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Species-specific and generic biomass equations for the regeneration of European tree species

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91

Abstract

93 [text]

Keywords

95 Tree biomass, allometric equations, forest regeneration

Introduction

97 Assessing forest productivity has a long tradition in forestry and forest ecosystem science.
98 During the last four decades, the interest in forest productivity has shifted from focusing on
99 tree and stand volume production to tree and stand biomass production (Parresol 1999). A
100 precise estimate of tree and forest biomass is of interest to many disciplines of forest,
101 ecosystem and climate change research, ranging from population ecology to remote sensing
102 and terrestrial ecosystem modelling, as well as to forest managers (Jenkins et al. 2003).
103 Particularly, it continues to be of increasing importance in recognition of the role forest
104 ecosystems have in the carbon cycle and the global climate system and also in compliance
105 with the second commitment period of the Kyoto Protocol (IPCC 2013), since forests can be
106 important carbon sinks and sources (Dixon et al. 1994; Valentini et al. 2000). Direct biomass
107 measurements in the field are very complex, laborious and time consuming (Sah et al. 2004).
108 Therefore, the use of relationships between tree biomass and tree parameters that can easily be
109 measured, mainly tree diameter at breast height (DBH) and/or tree height (H) are the most
110 common approach for estimating individual tree biomass (e.g. Annighöfer et al. 2012; Chave
111 et al. 2001; Djomo et al. 2010). There are several collections and generic meta-analyses

112 available for the latter approach resulting in species specific biomass equations (e.g. Falster et
113 al. 2015; Jenkins et al. 2003; Rojas-García et al. 2015; Ter-Mikaelian and Korzukhin 1997;
114 Wirth et al. 2004; Zianis et al. 2005). However, most published biomass equations focus on
115 larger trees (dbh ≥ 10 cm). Publications with biomass equations for juvenile trees of single
116 species are rare (e.g. Bartelink 1997; Chroust 1985; Pilli et al. 2006; Wirth et al. 2004).
117 Recently, biomass equations for shrub species of the understory were published (e.g. Berner
118 et al. 2015; Sah et al. 2004). Generally, however, biomass equations for seedlings and
119 saplings are hard to find (Pajtík et al. 2008). This may be due to their low individual tree size
120 which is far below merchantable wood dimensions and even the sum of their biomass is
121 believed to account only for a small fraction of total stand biomass, and associated carbon
122 stocks in forests (Brown 2002; Chave et al. 2001). Accurate biomass estimates for the
123 regeneration are nevertheless required for the increasing amount of afforestation and
124 reforestation sites, young successional forests, shelterwood systems, and open woodland
125 forests (e.g. Schroeder et al. 1997) and the modelling of their future development. In
126 particular, accurate estimates of regeneration biomass are of central importance to understand
127 and predict the dynamics in the carbon cycling of forests (Galik et al. 2009; Gonzalez-
128 Benecke et al. 2014a).
129 In Germany, a non-destructive estimation of the understory biomass ("PhytoCalc") was
130 repeatedly applied, which however does not directly allow estimating the biomass of single
131 trees in the regeneration (Bolte et al. 2009; Heinrichs et al. 2010). Norgren et al. (1995)
132 proposed a similar non-destructive approach for estimating seedling and sapling biomass,
133 using the projection area of a plant as explanatory variable for biomass in a computer-based
134 image analysis.
135 The aim of this paper is to generate species-specific and generic equations for aboveground
136 woody biomass in dependence of root-collar-diameter (RCD) and height (H) of seedlings and
137 saplings growing under common growth conditions in Central Europe. The respective
138 database includes original data from 6 European countries and 25 explorative or experimental
139 studies and represents 19 European tree species.

Material and Methods

141 *Data collection and processing*
142 The collected data set consists of 25 single original data sets on biomass, diameter and partly
143 height of the regeneration of European tree species that were directly made available by their
144 authors (Appendix A). The final data set consisted of 4225 single recordings of 19 Central
145 European tree species (Table 1) of which 5 species were conifers (n = 956 single
146 observations) and 14 species broadleaves (n = 3269).
147 Data compilation was restricted to the European continent (Fig. 1). Most data originated from
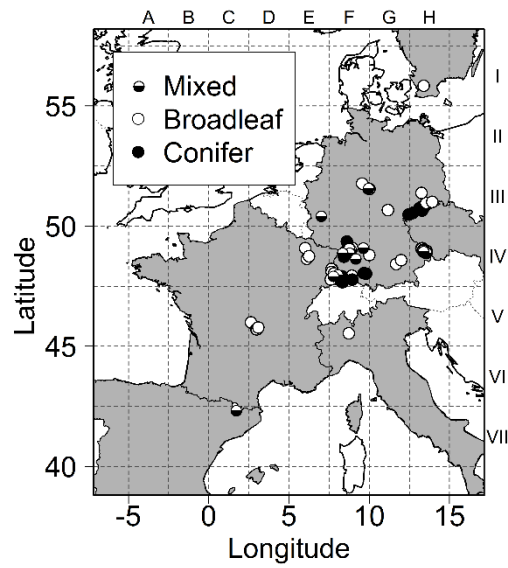148 Germany, followed by data from France and Spain.

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).

149

Table 1 Summary of plot characteristics and database for each species; T = tree 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 A.

Species	T	n	CNY	ASL (m)	AGB (g)	Database
Abies alba	C	58	DE ES	794.47 (235-1906)	543.99 (0.03-9949.22)	AME2013 EWB2009 HAM2014 KAE2006
Acer pseudoplatanus	B	21	DE FR	377.63 (171-1110)	1546.64 (1.25-13100)	CAQ2010 GEB2013 KAE2006 KAH2009 KUE2014
Betula pendula	B	2	DE ES	1606.16 (325-1906)	206.05 (0.14-5223.65)	AME2013 MUE2011
Carpinus betulus	B	2	DE	220.87 (220-238)	52.69 (0.16-265.45)	KAW2013 KUE2014
Fagus sylvatica	B	69	CZ DE FR	454.67 (173-1184)	694.28 (0.1-16200)	AMM2003 BAL2007 BAL2009 CAQ2010 EWB2009 GEB2013 GEL2001 HAB2009 HIR2010 HOF2008 KAE2006 KAH2009 LIN2014 PRO2008 SCH2012
Fraxinus excelsior	B	19	DE	426.49 (110-717)	2507.91 (3-19600)	GEB2013 KAE2006 KAH2009
Picea abies	C	53	CZ DE	424.77 (218-1227)	861.79 (2-12777.07)	EWB2009 KAE2006
Pinus sylvestris	C	4	DE ES	1112.21 (110-1906)	857.88 0.43-10188.83	AME2013 KAE2006 MUE2011
Pinus uncinata	C	1	ES	1906 (1906-1906)	1.37 (0.32-4.41)	AME2013
Prunus avium	B	1	DE	400 (400-400)	2031.07 (226.31-5617.41)	KAH2009
Prunus serotina	B	2	DE IT	207.06 (142-220)	821.32 (36.11-20348.33)	ANN2012 KAW2013
Pseudotsuga menziesii	C	2	DE	537 (444-630)	468.17 (27.19-1746.65)	KUE2011
Quercus petraea	B	5	DE FR	243.7 (110-412)	76.91 (0.32-2535.29)	BAL2011 COL1996 KAH2009
Quercus robur	B	12	DE SE	213.31 (90-493)	227.85 (1.4-8849.66)	AMM2003 KAE2006 KAW2013 KUE2014 LOE2006
Quercus rubra	B	1	DE	270.37 (238-238)	29 (8-70.45)	KUE2014
Robinia pseudoacacia	B	1	DE	220 (220-220)	176.01 (6.03-498.76)	KAW2013
Salix spec	B	1	DE	325 (325-325)	1604.52 (22.1-6486.4)	MUE2011
Sorbus aucuparia	B	34	CZ DE	969.5 (689-1190)	35.79 (1.31-159.18)	EWB2009
Tilia cordata	B	1	DE	400 (400-400)	578.69 131.49-1402.51)	HAB2009 KAH2009

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 1777 recordings measured AGB separately with (total AGB) and without leaves and needles (woody AGB). A total of 2152 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

165 regression fitting (loess {stats} in R Development Core Team 2013) separately for each tree
166 type (conifer, broadleaf).

167 As diameter measurement, most data sets provided root-collar-diameter (RCD) or the
168 diameter at stem base. However, some data sets used other diameter measurements (diameter
169 at 5 cm, 10 cm, 50 cm, 130 cm above ground). To convert all diameter measurements to root-
170 collar-diameter, correction factors were derived for conifer and broadleaf species from data
171 sets consisting of several diameter measurements for both tree types (data mainly from
172 KAE2006, compare Appendix A).

173 For broadleaf species, diameter measurements were transformed to RCD using:

174

$$RCD = T_x \, D_x \hspace{4cm} [1]$$

with RCD = root-collar-diameter; T_x = transformation factor for diameter measurements x
cm above ground ($T_5 = 1.08$; $T_{10} = 1.16$; $T_{50} = 1.33$; $T_{130} = 1.45$); D_x = diameter measured x
cm above ground.

175

176 For conifer species, diameter measurements were transformed to RCD using:

177

$$RCD = T_x \, D_x \hspace{4cm} [2]$$

with RCD = root-collar-diameter; T_x = transformation factor for diameter measurements x
cm above ground ($T_5 = 1.06$; $T_{10} = 1.13$; $T_{50} = 1.29$; $T_{130} = 1.45$); D_x = diameter measured x
cm above ground.

178

179 Mean values for transformation were derived from the relative diameter changes in the
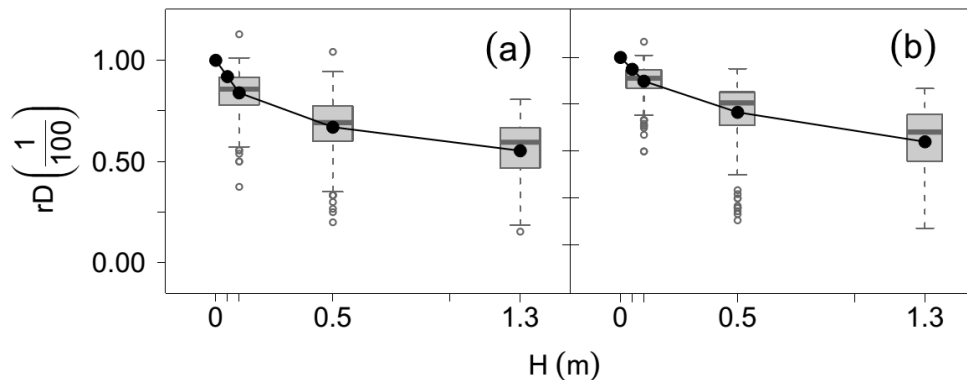180 different height classes (compare Fig. 2).

181

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.

182

183 *Biomass allometries and statistical analysis*
184 The biomass equations presented in this paper hold for aboveground parts of the regeneration
185 excluding leaves and needles. For each species and species type (broadleaf, conifer) we
186 developed allometric equations relating RCD, H and the factor RCD² H (in cm³) to biomass.
187 The mathematical model most commonly used for biomass prediction takes the form of
188 Snell's (1892) power equation $y = \beta 1 \, x^{\beta 2}$ (Kaitaniemi 2004; Zianis et al. 2005; Zianis and
189 Mencuccini 2004).

190 Biomass data mostly exhibits heteroscedasticity (Parresol 2001), which is an error variance
191 that is not constant over all observations. For this reason, the non-linear power equation is
192 often linearized to homogenize variance by logarithmic transformation of both dependent and
193 independent variables (ln y = ln β1 + β2 ln x) to allow fitting a linear regression to the data
194 (e.g. Bjarnadottir et al. 2007; Pilli et al. 2006; Sah et al. 2004). It is broadly accepted that this
195 transformation results in a systematic bias. Currently, this bias is being corrected for in
196 several ways by estimating a correction factor from the standard error (e.g. Baskerville 1972;
197 Beauchamp and Olson 1973; Madgwick and Satoo 1975, Madgwick and Satoo 1975; Parresol
198 1999; Sprugel 1983; Yandle and Wiant 1981), although no standard correction has been
199 proposed yet (Cienciala et al. 2008).

200 We used nonlinear least square regressions (nls {stats} in R Development Core Team 2013)
201 to fit power equations to the data and obtain estimates for the coefficients β1 and β2:

202

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

$$AGB = \beta1 \, H^{\beta2} \tag{4}$$

$$AGB = \beta1 \, (RCD^2 \, H)^{\beta2} \tag{5}$$

with AGB = aboveground biomass; RCD = root-collar-diameter; H = height; and β1 and
β2 = fitted coefficients

203

204 The heteroscedasticity of the data made a weighted analysis necessary (Bates and Watts
205 1988), to achieve minimum variance parameter estimates (Parresol 2001). Following Berner
206 et al. (2015), data was weighted by $y^{-0.5}$ to correct for non-random residuals and the tendency
207 of over-predicting the aboveground biomass (AGB) of small trees (compare Carroll and
208 Ruppert 1988; Huang et al. 1992). However, to make our data as comparable as possible to
209 other studies, we also fit models to logarithmically transformed data. We estimated
210 coefficients β1 and β2 in dependence of RCD, H and RCD² H (in cm³), since this still is a
211 standard method when dealing with biomass data (Zianis and Mencuccini 2004) (Appendix B,
212 Appendix C, Appendix D):

213

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

$$\ln(AGB) = \ln(\beta1) + \beta2 \, \ln(H) \tag{7}$$

$$\ln(AGB) = \ln(\beta1) + \beta2 \, \ln(RCD^2 \, H) \tag{8}$$

with ln = natural logarithm; AGB = aboveground biomass; RCD = root-collar-diameter;
H = height; and β1 and β2 = fitted coefficients

214

215 These logarithmically transformed models were back-transformed by multiplying the anti-log
216 of the intercept with the first-order correction factor suggested by Sprugel (1983):

217

$$CF = \exp(SEE^2 / 2) \tag{9}$$

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

218

219 Aside of estimating the coefficients β1 and β2 for each biomass model, we additionally
220 calculated standard errors of the regression coefficients (allowing model uncertainty to be
221 propagated into subsequent analyses (Berner et al. 2015)), p-values of the coefficients,
222 correlation between observations and fitted values, and root-mean-squared-error of the
223 nonlinear models for model evaluation. Residuals scatter was evaluated by calculating a
224 coefficient of determination for the residuals in dependence of 20 RCD-classes. Residuals
225 should be evenly distributed around zero throughout the classes, so coefficient of
226 determination values were also to be around zero. Biomass equations were calculated
227 separately for each species and generic biomass equations were calculated for all broadleaf
228 and conifer species each. Confidence intervals were calculated for the coefficients of the
229 nonlinear regression models, giving lower (2.5%) and upper (97.5%) confidence limits for
230 each coefficient (confint2 {nlstools} in R Development Core Team 2013).

231 Biomass equations for larger trees are usually based on the easily accessible DBH, while
232 biomass equations for seedlings and young saplings are based on RCD and/ or H as
233 explanatory variable. As the RCD is laborious to measure for a large sample size of small
234 trees, often only the H or height classes of the regeneration are recorded. To allow estimating
235 diameter from height measurements and *vice versa*, we have derived diameter-height curves
236 from our data for broadleaf and conifer species. Diameter-height curves are usually derived
237 by applying saturation functions like the Michaelis-Menton equation $H = β1 \, D / (β2 + D)$
238 (Menten and Michaelis 1913), Chapman-Richards equation $H = β1 \, (1 - \exp(- β2 \, D))^{β3}$
239 (Richards 1959), Weibull equation $H = β1 \, (1 - \exp(- β2 \, D^{β3}))$ (Weibull 1951) and others
240 (comp. Mehtätalo et al. 2015), because height growth thrives towards a threshold value. Since
241 this is not yet the case for trees in the regeneration stage, we used second-degree polynomials,
242 passing through the origin to describe the relationship of diameter and height:

243

$$H = β1 \, RCD + β2 \, RCD^2 \qquad\qquad [10]$$

with H = height; RCD = root-collar-diameter; β1 and β2 = fitted coefficients

244

245 All statistical analyses, fittings, and graphs were processed using the free software
246 environment R (R Development Core Team 2013).

247 **Results**

248 RCD, H and the factor of both ($RCD^2 \, H$) were significant predictors for the aboveground
249 biomass of each species and in the generic biomass equations ($p < 0.001$). Biomass equations
250 based on RCD as the predictor mainly resulted in correlations > 0.9, with a mean value
251 of 0.94 (± 0.06). The correlation based on H as predictor was slightly lower, with values
252 ranging from 0.43 (*Quercus rubra*) to 0.96 (*Betula pendula*) with a mean value
253 of 0.83 (± 0.13) (Table 2, Table 3). Biomass equations based on the $RCD^2 \, H$ also mainly
254 resulted in correlations > 0.9, with a mean value of 0.95 (± 0.05) (Table 4). Predictions based
255 on RCD produced a lower root-mean-squared-error of the fitted values (mean = 339.9 g)
256 compared to H as predictor (mean = 559.2 g), whereas lowest values were produced for the
257 factor $RCD^2 \, H$ (mean = 275.8 g).
258 The coefficient of determination (R^2_{res}) for the residuals showed a scatter around zero for
259 equations based on RCD and the factor $RCD^2 \, H$, but for the equations based on H the scatter
260 was around 0.4, which indicates that the residuals were not evenly distributed around zero and
261 showed a trend to increase with diameter.

262   The RCD range for most species was close to 100 mm, with some exeptions. Data on *Pinus*
263   *uncinata* had the smallest diameter range of 3.4 mm, with a maximum diameter 6.3 mm,
264   followed by *Quercus rubra* with a range of 12.2 mm and a maximum diameter of around
265   18 mm. *Carpinus betulus* and *Sorbus aucuparia* had small diameter ranges as well as low
266   maximum diameters (Table 2). The height of the species ranged from as small as 4 cm
267   (*Sorbus aucuparia*) up to 1210 cm (*Fraxinus excelsior*). For most species, individuals were
268   recorded with heights of at least 2 m, with *Pinus uncinata*, *Quercus rubra* and *Carpinus*
269   *betulus* being the exceptions. Most other species were well represented with height ranges of
270   around 400 cm and more (Table 3).
271

Table 2 Parameters of the biomass equations, estimating aboveground biomass (AGB) in g dry weight from the predictor variable root-collar-diameter (RCD). All biomass equations took the form of power equations (Equation [3]). n = number of observations for each species (in total = 4225 single observations); RCD range = diameter range of measured trees (mm), value in brackets stands for mean RCD; $\beta 1$ and $\beta 2$ = estimated model coefficients; se = standard error of the regression coefficients; p = significance values of coefficients; cor = correlation between observation and fit; RMSE = root-mean-squared-error of fit; R^2_{res} = coefficient of determination of residuals.

Species	n	RCD range (mm)		$\beta 1$	$\beta 2$	se ($\beta 1$)	se ($\beta 2$)	p ($\beta 1$)	p ($\beta 2$)	cor	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	0.04
Acer pseudoplatanus	130	4-100	(28.6)	0.023	2.862	0.015	0.15	0.13	< 0.001	0.934	1085.7	0.048
Betula pendula	58	3-107	(11.3)	0.266	2.126	0.049	0.042	< 0.001	< 0.001	0.995	83.2	0.002
Carpinus betulus	311	3-28	(14.0)	0.069	2.404	0.017	0.083	< 0.001	< 0.001	0.877	24.2	0.002
Fagus sylvatica	1182	1-114	(18.7)	0.114	2.517	0.012	0.025	< 0.001	< 0.001	0.962	578.6	0.15
Fraxinus excelsior	90	5-95	(37.0)	0.014	3.02	0.015	0.246	0.358	< 0.001	0.911	1779.1	0.111
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	95	3-95	(24.1)	0.015	2.881	0.008	0.117	0.055	< 0.001	0.972	427.8	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	0.03
Prunus avium	7	27-100	(60.3)	0.12	2.321	0.137	0.258	0.421	< 0.001	0.981	328.3	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	465	2-70	(15.6)	0.011	2.79	0.003	0.083	< 0.05	< 0.001	0.876	119.7	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	0.13
Quercus rubra	15	6-18	(12.3)	0.056	2.421	0.045	0.298	0.238	< 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	0.054	< 0.001	0.998	137.6	0.002
Sorbus aucuparia	40	3-29	(12.1)	0.145	2.06	0.073	0.165	0.054	< 0.001	0.918	15.7	0.017
Tilia cordata	10	28-65	(45.4)	0.006	2.95	0.009	0.392	0.544	< 0.001	0.963	110.3	0.026

278 Table 3 Parameters of the biomass equations, estimating aboveground biomass (AGB) in g dry weight from the predictor variable height (H). All biomass
279 equations took the form of power equations (Equation [4]). n = number of observations for each species (in total = 4097 single observations); H
280 range = height range of measured trees (cm), value in brackets stands for mean H; $\beta 1$ and $\beta 2$ = estimated model coefficients; se = standard error of the
281 regression coefficients; p = significance values of coefficients; cor = correlation between observation and fit; RMSE = root-mean-squared-error of fit;
282 R^2_{res} = coefficient of determination of residuals.

Species	n	H range (cm)		$\beta 1$	$\beta 2$	se ($\beta 1$)	se ($\beta 2$)	p ($\beta 1$)	p ($\beta 2$)	cor	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	90	40-1030	(354.1)	0.00421	2.12319	0.004	0.147	0.314	< 0.001	0.914	1397.9	0.338
Betula pendula	58	22-470	(94.0)	0	5.34264	0	0.359	0.65	< 0.001	0.958	231.1	0.147
Carpinus betulus	311	16-170	(80.8)	0.02242	1.69395	0.014	0.133	0.108	< 0.001	0.711	37.6	0.838
Fagus sylvatica	1142	8-1160	(168.0)	0.00149	2.30247	0	0.039	< 0.001	< 0.001	0.887	1005.3	0.377
Fraxinus excelsior	90	30-1213	(337.7)	0.00428	2.13866	0.004	0.135	0.278	< 0.001	0.925	1623.6	0.253
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	95	17-720	(130.7)	0.02025	1.9889	0.015	0.119	0.173	< 0.001	0.895	813.9	0.447
Pinus uncinata	46	16-29	(21.1)	0.00073	2.43282	0.001	0.337	0.351	< 0.001	0.733	0.5	0.429
Prunus avium	7	175-370	(271.7)	0	3.88746	0	0.699	0.815	< 0.05	0.953	508.5	0.09
Prunus serotina	211	90-850	(192.4)	0.00039	2.57002	0	0.079	0.052	< 0.001	0.94	772.2	0.308
Pseudotsuga menziesii	48	81-372	(201.7)	0.00457	2.11328	0.009	0.35	0.613	< 0.001	0.725	334.7	0.623
Quercus petraea	465	12-405	(64.2)	0.00737	2.01897	0.003	0.072	< 0.05	< 0.001	0.829	146	0.64
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	0.877	0.131	0.432	16.9	0.833
Robinia pseudoacacia	238	59-235	(151.2)	0.00122	2.33479	0.001	0.148	0.191	< 0.001	0.743	76.8	0.246
Salix spec	10	119-531	(338.8)	0.00001	3.1988	0	1.23	0.898	< 0.05	0.751	1393.9	0.604
Sorbus aucuparia	40	4-197	(99)	0.00109	2.16072	0.002	0.336	0.559	< 0.001	0.795	24.3	0.4
Tilia cordata	10	119-256	(178.8)	0.00074	2.58718	0.003	0.66	0.784	< 0.05	0.785	110.344	0.274

283

284

285 Table 4 Parameters of the biomass equations, estimating aboveground biomass (AGB) in g dry weight from the predictor variable RCD² H (cm³). All
286 biomass equations took the form of power equations (Equation [5]). n = number of observations for each species (in total = 4097 single observations);
287 RCD² H range = range of measured trees (cm³), value in brackets stands for mean RCD² H; β1 and β2 = estimated model coefficients; se = standard error
288 of the regression coefficients; p = significance values of coefficients; cor = correlation between observation and fit; RMSE = root-mean-squared-error of
289 fit; R²res = coefficient of determination of residuals.

Species	n	RCD² H range (cm³)		β1	β2	se (β1)	se (β2)	p (β1)	p (β2)	cor	RMSE (g)	R²res
Abies alba	399	0-47045	(2104.6)	1.87856	0.79034	0.263	0.014	< 0.05	< 0.001	0.971	364.7	0.006
Acer pseudoplatanus	90	6-93159	(15794.5)	0.20031	0.96443	0.106	0.049	0.062	< 0.001	0.956	1007.8	0.039
Betula pendula	58	2-53599	(1848.3)	0.3725	0.87948	0.04	0.01	< 0.001	< 0.001	0.998	45.2	0.003
Carpinus betulus	311	2-984	(217.9)	0.3562	0.92515	0.061	0.029	< 0.001	< 0.001	0.91	20.8	0.29
Fagus sylvatica	1142	0-132559	(4124.9)	0.62498	0.87386	0.05	0.007	< 0.001	< 0.001	0.974	490.1	0.108
Fraxinus excelsior	90	14-101911	(14945.5)	0.06826	1.07971	0.038	0.051	0.075	< 0.001	0.971	1008.2	0.036
Picea abies	368	3-72405	(3830.7)	2.24952	0.76318	0.321	0.014	< 0.001	< 0.001	0.961	559	0
Pinus sylvestris	95	2-63619	(4903.8)	0.75967	0.85003	0.231	0.03	< 0.05	< 0.001	0.975	406.8	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	7	1276-37000	(13084)	0.34369	0.91814	0.275	0.08	0.267	< 0.001	0.988	255.6	0.004
Prunus serotina	211	161-85170	(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	465	1-16366	(558.8)	0.52985	0.81162	0.1	0.022	< 0.001	< 0.001	0.893	115.4	0.453
Quercus robur	454	2-65307	(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	130-40185	(10735.7)	0.04368	1.12303	0.013	0.029	< 0.05	< 0.001	0.999	68.1	0.002
Sorbus aucuparia	40	3-1640	(271)	0.54829	0.75903	0.22	0.061	< 0.05	< 0.001	0.921	15.5	0.048
Tilia cordata	10	933-10020	(4312.4)	0.10615	1.02416	0.136	0.147	0.459	< 0.001	0.945	132.9	0.004

290 The estimated coefficient β1 ranged from 0.006 (*Tilia cordata*) to 0.4 (*Robinia pseudoacacia*)
291 for models based on RCD and was considerably smaller for the models based on H as
292 predictor (0 – 0.08). Coefficient β2 was evenly distributed around 2.5 for RCD models with a
293 maximal value of 3.02 (*Fraxinus excelsior*) and a minimal value of 1.94 (*Robinia*
294 *pseudoacacia*) (Table 2). Also for the H models, coefficient β2 was evenly distributed around
295 2.2 for most species, but three species showed β2 values out of the ordinary. Data for *Betula*
296 *pendula*, *Prunus avium* and *Salix spec* resulted in estimates for β2 that were around 5, 4, and 3
297 (Table 3), resulting in atypical curves with a pronounced slope for these species in
298 comparison to the other curves. Independent of the predictor variable (RCD, H or RCD² H),
299 coefficients β1 and β2 showed a negative correlation, for small values of β1 (RCD: β1 < 0.1,
300 correlation = -0.7862; H: β1 < 0.01, correlation = -0.3641; RCD² H: β1 < 1, correlation = -
301 0.8733), as also observed by Pilli et al. (2006) and Zianis and Mencuccini (2004).
302 Due to the considerable variety of single species observations, the significance of the
303 estimated coefficients (β1, β2) differed among the species (Table 2, Table 3, Table 4). With
304 RCD and RCD² H as predictor, all estimators for coefficient β2 were significant and also most
305 estimations of coefficient β1 (n = 11, n = 14, respectively). Coefficient β1 was particularly not
306 significantly different from zero for species with small numbers of observations (e.g. *Prunus*
307 *avium*, *Quercus rubra*, *Tilia cordata*), with *Acer pseudoplatanus* and *Fraxinus excelsior*
308 forming an exception. With H as predictor, also all estimators for coefficient β2 were
309 significant, aside of the estimations for *Quercus rubra*, where both coefficients were not
310 significant. However, most estimations of coefficient β1 were not significantly different from
311 zero (n = 14), whereby the coefficients β1 were very close to zero in the first place for the H
312 models.
313 For generic biomass equations, the original data were aggregated into conifer species and
314 broadleaf species and analyzed with respect to the same predictor variables as the species-
315 specific data (Fig. 3 a – d). Resulting generic biomass equations were:
316

$$AGB = 0.02822 \; RCD^{2.809} \qquad \text{(broadleaf species)} \qquad\qquad [11]$$

$$AGB = 0.1691 \; RCD^{2.369} \qquad \text{(conifer species)} \qquad\qquad [12]$$

$$AGB = 0.002597 \; H^{2.217} \qquad \text{(broadleaf species)} \qquad\qquad [13]$$

$$AGB = 0.02398 \; H^{1.982} \qquad \text{(conifer species)} \qquad\qquad [14]$$

$$AGB = 0.3613 \; RCD^2 \; H^{0.9217} \qquad \text{(broadleaf species)} \qquad\qquad [15]$$

$$AGB = 1.687 \; RCD^2 \; H^{0.7899} \qquad \text{(conifer species)} \qquad\qquad [16]$$

with AGB = aboveground biomass (g); RCD = root-collar-diameter (mm); H = height (cm);
mathematical model based on Equations [3], [4] and [5].
317

318 Estimated coefficients were significant for all models (p < 0.001). For the RCD models, the
319 standard error of the associated regression coefficients was se (β1) = 0.003 and
320 se (β2) = 0.023 for broadleaves and se (β1) = 0.022 and se (β2) = 0.03 for conifers.

For the H models, the standard error of the associated regression coefficients was se ($\beta 1$) = 0.00035 and se ($\beta 2$) = 0.021 for broadleaves and se ($\beta 1$) = 0.0056 and se ($\beta 2$) = 0.038 for conifers.

Finally, the the standard error of the associated regression coefficients for the RCD² H models was se ($\beta 1$) = 0.0208 and se ($\beta 2$) = 0.0054 for broadleaves and se ($\beta 1$) = 0.159 and se ($\beta 2$) = 0.0093 for conifers.

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 RCD² H models (R^2_{res} = 0.14, R^2_{res} = 0.01, respectively), but higher for H models (R^2_{res} = 0.38, R^2_{res} = 0.53, respectively). Confidence intervals for the coefficients of the models were wider for the H models, compared to the RCD models and RCD² H models Fig. 3 a – f, shaded grey area. Confidence intervals widened for all models in the direction of increasing RCD, H or RCD² H. In addition, values for the upper confidence limits were higher for all six models and both coefficients, compared to the lower confidence limits. Confidence limits were:

RCD model – broadleaf:
$\beta 1$ (2.5%, 97.5%) = 0.023, 0.034; $\beta 2$ (2.5%, 97.5%) = 2.764, 2.855;
RCD model – conifer:
$\beta 1$ (2.5%, 97.5%) = 0.1255, 0.2128; $\beta 2$ (2.5%, 97.5%) = 2.309, 2.429;
H model – broadleaf:
$\beta 1$ (2.5%, 97.5%) = 0.002, 0.003; $\beta 2$ (2.5%, 97.5%) = 2.177, 2.258;
H model – conifer:
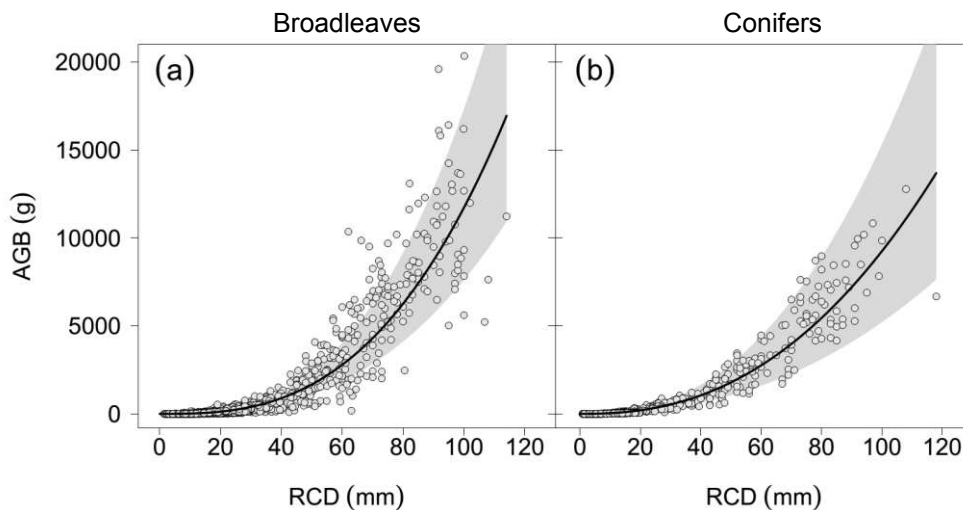$\beta 1$ (2.5%, 97.5%) = 0.013, 0.035; $\beta 2$ (2.5%, 97.5%) = 1.906, 2.057;
RCD² H model – broadleaf:
$\beta 1$ (2.5%, 97.5%) = 0.321, 0.402; $\beta 2$ (2.5%, 97.5%) = 0.911, 0.932;
RCD² H model – conifer:
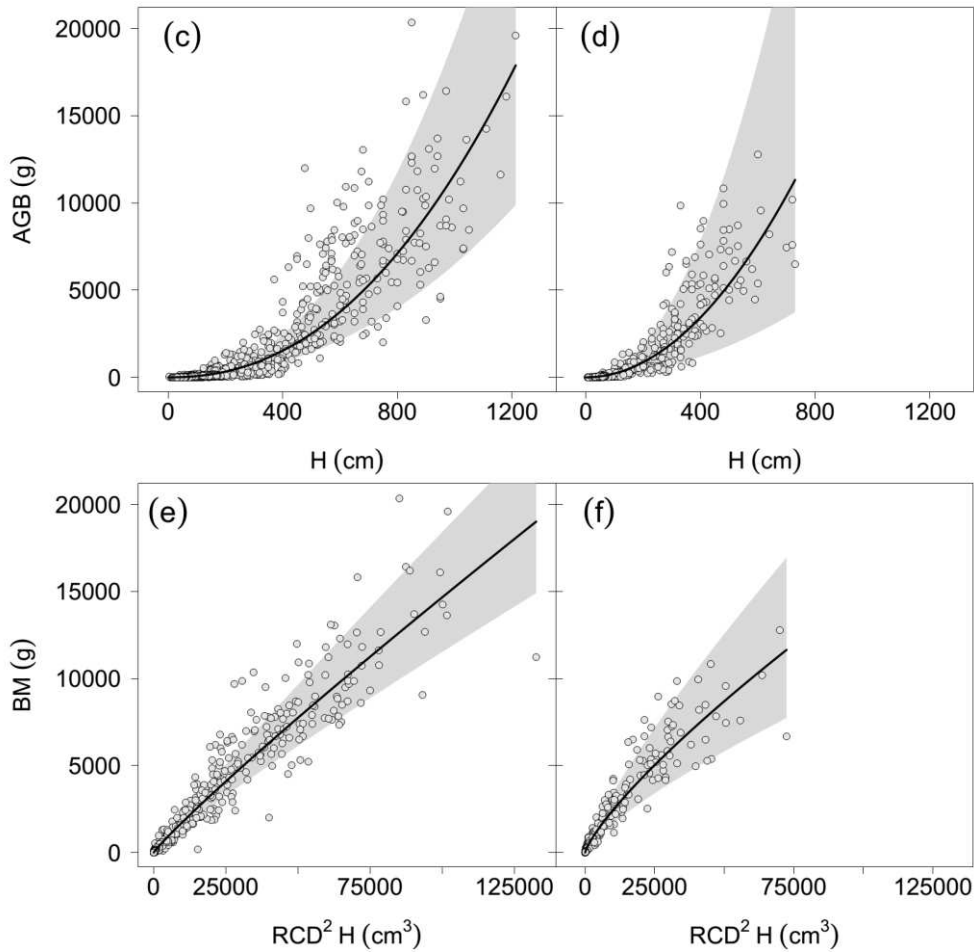$\beta 1$ (2.5%, 97.5%) = 1.375, 1.999; $\beta 2$ (2.5%, 97.5%) = 0.772, 0.808.

Fig. 3 Generic biomass curves (compare Equations [11] – [16]) based on root-collar-diameter (RCD) (a) and (b), height (H) (c) and (d), and RCD² 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 = 3269 (a), n = 956 (b), n = 3141 (c), n = 956 (d), n = 3141 (e), and n = 956 (f). Correlations between observation and fit were cor = 0.93 (a), cor = 0.95 (b), cor = 0.9 (c), cor = 0.89 (d), cor = 0.97 (e), and cor = 0.96 (f). Root-mean-squared-errors of fit were RMSE = 674.2 g (a), RMSE = 516.3 g (b), RMSE = 808.8 g (c), RMSE = 801.5 g (d), RMSE = 466 g (e), and RMSE = 475.5 g (f).

349

350 The generic RCD-H curves showed the strong relationship between both variables for
351 broadleaves and conifers (Fig. 4 a, b) and resulted in significant models (p < 0.001). Generic
352 height equations were:

353

$$H = 6.73 \, RCD + 0.0201 \, RCD^2 \qquad \text{(broadleaf species)} \qquad [17]$$

$$H = 5.49 \, RCD + 0.0001 \, RCD^2 \qquad \text{(conifer species)} \qquad [18]$$

with H = height (cm); RCD = root-collar-diameter (mm); mathematical model based on Equation [10].

354

355 Estimated coefficients (β_1, β_2) were significant for broadleaf species. For conifer species
356 coefficient β_1 was significantly different from zero, but β_2 was not (p = 0.957). Both models
357 had high coefficients of determination around 0.9, but the residual standard error was higher
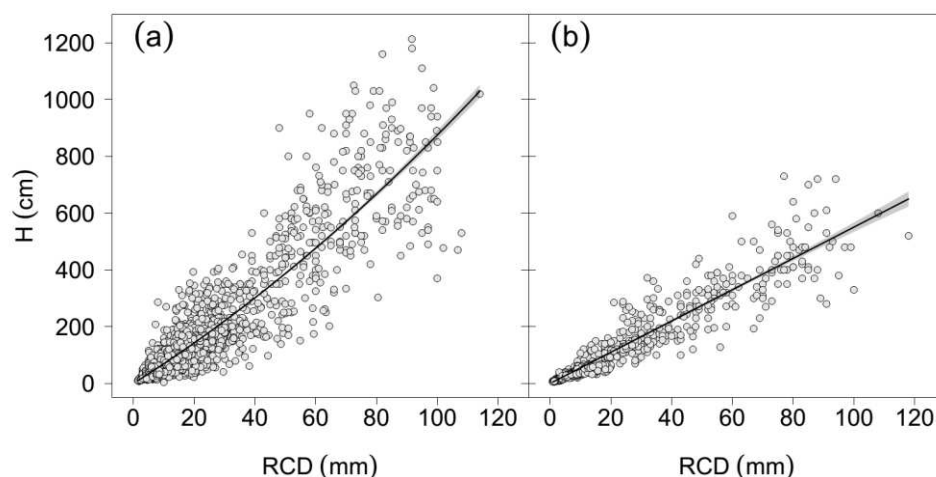358 for the broadleaf species, compared to the conifer species.

Fig. 4 Generic root-collar-diameter (RCD) – height (H) curves (compare Equations [15], [16]) with confidence intervals (shaded gray area) for broadleaf (a) and conifer (b) species. Number of observations were n = 3269 (a), n = 956 (b). The coefficient of determination was R² = 0.896 (a) and R² = 0.931 (b). Residual standard error in cm was RSE = 69.8 (a) and RSE = 43.6 (b).

Discussion

All species-specific biomass equations (Tables 2, 3, 4; Appendix B, C, D) were statistically significant (p < 0.05) and RCD proved to be a better single predictor variable than H, resulting in lower root-mean-squared-errors (RMSE) on average for the regeneration of forest trees. Even lower root-mean-squared-errors (RMSE) could be achieved on average (-21%) when using the predictor RCD² H instead of only RCD. Hence, the equations presented are a comprehensive collection to predict the biomass of forest regeneration and an alternative to existing non-destructive estimation approaches for young trees (Bolte et al. 2009; Norgren et al. 1995). Eventhough 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 (Equations [11] – [16]) 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 example presented a fractal model based on trunk diameter that suggested coefficient β2 taking a value of 8/3 (≈ 2.67), based on allometric theory. Zianis and Mencuccini (2004) calculated an empirical scaling exponent of β2 = 2.3679 based on a list of biomass equations. Differences of β2 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 β2 = 2.809 and β2 = 2.369, respectively (Equations [11], [12]), which is quite close to the values. Also species-specific root-collar-diameter dependent biomass equations (Table 2) resulted in an β2 value 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 β2 (< 2) are often reported for small plants (< a few meters). The estimates for β2 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

387 biomass estimation (e.g. Bjarnadottir et al. 2007; Gonzalez-Benecke et al. 2014a; Repola
388 2008). Aside of using the predictor RCD² H as combination of both, we decided not to use
389 height and diameter alone in the same equations, disregarding the fact that the data basis
390 would have allowed using such combinations. The main reason for this was that diameter and
391 height are highly collinear (Fig. 4). Not considering collinearity or multicollinearity of the
392 independent variables when used separately in regression analysis might result in biased
393 predictions (Ott 1993).
394 However, we also generally believe that measuring diameter and height of the regeneration is
395 quite laborious for large sample sizes, but is required for all biomass equations based on both
396 variables as predictors (e.g. Equations [5], [6], Table 4). Eventhough the predictor RCD² H
397 reduced the root-mean-squared-errors (RMSE), we suppose that the estimates solely based on
398 RCD result in comparably accurate biomass estimates (compare: correlation between
399 observation and fit in Tables 2 and 4), so that the additional work for also measuring H is not
400 necessarily justified for forest inventories.
401 The variability around the biomass equations increased with size of the explanatory variable
402 (Fig. 3), which is common for biomass equations (Zianis and Mencuccini 2004). Chave et al.
403 (2001) reported that the values of the estimated coefficients are strongly affected by the small
404 trees in the data set. This was also the case here because of the higher amount of
405 measurements of seedlings compared to saplings. The effect of small trees was particularly
406 pronounced for the logarithmically transformed data after back-transformation (Appendix B,
407 Appendix C, Appendix D), resulting in steep slopes for larger height and diameters and
408 possibly overestimating this part of the data, which can be problematic, aside of introducing a
409 bias through transformation. Applying nonlinear least square regressions allowed avoiding
410 these problems and we decided to give weights to our data to not systematically overestimate
411 the small range of the data in return. We consider this a pragmatic approach for biomass
412 estimation.
413 In regeneration stands, site conditions such as light availability, soil properties and resource
414 competition, can be expected to be among the most decisive factors determining growth rates,
415 especially height growth but also diameter, and growth architecture, in terms of biomass
416 allocation. Data compiled for this study represented a wide range of growth conditions,
417 especially for species with high numbers of plots and data sources, e.g. *Abies alba*, *Fagus*
418 *sylvatica* (Table 1), so that the provided equations can be assumed to be applicable for central
419 Europe (compare Wirth et al. 2004). Nevertheless, caution should be generally taken when
420 biomass estimates are extrapolated from plot to regional scale (Satoo and Madgwick 1982;
421 Zianis et al. 2005). In addition, each original study has been conducted for different purposes,
422 e.g. competition experiment (KAW2013), site preparation experiment (LOE2006),
423 provenance trial (GEL2001), and under different growth conditions, e.g. in situ (AME2013,
424 ANN2012), ex situ (BAL2011, KAW2013), differing light availability (PRO2008,
425 SCH2012), which may have increased the natural variability of the data or may have
426 introduced atypical plant architectures. The high variability of the data in combination with
427 the up to now limited size of the data base, in turn, hampered a detailed analysis of regional
428 differences in tree allometry or the effect of specific treatments, site or stand conditions.
429 These limitations should be considered when applying the presented biomass equations at plot
430 or stand scale.

431 Against this background, it would be highly desirable to minimize methodological differences
432 among biomass studies, by standardizing their methodologies (e.g. height of diameter
433 measurement, inclusion and / or exclusion of leaves and needles) as also claimed by Bi et al.
434 (2015), Cifuentes Jara et al. (2015b), and Cifuentes Jara et al. (2015a). Also, a standardized
435 quantification of the main site and stand factors influencing the allocation of tree growth (e.g.
436 light and water availability, soil properties, density, age, structure) could result in more
437 accurate general model predictions (e.g. Alemdag and Stiell 1982; António et al. 2007; Brown
438 1997; Gonzalez-Benecke et al. 2014b). Standards would facilitate compilation, evaluation and
439 application of existing and future biomass equations.

Acknowledgments

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Appendix

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

All co-authors: please, check this table and correct/ complement it where necessary

No.	Data set	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
(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
(3)	ANN2012	Ticino, Italy	2010	Prunus serotina (35)	Annighöfer et al. (2012) Biomass functions for the two alien tree speciesPrunus serotina Ehrh. and Robinia pseudoacaciaL. in floodplain forests of Northern Italy
(4)	BAL2007	Fontfreyde, France	2007	Fagus sylvatica (10)	Unpublished data
(5)	BAL2009	Fontfreyde, France	2009	Fagus sylvatica (9)	Unpublished data
(6)	BAL2011	Clermont-Ferrand, France (Greenhouse)	2011	Quercus petraea (24)	Unpublished data (laut Excel Sheet)
(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. **AND** 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	1983; 1993; 2000	Quercus petraea (426)	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. **AND** 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. **AND** Collet C, Frochot H, Ningre F 1999 Développement de jeunes chênes soumis à une compétition souterraine. Revue Forestière Française, 51: 298-308. FÜR Q. ROBUR (die ich rausgeschmissen habe, weil Daten fehlerhaft sein müssen!)
(9)	EWB2009	Bayrischer Wald, Germany	2009	Abies alba (40), Fagus sylvatica (40), Picea abies (40), Sorbus aucuparia (40)	Promberger (2010) Biomasse und sommerliches Äsungsangebot von Jungbäumen im Nationalpark Bayerischer Wald. Diplomarbeit
(10)	GEB2013	Göttingen, Germany greenhouse	2013	Acer pseudoplatanus (12), Fagus sylvatica (6), Fraxinus excelsior (12)	Masterarbeit, unpublished data

		experiment			
(11)	GEL2001	Graupa, Germany	2001	Fagus sylvatica (32)	Gellrich M, Steinke C, Schröder J (2001) Ergebnisse der Biomasseuntersuchungen für Probebäume des Buchenprovenienzversuches auf der Versuchsfläche "Pflanzgarten", LAF Graupa. Ergebnissbericht Technische Universität Dresden
(12)	HAB2009	Bechsted, Germany	2009 (?) gehört zu Kahl und Wirth	Fagus sylvatica (3), Tilia cordata (9)	
(13)	HAM2014	Sachsen, Germany	2010	Abies alba (194)	Hamm et al. (2014) Wachstumsreaktionen junger Weißtannen-Voraussaaten auf Begleitvegetation und Strahlungskonkurrenz. AFJZ 185:45-59
(14)	HIR2010	Sachsen, Germany	2010	Fagus sylvatica (88)	Masterarbeit (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. Fachrichtung Forstwissenschaften Tharandt 2011), unpublished data
(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 ?	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 vonBiomassefunktionenfürVerjüngungs-Bäume("NichtDerbholz"-Kollektiv) – erste Ergebnisse. DVFFA– Sektion Ertragskunde, Jahrestagung 2006
(17)	KAH2009	Bechsted, Germany	2009	Acer pseudoplatanus (12), Fagus sylvatica (5), Fraxinus excelsior (15), Prunus avium (7), Quercus petraea (15), Tilia cordata (1)	
(18)	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 &:305-315
(19)	KUE2011	Freiburg, Germany	2008	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 saplings). Forstarchiv 82, 184-194. **AND** Merkel (2009) Zur Ästigkeit von Douglasie unter Schirm. Diplomarbeit
(20)	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
(21)	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
(22)	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. **AND**: 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.
(23)	MUE2011	Freiburg, Germany	2011	Betula pendula (11), Pinus sylvestris (10), Salix spec (10)	Scherer-Lorenzen, M., Schulze, E.-D., Don, A., Schumacher, J. & Weller, E. (2007) Exploring the functional significance of forest diversity: A new long-term experiment with temperate tree species (BIOTREE). Perspectives in Plant Ecology, Evolution and Systematics, 9, 53-70. **FOR DETAILS ON SOIL, BUT DATA SAMPLING FROM 2011!**
(24)	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, 9p.; **and partly (? Not sure?) in**: Coll et al. (2003) Morphological and physiological responses of beech (Fagus sylvatica) seedlings to grass-induced belowground competition. Tree physiology 24:45-54
(25)	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 Manag 266:246-253

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Appendix B. Parameters of the biomass equations, estimating aboveground biomass (AGB) from the predictor variable root-collar-diameter (RCD). All models were significant (p < 0.001). Biomass equations took the form of Equation [6]. Parameters are: n = number of observations for each species (total = 4225 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 $\beta1$ (Equation [9]); $\exp(\beta1)$ = back-transformed anti-log of $\beta1$ multiplyed with CF; R^2 = multiple R-squared of the model; RSE = residual standard error.

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	130	-3.59	2.797	0.104	0.034	< 0.001	< 0.001	1.072	0.03	0.981	0.373
Betula pendula	58	-3.67	2.72	0.181	0.088	< 0.001	< 0.001	1.172	0.03	0.944	0.564
Carpinus betulus	311	-3.59	2.73	0.153	0.059	< 0.001	< 0.001	1.104	0.03	0.874	0.445
Fagus sylvatica	1182	-3.565	2.846	0.04	0.015	< 0.001	< 0.001	1.092	0.031	0.968	0.419
Fraxinus excelsior	90	-3.965	2.927	0.207	0.061	< 0.001	< 0.001	1.14	0.022	0.963	0.513
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	95	-3.508	2.728	0.095	0.034	< 0.001	< 0.001	1.08	0.032	0.985	0.392
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	7	-2.044	2.306	0.596	0.148	< 0.05	< 0.001	1.014	0.131	0.98	0.165
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	465	-3.918	2.565	0.1	0.038	< 0.001	< 0.001	1.137	0.023	0.906	0.506
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	40	-2.663	2.325	0.378	0.157	< 0.001	< 0.001	1.174	0.082	0.853	0.567
Tilia cordata	10	-3.284	2.485	1.2	0.317	< 0.05	< 0.001	1.041	0.039	0.885	0.282

Appendix C. Parameters of the biomass equations, estimating aboveground biomass (AGB) from the predictor variable height (H). All models were significant ($p < 0.001$), exept for Q. rubra ($p = 0.049$). Biomass equations took the form of Equation [7]. Parameters are: n = number of observations for each species (total = 4097 single observations); $\beta 1$ and $\beta 2$ = estimated model coefficients; se = standard error of the regression coefficients; p = significance values of coefficients; CF = correction factor for back-transformation of $\beta 1$ (Equation [9]); exp($\beta 1$) = back-transformed anti-log of $\beta 1$ multiplyed with CF; R^2 = multiple R-squared of the model; RSE = residual standard error.

Species	n	$\beta 1$	$\beta 2$	se($\beta 1$)	se($\beta 2$)	p($\beta 1$)	p($\beta 2$)	CF	exp($\beta 1$)	R^2	RSE
Abies alba	399	-8.072	2.829	0.089	0.025	< 0.001	< 0.001	1.236	0.00038589	0.97	0.651
Acer pseudoplatanus	90	-8.598	2.598	0.325	0.059	< 0.001	< 0.001	1.172	0.0002162	0.957	0.564
Betula pendula	58	-10.372	2.862	0.414	0.098	< 0.001	< 0.001	1.194	0.00003737	0.938	0.596
Carpinus betulus	311	-5.916	2.168	0.357	0.083	< 0.001	< 0.001	1.275	0.00343802	0.69	0.697
Fagus sylvatica	1142	-7.33	2.386	0.099	0.021	< 0.001	< 0.001	1.255	0.00082251	0.92	0.674
Fraxinus excelsior	90	-7.818	2.504	0.37	0.068	< 0.001	< 0.001	1.24	0.00049889	0.939	0.655
Picea abies	368	-5.486	2.316	0.128	0.029	< 0.001	< 0.001	1.122	0.00465274	0.946	0.481
Pinus sylvestris	95	-9.001	2.886	0.275	0.063	< 0.001	< 0.001	1.248	0.00015394	0.958	0.666
Pinus uncinata	46	-5.879	1.997	1.075	0.354	< 0.001	< 0.001	1.084	0.00303008	0.42	0.401
Prunus avium	7	-14.967	3.978	2.342	0.42	< 0.05	< 0.001	1.036	0.00000033	0.947	0.267
Prunus serotina	211	-5.448	2.175	0.313	0.061	< 0.001	< 0.001	1.091	0.00469647	0.859	0.418
Pseudotsuga menziesii	48	-7.99	2.583	0.786	0.15	< 0.001	< 0.001	1.132	0.00038354	0.865	0.497
Quercus petraea	465	-6.516	2.33	0.199	0.05	< 0.001	< 0.001	1.274	0.00188429	0.823	0.695
Quercus robur	454	-6.007	2.213	0.197	0.048	< 0.001	< 0.001	1.285	0.00316311	0.822	0.708
Quercus rubra	15	-8.935	2.646	5.563	1.217	0.132	< 0.05	1.21	0.00015937	0.267	0.617
Robinia pseudoacacia	238	-7.493	2.488	0.536	0.107	< 0.001	< 0.001	1.106	0.0006159	0.695	0.449
Salix spec	10	-16.01	3.876	2.353	0.409	< 0.001	< 0.001	1.189	0.00000013	0.918	0.588
Sorbus aucuparia	40	-2.56	1.22	1.02	0.23	< 0.05	< 0.001	1.869	0.14446644	0.426	1.118
Tilia cordata	10	-9.848	3.09	2.772	0.537	< 0.05	< 0.001	1.07	0.00005651	0.806	0.367

616 Appendix D. Parameters of the biomass equations, estimating aboveground biomass (AGB) from the predictor variable RCD² H (both in cm). All
617 models were significant (p < 0.001). Biomass equations took the form of Equation [8]. Parameters are: n = number of observations for each species
618 (total = 4097 single observations); β1 and β2 = estimated model coefficients; se = standard error of the regression coefficients; p = significance
619 values of coefficients; CF = correction factor for back-transformation of β1 (Equation [9]); exp(β1) = back-transformed anti-log of β1 multiplyed
620 with CF; R² = multiple R-squared of the model; RSE = residual standard error.

Species	n	β1	β2	se(β1)	se(β2)	p(β1)	p(β2)	CF	exp(β1)	R²	RSE
Abies alba	399	-0.672	0.956	0.022	0.016	< 0.001	< 0.001	1.076	0.549	0.99	0.383
Acer pseudoplatanus	90	-1.228	0.922	0.076	0.034	< 0.001	< 0.001	1.036	0.303	0.99	0.265
Betula pendula	58	-1.67	0.948	0.092	0.088	< 0.001	< 0.001	1.092	0.206	0.969	0.42
Carpinus betulus	311	-1.195	0.955	0.082	0.059	< 0.001	< 0.001	1.069	0.323	0.915	0.364
Fagus sylvatica	1142	-1.033	0.922	0.022	0.015	< 0.001	< 0.001	1.054	0.375	0.982	0.323
Fraxinus excelsior	90	-1.314	0.949	0.112	0.061	< 0.001	< 0.001	1.074	0.289	0.98	0.377
Picea abies	368	-0.164	0.868	0.042	0.029	< 0.001	< 0.001	1.052	0.892	0.976	0.317
Pinus sylvestris	95	-1.062	0.939	0.057	0.034	< 0.001	< 0.001	1.056	0.365	0.99	0.331
Pinus uncinata	46	-0.828	0.798	0.132	0.274	< 0.001	< 0.001	1.056	0.461	0.606	0.331
Prunus avium	7	-0.931	0.905	0.458	0.148	0.098	< 0.001	1.01	0.398	0.985	0.144
Prunus serotina	211	-0.774	0.921	0.107	0.06	< 0.001	< 0.001	1.033	0.476	0.947	0.256
Pseudotsuga menziesii	48	-0.626	0.89	0.132	0.07	< 0.001	< 0.001	1.019	0.545	0.98	0.194
Quercus petraea	465	-1.341	0.898	0.045	0.038	< 0.001	< 0.001	1.068	0.279	0.952	0.364
Quercus robur	454	-0.772	0.893	0.047	0.037	< 0.001	< 0.001	1.088	0.503	0.941	0.41
Quercus rubra	15	-1.397	0.931	0.342	0.207	< 0.05	< 0.001	1.018	0.252	0.933	0.186
Robinia pseudoacacia	238	-0.622	0.865	0.155	0.073	< 0.001	< 0.001	1.052	0.565	0.846	0.319
Salix spec	10	-2.103	1.013	0.387	0.111	< 0.05	< 0.001	1.035	0.126	0.984	0.262
Sorbus aucuparia	40	-0.432	0.721	0.297	0.157	0.153	< 0.001	1.269	0.824	0.781	0.691
Tilia cordata	10	-1.447	0.931	0.866	0.317	0.133	< 0.001	1.033	0.243	0.906	0.256