



Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate



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ABSTRACT

Biomass and leaf area equations are often required to assess or model forest productivity, carbon stocks and other ecosystem services. These factors are influenced by climate, age and stand structural attributes including stand density and tree species diversity or species composition. However, such covariates are rarely included in biomass and leaf area equations. We reviewed the literature and built a database of biomass and leaf area equations for 24 European tree species and 3 introduced species. The final dataset contained 973 equations. Most of the equations were site-specific and therefore restricted to the edaphic, climatic and stand structural conditions of the given site. To overcome this limitation, the database was used to develop regional species-specific equations that can be used in a wide range of stands and to quantify the effects of climate, age and stand structure on biomass or leaf area. The analysis showed considerable inter- and intra-specific variability in biomass relationships. The intra-specific variability was related to climate, age or stand characteristics, while the inter-specific variability was correlated with traits such as wood density, specific leaf area and shade tolerance. The analysis also showed that foliage mass is more variable than stem or total aboveground biomass, both within and between species, and these biomass components have contrasting responses to age and changes in stand structure. Despite the large number of published equations, many species are still not well represented. Therefore, generic equations were developed that include species-specific wood density instead of species identity. Further improvements may be possible if future studies quantify the stand structure of individual tree neighbourhoods instead of using the stand means for all trees sampled with the given stand.

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1. Introduction

Allometric relationships are critical for quantifying many aspects of ecology and forestry including the prediction of tree and stand variables to assess productivity, carbon stocks and other

ecosystem services at the tree, stand, landscape or regional levels (Henry et al., 2013; Chave et al., 2014; Paul et al., 2016). They are also required when quantifying or modelling forest functioning, such as how light, water, nutrient and carbon pools and fluxes respond to changes in climate or management.

Allometric relationships are often expressed in the form of Eq. (1), implying a 1% change in variable X will result in a b% change in variable Y.

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$$Y = aX^{b_{yx}} \quad (1)$$

The value of the exponent b has been hotly debated (Silesi, 2014) and hypothesised to relate to mechanical constraints that prevent trees from buckling (Greenhill, 1881; McMahon, 1973), hydraulic constraints (Ryan et al., 2006) and biophysical constraints. Contributions regarding the biophysical constraints include geometric scaling (Yoda et al., 1963; Gorham, 1979; Pretzsch et al., 2012), which suggests proportionality between different linear dimensions; linear tree dimensions (e.g., diameter) are related to quadratic or area-related dimensions (e.g., leaf area) as linear \propto quadratic^{1/2} and to cubic variables (e.g., biomass) as linear \propto cubic^{1/3} or quadratic \propto cubic^{2/3}. In contrast, the metabolic scaling theory describes resource distribution along hierarchical branching networks (West et al., 1999, 2009) and predicts that $b_{\text{biomass, diameter}} = 8/3$, $b_{\text{leaf area, diameter}} = 4/3$ (Pretzsch et al., 2012). However, b is usually not invariant for these relationships and the frequency distribution of b is not necessarily centred on the value of b predicted by the geometric or metabolic scaling theories (Coomes, 2006; Pretzsch, 2006; Ducey, 2012; Lines et al., 2012; Pretzsch and Dieler, 2012; Pretzsch et al., 2012, 2013; Silesi, 2014). Therefore, while the general allometric exponents may be useful for rough scaling they are less useful for modelling stand growth dynamics or for developing biomass and leaf area equations to upscale from tree measurements.

The variability in the exponent b is related to the fact that allometric relationships reflect current and past environmental conditions and provide information about within-tree carbon partitioning, which affects a tree's ability to acquire and compete for resources. Therefore, allometric relationships between diameter and biomass (foliage, stems or roots) or leaf area can vary with age (Wirth et al., 2004; Genet et al., 2011; Shaiek et al., 2011), stand density (Monserud and Marshall, 1999), species mixing (Laclau et al., 2008) and site characteristics (Wirth et al., 2004; Russell et al., 2015). As a result, equations developed using trees sampled from a single stand may be unbiased and precise for that situation but they are unlikely to be suitable for other ages or stands that differ in structure, climate or site characteristics (Muukkonen, 2007). Despite this, variables describing age, site and stand structural characteristics such as density, species composition or diversity are rarely included in biomass equations (Zianis et al., 2005) because this would require a larger sample of trees from a range of ages and site conditions.

In a recent review, only about 24% of equations were found to contain more than one independent variable, usually diameter (Henry et al., 2011). Nevertheless, for some species there are already many published biomass equations (Zianis et al., 2005) and the suitability of each equation for use in different stands can be determined, for example, by sampling some trees and comparing the measured biomass with the biomass predicted by the published site-specific equations (Freese, 1960; Pérez-Cruzado et al., 2015). However, this requires destructive biomass sampling in each target stand. It also requires that there is a published equation suitable for that stand, for which the likelihood declines as the number of published equations declines. An alternative approach is to use all of the published site-specific equations to develop new "regional" allometric equations that include independent variables such as climate, age, stand density and any other important site characteristics.

Several studies have developed regional species-specific or even generic (species independent) biomass equations (Pastor et al., 1984; Wirth et al., 2004; Lambert et al., 2005; Case and Hall, 2008; Seidl et al., 2010; Shaiek et al., 2011; Chave et al., 2014; de-Miguel et al., 2014; Paul et al., 2016). These often combine raw data from many different studies, but such data do not exist for many species or regions, or biomass data that was used to

develop site-specific equations has been lost or is unavailable. Therefore, some studies have used pseudo-observations calculated from published equations, such as predicted biomass values for each 1-cm or 5-cm diameter class (Jenkins et al., 2003; Muukkonen, 2007; Chojnacki et al., 2014) or a given number of pseudo-observations between the range of diameters sampled to produce the given site-specific equation (Pastor et al., 1984). Regardless of the approach used, most of the resulting regional or generic equations (i.e. generalized equations) have included only tree-level variables (e.g., diameter, height) and/or species-level variables (e.g., wood density) and therefore average out or group the variability in tree biomass that might otherwise be explained by age, climate, soils, stand density or species mixing (Wirth et al., 2004; Chojnacki et al., 2014; Weiskittel et al., 2015). Such variables could facilitate the development of biomass equations that are applicable to a wider range of sites and stands, and can be used to examine the effects of these factors on stand growth and biomass stocks.

Despite the large number of published equations, many European species are still not well represented. Therefore, the first objective of this study was to develop a database containing biomass and leaf area equations for 24 European tree species and 3 introduced species (*Pseudotsuga menziesii*, *Robinia pseudoacacia* and *Prunus serotina*) that are currently considered important by European foresters. The review of the literature resulted in a total of 973 equations, including raw data sets obtained from tables in publications or from our previous work. These data were used to test the hypotheses that: (1) foliage or branch mass are more variable than stem, coarse root or total aboveground biomass; (2) age, trees per hectare, basal area and climate all influence the relationships between tree diameter and biomass or leaf area; (3) these variables have contrasting effects on different biomass components; (4) there are significant differences between species in terms of their response to age, trees per hectare, basal area and climate, and these differences vary in relation to traits such as specific leaf area, wood density and shade tolerance. Our second objective was to develop generalized regional equations for each species, or species group, and each biomass component or leaf area, which include the independent variables age, trees per hectare, basal area, mean annual precipitation or mean annual temperature and can therefore be used in a wider range of forest types.

2. Material and methods

2.1. Selection of equations

A literature search was used to find biomass and leaf area equations for 27 species (and several species groups) summarised in Table 1. For most species the equations included a wide range of sites across the current species distributions within Europe and are therefore assumed to be representative of the given species within Europe. These ranges, for each species, are indicated in Table 2 in terms of stand and site characteristics. Species selection was based on the availability of equations, but also reflects the economic importance of the species. Equations were excluded when the diameter range or number of sample trees was not provided. They were also excluded when they did not include diameter at 1.3 m as an independent variable. Equations based on root collar diameter (often 0.1 m) were also excluded. Height-diameter relationships for a given species can vary with age and site characteristics (Watt and Kirschbaum, 2011). Therefore to avoid adding bias that may result from height predictions, equations with height were only used when no diameter-only equations were available from the same study. If height was included in the equation, it was predicted using the diameter-height equation provided in

Table 1

The number of published equations or data sets found for each component.

Species	Equations per species distribution ^a	Number of equations/raw data sets								
		Foliage mass or leaf area	Live branch	Dead branch	Live & dead branch	Stem	Stem & branch	Aboveground	Root	Total ^c
<i>Abies alba</i>	6.7	1				3	1	4	1	0/10
<i>Acer pseudoplatanus</i>	(>110)	3			5	5	7	1	1	1/21
<i>Alnus glutinosa</i>	48.6	3			3	4	3	4	1	0/18
<i>Alnus incana</i>	(>100)	4			4	3	4	4	1	0/20
<i>Betula pendula</i>	8.7	2			5	5	5	3		6/14
<i>Betula pubescens</i>	5.4	3	1	1	4	4	4	8	1	0/26
<i>B. pendula</i> or <i>B. pubescens</i> ^b	10.1	7	3	3	13	13	17	13	3	12/60
<i>Carpinus betulus</i>	14	1			4	3	4	1	1	0/14
<i>Castanea sativa</i>	27.3	4			5	6	5	9	1	0/30
<i>Fagus sylvatica</i>	9.9	10	2	1	13	12	14	9	10	3/68
<i>Fraxinus excelsior</i>	58.7	7			7	7	10	4	2	3/34
<i>Larix decidua</i>	36.1	4	3	3	5	5	4	5	1	0/30
<i>Picea abies</i>	6	28	12	12	19	15	16	18	7	16/111
<i>Pinus cembra</i>	(>10.0)							2		0/2
<i>Pinus nigra</i>	8.6	2			2	3	1	5	2	3/12
<i>Pinus pinaster</i>	25	14	1	1	10	14	6	14	5	6/59
<i>Pinus sylvestris</i>	3.5	22	7	7	16	15	18	15	9	2/107
<i>Populus alba</i>	(>30)	1			1	1	1	1	1	0/6
<i>Populus tremula</i>	25.4	3			3	4	3	3		0/16
<i>P. alba</i> , <i>P. tremula</i> and <i>P. tremula hybrids</i> ^b	5				10	11	11	6	1	12/31
<i>Prunus avium</i>	(>10)	2								0/2
<i>Prunus serotina</i>	1				2	2	3	1		0/9
<i>Pseudotsuga menziesii</i>	342.6	40	17	14	23	26	18	19	4	15/138
<i>Quercus ilex</i>	13.5	5			4	5	5	7	3	5/24
<i>Quercus petraea</i>	9.1				4	5	11		1	13/8
<i>Quercus robur</i>	9	3			6	6	8	2	2	13/14
<i>Q. petraea</i> or <i>Q. robur</i> ^b	11.3	3	1		13	13	24	2	4	27/33
<i>Robinia pseudoacacia</i>	51.9	3			6	6	5	4	3	0/27
<i>Sorbus aucuparia</i>	(>25)	1			1	1	1	1		0/5
<i>Tilia cordata</i> or <i>platyphyllas</i>	15					1	1	1		0/3

^a The number of equations divided by the percentage of Europe's forest area where that species occurs (from Köble and Seufert, 2001). The numbers in parentheses are for species that had no area available in Köble and Seufert (2001), so their area was assumed to occupy <0.2%, which would result in the numbers in parentheses.

^b Several species from the same genera were grouped because some studies did not differentiate the species. For such groups, the data from each species was combined (not only the studies that did not differentiate the species).

^c Number of raw data sets/number of equations.

the given study or published diameter-height equations (Merganič et al., 2011; Pretzsch et al., 2013; Özcelik et al., 2014). The predicted range in height was forced to match the height range reported for the sample trees by multiplying all values by a constant, thereby preserving the shape of the height-diameter relationship. Equations with incorrect parameters (identified by their implausible biomass or leaf area predictions) were also not used. While several general equations have been developed for some of the species in Table 1 (Wirth et al., 2004; Muukkonen, 2007), we did not use those general equations and instead aimed to use the equations that were used to develop those general equations.

Many different biomass components can be defined for trees, but for a given component the definitions can vary between studies. For example, roots may be sampled down to minimum diameters of 1 cm, 0.5 cm or 0.2 cm (Jenkins et al., 2003; Wirth et al., 2004), stem can begin at the base of the tree and extend up to a minimum diameter of 5 cm (Canadell et al., 1988) or it may only include the straight part of the stem (Annighöfer et al., 2012). This will add an error to the regional or generic equations that are produced. In addition to leaf area, we searched for equations that predict the biomass components of foliage, branch wood (total, live or dead, all including the bark), stem (including wood and bark), stem and branch (including stem + branch wood and bark), aboveground (including stem + branch wood and bark + foliage) and roots. Where the studies divided the components even further (e.g., stem wood and stem bark), we used both equations to calculate the stem or we combined the aboveground components to get aboveground mass.

When a study provided equations for leaf mass but not leaf area, or vice versa, the specific leaf area (SLA, m² kg⁻¹) was used to pre-

dict the leaf area from the leaf mass, or vice versa. Here, leaf area strictly refers to one-sided projected area. SLA can decline with tree age and this relationship was obtained for each species using published SLA-age data that was fitted to Eq. (2).

$$SLA(t) = SLA_1 + (SLA_0 - SLA_1)e^{-(\ln 2)(t/t_\sigma)^2} \quad (2)$$

where SLA_0 and SLA_1 are the values of SLA in young and older stands, respectively, and t_σ is the age at which $SLA = \frac{1}{2}(SLA_0 + SLA_1)$ (Sands and Landsberg, 2002). The SLA data are provided as supplementary information Table A.1 of Appendix A and SLA-age relationships are shown in Fig. B.1 of Appendix B.

2.2. Calculation of pseudo-observations

The compiled equations were used to generate pseudo-observations for use in fitting the regional allometric models. Although raw data are strongly favoured above pseudo-observations, raw data were not available for many of the equations in this study. Restricting the data set only to raw data would therefore have severely restricted the ranges of stand conditions, climates, ages and tree sizes available and thus greatly limited our ability to examine the effects of these factors on biomass relationships. Therefore, pseudo-observations were generated for many of the published equations. The equations and their pseudo-observations are provided in Table A.2 of Appendix A. Several approaches have been used to generate pseudo-observations in biomass studies. One method involves calculating one or more pseudo-observations per 1-cm (or n-cm) diameter class (Muukkonen, 2007; Chojnacki et al., 2014; de-Miguel et al.,

Table 2

Characteristics of the species and the mean (minimum/maximum) characteristics of the stands where those equations or data sets were obtained.

Species	Wood density (g cm ⁻³) ^a	Shade tolerance ^a	Specific leaf area (m ² kg ⁻¹) ^b	Diameter (cm)	Age (years)	Basal area (m ² ha ⁻¹)	Trees per ha	Latitude (°)	Longitude (°)	Mean annual temperature (°C) ^c	Mean annual precipitation (mm) ^c
<i>Abies alba</i>	0.35	4.6	9.08	34 (5.7/80)	32.7 only			47.0 (42.7/56.0)	8 (0.8/15.7)	8.4 (6.3/11.3)	999 (718/1144)
<i>Acer pseudoplatanus</i>	0.51	3.73	19.51	8.4 (0.1/88.2)	13.4 (4.8/143.8)	20.4 (17.7/30.6)	21,179 (8202/39,870)	50.9 (45.6/56.0)	6.8 (-87.3/19.3)	7.6 (5.6/8.6)	810 (697/1287)
<i>Alnus glutinosa</i>	0.44	2.71	14.93	14.9 (1/47.3)	26.3 (11/49)	22.3 (12.2/32.5)	8756 (1114/16,399)	56.1 (42.4/59.5)	11.9 (1.6/16)	6.5 (5.8/7.8)	712 (569/1011)
<i>Alnus incana</i>	0.44	2.3	14.93	9.3 (0.7/24.6)	19.5 (6.5/40)	27.6 (10.3/33.4)	13,730 (1854/27,719)	60.4 (57.3/61.8)	16.8 (10.8/26.1)	4.4 (2.9/6.7)	678 (630/753)
<i>Betula pendula</i>	0.53	2.03	9.84	7.7 (1/25.5)	12.4 (6.5/20)	14.9 (7.7/19.8)	13,202 (466/22,684)	57.8 (49.9/62.0)	12.1 (5.3/26.1)	6 (3/9.5)	717 (630/809)
<i>Betula pubescens</i>	0.53	1.85	9.84	4.8 (0.5/15)	9.2 (8/12)	14.6 (10.6/21.3)	28,919 (3060/69,527)	61.3 (52.0/69.7)	22.8 (10.4/27.3)	3.3 (-1.1/8.2)	576 (414/723)
<i>B. pendula</i> or <i>B. pubescens</i> ^d				8.5 (0.5/38)	17.5 (6.5/44)	15.5 (7.7/21.3)	20,170 (466/69,527)	60.7 (49.9/69.7)	17.7 (-3.1/27.3)	3.8 (-1.1/9.5)	659 (414/1287)
<i>Carpinus betulus</i>	0.71	3.97	19.83	24 (0.1/75)	14.9 (12/32)	23.3 (21.3/35.1)	7921 (168/15,466)	45.5 (36.4/52.0)	26.5 (7.6/52)	9.7 (1.4/13.7)	672 (418/1523)
<i>Castanea sativa</i>	0.46	3.15	14.34	21.4 (1/64.2)	57.4 (12.3/100)	30.9 (28.4/43.2)	3002 (1597/3970)	40.7 (37.5/46.1)	-4.4 (-7.6/15)	12.3 (6.8/15.8)	740 (468/1275)
<i>Fagus sylvatica</i>	0.59	4.56	21.54	27.1 (0.5/84)	64.2 (8/145)	24.1 (2.9/73.8)	3726 (196/16,815)	49.4 (42.3/56.0)	6.2 (-4.2/16.2)	8.9 (1.4/11.3)	766 (537/1523)
<i>Fraxinus excelsior</i>	0.56	2.66	17.08	7.7 (0.1/69.3)	12.2 (4.6/114.2)	21.4 (17.7/28.8)	17,082 (1000/35,620)	50.9 (45.2/59.5)	11.4 (-3.3/19.3)	8.3 (6.7/10.9)	802 (549/1325)
<i>Larix decidua</i>	0.47	1.46	12.18	30.4 (4/90.1)	24 (20/28)	28.6 (28.6/28.6)	2390 (2280/2500)	46.8 (43.9/50.6)	-12.6 (-91.9/15.7)	6.7 (2.9/11.3)	856 (744/1126)
<i>Picea abies</i>	0.37	4.45	5.76	22.8 (0.4/82)	47.9 (17/152)	34.9 (2.4/62)	4301 (308/17,388)	54.1 (42.7/67.0)	1.2 (-91.9/26.7)	5.6 (-0.3/11.3)	769 (521/1280)
<i>Pinus cembra</i>	0.42	2.87	4.6	32.2 (7.7/56.3)				46.1 (46.1/46.1)	11.1 (11.1/11.1)	11.3 (11.3/11.3)	874 (874/874)
<i>Pinus nigra</i>	0.42	2.1	- ^c	29.5 (6/77.3)	21.1 (13/62)	39.9 (39.9/39.9)	2500 (2500/2500)	41.9 (40.6/51.2)	20.6 (-1.6/33.7)	10.9 (9.1/13.4)	727 (522/931)
<i>Pinus pinaster</i>	0.41	2.21	2.97	24.9 (1/64)	26.9 (7.6/64)	38.8 (17.1/66.7)	2183 (223/23,614)	41.2 (32.8/44.7)	10.6 (-8.1/117)	12.8 (10/15.9)	818 (381/1298)
<i>Pinus sylvestris</i>	0.42	1.67	4.28	18.4 (1/76)	48.7 (10/165)	25.2 (16/37.6)	4645 (223/17,388)	55.9 (41.2/69.3)	14.1 (-4.2/26.7)	6.2 (0.8/11.3)	702 (492/1340)
<i>Populus alba</i>	0.35	2.3	9.84	5.4 (0.1/10.7)	8 (8/8)			44.5 (44.5/44.5)	26.7 (26.7/26.7)	11 (11/11)	550 (550/550)
<i>Populus tremula</i>	0.37	2.22	9.84	11.3 (1/40)	18.4 (10/46)	32.6 (26.1/37.5)	9549 (1246/17,805)	58.7 (51.2/61.0)	12.5 (5.3/17)	5.7 (3.1/9.5)	712 (622/809)
<i>Populus alba</i> , <i>P. tremula</i> and <i>P. tremula hybrids</i> ^d				13.5 (0.1/44.7)	16.5 (7/46)	30.3 (10.6/37.5)	5834 (440/17,805)	55.1 (44.5/61.0)	13.2 (7.5/26.4)	8 (5.1/11)	672 (550/920)
<i>Prunus avium</i>	0.47	3.33	12.43	5.5 (1/10)			167 (167/167)	43.8 (43.8/43.8)	1.7 (1.7/1.7)	12.9 (12.9/12.9)	724 (724/724)
<i>Prunus serotina</i>	0.68	2.46	- ^c	23.7 (0.9/49.6)	31.9 (27.5/45)	37.7 (37.7/37.7)		43.9 (39.6/45.3)	-13.3 (-80/8.9)	12.4 (10.9/12.9)	1012 (993/1069)
<i>Pseudotsuga menziesii</i>	0.43	2.78	5.98	26.6 (1/163)	40.2 (10/262)	46.4 (0.5/75)	3893 (235/12,000)	46.1 (35.3/56.0)	-108.6 (-123.9/11.7)	7.7 (4.2/10.9)	1121 (347/2315)
<i>Quercus ilex</i>	0.82	3.02	4.83	17.9 (1/90)	78.7 (31/133)	27.2 (16.3/38.8)	6271 (1814/10,865)	37.9 (32.9/43.7)	3.6 (-5.4/15)	16.2 (8.2/21.7)	456 (59/760)
<i>Quercus petraea</i>	0.56	2.73	14.81	20.4 (3/77.1)	61 (20/198)	19.9 (7.7/35.1)	4523 (1419/10,700)	51.5 (48.7/54.4)	3 (-3.1/8)	7.7 (6.8/9.5)	987 (745/1287)
<i>Quercus robur</i>	0.56	2.45	14.81	29 (4/67.5)	75.2 (20/122)	32.4 (14.3/41.9)	1105 (375/6137)	46.6 (42.7/51.3)	-1.3 (-8/7.5)	10.3 (7.8/11.7)	953 (746/1284)
<i>Q. petraea</i> or <i>Q. robur</i> ^d				24 (1/77.1)	64.2 (10/198)	26.8 (7.7/41.9)	2235 (163/10,700)	48.9 (42.7/54.4)	3 (-8/15.3)	8.9 (1.4/11.7)	936 (626/1523)
<i>Robinia pseudoacacia</i>	0.68	1.72	24.84	11.3 (0.1/40.1)	15.3 (8/27.5)	31.2 (24.8/37.7)	3551 (3551/3551)	43.1 (35.1/51.2)	32.3 (-83.4/109)	10.4 (8.6/12.9)	712 (462/1915)
<i>Sorbus aucuparia</i>	0.63	2.73	- ^c	5.5 (1/10)	11 (11/11)			59.5 (59.5/59.5)	10.8 (10.8/10.8)	6.7 (6.7/6.7)	753 (753/753)
<i>Tilia cordata</i> or <i>platyphyllas</i>	0.42	4.18	22.11	26.6 (4/58.6)	73.6 (73.6/73.6)			34.6 (24.8/54.4)	8.1 (-3.1/13.7)	6.9 (6.8/6.9)	870 (662/1287)

^a See Table B.3 for more information (Niinemets and Valladares, 2006; Zanne et al., 2009).^b Means calculated from data in Table A.1.^c Specific-leaf area data was not available for these species.^d Several species from the same genera were grouped because some studies did not differentiate the species. For such groups, the data from each species was combined (not only the studies that did not differentiate the species).^e The climate data was obtained from Hijmans et al. (2005).

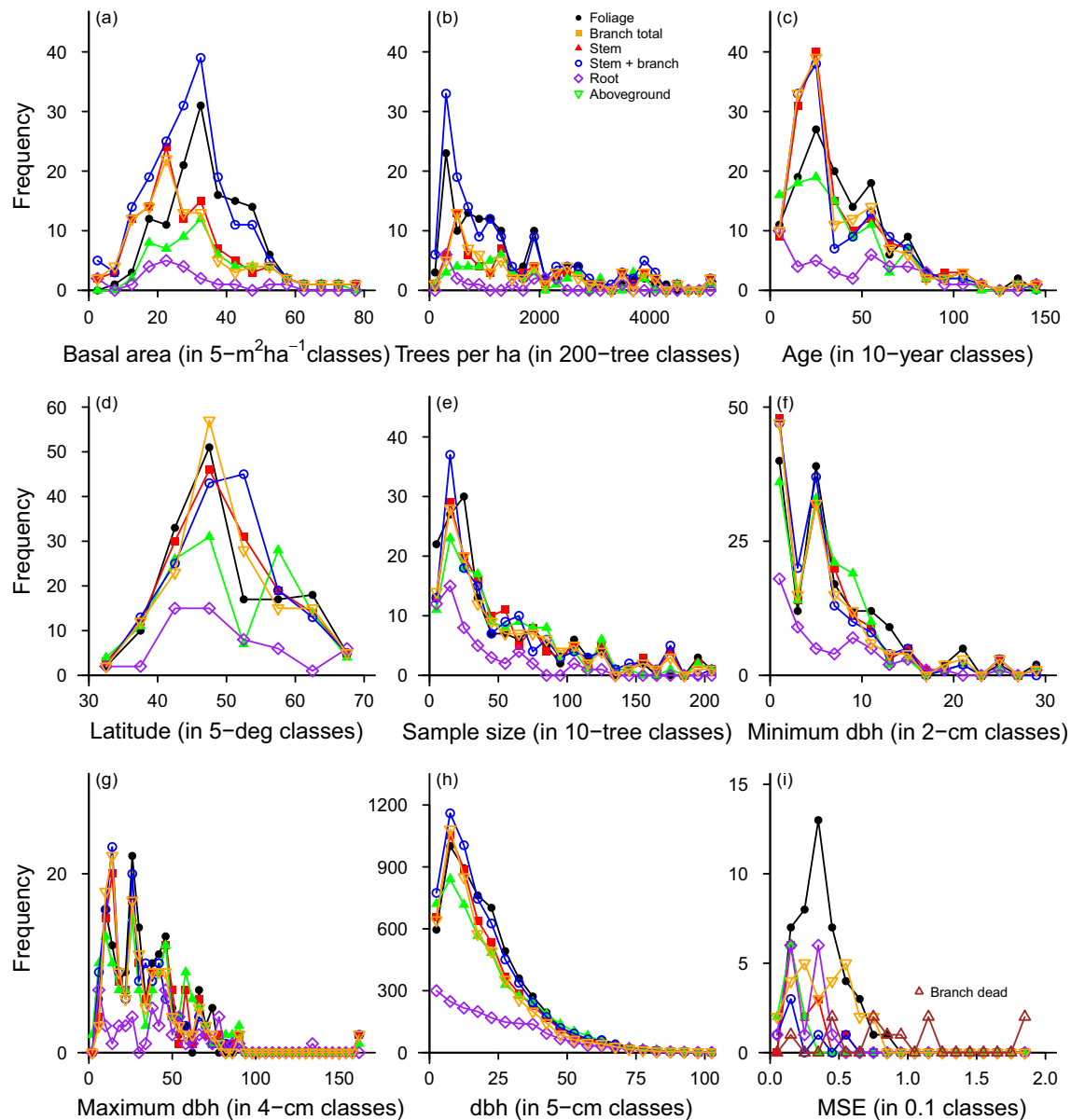


Fig. 1. Frequency distributions of stand variables, including basal area (a), trees per ha (b), age (c) and latitude (d), as well as sample characteristics including the sample size (e), the minimum diameter (dbh) sampled (f), the maximum diameter sampled (g), the distribution of diameter pseudo-observations (h) and the mean square error (i). The frequency indicates the number of equations or raw data sets that included the value on the x-axis, except for (h) which includes all individual pseudo-observations or raw data points. This figure summarizes the data provided in Table A.2. In addition to the pseudo-observations, the raw data was also included when available. Note that for clarity, the x-axes do not extend to their maximum for (b) maximum = 70,000, (e) maximum = 4213 and (h) maximum = 163.

2014). Another method involves the use of an equal number of pseudo-observations per equation (Pastor et al., 1984; Jenkins et al., 2003). In this study, equal numbers of pseudo-observations were used for each equation instead of pseudo-observations at each n-cm class. This was necessary because some equations had a much larger diameter range than others and they would have had a correspondingly higher number of pseudo-observations. Equations with large numbers of pseudo-observations (due to large diameter ranges) would bias the data set towards the values of the climate, age and stand structural variables associated with the given equation. The distributions of diameter, age, basal area and trees per hectare are shown in Fig. 1. The median sample size for all equations was 33. Therefore, 33 pseudo-observations were calculated for each equation that were evenly distributed between the smallest and largest diameter used to develop the given equa-

tion. This is larger than the n in some previous studies (e.g., Pastor et al., 1984; Jenkins et al., 2003; Chojnacki et al., 2014). The larger n was used to reduce the possibility of overestimating the parameters (and hence biomass), which can result from small sample sizes (Duncanson et al., 2015). Where studies included the raw data in published tables or the raw data were provided by the authors, the raw data were used instead of pseudo-observations (10%; 105 raw data sets but 868 equations).

As is often the case, there was a bias towards the smaller diameter classes (Fig. 1h). To reduce the influence of tree size distribution, Duncanson et al. (2015) binned data by calculating the median value of the dependent variable in equally spaced independent variable bins. However, this approach can underestimate the variability of the equations (Jucker et al., 2017). Furthermore, binning could not be done in this study because there was more than

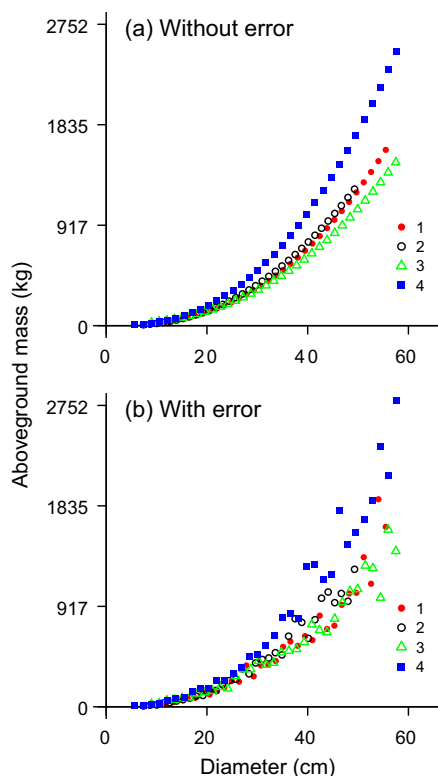


Fig. 2. The pseudo-observations calculated from four published equations for *Abies alba* predicting aboveground biomass (kg/tree) without (a) or with (b) the model error taken into account. The equation numbers in the legend refer to the equations in Table A.2. In the legends 1 = (Fattorini et al., 2004; Gasparini et al., 2006), 2 = (Nord-Larsen and Nielsen, 2015), 3 = (Ruiz-Peinado et al., 2011), 4 = (Tabacchi et al., 2011).

one independent variable and binning would require a complete matrix of diameter, age, climate and stand variables, which does not exist in this data set.

While the pseudo-observation datasets could potentially be used to examine the variability between equations, they do not include the variability within a given equation (or site) and therefore will lead to underestimation of errors of regional equations (Case and Hall, 2008; de-Miguel et al., 2014). The within-equation error includes the uncertainty of the parameter estimates as well as the residual error of the equation (Breidenbach et al., 2014). The latter can be approximated by randomly generating pseudo-observations by assuming a normal distribution of residuals with a mean of zero and the variance (mean square error of the residuals; MSE) reported for the given equation (de-Miguel et al., 2014). This recovers the within- and between-equation variability of the original field measurements (de-Miguel et al., 2014). In order to illustrate this we show the pseudo-observations calculated from all (four) published equations for estimation of aboveground biomass of the first species listed in our database, *Abies alba* (Fig. 2).

It was possible to obtain usable variance values for only 14% of the published equations and this includes MSE values that were calculated by fitting Eq. (3) to each of the raw data sets that were included in the database. This scarcity of model variance information resulted because many studies did not report model errors or it was not clear what the error terms actually were. For example, the names given to the errors varied widely and we generally used values that were called standard deviation, MSE, Root MSE, Sy,x, se, residual error, residual standard error, residual deviation and mean error. To ensure compatibility, we only used the MSE values from equations fitted to ln-transformed biomass components or leaf area. The MSE values for the 86% of equations for which we did

not have a model error value were estimated based on the observation that the MSE values appeared to vary between biomass components and also between broad-leaved and coniferous species. Therefore, we filled in the missing MSE values using the mean MSE values for each of these combinations (Fig. B.2). The MSE was only available for 10 leaf area equations and therefore the mean MSE was used for all other leaf area equations. From here on, Dataset 1 refers to the dataset with pseudo-observations that ignore within-equation variability, and Dataset 2 refers to the dataset containing the pseudo-observations that were calculated by taking into account the MSE values. Both datasets contained the raw biomass or leaf area data (105 of the 973 equations). The regional equations were fitted using Dataset 1, while Dataset 2 was only used to estimate a more realistic MSE of the regional equations (MSE_{real}).

2.3. Candidate independent variables

The selection of candidate independent variables for biomass equations should be based on clear hypotheses and theory (Sileshi, 2014). Furthermore, when using published equations or published data sets, the independent variables are restricted to variables that were described in the publications and that are measured in a standard/comparable way in each study. This therefore restricts the variables to stem diameter, tree age, stand basal area, trees per hectare, latitude, longitude (and therefore climate) and species proportions. Tree size, in terms of diameter or height, is a clear candidate variable and is included in the vast majority of equations. It indirectly provides information about the trees' history. Age is another strong candidate variable because many studies have shown that allometry and biomass partitioning are affected by age (Wirth et al., 2004; Litton et al., 2007; Genet et al., 2011; Shaiek et al., 2011). The number of trees per hectare and mean diameter are allometrically related as described by the self-thinning law (Reineke, 1933; Yoda et al., 1963), so trees per hectare is also a good candidate variable. For a given number of trees per ha, a stand can have a wide range of basal area values. Therefore, basal area or mean diameter may also be required to more adequately describe the stand structure. Biomass relationships may also vary between sites due to differences in climate and soils or because the provenances and genotypes of the given species vary (Litton et al., 2007; Poorter et al., 2012; Reich et al., 2014). Mean annual temperature and mean annual precipitation were predicted from latitude and longitude using the WorldClim database (Hijmans et al., 2005). Provenance and genotype information are often not provided and it was assumed that latitude may approximate some of these effects, and it is provided in nearly all studies.

Variables such as tree species proportion are too specific to be useful unless the equations are only designed for a specific forest type. This is because there is an extremely high number of potential species combinations and proportions where any given species can occur, and this variability in species composition cannot be quantified using a single stand variable (Forrester et al., 2017). Therefore, alternative variables have been proposed that quantify the horizontal (basal area, trees per ha) or vertical stand structure (tree dominance status) and that are weighted, if necessary, by traits assumed to indicate species-specific competitive ability, such as wood density, specific leaf area and shade tolerance (Forrester et al., 2017).

2.4. Regional equations

Regional equations (Eqs. (3)–(21)) for each species and component were fitted using linear mixed models. The pseudo-observations (or raw data) belonging to a given published equation

were given a unique number to identify the published equation from which they were obtained (this number ranged from 1 to 982). This unique equation number was included as the random variable to account for within study correlation (pseudo-observations from a given published equation are not independent of each other). The fixed effects were the independent variables including tree diameter (d , cm) at 1.3 m, age (A , years), stand basal area (BA , $m^2 ha^{-1}$), the number of trees per hectare (TPH), latitude ($^\circ$), mean annual temperature ($^\circ C$) and mean annual precipitation (mm). The biomass, leaf area, diameter, age and TPH were all ln-transformed to reduce homoscedasticity and to produce linear relationships with biomass or leaf area. The following functional forms were compared:

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \varepsilon \quad (3)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 BA + \varepsilon \quad (4)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 \ln(A) + \varepsilon \quad (5)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 \ln(TPH) + \varepsilon \quad (6)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 \text{Latitude} + \varepsilon \quad (7)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 \text{Prec} + \varepsilon \quad (8)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 \text{Temp} + \varepsilon \quad (9)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 BA + \beta_3 \ln(A) + \varepsilon \quad (10)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 BA + \beta_3 \ln(TPH) + \varepsilon \quad (11)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 BA + \beta_3 \text{Latitude} + \varepsilon \quad (12)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 BA + \beta_3 \text{Prec} + \varepsilon \quad (13)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 BA + \beta_3 \text{Temp} + \varepsilon \quad (14)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 \ln(A) + \beta_3 \ln(TPH) + \varepsilon \quad (15)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 \ln(TPH) + \beta_3 \text{Prec} + \varepsilon \quad (16)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 \ln(TPH) + \beta_3 \text{Temp} + \varepsilon \quad (17)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 \ln(TPH) + \beta_3 \text{Latitude} + \varepsilon \quad (18)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 \ln(A) + \beta_3 \text{Prec} + \varepsilon \quad (19)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 \ln(A) + \beta_3 \text{Temp} + \varepsilon \quad (20)$$

$$\ln(Y) = \ln\beta_0 + \beta_1 \ln(d) + \beta_2 \ln(A) + \beta_3 \text{Latitude} + \varepsilon \quad (21)$$

where ε is an error term that is assumed to be normally distributed with a mean (μ) of 0 and standard deviation of σ . In order to correct for the bias that results from back-transforming predictions of Y , a correction factor (CF) was calculated from the mean of the pseudo-observations divided by the mean of the values predicted by the regional equation (Snowden, 1991).

To compare the effect of each independent variable on each biomass component and to determine whether these responses were related to species traits, Eqs. (22)–(24) were used after standardising all independent variables by subtracting the mean from the variable value and then dividing it by the standard deviation of the given variable. The standardised independent variables then each have a mean (μ) of 0 and a standard deviation (σ) of 1. If the independent variable was ln-transformed, then the transformed values were standardised to $\mu = 0$ and $\sigma = 1$. Therefore,

the slope parameters (hereafter called beta weights) in Eqs. (22)–(24) were used to provide the effect size for each variable. Beta weights (standardised coefficients) are scale free, and quantify how many standard deviations the dependent variable (Y) will change per standard deviation increase in the independent variable (X). Thus they can be used as effect size estimates (Peterson and Brown, 2005; Nieminen et al., 2013). In this analysis, the effect size of all independent variables was compared in order to identify those that have the largest influence on biomass or leaf area.

$$\begin{aligned} \ln(Y) = & \ln\beta_0 + \beta_1 \ln(d) + \beta_2 BA + \beta_3 \ln(A) + \beta_4 \ln(TPH) \\ & + \beta_5 \text{Prec} + \beta_6 \text{Temp} + \beta_7 SLA + \beta_8 \ln(d) \times SLA + \beta_9 BA \\ & \times SLA + \beta_{10} \ln(A) \times SLA + \beta_{11} \ln(TPH) \times SLA \\ & + \beta_{12} \text{Prec} \times SLA + \beta_{13} \text{Temp} \times SLA + \varepsilon \end{aligned} \quad (22)$$

$$\begin{aligned} \ln(Y) = & \ln\beta_0 + \beta_1 \ln(d) + \beta_2 BA + \beta_3 \ln(A) + \beta_4 \ln(TPH) \\ & + \beta_5 \text{Prec} + \beta_6 \text{Temp} + \beta_7 \rho + \beta_8 \ln(d) \times \rho + \beta_9 BA \times \rho \\ & + \beta_{10} \ln(A) \times \rho + \beta_{11} \ln(TPH) \times \rho + \beta_{12} \text{Prec} \times \rho \\ & + \beta_{13} \text{Temp} \times \rho + \varepsilon \end{aligned} \quad (23)$$

$$\begin{aligned} \ln(Y) = & \ln\beta_0 + \beta_1 \ln(d) + \beta_2 BA + \beta_3 \ln(A) + \beta_4 \ln(TPH) \\ & + \beta_5 \text{Prec} + \beta_6 \text{Temp} + \beta_7 ST + \beta_8 \ln(d) \times ST + \beta_9 BA \\ & \times ST + \beta_{10} \ln(A) \times ST + \beta_{11} \ln(TPH) \times ST + \beta_{12} \text{Prec} \\ & \times ST + \beta_{13} \text{Temp} \times ST + \varepsilon \end{aligned} \quad (24)$$

where d , BA , A , TPH , $Temp$, $Prec$ and SLA are as defined earlier for Eqs. (3)–(21), ρ is the wood density (oven dry mass per fresh volume; $g cm^{-3}$) (Zanne et al., 2009) and ST is the shade tolerance from Niinemets and Valladares (2006) (Table B.3). SLA is the mean SLA for the given species obtained from the published values in Table A.1. Eq. (23), which contains wood density, was also fitted to Datasets 1 and 2 without standardising the independent variables. This was done to provide generic (species independent) models that can be applied to species that are not well represented in the data base. These generic equations were fitted to all data in Dataset 1. Eqs. (3)–(21) were fitted using the *nlme* package in R (Pinheiro et al., 2013) and using the REML method, which maximises the restricted log-likelihood.

2.5. Verification and quality of fit

Verification or validation of the final models based on Eqs. (3)–(21) was done based on the K-fold or leave-one-out methods of cross-validation (Arlot and Celisse, 2010; Picard et al., 2012) whereby Eqs. (3)–(21) were fitted to the pseudo-observations (or raw data sets) from all but one of the published equations, and then the predictions of the resulting regional model were compared with the pseudo-observations (or raw data sets) of the excluded published equation. This was repeated until all of the published equations had been used as validation data.

To check for collinearity between independent variables, variance inflation factors (VIF) were calculated using the *corvif* function in the *AED* package in R (Zuur et al., 2009). VIF above 5 indicate high multicollinearity between independent variables (Sileshi, 2014). While many biomass studies include variables that are highly correlated (e.g., diameter and height), we avoided this to ensure that the parameter estimates represented causal relationships as closely as possible.

The uncertainty of the model parameters was examined using the percent relative standard errors PRSE (Eq. (25); Sileshi, 2014).

$$PRSE (\%) = 100 \frac{\text{parameter standard error}}{\text{parameter estimate}} \quad (25)$$

PRSE values more than 50% were considered unreliable. Akaike's information criterion (AIC) was used to examine whether any of the regional equations were over-parameterised. However, Eqs. (3)–(21) were often fitted to different subsets of data because different published equations provided different combinations of the independent variables. Therefore the Bayesian information criterion (BIC) was also used because it takes the sample size into account.

The precision of the regional equations was quantified using the square root of the mean square error (RMSE) using Eq. (26) calculated from the ln-transformed data.

$$RMSE = \sqrt{\frac{\sum_{i=1}^n (P_i - O_i)^2}{n}} \quad (26)$$

where O are the observed values and P are the predicted values. The precision was also quantified using the mean absolute percentage error (MAPE) using Eq. (27) and the back-transformed predicted values that had been corrected for the bias using the correction factor (CF) described above from Snowden (1991).

$$MAPE (\%) = \frac{100}{n} \sum_{i=1}^n \frac{|O_i - P_i|}{O_i} \quad (27)$$

The bias was quantified using Eq. (28) (Sileshi, 2014), also using the back-transformed predicted values that had been corrected for the bias using the CF described above from Snowden (1991).

$$Bias (\%) = \frac{100}{n} \sum_{i=1}^n \frac{P_i - O_i}{O_i} \quad (28)$$

Linear regression of the observed (y-axis) against the predicted values (all ln-transformed) were used to examine how well the models fit the observed data. This was used to test whether the slope was significantly different from 1 and whether the intercept was significantly different from 0 (Sileshi, 2014) by calculating 95% confidence intervals (standard error of parameter $\times 1.96$) for the slope and intercept. During the validation, the mean PRSE, RMSE, MAPE and Bias were calculated from all the K-fold validations for the given general equation. All analyses were performed using R software version 3.3.1 (R Core Team, 2016).

3. Results

The final dataset contained pseudo-observations for 27 species from 868 equations and 105 raw data sets (973 in total) (Table 1). This included 60,294 biomass or leaf area samples from the reviewed studies. The equations covered a broad range of stand characteristics, with basal areas ranging from <5 to >75 m² ha⁻¹ and stand densities ranging from <200 to 70,000 trees per hectare (Fig. 1a, b). However, there was a clear skew towards the smaller tree sizes and younger ages (Fig. 1c, h). The equations were dis-

tributed across the latitudinal range of Europe with a peak in the middle, at latitudes of about 45–50° (Fig. 1d). While many of the sample sizes were small (<30 trees) there were also many that contained >50 trees (Fig. 1e).

All validation equations and final equations are listed in Table A.4. The final equations that were valid (e.g., $P < 0.05$ for all variables, VIF < 5 and PRSE < 50%) are listed in Table A.5. Focusing only on equations in the form of Eq. (3), the confidence intervals for the exponent β_1 , averaged across all species, often contained the value predicted by the metabolic scaling theory (although it was usually close to the upper limit) and often did not contain the value predicted by the geometric scaling theory (Table 3).

3.1. Intra-specific variability

In agreement with our first hypothesis, the foliage mass, and to a lesser extent branch mass, was generally more variable for a given diameter than stem mass (Fig. 3, see also Figs. B.3–B.25). This is indicated by the greater mean RMSE_{real} for foliage (0.42) and total branch mass (0.54) compared with stem (0.33), stem + branch mass (0.28) and aboveground mass (0.18), with intermediate RMSE for root mass (0.37) (from Table A.5).

Using the RMSE when calculating the pseudo-observations, as shown in Fig. 2, resulted in RMSE_{real} that were on average 76% larger (0.404 compared with 0.230) than those calculated when the RMSE of the individual equations was not considered when calculating the pseudo-observations.

For many species, there were enough equations available to test whether the biomass components were influenced by age, basal area, trees per ha, climate or latitude. These variables were significant in 387 out of the 576 regional equations listed in Table A.5, which is consistent with our second hypothesis that these variables influence diameter-biomass relationships. The parameter estimates in Table A.5 show that climate, age and the stand variables have contrasting effects on different biomass components and species. Stem, stem + branch and aboveground mass often tended to increase (for a given diameter) with all of these independent variables (except climate and latitude where effects were more variable). In contrast, foliage mass and leaf area sometimes declined (for a given diameter) with increasing age, basal area and trees per ha. For most species or species groups (24 out of 31) equations that contained diameter only (Eq. (3)) had, on average, similar or higher RMSE, MAPE and Bias than the other equations (Table 4). There was no clear trend as to whether age, basal area, trees per ha, precipitation or temperature was the best independent variable to add to the equations.

3.2. Inter-specific variability

Wide inter-specific variability was observed in biomass components, especially foliage mass (Fig. 4). The biomass components for which there was a lot of intra-specific variability also showed a lot of inter-specific variability. For example, for a diameter of 60 cm, the predicted foliage mass (kg per tree) varied by 767% from about 15 kg in *C. betulus* to 130 kg in *P. abies*, while stem mass varied by 160% from about 1000 kg in *P. pinaster* to 2600 kg in *C. betulus*.

The inter-specific variability in the biomass – diameter relationship was generally high for foliage mass and lower for stem mass (Figs. 4 and 5). Examination of the effect sizes (beta-weights) showed that diameter always had the greatest influence on biomass (Figs. 6 and 7). Increasing basal area generally reduced leaf area, leaf mass and branch mass. Increasing age generally increased stem mass but reduced root mass; for a given diameter older trees had less root mass than younger trees (Fig. 6). Foliage biomass or leaf area increased with temperature or precipitation for low trait values (SLA, wood density and shade tolerance) but

Table 3
Mean β_1 of Eq. (3) and its 95% confidence interval for all of the final equations in Table A.5.

Component	Mean (95% confidence interval)
Aboveground	2.41 (2.12/2.70) ^b
Stem and branch mass	2.37 (2.09/2.65) ^{a,b}
Stem mass	2.39 (2.08/2.70) ^b
Live branch mass	2.15 (0.16/4.14)
Total branch mass	2.31 (1.72/2.89) ^b
Foliage mass	1.83 (1.13/2.53) ^{a,b}
Root mass	2.27 (1.74/2.80) ^b

^a Interval does not contain the β_1 predicted by the metabolic scaling theory (2.67).

^b Interval does not contain the β_1 predicted by the geometric scaling theory (3).

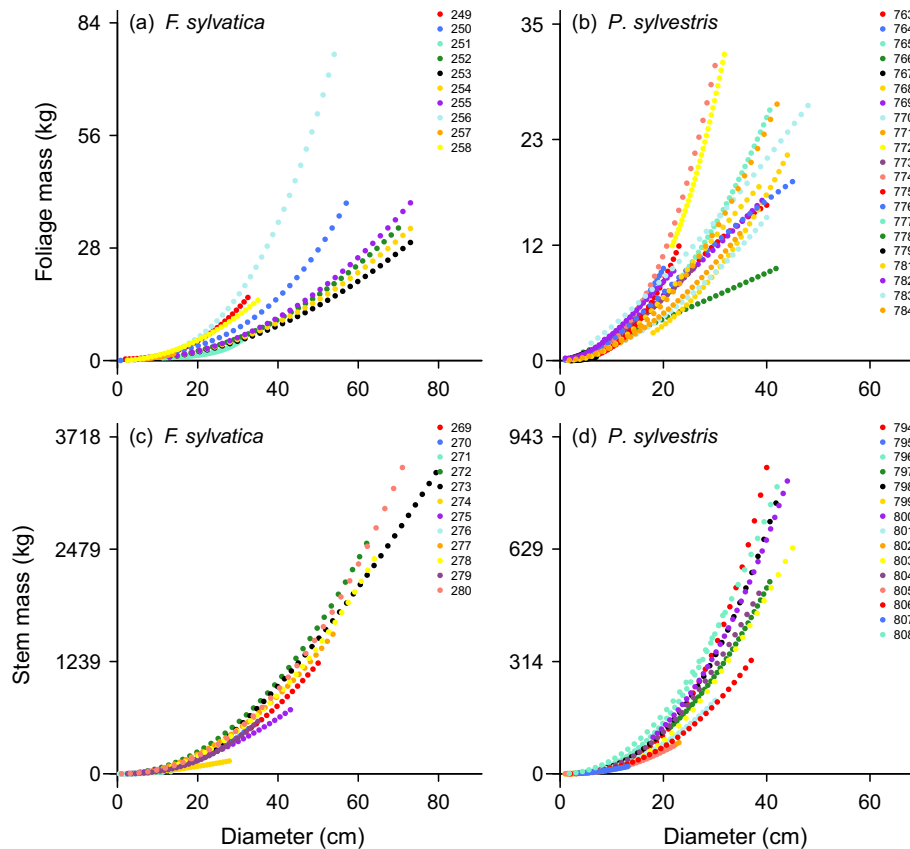


Fig. 3. The pseudo-observations for individual tree foliage mass (a, b) and stem mass (c, d) for two contrasting species that were well represented in the data set, *Fagus sylvatica* (a, c, deciduous, broad-leaved) and *Pinus sylvestris* (b, d, evergreen conifer). The numbers in the legends represent the equation number in the database (Table A.2) that identifies the source of the published equation used to produce the pseudo-observations. One raw data set was excluded from (b) to improve clarity.

decreased for high trait values. For the other component-independent variable combinations, there were often contrasting responses ranging from increases to decreases in biomass. This is consistent with our third hypothesis that stand characteristics and age have contrasting effects on different biomass components.

Wood traits (wood density, SLA or shade tolerance) were significantly correlated with inter-specific variability for more than half of all possible combinations of biomass components and independent variables, consistent with our fourth hypothesis. For example, the effect of diameter on leaf mass declined as all wood traits increased (Fig. 6).

Eq. (23) was also fitted for all species before the data were standardised. This enabled the development of a generic equation for each biomass component and leaf area that could be used for any species in our data set. However, it should be noted that the species-specific regional models are expected to be the most accurate and the generic model fitted to Eq. (23) is intended to be used only for rarer species until those species are better represented.

4. Discussion

4.1. Intra-specific variability

For a given diameter, there was considerable intra-specific variability and this was greater for the shorter lived components such as foliage and branches than for longer lived components, like stems. This finding is consistent with our first hypothesis and with previous studies (Wirth et al., 2004; Saint-André et al., 2005; António et al., 2007; Genet et al., 2011; Xiang et al., 2011, 2016; Clough et al., 2016). Shorter lived tissues such as foliage, branches

and fine roots may turn over more readily and rapidly as conditions become more or less favourable thereby making them more variable for a given diameter than structural support components, such as stems.

It follows therefore that the intra-specific variability not only reflects tree age and genetics but that it can also indicate how trees have responded to previous growing conditions. When biomass equations are developed, it is common to average out this variability or to group it all together (Sileshi, 2014; Weiskittel et al., 2015) by developing regional or generic models that include a single independent variable (e.g., dbh) or a compound variable that includes dbh; Chave et al., 2014) or by assigning the variability to the random variables in mixed models (de-Miguel et al., 2014). Alternatively, this study shows that such intra-specific variability can be partitioned to some of the independent variables that are causing this variability such as age, basal area, trees per ha, climate and latitude, instead of to random effects, consistent with our second hypothesis. An advantage of this approach is that the effects of climate, age, stand basal area and trees per ha on biomass stocks can be predicted and the size and direction of their effects are clearly evident from the model parameters.

It is worth noting that the difference in biomass predictions for a given diameter often differed by more than 50% for the same species and component, and sometimes by more than 100% (e.g., Fig. 3). This highlights the risk of applying species-and-site specific published biomass equations to stands where they were not developed. Even for the regional equations developed in this study, it is critical to note the ranges in all independent variables, because these should include the values of the target stands to avoid extrapolating beyond the range of data used to develop the equations.

Table 4

Mean values of statistics for Eq. (3) (with only diameter as an explanatory variable) compared with all other equations (All ex. 3), which also included stand and climatic variables (Eqs. (4)–(21)). PRSE = percent relative standard errors (Eq. (25)), AIC = Akaike's information criterion, BIC = Bayesian information criterion, RMSE = square root of the mean square error (Eq. (26)), MAPE = mean absolute percentage error (Eq. (27)) and Bias = bias calculated using Eq. (28).

Species	Equation	Mean AIC	Mean BIC	Mean RMSE	Mean MAPE	Mean Bias
All species	All ex. 3	539	570	0.264	22	11.4
	3	955	979	0.279	23.2	12.6
Broadleaved species	All ex. 3	497	525	0.296	34.1	23.6
	3	501	522	0.286	24.3	13.6
Coniferous species	All ex. 3	−134	−105	0.231	16.5	6.4
	3	227	250	0.259	20.8	9.8
<i>Abies alba</i>	3	−211	−200	0.085	5.4	−0.3
<i>Acer pseudoplatanus</i>	All ex. 3	54	70	0.284	20.3	1
	3	32	44	0.255	18.3	2.5
<i>Alnus glutinosa</i> or <i>Alnus incana</i>	All ex. 3	−64	−44	0.159	12.2	1.1
	3	131	148	0.223	18	6.6
<i>Alnus glutinosa</i>	All ex. 3	−92	−80	0.13	10.2	0.3
	3	−40	−29	0.204	16.8	4.5
<i>Alnus incana</i>	All ex. 3	−311	−298	0.047	3.7	−0.2
	3	−138	−127	0.135	9.6	−0.3
<i>B. pendula</i> or <i>B. pubescens</i>	All ex. 3	−41	−27	0.869	39.5	7.8
	3	−8	5	0.285	31.5	22.8
<i>Betula pendula</i>	All ex. 3	−140	−127	0.097	7.2	0.8
	3	−43	−33	0.2	17.9	7
<i>Betula pubescens</i>	All ex. 3	−213	−201	0.062	5.5	−0.9
	3	−195	−183	0.138	10.6	0.5
<i>Carpinus betulus</i>	All ex. 3	−144	−131	0.142	12.1	−3.1
	3	−59	−48	0.197	16.2	−2.8
<i>Castanea sativa</i>	All ex. 3	6	20	0.283	23.5	5.1
	3	12	25	0.257	17.5	−3.1
<i>Fagus sylvatica</i>	All ex. 3	−91	−73	0.306	36	21.6
	3	−56	−41	0.205	19	9.2
<i>Fraxinus excelsior</i>	All ex. 3	114	130	0.322	25.1	3.5
	3	157	170	0.313	25.6	−6.5
<i>Larix decidua</i>	All ex. 3	−137	−126	0.13	11.2	2.2
	3	−92	−80	0.181	13.5	1.2
<i>Picea abies</i>	All ex. 3	−87	−66	0.202	14.5	5.5
	3	−84	−67	0.219	15.9	7.1
<i>Pinus cembra</i>	3	−190	−181	0.05	4.2	0.6
<i>Pinus nigra</i>	3	−56	−47	0.134	8.4	0.5
<i>Pinus pinaster</i>	All ex. 3	−159	−140	0.168	13.2	6.2
	3	−105	−92	0.195	14.7	5.8
<i>Pinus sylvestris</i>	All ex. 3	−155	−133	0.195	14.9	6.1
	3	−58	−42	0.218	17	5.3
<i>Populus alba</i> , <i>P. tremula</i> and <i>P. tremula</i> hybrids	All ex. 3	3	19	0.22	18.9	11.7
	3	−168	−155	0.147	12.6	6.9
<i>Prunus avium</i> or <i>Prunus serotina</i>	3	−51	−42	0.164	14.3	4.1
<i>Prunus avium</i>	3	−31	−22	0.16	13.3	1.4
<i>Prunus serotina</i>	3	−56	−47	0.17	15.8	7.4
<i>Pseudotsuga menziesii</i>	All ex. 3	−3	19	0.262	21.8	8.2
	3	92	109	0.262	21.7	7.2
<i>Quercus ilex</i>	All ex. 3	190	209	0.212	15.4	4
	3	96	109	0.203	15	1.8
<i>Quercus petraea</i>	All ex. 3	−355	−339	0.085	6.3	−0.6
	3	−162	−153	0.16	14	1.9
<i>Q. petraea</i> or <i>Q. robur</i>	All ex. 3	−122	−105	0.182	19.3	13.3
	3	−145	−133	0.157	14.3	5.7
<i>Quercus robur</i>	All ex. 3	−111	−98	0.128	10.1	5.5
	3	−73	−63	0.147	11.7	3.8
<i>Robinia pseudoacacia</i>	All ex. 3	−151	−138	0.097	8.2	3.8
	3	−84	−73	0.153	11.7	4.1

Not only the magnitude, but also the direction of the response to these independent variables differed between components, consistent with our third hypothesis and with previous meta-analyses (Litton et al., 2007; Poorter et al., 2012). For example, foliage mass declined with increasing basal area while stem mass did not change (Fig. 6). In relatively open and low basal area stands, biomass partitioning can be more to foliage to maximise light absorption because competition for soil resources is relatively low and there is less incentive for height (and stem) growth to outcompete neighbours. On the other hand, in dense stands there is less space for expanding crowns or fine-root systems and more biomass may be partitioned to the stems in order to grow taller to maintain a competitive position within the canopy (Poorter et al., 2012). Stand

density or species composition have also been found to influence biomass relationships in other studies (Monserud and Marshall, 1999; Wirth et al., 2004; Laclau et al., 2008). Roots were more variable in terms of their response to basal area, but it was not possible to divide this component into fine, medium and coarse roots, which prevents the patterns in root mass from being examined in detail.

The response to age was also consistent with previous studies that have found declines in foliage mass or leaf area and increases in stem mass as trees age (Porte et al., 2000; Porté et al., 2002; Saint-André et al., 2005; Wutzler et al., 2008; Genet et al., 2011; Shaiek et al., 2011). Age had a varied effect on root mass, consistent with previous work, where central European *F. sylvatica* fine, med-

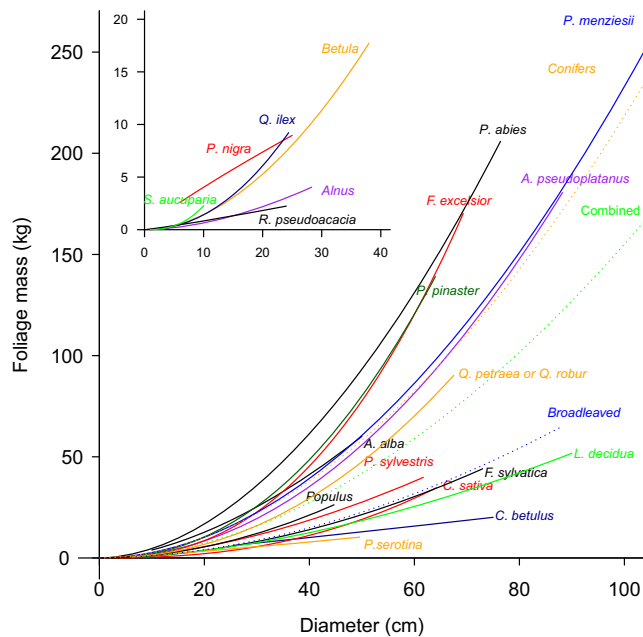


Fig. 4. The relationships between foliage mass and diameter for various European species. The lines are Eq. (3) fitted to all available data for the given species (Table A.2) and are provided in Table A.5. The dotted lines show the same relationships after dividing the data into broad-leaved species (dotted blue line), conifers (dotted orange line) or all species (dotted green line). The inset is the same relationship for species with small ranges of pseudo-observations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

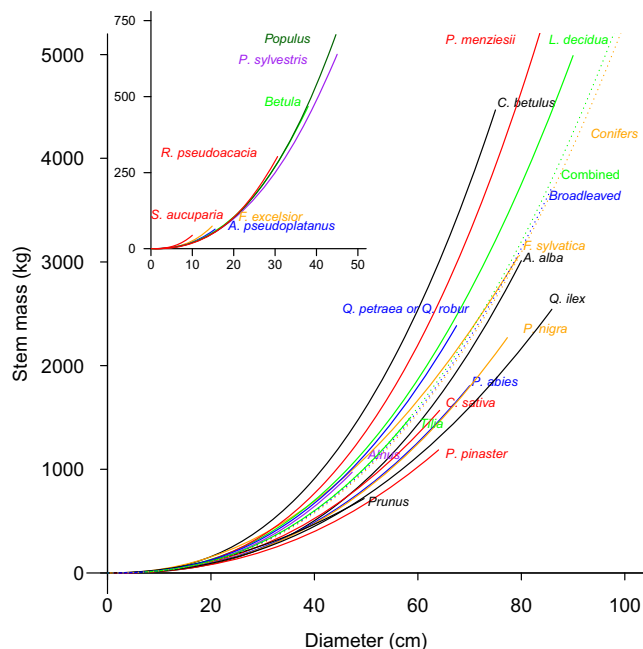


Fig. 5. The relationships between stem mass and diameter for various European species. The lines are Eq. (3) fitted to all available data for the given species (Table A.2) and are provided in Table A.5. The dotted lines show the same relationships after dividing the data into broad-leaved species (dotted blue line), conifers (dotted orange line) or all species (dotted green line). The inset is the same relationship for species with small ranges of pseudo-observations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

reduced with age for a given diameter (but not medium or coarse roots) (Saint-André et al., 2005). The variability in this study is likely to reflect the variable definition of roots used in the reviewed studies and that different components (fine, medium and coarse roots) do not necessarily respond to age or stand structure in the same way, similar to the contrasting aboveground responses of stem mass versus foliage mass (Saint-André et al., 2005).

4.2. Inter-specific variability

The considerable inter-specific variability in dbh – biomass (or crown or height) relationships has been found to correlate with species traits such as wood density, such that for a given diameter, biomass increases (or height declines) for species with higher wood density (Ketterings et al., 2001; Chave et al., 2005; Dietze et al., 2008; van Breugel et al., 2011; Ducey, 2012; Chojnacki et al., 2014). This study shows that this pattern not only exists for dbh-biomass relationships, but that relationships between biomass and age, basal area, trees per ha and climate also vary between species in relation to the species-specific wood density, shade tolerance or specific leaf area. For example, increasing basal area reduced foliage mass more for low wood density species but increased it for high wood density species. This may reflect a lower tolerance to competition of the low wood density species (Kunstler et al., 2016). The increase in stem mass with increasing age was greater for species with low wood density or low SLA. Since wood density is globally negatively correlated with a species' competitive effect on neighbours as well as its ability to tolerate competition (Kunstler et al., 2016), this may reflect a higher partitioning of biomass to stems (or height) as trees age in response to competition. Similarly, the contrasting responses of height, crown length or crown diameter to stem diameter or stand structural characteristics were correlated with wood density or shade tolerance for 17 European species (Forrester et al., 2017).

The inclusion of wood density in biomass equations can make them generic (e.g., Eq. (23)), so that they can also be used for rarer species (e.g., *Prunus avium*, *Tilia*, *Sorbus* or *Pinus cembra*) that are not well represented in datasets (Chave et al., 2004; Dietze et al., 2008; van Breugel et al., 2011). While the species-specific regional equations are likely to be more accurate for the range of stand conditions where they were developed, the generic equations where species identity is quantified as wood density may be a short term solution for rare species until they are better represented with biomass samples. Of the three generic equations used in this study (Eqs. (22)–(24)), our focus was on Eq. (23), which is based on wood density, because this trait is easier to obtain than shade tolerance (Eq. (24)) and is assumed to be less variable within a species than SLA (Eq. (22)). However, even wood density can vary between individuals of the same species (e.g., Niinemets, 2015).

4.3. Important considerations about the dataset

A source of error for the general equations produced in this study was the variability in definitions for a given biomass component. Different studies typically have different questions and therefore good reasons for varying the definitions. However, this would have inflated the error of the general equations.

The large dataset used for this study helps to make the equations in Tables A.5 and A.6 more widely applicable. However, despite the wide range in conditions these equations are still subject to at least three sources of uncertainty. The first is the inherent variability in the population (e.g., RMSE), which we aimed to partition, at least partly, to stand variables, climate and age. The second is the sample size (van Breugel et al., 2011; Roxburgh et al., 2015). Many of the published equations were developed from small sample sizes (Fig. 1e), which can lead to overestimates of

ium and coarse roots were not influenced by age (Genet et al., 2011) but increased with age in another study (Wirth et al., 2004; Wutzler et al., 2008). Fine roots of *Eucalyptus* were also

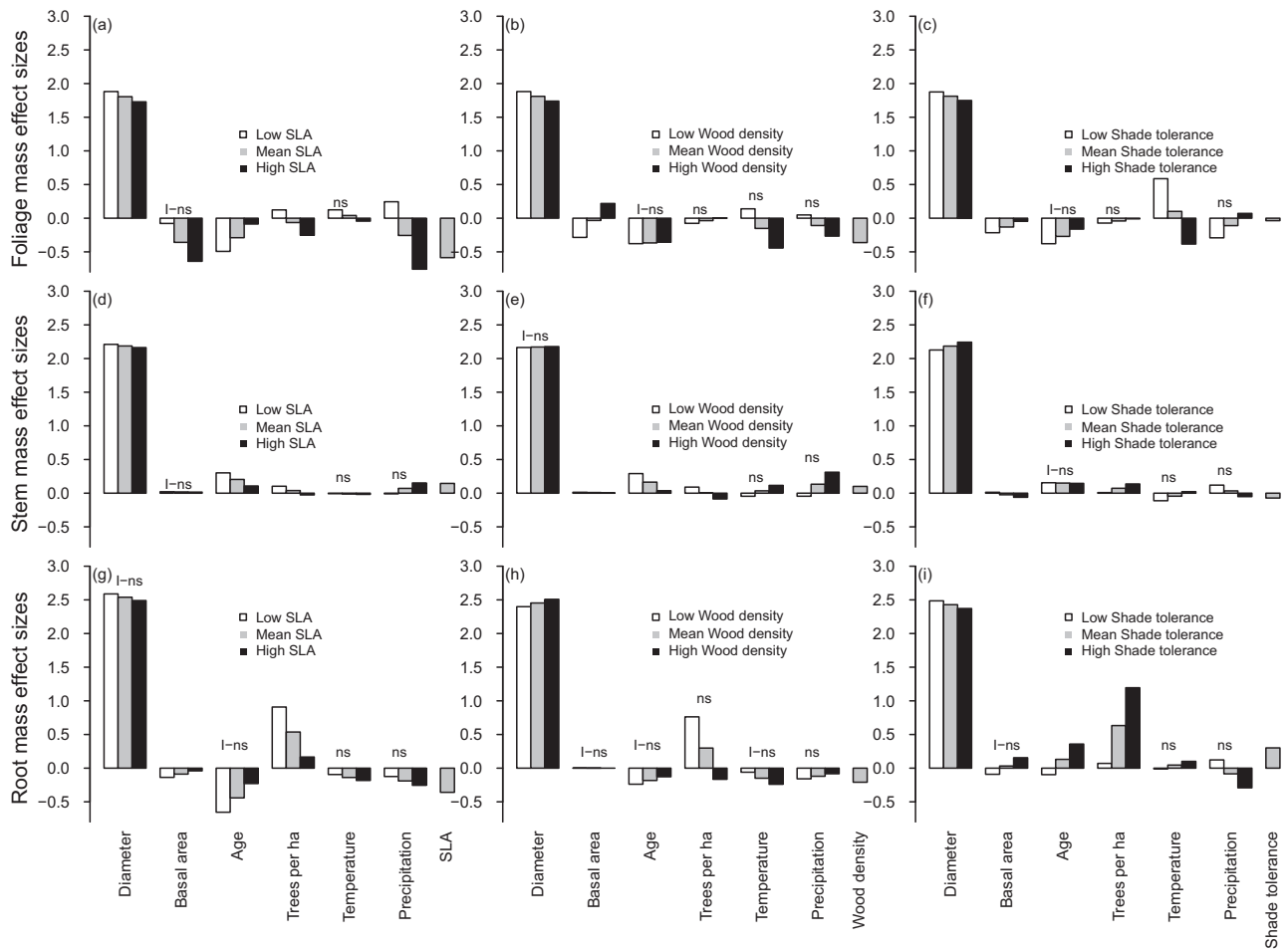


Fig. 6. The effect sizes (beta weights) of independent variables used to predict foliage mass (a–c), stem mass (d–f) and root mass (g–i) using Equations (22)–(24). The effect sizes are quantified as the slopes of the variables on the x-axis, all of which have been standardised (mean = 0 and standard deviation = 1). “I-ns” indicates that there was no significant interaction between the given x-axis variable and the trait (specific leaf area (SLA), wood density, shade tolerance). “ns” indicates that the x-axis variable was not significant in the model. The statistical information is in Table A.6. For the trait levels, Low = Mean – 1 standard deviation, Mean = Mean of all species, High = Mean + 1 standard deviation.

biomass due to the overestimation of parameters (Duncanson et al., 2015). While the median sample size was 33 observations for the published equations used in this study, previous studies have recommended at least 40–50 or more, depending on the type of tree species (Roxburgh et al., 2015). Therefore, the pseudo-observations derived from the published equations that were based on small data sets may have been slightly overestimated and there is no way of knowing how this could have influenced the regional or generic equations developed in this study. The accuracy of biomass models is inherently dependent on the accuracy of the raw data, or in our case, the pseudo-observations.

The third source of uncertainty is related to the diameter distributions because biomass predictions are most precise near the mean stem diameter that was used to fit the equation (van Breugel et al., 2011). If the equation is applied to a population with a different diameter distribution, then the precision will be reduced (Snowdon et al., 2002; van Breugel et al., 2011). That is, the uncertainty in the predictions depends on the characteristics of the population where the biomass equations are applied and not only on the sample size and characteristics of the population used to develop the equation (Roxburgh et al., 2015). Therefore, when deciding which trees to sample for biomass, it is pertinent to consider the diameter distribution of the population where the final equation will be applied (Roxburgh et al., 2015). While the diameter distributions of the pseudo-observations are shown in Fig. 1h, and

could also be calculated for each species-component using the data in Table A.2, the studies where the equations were obtained rarely described the diameter distributions of their sample trees or of the population where the equations were expected to be applied.

The MSE_{real} of the general models, which were developed after incorporating the error of the published equations (e.g., Fig. 2) were probably overestimates of the error. This is because many studies did not provide information about age, basal area or trees per ha. Therefore, the variability in biomass resulting from those variables could not be partitioned to those variables in the fitted equations, thereby inflating their MSE_{real} . However, even when the stand variables are provided, they are means for the whole stand and are therefore not specific to individual sample trees. In reality, within-stand variability probably results in individual trees experiencing different neighbourhood basal areas, trees per ha and species compositions. Therefore, the MSE_{real} in Tables A.5 and A.6 are provided only as estimates of the model errors in case they are required for calculating the prediction errors. To improve the MSE_{real} , and to account for within-stand variability, future studies may benefit from using a neighbourhood index approach to quantify the structural variability within single stands so that instead of assigning the same value of each structural variable to all sample trees from a given stand, each tree is assigned the actual structural information for its neighbourhood (e.g., Thorpe et al., 2010; Forrester, 2015). This would also make better use of the biomass

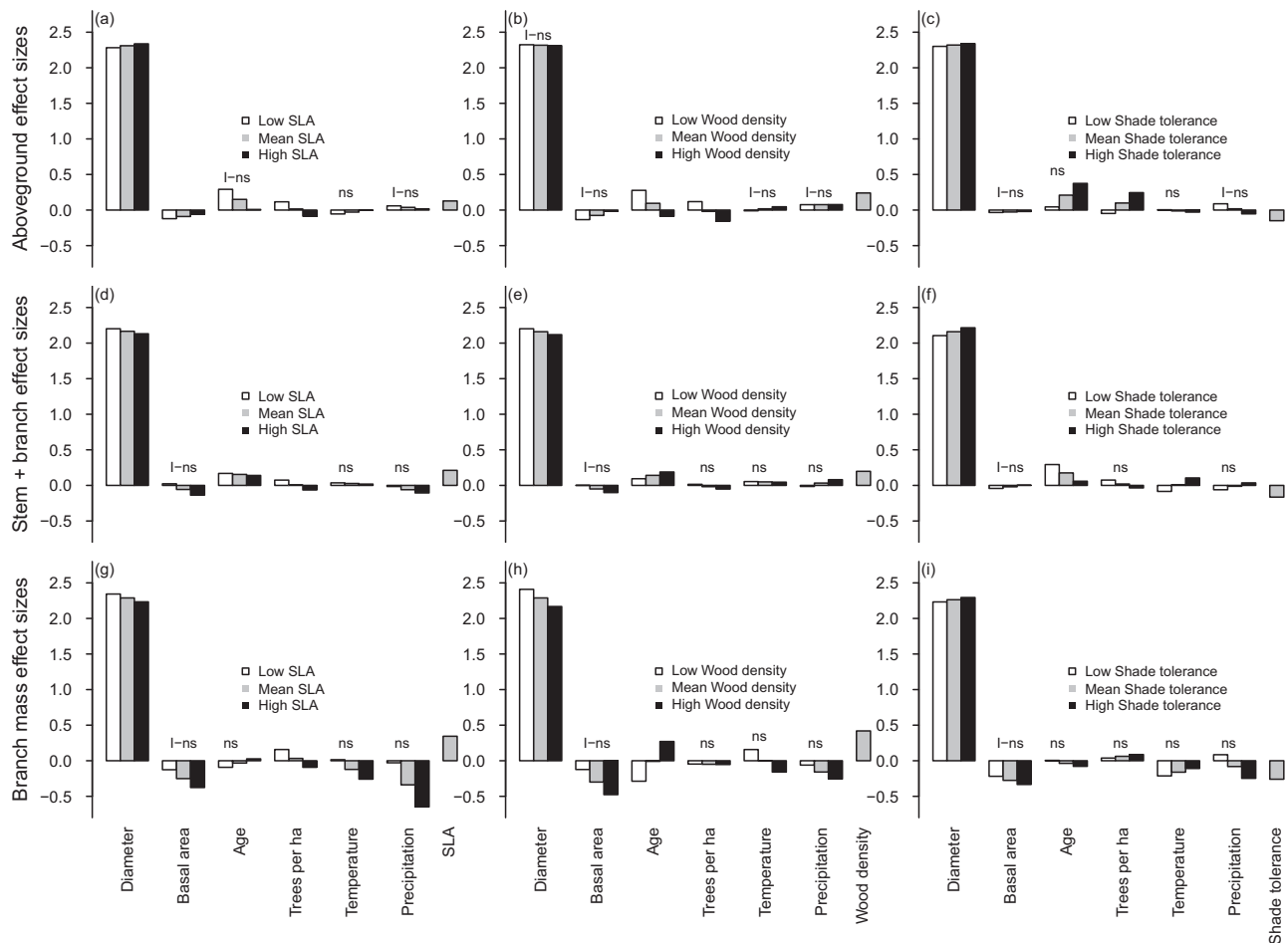


Fig. 7. The effect sizes (beta weights) of all independent variables used to predict aboveground mass (a–c), stem + branch mass (d–f) and total branch mass (g–i) using Eqs. (22)–(24). The effect sizes are quantified as the slopes of the variables on the x-axis, all of which have been standardised (mean = 0 and standard deviation = 1). “I-ns” indicates that there was no significant interaction between the given x-axis variable and the trait (specific leaf area (SLA), wood density, shade tolerance). “ns” indicates that the x-axis variable was not significant in the model. The statistical information is in Table A.6. For the trait levels, Low = Mean – 1 standard deviation, Mean = Mean of all species, High = Mean + 1 standard deviation.

data, which is typically very expensive and time consuming to collect relative to the collection of neighbourhood index information.

4.4. Next steps

Vertical stand structure has been shown to be one of the most important variables for predicting live-crown lengths in a range of European tree species (Forrester et al., 2017) and may also be worth considering when predicting leaf mass or leaf area. Vertical structure can be quantified using the relative height, calculated as the height of the sample tree divided by the mean height of the stand (or neighbourhood). In the same study the stand basal area variable was weighted by the wood density of the species within the plots while assuming that the wood density approximated any differences in the species competitive abilities (Forrester et al., 2017). This was done so that the equations could be applied to stands with contrasting species compositions without directly including the species composition in the equations. A similar approach may be required for biomass equations if it is found that species interactions influence biomass relationships (e.g., Laclau et al., 2008) and those effects of species interactions are not adequately explained using stand variables such as relative height, basal area and trees per ha.

Alternatively, instead of using stand variables, a single tree variable could be used that is influenced by climate, species mixing and all stand structural characteristics. For example, crown diameter and height were found to be adequate for predicting biomass

for a wide range of species from a wide range of forest types (Jucker et al., 2017) and other studies have also found that crown characteristics were good for predicting leaf area (Ledermann and Neumann, 2006). The reason for the strong correlations between crown dimensions and tree biomass are that crown dimensions are sensitive to many stand structural and climatic characteristics and can therefore potentially replace all of those variables in biomass equations. Also, the crown and height variables probably reflect the past growing conditions experienced by the tree better than the current stand structural conditions. Unfortunately, crown dimensions are time consuming to measure directly, are measured in many different ways and are rarely available for all trees in a stand, which prevents them from being a current practical solution. However, this may change in future as methods such as terrestrial laser scanning (Seidel et al., 2011) and remote sensing of crowns and heights becomes more practical. Therefore, while there are increasingly more variables being added to equations (Henry et al., 2011), we suggest that these should be variables known to be sensitive to stand structure.

It is worth considering that the more independent variables an equation contains, the higher the probability that it cannot be used in other studies because some of those independent variables are unavailable. Many of the studies reviewed provided only the “optimal” equation, although the combination of independent variables in those equations varied between species or studies. Therefore, this study focused on relatively simple equations (Eqs.

(3)–(21)) and all equations for the given species and component that were valid are provided (not only the best equations) so that potential users can select the equations based on their available data and objectives.

In conclusion, there was considerable inter- and intra-specific variability in biomass relationships. Intra-specific variability could be explained using age or stand characteristics while the inter-specific variability was related to traits such as wood density, specific leaf area and shade tolerance. Using this information, regional biomass equations were developed for 27 species and several species groups that summarise much of the information about European biomass equations in the literature, and that can be used in a wider range of forest types than the individual site-specific equations in the publications. However, while nearly 1000 equations or raw datasets were found for the species in this study, many individual species were not well represented. This was in terms of the range of ages or stand conditions where the data was collected, but it can also be illustrated by considering the number of equations per land area where the given species occurs (Table 1). Based on this calculation, many of the species with a high number of equations (*P. sylvestris*, *F. sylvatica*, *P. abies*) have a low value (<10 equations per land area) because they are so widely distributed. Our data set has been provided as Supplementary information with this study (Table A.2) so that regional species-specific or generic equations can be refined for specific regions or any other purposes that have not been considered in this study. While this dataset can easily be updated as new equations are published, a much more valuable database could be developed by adding more of the historic raw data on which the original published equations were based, as currently done in the US (Weiskittel et al., 2015) and elsewhere (Falster et al., 2015), and by targeting new biomass sampling to fill in the gaps of the database in terms of the distributions of independent variables (diameter, stand structural variables etc.), species representation relative to their abundance and sample distributions that are as close as possible to the diameter distributions in the target stands.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.04.011>.

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