretzsch H (2014) Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. For Ecol Manag 327:251–264. doi:10.1016/j.foreco.2014.04.027

Pretzsch H, Biber P (2010) Size-symmetric versus size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in central Europe.pdf. Can J For Res 40:370–384. doi:10.1139/D09-195

Pretzsch H, Biber P, Uhl E, Hense P (2012a) Coarse root–shoot allometry of *Pinus radiata* modified by site conditions in the Western Cape province of South Africa. South For J For Sci 74:237–246. doi:10.2989/20702620.2012.741794

Pretzsch H, Uhl E, Biber P et al (2012b) Change of allometry between coarse root and shoot of Lodgepole pine (*Pinus contorta* DOUGL. ex. LOUD) along a stress gradient in the sub-boreal forest zone of British Columbia. Scand J For Res 27:532–544

Reineke LH (1933) Perfecting a stand-density index for even-aged forests. J Agric Res 46:627–638

Ruiz-Peinado C-I, del Rio C-I, Montero C-I et al (2011) New models for estimating the carbon sink capacity of Spanish softwood species. Forest Syst 20:176–188. doi:10.5424/fs/2011201-11643

Snell O (1892) Die Abhängigkeit des Hirngewichtes von dem Körpergewicht und den geistigen Fähigkeiten. Eur Arch Psychiatry Clin Neurosci 23:436–446

Uhl E, Biber P, Ulbricht M et al (2015) Analysing the effect of stand density and site conditions on structure and growth of oak species using Nelder trials along an environmental gradient: experimental design, evaluation methods, and results. For Ecosyst. doi:10.1186/s40663-015-0041-8

Vejpustková M, Zahradník D, Čihák T, Šrámek V (2015) Models for predicting aboveground biomass of European beech (*Fagus sylvatica* L.) in the Czech Republic. J For Sci 61:45–54. doi:10.17221/100/2014-JFS

Wirth C, Schumacher J, Schulze E-D (2004) Generic biomass functions for Norway spruce in Central Europe—a meta-analysis approach toward prediction and uncertainty estimation. Tree Physiol 24:121–139

Xue L, Jacobs DF, Zeng S et al (2012) Relationship between aboveground biomass allocation and stand density index in *Populus × euramericana* stands. Forestry 85:611–619. doi:10.1093/forestry/cps071

Zhao D, Kane M, Teskey R, Markewitz D (2016) Modeling aboveground biomass components and volume-to-weight conversion ratios for loblolly pine trees. For Sci 62:463–473. doi:10.5849/forsci.15-129

Zianis D, Suomen Metsätieteellinen Seura, Metsäntutkimuslaitos (eds) (2005) Biomass and stem volume equations for tree species in Europe. Finnish Society of Forest Science, Finnish Forest Research Institute, Helsinki