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Species-specific and generic biomass equations for seedlings and saplings of European tree species

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Abstract Biomass equations are a helpful tool to estimate the tree and stand biomass production and standing stock. Such estimations are of great interest for science but also of great importance for global reports on the carbon cycle and the global climate system. Even though there are various collections and generic meta-analyses available with biomass equations for mature trees, reports on biomass equations for juvenile trees (seedlings and saplings) are mainly missing. Against the background of an increasing amount of reforestation and afforestation projects and forests in young successional stages, such equations are required. In this study we have collected data

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from various studies on the aboveground woody biomass of 19 common tree species growing in Europe. The aim of this paper was to calculate species-specific biomass equations for the aboveground woody biomass of single trees in dependence of root-collar-diameter (RCD), height (H) and the combination of the two (RCD^2 H). Next to calculating species-specific biomass equations for the species available in the dataset, we also calculated generic biomass equations for all broadleaved species and all conifer species. The biomass equations should be a contribution to the pool of published biomass equations, whereas the novelty is here that the equations were exclusively derived for young trees.

Introduction

Assessing forest productivity has a long tradition in forestry and forest ecosystem science. During the last four decades, the interest in forest productivity has shifted from focusing on tree and stand timber production to tree and stand biomass production, below and above ground, differentiated for all tree compartments (Parresol 1999). A precise estimate of tree and forest biomass is of interest to many disciplines of forest, ecosystem and climate change research, ranging from population ecology to remote sensing and terrestrial ecosystem modeling, as well as to forest managers (Jenkins et al. 2003). Particularly, it continues to be of increasing importance in recognition of the role forest ecosystems have in the carbon cycle and the global climate system and also in compliance with the second commitment period of the Kyoto Protocol (IPCC 2013), since forests can be important carbon sinks and sources (Dixon et al. 1994; Valentini et al. 2000). Direct

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biomass measurements in the field are very complex, laborious and time consuming (Sah et al. 2004). Therefore, the use of relationships between tree biomass and tree parameters that can easily be measured, mainly tree diameter at breast height (DBH) and/or tree height (H) are the most common approach for estimating individual tree biomass (e.g., Annighöfer et al. 2012; Chave et al. 2001; Djomo et al. 2010). There are several collections and generic meta-analyses available for the latter approach resulting in species-specific biomass equations (e.g., Falster et al. 2015; Jenkins et al. 2003; Rojas-García et al. 2015; Ter-Mikaelian and Korzukhin 1997; Wirth et al. 2004; Zianis et al. 2005). However, most published biomass equations focus on larger trees (DBH ≥ 10 cm). Recently, biomass equations for shrub species and understory trees were published (e.g., Berner et al. 2015; Sah et al. 2004). Publications with species-specific biomass equations for juvenile trees (seedlings and saplings) are rare (e.g., Bartelink 1997; Chroust 1985; Pajtík et al. 2008; Pilli et al. 2006; Wirth et al. 2004). This may be due to their low individual tree size which is far below merchantable wood dimensions and even the sum of their biomass is believed to account only for a small fraction of total stand biomass and associated carbon stocks in forests (Brown 2002; Chave et al. 2001). Accurate biomass estimates for seedlings and saplings are nevertheless required for the increasing amount of afforestation and reforestation sites, young successional forests as a result of disturbances, shelterwood systems, uneven-aged stands, and open woodland forests (e.g., Schroeder et al. 1997) and the modeling of their future development. In particular, accurate estimates of seedling and sapling biomass are of central importance to understand and predict the dynamics in the carbon cycling of forests (Galik et al. 2009; Gonzalez-Benecke et al. 2014a).

Allometric-based biomass estimations are an improvement over several other alternative methods. In Germany, a non-destructive estimation of the understory biomass ("PhytoCalc") was repeatedly applied, which, however, does not directly allow estimating the biomass of single individuals in the regeneration layer (Bolte et al. 2009; Heinrichs et al. 2010). Norgren et al. (1995) proposed a similar non-destructive approach for estimating seedling and sapling biomass, using the projection area of a plant canopy as explanatory variable for biomass in a computer-based image analysis.

The aim of this paper is to generate species-specific and generic equations for aboveground woody biomass of single trees in dependence of root-collar-diameter (RCD) and height (H) of seedlings and saplings growing under more or less common growth conditions in Europe. The respective database includes original data from 6 European countries and 27 explorative or experimental studies and

represents 19 tree species, 15 species native to Europe and 4 non-native species.

Materials and methods

Data collection and processing

The collected dataset consists of 27 single original datasets on biomass, diameter and partly height of seedlings and saplings of European tree species that were directly made available by their authors (Appendix 1). The final dataset consisted of 4468 single recordings of 19 tree species occurring in Europe (Table 1) of which 5 species were conifers ($n = 961$ single observations) and 14 species broadleaves ($n = 3507$).

Data compilation was restricted to the European continent (Fig. 1). Most data originated from Germany, followed by data from France and Spain.

All recordings consisted of at least one diameter measurement paired with a biomass measurement. Here, only

aboveground biomass (AGB) measurements were considered. Data for belowground biomass are also already included in the database but up to now; they are not sufficient for the development of generalized, species-specific equations. A total of 1827 recordings measured AGB separately with (total AGB) and without leaves and needles (woody AGB). A total of 2345 recordings only measured woody AGB and 296 only measured total AGB. To standardize measurements to wood AGB, the total AGB measurements ($n = 216$ broadleaves, $n = 80$ conifers) were converted to woody AGB by using the records consisting of both biomass measurements and applying local polynomial regression fitting [function "loess" in R (R Development Core Team 2013) package "stats" (Cleveland et al. 1992)] separately for each tree type (conifer, broadleaf).

As diameter measurement, most datasets provided RCD or the diameter at stem base. However, some datasets used other diameter measurements (diameter at 5, 10, 50, 130 cm above ground). To convert all diameter measurements to RCD, correction factors were derived for conifer and broadleaf species from datasets consisting of several

Table 1 Summary of plot characteristics and database for each species

Species	S	n	CNY	ASL (m)	AGB (g)	Database
Abies alba	C	58	DE ES	794 (235–1906)	544 (0–9949)	AME2013 DIR2010 HAM2014 KAE2006
Acer pseudoplatanus	B	22	DE FR	411 (171–1110)	950 (1–13100)	CAQ2010 GEB2013 KAE2006 KUE2014 SEE2011 SLO2003 WAK2009
Betula pendula	B	3	DE ES	1510 (325–1906)	190 (0–5224)	AME2013 MUE2014 SLO2003
Carpinus betulus	B	3	DE	224 (220–400)	52 (0–265)	KAW2013 KUE2014 SLO2003
Fagus sylvatica	B	70	CZ DE FR	455 (173–1184)	670 (0–16200)	AMM2003 BAL2007 BAL2009 CAQ2010 DIR2010 GEB2013 GEL2001 HIR2011 HOF2008 KAE2006 LIN2014 MUE2014 PRO2008 SCH2012 SEE2011 SLO2003 WAK2009
Fraxinus excelsior	B	20	DE	442 (110–717)	1393 (3–19600)	GEB2013 KAE2006 SEE2011 SLO2003 WAK2009
Picea abies	C	53	CZ DE	425 (218–1227)	862 (2–12777)	DIR2010 KAE2006 SCH2012
Pinus sylvestris	C	5	DE ES	1077 (110–1906)	815 (0–10189)	AME2013 KAE2006 MUE2014 SLO2003
Pinus uncinata	C	1	ES	1906 (1906–1906)	1 (0–4)	AME2013
Prunus avium	B	1	DE	400 (400–400)	1189 (7–5617)	SLO2003 WAK2009
Prunus serotina	B	2	DE IT	207 (142–220)	821 (36–20348)	ANN2012 KAW2013
Pseudotsuga menziesii	C	2	DE	537 (444–630)	468 (27–1747)	KUE2011
Quercus petraea	B	5	DE FR	245 (110–412)	76 (0–2535)	BAL2011 COL1996 COL2006 SLO2003 WAK2009
Quercus robur	B	12	DE SE	270 (90–493)	228 (1–8850)	AMM2003 KAE2006 KAW2013 KUE2014 LOE2006
Quercus rubra	B	1	DE	238 (238–238)	29 (8–70)	KUE2014
Robinia pseudoacacia	B	1	DE	220 (220–220)	176 (6–499)	KAW2013
Salix spec	B	1	DE	325 (325–325)	1605 (22–6486)	MUE2014
Sorbus aucuparia	B	35	CZ DE	906 (400–1190)	33 (1–159)	DIR2010 SLO2003
Tilia cordata	B	1	DE	400 (400–400)	387 (2–1403)	MUE2014 SLO2003 WAK2009

S, species type (B, broadleaf; C, conifer); n, number of plots; CNY, Country; ASL, plot height above sea level (m); AGB, aboveground biomass excluding leaves and needles (g). ASL and AGB are presented as mean values with minimum and maximum values in brackets. Abbreviations of Database refer to Appendix 1
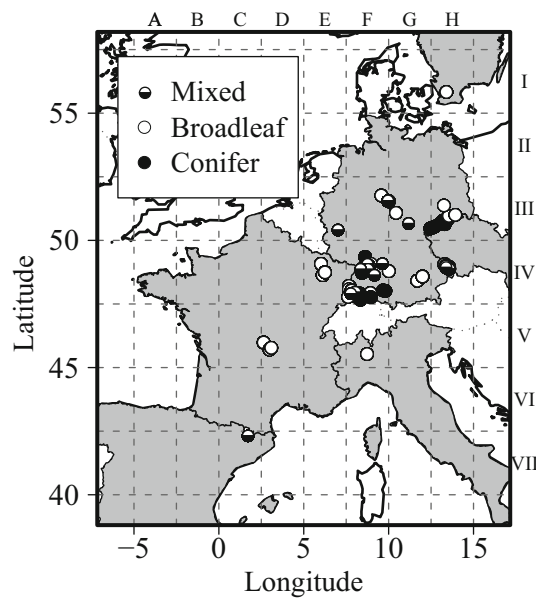
Fig. 1 Map of data source locations. Plots are distinguished according to the tree species types ('Mixed' = sites with broadleaf and coniferous species; 'Broadleaf' = sites with broadleaf species; 'Conifer' = sites with coniferous species). Countries where data were collected are shaded gray

diameter measurements for both tree types (data mainly from KAE2006, compare Appendix 1). Mean values for transformation were derived from the relative diameter changes in the different height classes (compare Fig. 2).

Diameter measurements were transformed to RCD using:

$$RCD = T_x D_x \tag{1}$$

with RCD = root-collar-diameter (mm); T_x = transformation factor for diameter measurements × cm above ground (broadleaf species: $T_5 = 1.08$; $T_{10} = 1.16$; $T_{50} = 1.33$; $T_{130} = 1.45$ and conifer species $T_5 = 1.06$; $T_{10} = 1.13$; $T_{50} = 1.29$; $T_{130} = 1.45$); $T_x = 1/rD$; rD = relative diameter change (Fig. 2); D_x = diameter measured × cm above ground.

Biomass allometries and statistical analysis

The biomass equations presented in this paper hold for aboveground parts of seedlings and saplings excluding leaves and needles. For each species and species type (broadleaf, conifer), we developed allometric equations relating RCD (in mm), H (in cm) and the factor $RCD^2 H$ (in cm³) to biomass. The mathematical model most commonly used for biomass prediction takes the form of Snell's (1892) power equation $y = \beta1 \, x^{\beta2}$ (Kaitaniemi 2004; Zianis et al. 2005; Zianis and Mencuccini 2004).

Biomass data mostly exhibits heteroscedasticity (Parresol 2001), which is an error variance that is not constant over all observations. For this reason, the nonlinear power equation is often linearized to homogenize variance by logarithmic transformation of both dependent and independent variables (ln $y = \ln \beta1 + \beta2 \ln x$) to allow fitting a linear regression to the data (e.g., Bjarnadottir et al. 2007; Pilli et al. 2006; Sah et al. 2004). It is broadly accepted that this transformation results in a systematic bias. Currently, this bias is being corrected for in several ways by estimating a correction factor from the standard error (e.g., Baskerville 1972; Beauchamp and Olson 1973; Madgwick and Satoo 1975, 1975; Parresol 1999; Sprugel 1983; Yandle and Wiant 1981), although no standard correction has been proposed yet (Cienciala et al. 2008).

As an alternative to fitting a linear model to log-transformed measurements, we used nonlinear least square regressions (function "nls" in R package "stats" (Bates and Chambers 1992)) to fit power equations to the data and obtain estimates for the coefficients $\beta1$ and $\beta2$:

$$AGB = \beta1 \, RCD^{\beta2} \tag{2}$$

$$AGB = \beta1 \, H^{\beta2} \tag{3}$$

$$AGB = \beta1 \left(RCD^2 H\right)^{\beta2} \tag{4}$$

with AGB = aboveground biomass (g); RCD = root-collar-diameter (mm); H = height (cm); the factor $RCD^2 H$ (cm³); and $\beta1$ and $\beta2$ = fitted coefficients.

The heteroscedasticity of the data made a weighted analysis necessary (Bates and Watts 1988), to achieve minimum variance parameter estimates (Parresol 2001). Following Berner et al. (2015), data were weighted by $y^{-0.5}$ to correct for non-random residuals and the tendency of over-predicting AGB of small trees (compare Carroll and Ruppert 1988; Huang et al. 1992). However, to make our data as comparable as possible to other studies, we also fit models to logarithmically transformed data [function "lm" in R package "stats" (Chambers 1992)]. We estimated coefficients $\beta1$ and $\beta2$ in dependence of RCD, H and RCD^2 H (in cm³), since this still is a standard method when dealing with biomass data (Zianis and Mencuccini 2004) (Appendixes 2, 3, 4):

$$\ln(AGB) = \ln(\beta1) + \beta2 \ln(RCD) \tag{5}$$

$$\ln(AGB) = \ln(\beta1) + \beta2 \ln(H) \tag{6}$$

$$\ln(AGB) = \ln(\beta1) + \beta2 \ln\left(RCD^2 H\right) \tag{7}$$

with ln = natural logarithm; AGB = aboveground biomass (g); RCD = root-collar-diameter (mm); H = height (cm); the factor $RCD^2 H$ (cm³); and $\beta1$ and $\beta2$ = fitted coefficients.

Fig. 2 Relative diameter change (rD) in dependence of stem height (H) where diameter was measured for broadleaf (**a**) and coniferous (**b**) species. The height (H) value of 0 refers to the root-collar-diameter (RCD) measurements
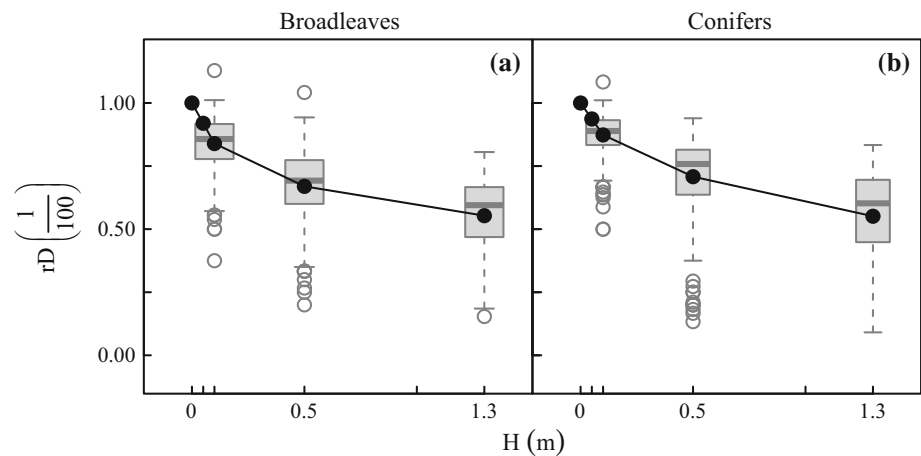
These logarithmically transformed models were back-transformed by multiplying the anti-log of the intercept with the first-order correction factor suggested by Sprugel (1983):

$$CF = \exp\left(SEE^2/2\right) \qquad (8)$$

with CF = correction factor; SEE = standard error of the estimate based on natural logarithms.

Aside of estimating the coefficients $\beta1$ and $\beta2$ for each biomass model, we additionally calculated standard errors of the regression coefficients [allowing model uncertainty to be propagated into subsequent analyses (Berner et al. 2015)], p values of the coefficients, coefficients of Pearson's correlation between observed and fitted values, and root-mean-squared-error of the nonlinear models for model evaluation. Residuals scatter was evaluated by calculating a coefficient of determination for the residuals in dependence of 20 RCD-classes. Residuals should be evenly distributed around zero throughout the classes, so should coefficient of determination values. Biomass equations were calculated separately for each species, and generic biomass equations were calculated for all broadleaf and conifer species each. Confidence intervals were calculated for the coefficients of the nonlinear regression models, giving lower (2.5 %) and upper (97.5 %) confidence limits for each coefficient [function "confint2" in R package "nlstools" (Baty and Delignette-Muller 2015)].

All statistical analyses, model fitting, and graphs were processed using the free software environment R, version 3.1.0 (R Development Core Team 2013).

Results

The RCD range for most species was close to 100 mm, with some exceptions. Data on *Pinus uncinata* had the smallest diameter range of 3.4 mm, with a maximum diameter of

only 6.3 mm, followed by *Quercus rubra* with a range of 12.2 mm and a maximum diameter of around 18 mm. *Carpinus betulus*, *Pseudotsuga menziesii*, and *Sorbus aucuparia* had small diameter ranges as well as low maximum diameters (Table 2). The height of the species ranged from as small as 4 cm (*Sorbus aucuparia*) up more than 1000 cm for *Acer pseudoplatanus* (1030 cm), *Fagus sylvatica* (1160 cm), and *Fraxinus excelsior* (1210 cm). For most species, individuals with maximum heights of at least 200 cm were recorded, with *Pinus uncinata* (max. 29 cm), *Quercus rubra* (max. 120 cm) and *Carpinus betulus* (max. 170 cm) being the exceptions. Height ranges were around 200–300 cm for *Prunus avium*, *Pseudotsuga menziesii*, and *Tilia cordata*. Most other species were well represented with height ranges of around 400 cm and far more (Table 3).

RCD, *H* and the product of both (RCD^2 H) were significant predictors for the AGB of each species and in the generic biomass equations ($p < 0.001$). Biomass equations based on RCD as the predictor mainly resulted in correlations between observed and fitted values greater than 0.9, with a mean value of 0.94 (±one standard deviation of 0.06). Lower correlations based on RCD were only found for *Carpinus betulus* (0.88), *Pinus unicata* (0.77), and *Robinia pseudoacacia* (0.82) (Table 2). The correlations based on *H* as predictor was slightly lower, with a mean value of 0.83 (±0.13). All species had correlations above 0.7 with a maximal value of 0.96 for *Betula pendula*. *Quercus rubra* formed the only exception with a correlation value of only 0.43 (Table 3) based on *H* as predictor value. Biomass equations based on RCD^2 H also mainly resulted in correlations greater than 0.9, with a mean value of 0.95 (±0.05) (Table 4). Again *Pinus unicata* (0.84) and *Robinia pseudoacacia* (0.85) formed the exceptions. Predictions based on RCD resulted in a lower RSME of the fitted values (mean = 296 ± 344 g) compared to *H* as predictor (mean = 507 ± 447 g), whereas lowest values were derived for RCD^2 H (mean = 241 ± 245 g) (Tables 2, 3, 4).

Table 2 Parameters of the biomass equations, estimating aboveground biomass (AGB) in g dry weight from the predictor variable root-collar-diameter (RCD)

Species	n	RCD range (mm)	β1	β2	se (β1)	se (β2)	p (β1)	p (β2)	Corr	RMSE (g)	R^2_{res}
Abies alba	399	1–99 (13.8)	0.169	2.402	0.031	0.043	<0.001	<0.001	0.97	373.7	0.040
Acer pseudoplatanus	215	4–100 (21.2)	0.025	2.849	0.012	0.113	<0.05	<0.001	0.94	843.4	0.031
Betula pendula	63	3–107 (10.9)	0.259	2.132	0.046	0.04	<0.001	<0.001	0.994	80.5	0.002
Carpinus betulus	316	3–28 (13.9)	0.068	2.41	0.017	0.082	<0.001	<0.001	0.878	24	0.002
Fagus sylvatica	1230	1–114 (18.5)	0.113	2.518	0.012	0.024	<0.001	<0.001	0.962	567.3	0.150
Fraxinus excelsior	165	5–95 (25.8)	0.015	3.004	0.011	0.173	0.19	<0.001	0.923	1314.2	0.109
Picea abies	368	3–118 (23.9)	0.202	2.329	0.041	0.046	<0.001	<0.001	0.952	616.9	0.014
Pinus sylvestris	100	3–95 (23.2)	0.015	2.881	0.007	0.114	<0.05	<0.001	0.972	416.9	0.003
Pinus uncinata	46	3–6 (4.2)	0.063	2.076	0.027	0.276	<0.05	<0.001	0.771	0.5	0.030
Prunus avium	12	7–100 (38.6)	0.115	2.33	0.091	0.179	0.24	<0.001	0.988	250.4	0
Prunus serotina	211	12–100 (27.8)	0.02	2.962	0.003	0.038	<0.001	<0.001	0.981	427.7	0.004
Pseudotsuga menziesii	48	10–52 (25.6)	0.218	2.269	0.076	0.094	<0.05	<0.001	0.976	103.8	0.008
Quercus petraea	470	2–70 (15.6)	0.011	2.788	0.003	0.083	<0.05	<0.001	0.876	119.1	0.218
Quercus robur	502	3–100 (13.9)	0.027	2.769	0.003	0.029	<0.001	<0.001	0.986	175.2	0.130
Quercus rubra	15	6–18 (12.3)	0.056	2.421	0.045	0.298	0.24	<0.001	0.95	5.7	0.005
Robinia pseudoacacia	238	7–39 (21.2)	0.414	1.942	0.122	0.091	<0.05	<0.001	0.821	65.2	0.191
Salix spec.	10	10–91 (42.4)	0.063	2.562	0.028	0.102	0.05	<0.001	0.998	137.6	0.002
Sorbus aucuparia	45	3–29 (11.6)	0.143	2.064	0.064	0.148	<0.05	<0.001	0.922	14.9	0.014
Tilia cordata	15	6–65 (33.3)	0.006	2.952	0.007	0.303	0.43	<0.001	0.978	90.1	0

All biomass equations took the form of power equations (Eq. 2). *n*, number of observations for each species (in total = 4468 single observations); RCD range, diameter range of measured trees (mm), value in brackets stands for mean RCD; β1 and β2, estimated model coefficients; se, standard error of the regression coefficients; *p*, significance values of coefficients; corr, correlation between observation and fit; RMSE, root-mean-squared-error of fit; R^2_{res}, coefficient of determination of residuals

The coefficient of determination R^2_{res} for the residuals (R^2_{res}) showed a scatter around zero for equations based on RCD (mean = 0.05) and the factor $RCD^2 H$ (mean = 0.07). For the equations based on *H*, the scatter was around 0.43, indicating that the residuals were not evenly distributed around zero with *H* as predictor variable and showed a trend to increase with height (Tables 2, 3, 4).

The estimated coefficient β1 ranged from 0.006 (*Tilia cordata*) to 0.4 (*Robinia pseudoacacia*) for models based on RCD and was considerably smaller for the models based on *H* as predictor, ranging from 0 (*Betula pendula*, *Prunus avium*) to 0.08 (*Picea abies*) (Tables 2, 3). Coefficient β2 was evenly distributed around 2.5 for RCD models with a maximal value of 3.004 (*Fraxinus excelsior*) and a minimal value of 1.94 (*Robinia pseudoacacia*) (Table 2). Also for the *H* models, coefficient β2 was evenly distributed around 2.2 for most species, but three species showed β2 values out of the ordinary. Data for *Betula pendula*, *Prunus avium* and *Salix* spec. resulted in estimates for β2 that were around 5, 4, and 3 (Table 3), resulting in atypical curves with a pronounced slope for these species in comparison with the other curves.

Irrespective of the predictor variable (RCD, *H* or RCD^2 H), coefficients β1 and β2 showed a negative

correlation, for small values of β1 (RCD: β1 < 0.1, correlation = −0.88; H: β1 < 0.01, correlation = −0.46; RCD^2 H: β1 < 1, correlation = −0.87), as also observed by Pilli et al. (2006) and Zianis and Mencuccini (2004).

Due to the considerable variety of single species observations, the significance of the estimated coefficients (β1, β2) differed among the species (Tables 2, 3, 4). With RCD and RCD^2 H as predictor, all estimators for coefficient β2 were significant and also most estimations of coefficient β1 (*n* = 14, *n* = 16, respectively). Coefficient β1 was particularly not significantly different from zero for species with small numbers of observations (e.g., *Prunus avium*, *Quercus rubra*, *Tilia cordata*), with *Fraxinus excelsior* forming an exception (Tables 2, 4). With *H* as predictor, also all estimators for coefficient β2 were significant, aside of the estimations for *Quercus rubra*, where both coefficients were not significant (Table 3). However, most estimations of coefficient β1 were not significantly different from zero (*n* = 14), whereby the coefficients β1 were very small and close to zero in the first place for the *H* models.

For generic biomass equations, the original data were aggregated into conifer species and broadleaf species and analyzed with respect to the same predictor variables as the species-specific data (Fig. 3a–f). Resulting generic biomass

Table 3 Parameters of the biomass equations, estimating aboveground biomass (AGB) in g dry weight from the predictor variable height (H)

Species	n	H range (cm)	$\beta1$	$\beta2$	se ($\beta1$)	se ($\beta2$)	p ($\beta1$)	p ($\beta2$)	Corr	RMSE (g)	R^2_{res}
Abies alba	399	6–590 (75.3)	0.03118	1.961	0.011	0.059	<0.05	<0.001	0.917	616.1	0.526
Acer pseudoplatanus	175	18–1030 (232)	0.00165	2.26095	0.001	0.1	0.14	<0.001	0.926	1020.7	0.381
Betula pendula	63	22–470 (92)	0	5.34214	0	0.344	0.64	<0.001	0.958	221.7	0.147
Carpinus betulus	316	16–170 (80.2)	0.02147	1.70301	0.013	0.131	0.1	<0.001	0.715	37.4	0.837
Fagus sylvatica	1190	8–1160 (167.1)	0.00135	2.31682	0	0.038	<0.001	<0.001	0.887	987.7	0.375
Fraxinus excelsior	165	23–1213 (241.3)	0.00158	2.28364	0.001	0.094	0.12	<0.001	0.932	1224.6	0.292
Picea abies	368	20–730 (118.7)	0.08422	1.78966	0.024	0.046	<0.001	<0.001	0.894	904.5	0.397
Pinus sylvestris	100	10–720 (124.9)	0.02022	1.9891	0.014	0.116	0.16	<0.001	0.897	793.3	0.445
Pinus uncinata	46	16–29 (21.1)	0.00073	2.43282	0.001	0.337	0.35	<0.001	0.733	0.5	0.429
Prunus avium	12	51–370 (183.8)	0	3.88355	0	0.492	0.73	<0.001	0.971	388.5	0.445
Prunus serotina	211	90–850 (192.4)	0.00039	2.57002	0	0.079	0.05	<0.001	0.94	772.2	0.308
Pseudotsuga menziesii	48	81–372 (201.7)	0.00457	2.11328	0.009	0.35	0.61	<0.001	0.725	334.7	0.623
Quercus petraea	470	12–405 (64.4)	0.00684	2.03158	0.003	0.072	<0.05	<0.001	0.828	145.5	0.641
Quercus robur	454	13–900 (78.8)	0.00936	2.05293	0.003	0.044	<0.001	<0.001	0.909	468.3	0.14
Quercus rubra	15	75–120 (97.3)	0.00099	2.20817	0.006	1.371	0.88	0.13	0.432	16.9	0.833
Robinia pseudoacacia	238	59–235 (151.2)	0.00122	2.33479	0.001	0.148	0.19	<0.001	0.743	76.8	0.246
Salix spec.	10	119–531 (338.8)	0.00001	3.1988	0	1.23	0.9	<0.05	0.751	1393.9	0.604
Sorbus aucuparia	45	4–197 (97.6)	0.00044	2.33729	0.001	0.321	0.54	<0.001	0.799	23.3	0.402
Tilia cordata	15	26–256 (131.3)	0.00061	2.62245	0.002	0.498	0.71	<0.001	0.877	206.7	0.108

All biomass equations took the form of power equations (Eq. 3). n, number of observations for each species (in total = 4340 single observations); H range, height range of measured trees (cm), value in brackets stands for mean H; $\beta1$ and $\beta2$, estimated model coefficients; se, standard error of the regression coefficients; p, significance values of coefficients; *corr*, correlation between observation and fit; *RMSE*, root-mean-squared-error of fit; R^2_{res}, coefficient of determination of residuals

equations are presented in Table 5. Estimated coefficients were significant for all models ($p < 0.001$). All models also resulted in correlations greater than 0.9, with a mean value of 0.93 (±0.03). Only the generic model for conifers based on H as predictor resulted in a lower correlation of 0.89 (Table 5). Predictions based on $RCD^2 H$ resulted in the lowest RSME of the fitted values (mean = 461 ± 18 g), followed by predictions based on RCD (mean = 583 ± 96 g), and H (mean = 792 ± 10 g) (Table 5). The coefficient of determination for the residuals was low for RCD models of broadleaf and conifer species ($R^2_{res} = 0.13$, $R^2_{res} = 0.05$, respectively) and for the $RCD^2\ H$ models ($R^2_{res} = 0.14$, $R^2_{res} = 0.01$, respectively), but higher for H models ($R^2_{res} = 0.37$, $R^2_{res} = 0.53$, respectively). For the RCD and H models, the standard error of the associated regression coefficients $\beta1$ and $\beta2$ was around 0.02. The standard error of the associated regression coefficients for the $RCD^2\ H$ models was higher, with a mean value of around 0.05 (Table 5).

Confidence intervals for the coefficients of the models were wider for the H models, compared to the RCD models and $RCD^2\ H$ models (Fig. 3a–f, shaded gray area). Confidence intervals widened for all models in the direction of increasing RCD, H or $RCD^2\ H$. In addition, values for the upper confidence limits were higher for all six models and

both coefficients, compared to the lower confidence limits (Table 5).

Discussion

All species-specific biomass equations (Tables 2, 3, 4; Appendixes 2, 3, 4) were statistically significant ($p < 0.05$) and RCD proved to be a better single predictor variable than H, resulting in lower RMSE on average for the seedlings and saplings of forest trees. Even lower RMSE could be achieved on average (-21 %) when using the predictor $RCD^2 H$ instead of only RCD. Hence, the equations presented are a comprehensive collection to predict the biomass of seedlings and saplings and an alternative to existing non-destructive biomass estimation approaches (Bolte et al. 2009; Norgren et al. 1995). Even though species-specific models are expected to provide more accurate estimates of biomass and/or carbon than mixed-species models (Buech and Rugg 1989; Sah et al. 2004), generic equations as developed here for broadleaf and conifer species (Table 5) can be a helpful tool to estimate biomass of species not considered in this study (e.g., Brown 1976; Nelson et al. 1999).

In any case, the equations are more precise than existing comparably coarse approaches. West et al. (1999), for

Table 4 Parameters of the biomass equations, estimating aboveground biomass (AGB) in g dry weight from the predictor variable $RCD^2 H$ (cm^3)

Species	n	$RCD^2 H$ range (cm^3)	$\beta 1$	$\beta 2$	se ($\beta 1$)	se ($\beta 2$)	p ($\beta 1$)	p ($\beta 2$)	Corr	RMSE (g)	R^2_{res}
Abies alba	399	0–47,045 (2104.6)	1.87856	0.79034	0.263	0.014	<0.001	<0.001	0.971	364.7	0.006
Acer pseudoplatanus	175	4–93,159 (8198.2)	0.21103	0.95964	0.077	0.033	<0.05	<0.001	0.963	722.1	0.035
Betula pendula	63	2–53,599 (1704.1)	0.37119	0.87982	0.038	0.01	<0.001	<0.001	0.998	43.4	0.003
Carpinus betulus	316	2–984 (214.9)	0.35633	0.92508	0.06	0.028	<0.001	<0.001	0.912	20.6	0.29
Fagus sylvatica	1190	0–132,559 (3969.9)	0.62342	0.87409	0.048	0.007	<0.001	<0.001	0.974	480.2	0.108
Fraxinus excelsior	165	6–101,911 (8271.2)	0.07555	1.07047	0.03	0.036	<0.05	<0.001	0.975	745.5	0.042
Picea abies	368	3–72,405 (3830.7)	2.24952	0.76318	0.321	0.014	<0.001	<0.001	0.961	559	0
Pinus sylvestris	100	2–63,619 (4659.1)	0.75897	0.85012	0.224	0.029	<0.05	<0.001	0.975	396.5	0.02
Pinus uncinata	46	1–10 (4)	0.38946	0.87595	0.059	0.09	<0.001	<0.001	0.839	0.4	0.014
Prunus avium	12	26–37,000 (7649.4)	0.34321	0.91827	0.192	0.056	0.1	<0.001	0.993	195.2	0.002
Prunus serotina	211	161–85,170 (3655.1)	0.41845	0.93306	0.049	0.011	<0.001	<0.001	0.984	397.3	0.015
Pseudotsuga menziesii	48	86–8977 (2088.9)	0.42058	0.92076	0.149	0.042	<0.05	<0.001	0.972	111.7	0.053
Quercus petraea	470	1–16,366 (554.1)	0.5274	0.81213	0.099	0.022	<0.001	<0.001	0.893	114.8	0.453
Quercus robur	454	2–65,307 (1602.5)	0.67311	0.85202	0.066	0.009	<0.001	<0.001	0.987	176.9	0.055
Quercus rubra	15	32–346 (163.9)	0.10626	1.09349	0.056	0.097	0.08	<0.001	0.969	4.5	0.001
Robinia pseudoacacia	238	31–2802 (800.4)	0.98644	0.77535	0.229	0.033	<0.001	<0.001	0.85	60	0.224
Salix spec.	10	130–40,185 (10735.7)	0.04368	1.12303	0.013	0.029	<0.05	<0.001	0.999	68.1	0.002
Sorbus aucuparia	45	3–1640 (246.3)	0.52384	0.76575	0.187	0.055	<0.05	<0.001	0.924	14.7	0.046
Tilia cordata	10	933–10,020 (4312.4)	0.10615	1.02416	0.136	0.147	0.459	<0.001	0.945	132.9	0.004

All biomass equations took the form of power equations (Eq. 4). n, number of observations for each species (in total = 4340 single observations); $RCD^2 H$ range, range of measured trees (cm^3), value in brackets stands for mean $RCD^2 H$; $\beta 1$ and $\beta 2$, estimated model coefficients; se, standard error of the regression coefficients; p, significance values of coefficients; *corr*, correlation between observation and fit; *RMSE*, root-mean-squared-error of fit; R^2_{res}, coefficient of determination of residuals

example, presented a fractal model based on trunk diameter that suggested coefficient $\beta 2$ taking a value of 8/3 (≈ 2.67), based on allometric theory. With their "Pipe-model theory," the pioneers of this approach (Shinozaki et al. 1964a, b) postulated a stable relation between assimilate mass and cross-sectional stem surface area of nutrient and water transporting surface of single trees. Anzola-Jürgenson 2002; Enquist and Niklas 2001; West et al. 1999) generalized this approach to a global and universal allocation rule in plant biology, which can be explained with plant architecture and hydrometric principles. It can be assumed that seedlings and saplings with a hardly pithied cross-sectional stem surface follow this 8/3 rule quite stringently, because the cross-sectional stem surface area fully functions as water transportation area. However, it can be assumed that increasing tree dimensions, pithiness and shift of water transport from the whole surface area to sapwood or single tree rings, will result in a gradual move away from the general $DBH^{8/3}$ relationship. Zianis and Mencuccini (2004) calculated an empirical scaling exponent of $\beta 2 = 2.3679$ based on a list of biomass equations. Differences of $\beta 2$ are a result of differences in species wood density and growth architecture (Ketterings et al. 2001). Here, generic models for broadleaf and conifer species resulted in $\beta 2 = 2.807$ and $\beta 2 = 2.37$, respectively

(Table 5), which is quite close to the values. Also species-specific RCD-dependent biomass equations (Table 2, Appendix 2) resulted in $\beta 2$ values in the range of roughly 2–3. This is in line with the equations reviewed by Zianis and Mencuccini (2004) but slightly contradicts Pilli et al. (2006), who found that very low values of $\beta 2$ (<2) are often reported for small plants (only a few meters high). The estimates for $\beta 2$ were more heterogeneous for the biomass models based on H as explanatory variable (Table 3), which was especially due to the species *Betula pendula*, *Prunus avium* and *Salix* spec. Some previous studies have used combinations of diameter and height as independent variables for biomass estimation (e.g., Bjarnadottir et al. 2007; Gonzalez-Benecke et al. 2014a; Repola 2008). Aside of using the predictor $RCD^2 H$ as combination of both, we decided not to use height and diameter alone in the same equations, disregarding the fact that the data basis would have allowed using such combinations. The main reason for this was that diameter and height are highly collinear. Not considering collinearity or multicollinearity of the independent variables, when used separately in regression analysis, might result in biased predictions (Ott 1993).

However, we also generally believe that measuring diameter and height of seedlings and saplings is quite
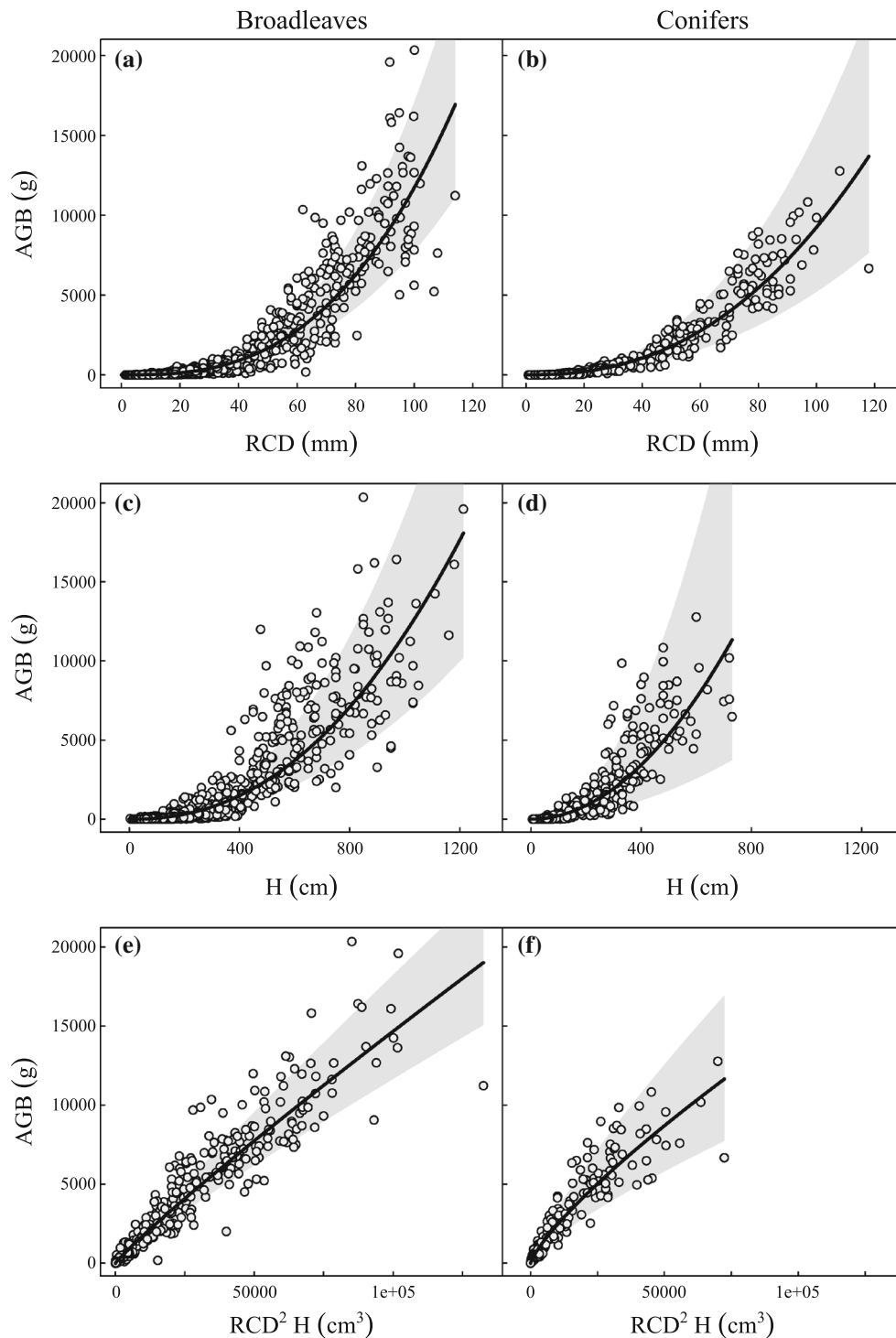
Fig. 3 Generic aboveground biomass (AGB) curves based on root-collar-diameter (RCD) (**a**) and (**b**), height (H) (**c**) and (**d**), and $RCD^2 H$ (**e**) and (**f**) with confidence intervals (shaded gray area) for broadleaf (**a**, **c**, **e**) and conifer (**b**, **d**, **f**) species. Number of observations were $n = 3507$ (**a**), $n = 961$ (**b**), $n = 3379$ (**c**), $n = 961$ (**d**), $n = 3379$ (**e**), and $n = 961$ (**f**). Correlation coefficients between observed and fitted values were between corr $= 0.89$ and corr $= 0.97$, root-mean-squared-errors of fit were between RMSE $= 449$ g and RMSE $= 799$ g (compare Table 5)

laborious for large sample sizes, but is required for all biomass equations based on both variables as predictors (e.g., Eqs. (4), (7), Table 4). Even though the predictor

$RCD^2 H$ reduced the RMSE and produced more accurate estimates than RCD alone, the gain in accuracy (compare: correlation between observation and fit in Tables 2 and 4)

Table 5 Parameters of the generic biomass equations, estimating aboveground biomass (AGB) in g dry weight from the predictor variables root-collar-diameter RCD (mm), height H (cm), and $RCD^2 H$ (cm^3)

S	Var	n	$\beta 1$	$\beta 2$	se ($\beta 1$)	se ($\beta 2$)	p ($\beta 1$)	p ($\beta 2$)	CI $\beta 1$ (2.5–97.5 %)	CI $\beta 2$ (2.5–97.5 %)	Corr	RMSE (g)	R^2_{res}
B	RCD	3507	0.028	2.807	0.003	0.022	<0.001	<0.001	(0.023–0.034)	(2.764–2.851)	0.93	651	0.13
C	RCD	961	0.169	2.37	0.022	0.03	<0.001	<0.001	(0.125–0.212)	(2.31–2.429)	0.95	515	0.05
B	H	3379	0.002	2.249	0	0.02	<0.001	<0.001	(0.002–0.003)	(2.21–2.288)	0.9	785	0.37
C	H	961	0.024	1.982	0.006	0.038	<0.001	<0.001	(0.013–0.035)	(1.907–2.057)	0.89	799	0.53
B	RCD^{2}H	3379	0.361	0.922	0.02	0.005	<0.001	<0.001	(0.323–0.4)	(0.912–0.932)	0.97	449	0.14
C	RCD^{2}H	961	1.687	0.79	0.159	0.009	<0.001	<0.001	(1.376–1.998)	(0.772–0.808)	0.96	474	0.01

All biomass equations took the form of power equations (Eq. 2–4). S, species type (B, broadleaf; C, conifer); *Var* predictor variable used in the generic biomass equations, n, number of observations for each equation, $\beta 1$ and $\beta 2$, estimated model coefficients; se, standard error of the regression coefficients; p, significance values of coefficients; CI, lower and upper confidence limits for model coefficients, corr, correlation between observation and fit; RMSE, root-mean-squared-error of fit (g); R^2_{res}, coefficient of determination of residuals

does not necessarily justify the additional work for also measuring H in these cases for biomass estimations from forest inventories. But also H alone proved to be a reliable predictor for the biomass of the seedlings and saplings (compare: correlation between observation and fit in Table 3), even though the accuracy in terms of RMSE was lowest, compared to the other predictors. The advantage of only measuring H is that recording H for seedlings and saplings is usually considered to be less laborious than measuring RCD, especially in conditions with very dense forest regeneration.

The variability around the biomass equations increased with size of the explanatory variable (Fig. 3), which is common for biomass equations (Zianis and Mencuccini 2004). Chave et al. (2001) reported that estimated coefficients were strongly affected by small trees in their dataset. This was also the case here because of the higher amount of measurements of seedlings compared to saplings. The effect of small trees was particularly pronounced for the logarithmically transformed data after back-transformation (Appendixes 2, 3, 4), resulting in steep slopes for larger height and diameters and possibly overestimating this part of the data, which can be problematic, aside of introducing a bias through transformation. Applying nonlinear least square regressions allowed avoiding these problems by giving weights to our data to not systematically overestimate the small range of the data in return. We consider this a pragmatic approach for biomass estimation.

In juvenile stands, site conditions such as light availability, soil properties and resource competition, can be expected to be among the most decisive factors determining growth rates, especially height growth but also diameter, and growth architecture, in terms of biomass allocation. Data compiled for this study represented a wide range of growth conditions, especially for species with high numbers of plots, observations, and data sources, e.g., *Abies alba*,

Fagus sylvatica, *Picea abies* (Table 1), so that the provided equations can be assumed to be applicable for Europe (compare Wirth et al. 2004). Nevertheless, caution should be generally taken when biomass estimates are extrapolated from plot to regional scale (Satoo and Madgwick 1982; Zianis et al. 2005) or beyond the observed data range. In addition, each original study has been conducted for different purposes, e.g., as competition experiment (KAW2013), site preparation experiment (LOE2006), provenance trial (GEL2001), and under different growth conditions, e.g., in situ (AME2013, ANN2012), ex situ (BAL2011, KAW2013), differing light availability (PRO2008, SCH2012), which may have increased the natural variability of the data or may have introduced atypical plant architectures (compare references in Appendix 1). The high variability of the data in combination with the up to now limited size of the data base, in turn, hampered a detailed analysis of regional differences in tree allometry or the effect of specific treatments, site or stand conditions. These limitations should be considered when applying the presented biomass equations at plot or stand scale.

Against this background, it would be highly desirable to minimize methodological differences among biomass studies, by standardizing their methodologies (e.g., height of diameter measurement, inclusion and/or exclusion of leaves and needles) as also claimed by Bi et al. (2015), Cifuentes et al. (2015a, b). Also, a standardized quantification of the main site and stand factors influencing the allocation of tree growth (e.g., light and water availability, soil properties, density, age, structure, browsing pressure) could result in more accurate general model predictions (e.g., Alemdag and Stiell 1982; António et al. 2007; Brown 1997; Gonzalez-Benecke et al. 2014b). Standards would facilitate compilation (GlobAllomeTree platform by the FAO as good initiative), evaluation and application of existing and future biomass equations.

Appendix 1

Dataset references and responsible scientists. Presented are the names of the datasets as used in this study and the publication they refer to

No.	Dataset	Region	Sampling year	Species	Bibliographic references
(1)	AME2013	Catalonia, Spain	2011	*Abies alba* (48), *Betula pendula* (47), *Pinus sylvestris* (45), *Pinus uncinata* (46)	Ameztegui, A., Coll, L. (2013) Unraveling the role of light and biotic interactions on seedling performance of four Pyrenean species along environmental gradients. Forest Ecology and Management 303: 25–34, DOI 10.1016/j.foreco.2013.04.011
(2)	AMM2003	Freising, Germany	1999	*Fagus sylvatica* (107), *Quercus robur* (107)	Ammer C (2003) Growth and biomass partitioning of *Fagus sylvatica* L. and Quercus robur L. seedlings in response to shading and small changes in the R/FR-ratio of radiation. Annals of Forest Science 60: 163–171, DOI 10.1051/forest:2003009
(3)	ANN2012	Ticino, Italy	2010	*Prunus serotina* (35)	Annighöfer et al. (2012) Biomass functions for the two alien tree species Prunus serotina Ehrh. And Robinia pseudoacacia L. in floodplain forests of Northern Italy. European Journal of Forest Research 131:1619–1635, DOI 10.1007/s10342-012-0629-2
(4)	BAL2007	Fontfreyde, France	2007	*Fagus sylvatica* (10)	Balandier (2007) Unpublished data
(5)	BAL2009	Fontfreyde, France	2009	*Fagus sylvatica* (9)	Balandier (2009) Unpublished data
(6)	BAL2011	Clermont-Ferrand, France (Greenhouse)	2011	*Quercus petraea* (24)	Balandier (2011) Unpublished data
(7)	CAQ2010	Graoully Forest, France	2005, 2006, 2007	*Acer pseudoplatanus* (40), *Fagus sylvatica* (176)	Caquet B, Montpied P, Dreyer E, Epron D, Collet C 2010 Response to canopy opening does not act as a filter to *Fagus sylvatica* and Acer sp. Advance regeneration in a mixed temperate forest. Ann For Sci 67:105
					Caquet B, Barigah T, Cochard H, Montpied P, Collet C, Dreyer E, Epron D 2009 Hydraulic properties of naturally regenerated beech saplings respond to canopy opening. Tree Physiol. 29:1395–1405.
(8)	COL1996	Champenoux, France	1993	*Quercus petraea* (197)	Collet C, Guehl JM, Frochot H, Ferhi A 1996 Effect of two forest grasses differing in their growth dynamics on the water relations and the growth of Quercus petraea seedlings. Can J Bot, 74: 1562–1571
(9)	COL2006	Champenoux, France	2000	*Quercus petraea* (229)	Collet C, Löf M, Pagès L 2006 Root system development of oak seedlings analyzed using a root architectural model. Effects of competition with grass. Plant and Soil, 279: 367–383.
(10)	DIR2010	Bayerischer Wald, Germany	2009	*Abies alba* (40), *Fagus sylvatica* (40), *Picea abies* (40), *Sorbus aucuparia* (40)	Dirnberger (2010) Unpublished data, Diploma thesis: Biomasse und sommerliches Äsungsangebot von Jungbäumen im Nationalpark Bayerischer Wald. University of applied Sciences, Weihenstephan
(11)	GEB2013	Göttingen, Germany greenhouse experiment	2013	*Acer pseudoplatanus* (12), *Fagus sylvatica* (6), *Fraxinus excelsior* (12)	Gebereyesus (2013) Unpublished data, Master thesis: Biomass estimations of regeneration trees (DBH < 7 cm) in temperate forests. Georg-August-University, Göttingen

No.	Dataset	Region	Sampling year	Species	Bibliographic references
(12)	GEL2001	Graupa, Germany	2001	*Fagus sylvatica* (32)	Gellrich M, Steinke C, Schröder J (2001) Ergebnisse der Biomasseuntersuchungen an ausgewählten Probebäumen des Rotbuchen-Herkunftsversuches 1990, Versuchsfläche RBU-V03 Graupa, Nordteil, Staatsbetrieb Sachsenforst, Ergebnisbericht Technische Universität Dresden für Probebäume des Buchenprovenienzversuches auf der Versuchsfläche "Pflanzgarten," LAF Graupa. University of Technology Dresden, Tharandt
(13)	HAM2014	Sachsen, Germany	2010	*Abies alba* (194)	Hamm T, Weidig J, Huth F, Kuhlisch W, Wagner S et al. (2014) Wachstumsreaktionen junger Weißtannen-Voraussaaten auf Begleitvegetation und Strahlungskonkurrenz. AFJZ 185:45–59
(14)	HIR2011	Sachsen, Germany	2010	*Fagus sylvatica* (88)	Hirschfelder (2011) Unpublished data, Master thesis: Die Untersuchung der Wachstumsparameter und der Wurzeldeformationen von Rotbuchen-Voranbauten (*Fagus sylvatica* L.) aus Saat und Pflanzung unter einem Fichtenschirm (Picea abies [L.] KARST.) im Tharandter Wald. University of Technology Dresden, Tharandt
(15)	HOF2008	Freising, Landshut Germany	2004	*Fagus sylvatica* (289)	Hofmann R, Ammer C (2008) Biomass partitioning of beech seedlings under the canopy of spruce. Austrian Journal of forest science (1):51–66
(16)	KAE2006	Baden-Württemberg, Germany	2005, 2006	*Abies alba* (117), *Acer pseudoplatanus* (51), *Fagus sylvatica* (149), *Fraxinus excelsior* (63), *Picea abies* (156), *Pinus sylvestris* (40), *Quercus robur* (44)	Kändler et al. (2006) Herleitung von Biomassefunktionen für Verjüngungsbäume ("Nicht Derbholz"-Kollektiv)—erste Ergebnisse. DVFFA—Sektion Ertragskunde, Jahrestagung 2006
(17)	KAW2013	Göttingen, Germany	2011	*Carpinus betulus* (296), *Prunus serotina* (176), *Quercus robur* (288), *Robinia pseudoacacia* (238)	Kawaletz et al. (2013) Exotic tree seedlings are much more competitive than natives but show underyielding when growing together. J Plant Eco 6:305–315, DOI 10.1093/jpe/rts044
(18)	KUE2011	Freiburg, Germany	2008, 2012	*Pseudotsuga menziesii* (48)	Kühne et al. (2011) Einfluss von Überschirmung, Dichtstand und Pflanzengröße auf die Wurzelentwicklung natürlich verjüngter Douglasien. (Effects of canopy closure, crowding and plant size on root system development in Douglas-fir seedlings). Forstarchiv 82, 184–194, DOI 10.4432/0300-4112-82-184 Kuehne et al. (2015) Root system development in naturally regenerated Douglas-fir saplings as influenced by canopy closure and crowding. Journal of Forest Science 61, 406–415, DOI: 10.17221/53/2015-JFS
					Merkel (2009) Unpublished data, Diploma thesis: Zur Ästigkeit von Douglasie unter Schirm. Rottenburg University of Applied Forest Sciences, Rottenburg
(19)	KUE2014	Freiburg, Germany	2012	*Acer pseudoplatanus* (15), *Carpinus betulus* (15), *Quercus robur* (15), *Quercus rubra* (15)	Kühne et al. (2014) A comparative study of physiological and morphological seedling traits associated with shade tolerance in introduced red oak (Quercus rubra) and native hardwood tree species in southwestern Germany. Tree Physiology 34, 184–193, DOI 10.1093/treephys/tpt124

No.	Dataset	Region	Sampling year	Species	Bibliographic references
(20)	LIN2014	Solling, Germany	2012	*Fagus sylvatica* (30)	Lin N, Bartsch N, Vor T (2014) Long-term effects of gap creation and liming on understory vegetation with a focus on tree regeneration in a European beech (*Fagus sylvatica* L.) forest. Annals of forest science 57(2): 249–262, DOI 10.15287/afr.2014.274
(21)	LOE2006	Skarhul, Sweden	2004	*Quercus robur* (48)	Löf M, Rydberg D, Bolte A (2006): Mounding site preparation for forest restoration: Survival and growth response in Quercus robur L. seedlings. For. Ecol. Manage. 232: 19–25, DOI 10.1016/j.foreco.2006.05.003
					Bolte A, Löf M (2010): Root spatial distribution and biomass partitioning in Quercus robur L. seedlings: the effects of mounding site preparation. Eur. J. Forest Res. 129, 4: 603–612, DOI 10.1007/s10342-010-0360-9
(22)	MUE2014	Bechstedt, Kaltenborn, Germany	2010, 2011	*Betula pendula* (11), *Fagus sylvatica* (3), *Pinus sylvestris* (10), *Salix* spec. (10), *Tilia cordata* (9)	Müller S (2014) Unpublished data, Dissertation: Architectural light foraging syndromes of juvenile temperate broad leaved trees. Albert-Ludwigs Universität Freiburg.
(23)	PRO2008	Charensat, France	2004	*Fagus sylvatica* (54)	Provendier D, Balandier P (2008) Compared effects of competition by grasses (Graminoids) and broom (Cytisus scoparius) on growth and functional traits of beech saplings (*Fagus sylvatica*). Ann For Sci (65) 510, DOI 10.1051/forest:2008028
(24)	SCH2012	Göttingen, Germany greenhouse experiment	2008	*Fagus sylvatica* (184), *Picea abies* (172)	Schall P, Lödige C, Beck M., Ammer C (2012) Biomass allocation to roots and shoots is more sensitive to shade and drought in European beech than in Norway spruce seedlings. For Eco Manage 266:246–253, DOI 10.1016/j.foreco.2011.11.017
(25)	SEE2011	Hainich, Thuringia, Germany	2008	*Acer pseudoplatanus* (80), *Fagus sylvatica* (43), *Fraxinus excelsior* (70)	Seele (2008) Unpublished data, Dissertation: The influence of deer browsing on natural forest regeneration. Friedrich-Schiller-University, Jena
(26)	SLO2003	Bechstedt, Germany	2003	*Acer pseudoplatanus* (5), *Betula pendula* (5), *Carpinus betulus* (5), *Fagus sylvatica* (5), *Fraxinus excelsior* (5), *Pinus sylverstris* (5), *Prunus avium* (5), *Quercus petraea* (5), Sorbus aucuparia (5), *Tilia cordata* (5)	Scherer-Lorenzen (2003) Unpublished data
(27)	WAK2009	Bechstedt, Kaltenborn Germany	2009	*Acer pseudoplatanus* (12), *Fagus sylvatica* (5), *Fraxinus excelsior* (15), *Prunus avium* (7), *Quercus petraea* (15), *Tilia cordata* (1)	Wirth and Kahl (2009) Unpublished data

Appendix 2

Parameters of the biomass equations, estimating aboveground biomass (AGB) from the predictor variable root-collar-diameter (RCD)

Species	n	$\beta1$	$\beta2$	se ($\beta1$)	se ($\beta2$)	p ($\beta1$)	p ($\beta2$)	CF	exp ($\beta1$)	R^2	RSE
Abies alba	399	−3.489	2.854	0.034	0.016	<0.001	<0.001	1.089	0.033	0.988	0.413
Acer pseudoplatanus	215	−3.196	2.707	0.092	0.033	<0.001	<0.001	1.089	0.045	0.969	0.412
Betula pendula	63	−3.647	2.72	0.175	0.086	<0.001	<0.001	1.162	0.03	0.943	0.548
Carpinus betulus	316	−3.593	2.731	0.15	0.058	<0.001	<0.001	1.103	0.03	0.876	0.443
Fagus sylvatica	1230	−3.512	2.835	0.042	0.016	<0.001	<0.001	1.101	0.033	0.964	0.438
Fraxinus excelsior	165	−3.352	2.775	0.145	0.048	<0.001	<0.001	1.133	0.04	0.953	0.499
Picea abies	368	−3.084	2.676	0.085	0.029	<0.001	<0.001	1.091	0.05	0.959	0.418
Pinus sylvestris	100	−3.575	2.738	0.104	0.038	<0.001	<0.001	1.101	0.031	0.981	0.439
Pinus uncinata	46	−2.595	1.958	0.392	0.274	<0.001	<0.001	1.066	0.08	0.537	0.358
Prunus avium	12	−2.892	2.509	0.235	0.07	<0.001	<0.001	1.03	0.057	0.992	0.244
Prunus serotina	211	−3.748	2.902	0.195	0.06	<0.001	<0.001	1.052	0.025	0.919	0.317
Pseudotsuga menziesii	48	−2.408	2.522	0.22	0.07	<0.001	<0.001	1.032	0.093	0.966	0.25
Quercus petraea	470	−3.902	2.561	0.101	0.039	<0.001	<0.001	1.139	0.023	0.904	0.51
Quercus robur	502	−3.286	2.612	0.092	0.037	<0.001	<0.001	1.134	0.042	0.907	0.501
Quercus rubra	15	−1.595	1.929	0.515	0.207	<0.05	<0.001	1.035	0.21	0.869	0.261
Robinia pseudoacacia	238	−2.083	2.325	0.22	0.073	<0.001	<0.001	1.064	0.133	0.813	0.352
Salix spec	10	−3.299	2.686	0.402	0.111	<0.001	<0.001	1.029	0.038	0.986	0.239
Sorbus aucuparia	45	−2.598	2.305	0.345	0.146	<0.001	<0.001	1.156	0.086	0.853	0.539
Tilia cordata	15	−4.823	2.882	0.364	0.109	<0.001	<0.001	1.06	0.009	0.982	0.341

All models were significant ($p < 0.001$). Biomass equations took the form of Eq. (5). Parameters are: n = number of observations for each species (total = 4468 single observations); $\beta1$ and $\beta2$ = estimated model coefficients; se = standard error of the regression coefficients; p = significance values of coefficients; CF = correction factor for back-transformation of $\beta1$ (Eq. 8); exp($\beta1$) = back-transformed anti-log of $\beta1$ multiplied with CF; R^2 = multiple R-squared of the model; *RSE* residual standard error

Appendix 3

Parameters of the biomass equations, estimating aboveground biomass (AGB) from the predictor variable height (H)

Species	n	$\beta1$	$\beta2$	se ($\beta1$)	se ($\beta2$)	p ($\beta1$)	p ($\beta2$)	CF	exp ($\beta1$)	R^2	RSE
Abies alba	399	−8.072	2.829	0.089	0.025	<0.001	<0.001	1.236	0.000386	0.97	0.651
Acer pseudoplatanus	175	−7.21	2.331	0.237	0.047	<0.001	<0.001	1.213	0.000896	0.934	0.621
Betula pendula	63	−10.348	2.858	0.399	0.095	<0.001	<0.001	1.181	0.000038	0.937	0.577
Carpinus betulus	316	−5.932	2.171	0.35	0.081	<0.001	<0.001	1.271	0.003374	0.695	0.693
Fagus sylvatica	1190	−7.308	2.377	0.099	0.021	<0.001	<0.001	1.254	0.000841	0.917	0.673
Fraxinus excelsior	165	−7.521	2.411	0.317	0.062	<0.001	<0.001	1.29	0.000699	0.903	0.714
Picea abies	368	−5.486	2.316	0.128	0.029	<0.001	<0.001	1.122	0.004653	0.946	0.481
Pinus sylvestris	100	−8.319	2.75	0.316	0.073	<0.001	<0.001	1.393	0.00034	0.936	0.814
Pinus uncinata	46	−5.879	1.997	1.075	0.354	<0.001	<0.001	1.084	0.00303	0.42	0.401
Prunus avium	12	−11.382	3.335	0.779	0.155	<0.001	<0.001	1.085	0.000012	0.979	0.405
Prunus serotina	211	−5.448	2.175	0.313	0.061	<0.001	<0.001	1.091	0.004696	0.859	0.418
Pseudotsuga menziesii	48	−7.99	2.583	0.786	0.15	<0.001	<0.001	1.132	0.000384	0.865	0.497
Quercus petraea	470	−6.479	2.318	0.199	0.05	<0.001	<0.001	1.275	0.001959	0.82	0.697
Quercus robur	454	−6.007	2.213	0.197	0.048	<0.001	<0.001	1.285	0.003163	0.822	0.708
Quercus rubra	15	−8.935	2.646	5.563	1.217	0.13	< 0.05	1.21	0.000159	0.267	0.617
Robinia pseudoacacia	238	−7.493	2.488	0.536	0.107	<0.001	<0.001	1.106	0.000616	0.695	0.449
Salix spec	10	−16.01	3.876	2.353	0.409	<0.001	<0.001	1.189	0.0000001	0.918	0.588

Species	n	$\beta1$	$\beta2$	se ($\beta1$)	se ($\beta2$)	p ($\beta1$)	p ($\beta2$)	CF	exp ($\beta1$)	R^2	RSE
Sorbus aucuparia	45	−2.591	1.209	0.982	0.221	< 0.05	<0.001	1.79	0.134188	0.411	1.079
Tilia cordata	15	−9.128	2.946	0.578	0.123	<0.001	<0.001	1.073	0.000117	0.978	0.375

All models were significant ($p < 0.001$), except for Q. rubra ($p = 0.049$). Biomass equations took the form of Eq. (6). Parameters are: n = number of observations for each species (total = 4097 single observations); $\beta1$ and $\beta2$ = estimated model coefficients; se = standard error of the regression coefficients; p = significance values of coefficients; CF = correction factor for back-transformation of $\beta1$ (Eq. 8); exp($\beta1$) = back-transformed anti-log of $\beta1$ multiplied with CF; R^2 = multiple R-squared of the model; *RSE* residual standard error

Appendix 4

Parameters of the biomass equations, estimating aboveground biomass (AGB) from the predictor variable RCD^2 H (both in cm)

Species	n	$\beta1$	$\beta2$	se ($\beta1$)	se ($\beta2$)	p ($\beta1$)	p ($\beta2$)	CF	exp ($\beta1$)	R^2	RSE
Abies alba	399	−0.672	0.956	0.022	0.005	<0.001	<0.001	1.076	0.549	0.99	0.383
Acer pseudoplatanus	175	−0.786	0.873	0.049	0.008	<0.001	<0.001	1.039	0.473	0.987	0.277
Betula pendula	63	−1.652	0.948	0.089	0.022	<0.001	<0.001	1.087	0.208	0.968	0.408
Carpinus betulus	316	−1.187	0.954	0.08	0.016	<0.001	<0.001	1.068	0.326	0.917	0.362
Fagus sylvatica	1190	−1.019	0.921	0.022	0.004	<0.001	<0.001	1.054	0.38	0.981	0.323
Fraxinus excelsior	165	−1.052	0.918	0.078	0.012	<0.001	<0.001	1.07	0.373	0.974	0.367
Picea abies	368	−0.164	0.868	0.042	0.007	<0.001	<0.001	1.052	0.892	0.976	0.317
Pinus sylvestris	100	−1.042	0.936	0.056	0.01	<0.001	<0.001	1.057	0.373	0.989	0.332
Pinus uncinata	46	−0.828	0.798	0.132	0.097	<0.001	<0.001	1.056	0.461	0.606	0.331
Prunus avium	12	−1.065	0.919	0.123	0.017	<0.001	<0.001	1.013	0.349	0.997	0.161
Prunus serotina	211	−0.774	0.921	0.107	0.015	<0.001	<0.001	1.033	0.476	0.947	0.256
Pseudotsuga menziesii	48	−0.626	0.89	0.132	0.019	<0.001	<0.001	1.019	0.545	0.98	0.194
Quercus petraea	470	−1.34	0.898	0.045	0.009	<0.001	<0.001	1.068	0.28	0.951	0.364
Quercus robur	454	−0.772	0.893	0.047	0.011	<0.001	<0.001	1.088	0.503	0.941	0.41
Quercus rubra	15	−1.397	0.931	0.342	0.069	<0.05	<0.001	1.018	0.252	0.933	0.186
Robinia pseudoacacia	238	−0.622	0.865	0.155	0.024	<0.001	<0.001	1.052	0.565	0.846	0.319
Salix spec	10	−2.103	1.013	0.387	0.046	<0.05	<0.001	1.035	0.126	0.984	0.262
Sorbus aucuparia	45	−0.474	0.726	0.273	0.058	0.09	<0.001	1.238	0.77	0.784	0.653
Tilia cordata	15	−1.84	0.977	0.191	0.028	<0.001	<0.001	1.033	0.164	0.99	0.255

All models were significant ($p < 0.001$). Biomass equations took the form of Eq. (7). Parameters are: n = number of observations for each species (total = 4340 single observations); $\beta1$ and $\beta2$ = estimated model coefficients; se = standard error of the regression coefficients; p = significance values of coefficients; CF = correction factor for back-transformation of $\beta1$ (Eq. 8); exp($\beta1$) = back-transformed anti-log of $\beta1$ multiplied with CF; R^2 = multiple R-squared of the model; *RSE* residual standard error

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