

# On the Genetic Affinity of Individual Tree Biomass Allometry in Poplar Short Rotation Coppice

N. Oliveira<sup>1,2</sup> & R. Rodríguez-Soalleiro<sup>2</sup> & C. Pérez-Cruzado<sup>2,3</sup> & I. Cañellas<sup>1</sup> & H. Sixto<sup>1</sup>

<sup>1</sup> Forest Research Centre, National Institute for Agriculture and Food Research and Technology (INIA-CIFOR), Ctra. de la Coruña km 7,5, E-28040 Madrid, Spain

<sup>2</sup> Sustainable Forest Management Group, University of Santiago de Compostela, C/Benigno Ledo s/n, E-27002 Lugo, Spain

<sup>3</sup> Chair of Forest Inventory and Remote Sensing, Georg-August-Universität Göttingen, Göttingen D-37077, Germany

## Abstract

Woody biomass is one of our main resources available to enhance the bio-economy, but its production varies considerably depending on the species, the environment and crop management. The variability associated with these crops complicates the estimation of biomass through prediction models. The specificity of environment or genotype level limits the application of many of the models, which are often developed for use at local geographical levels. Although generalizations involve some loss of accuracy, the inclusion of a wide range of data for a wide range of environments and genotypes can improve model applicability. A total of 11,265 data from short-rotation, high-density poplar plantations (from 22 sites in Spain, covering 29 genotypes belonging to 7 different taxonomic groups) were used to develop biomass prediction models under Mediterranean conditions and to test whether similarities in individual tree biomass allometry occur within the taxonomic group level. A general model and both taxonomic group- and genotype-level models were fitted using weighted nonlinear regression. The simplified model, in which only the basal diameter is included, presented the best model performance, explaining 87% of the variability. The allometric similarities among different genotypes were evaluated in order to explore the relationship between the most frequently used poplar genotypes in the Mediterranean area, and although certain groups were identified, it was not possible to relate these similarities among different genotypes to their taxonomic group affinity. This was also confirmed by comparing the performance of the general models with the taxonomic group-level models when predicting at the genotype level. Although estimates made using the general models are relatively precise, the use of genotype-level models is recommended for more accurate predictions.

**Highlights:** The allometric similarities among genotypes were not related to their taxonomic group affinity.

Countrywide biomass prediction models for short-rotation poplar plantations were developed.

A general model as well as taxonomic group-level and genotype-level models were fitted.

The use of genotype-level models is recommended for more accurate predictions.

**Keywords:** *Populus* spp. . Biomass . Short-rotation forestry (SRF) . Allometric models. Weighted nonlinear regression . Generalized model

## Introduction

The use of biomass as a resource to further the development of the bio-economy is currently a major avenue of research in the field of bioenergy. There are a variety of sources of biomass, and among the crops used for this purpose, woody species have gained particular importance [1] and are now a commercial reality in many parts of the world [2].

The main aim with regard to these crops is to achieve higher, more efficient production as well as sustainability, and this requires a broad understanding of the factors involved in the production process. Total biomass production varies considerably, due not only to factors related to species and site conditions, but also to plantation management [3].

43 The suitability of the *Salicaceae* family for lignocellulosic biomass production using high-density crops in short-  
44 rotation coppice (SRC) is well documented [4, 5]. *Populus* spp. are considered highly favorable for this purpose  
45 under Mediterranean conditions, whether unirrigated [6] or irrigated [7], depending on the area. Nevertheless,  
46 wide genetic variability in biomass production is found among *Populus* spp. and their hybrids, and even among  
47 genotypes of the same taxonomic group [8]. Additionally, site conditions, crop management and all the  
48 interactions between them play an important role in determining the production attained [3].

49 The ability to predict production levels is particularly important when the economic viability of a given crop is to  
50 be assessed [9] or when decisions regarding rotation length must be taken. The allometric prediction models based  
51 on empirical data allow estimates of biomass stock and yield at the genotype level or in accordance with specific  
52 plantation conditions. The fact that biomass estimation models are site-specific [10] or genotype-specific [7]  
53 clearly limits their practical use as management tools for predicting biomass and crop management planning. The  
54 main constraint in this respect is the lack of models for some genotypes, although this is usually addressed by  
55 using models fitted for close genotypes according to the progenitor species (same hybrid group). This is a common  
56 procedure for biomass estimation in highly diverse natural forest, where the characteristics (such as wood-specific  
57 gravity) of the genotypes of the same species, genus and even family are averaged in order to make predictions  
58 when information specific to a given species is lacking [11]. This procedure assumes that biomass allometry is  
59 driven mainly by taxonomic affinity due to their common progenitor species. This is also the case for biomass  
60 estimation in SRC, where biomass models for taxonomically proximate genotypes are commonly used in the case  
61 of genotypes for which there are no published biomass models [8].

62 However, the use of general models for genotype-specific estimations, while allowing greater flexibility, can  
63 involve a considerable loss of accuracy. Hence, the calibration of generalized biomass models for large regions  
64 must be based upon a sample of site and climatic conditions encompassing the range of environmental conditions  
65 covered [12, 13]. This is both costly and time-consuming.

66 While much of the research related to biomass modelling for SRC has focused on developing site- and  
67 genotypespecific biomass models [14–16], there are also some examples of models developed at higher  
68 hierarchical levels [8, 17]. In any case, there has been little research focusing on the loss of accuracy and precision  
69 in biomass estimation at the genotype level due to the use of widely applicable general models. In addition, the  
70 validity of biomass models for other genotypes of the same or even other taxonomic groups has not been studied  
71 in depth.

72 The aims of this study are i) to evaluate the similarities in biomass allometry among different genotypes, and ii)  
73 to evaluate the accuracy and precision associated with using biomass models fitted at different hierarchical levels:  
74 generalized, taxonomic group and genotype-specific models fitted for an extensive dataset which includes  
75 information on different poplar genetic material and site conditions in the Mediterranean area under irrigation  
76 management.

## 77 **Materials and methods**

### 78 **Data**

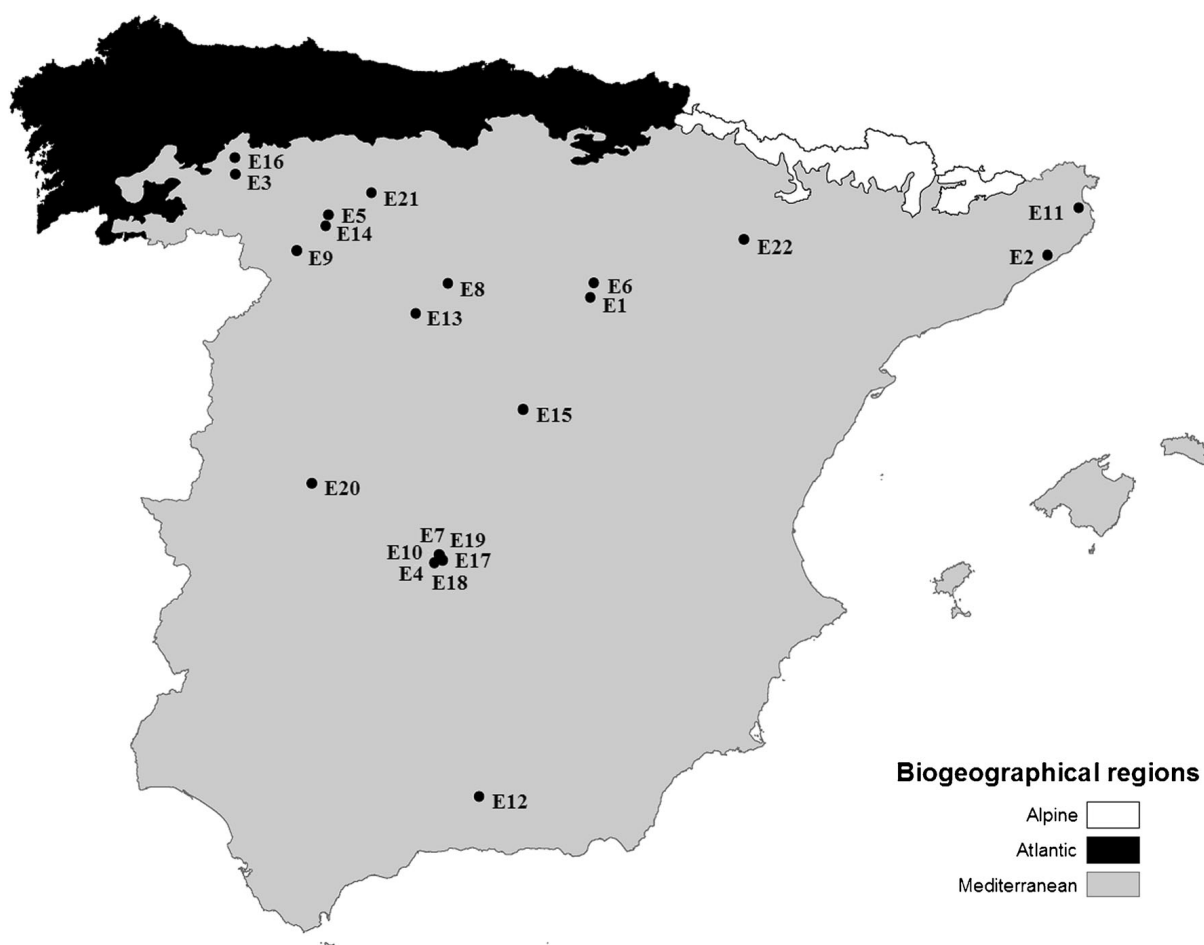
79 An extensive dataset of *Populus* spp. growing under an SRC regime at 22 established sites in Spain was used in  
80 this study (Fig. 1). The sites cover a wide range of conditions (Table 1) and are highly representative of the areas  
81 where this crop is present, ranging from temperate to warm Mediterranean climates. Twenty-nine genotypes of  
82 seven different taxonomic groups were included in the network of plots (Table 2) [18].

83 Plantations were established in early spring during the period from 2005 to 2010 using hardwood cuttings 20–30  
84 cm in length. Density ranged from 4762 cuttings ha<sup>-1</sup> to 33,333 cuttings ha<sup>-1</sup> in a design consisting of single rows  
85 3 m apart.

86 Similar management was applied at all sites for all genotypes, including fertilization during soil tillage according  
87 to the specific soil characteristics, pre-emergence treatment with oxyfluorfen (4 l ha<sup>-1</sup>) to control weeds, and drip  
88 or flood irrigation (to field capacity) during the summer months [19]. The summer drought, characteristic of the

89 Mediterranean climate, necessitated the application of irrigation at all the sites. A rotation length of 3 years was  
90 established for all but three of the sites (E4, E5 and E17), where a 4-year rotation was determined due to poor  
91 development. In the plots established at E1, trees were cut back 1 year after planting in order to stimulate sprouting  
92 [20, 21]. Hence, the stages of development covered in this study at the end of the first rotation were R3S3, R4S3  
93 and R4S4, denoting root age as R and stem age as S.

94 Measurements were taken annually after planting. The diameter over bark at 10 cm above ground level (*Db*, mm),  
95 accounting for the size of the shoots at the usual harvesting height, was measured using a digital caliper. The total  
96 height of the highest shoot (*Ht*, cm) was also measured with a measuring pole. The number of shoots and the  
97 density of living trees per plot were also recorded. The above-ground woody biomass was evaluated in all plots  
98 by destructive analysis at the end of the rotation, once leaves had fallen. Total above-ground dry woody biomass  
99 (*Ws*, g dry matter [DM]) was determined for each sample from the fresh weight, and the estimated wood moisture  
100 by randomly selecting whole plants from each of the plots and then oven-drying a sample randomly selected for  
101 each genotype to a constant weight at 105 °C.



102

103 **Fig. 1** Locations of the experimental sites

## 104 **Statistical Analysis**

### 105 *Fitting and Evaluating Biomass Models at Different Hierarchical Levels*

106 We fitted regression models at three levels: 1) a joint general model for all the genotypes, sites and management  
107 schemes (density and rotation length) included in the study; 2) taxonomic group-level models, by taking into  
108 account the hybrid group of each tested genotype (see Table 2), excluding those taxonomic groups which were  
109 present at only one site or contained only one genotype (*P. × generosa* × *P.nigra* L., *P. nigra* L. and *P.*

110 *trichocarpa*); and 3) genotype-level models for each of 18 genotypes (after excluding those which were present  
 111 at only a single site).

112 Due to the lack of homogeneity in the residual variances, weighted nonlinear regression was used to correct  
 113 heteroscedasticity, frequently present in individual tree biomass data [22]. Each observation was weighted by the  
 114 inverse of its basal diameter variance ( $1/D_b^2$ ). This weighting factor stabilized the variances and provided  
 115 homogeneous studentized residuals.

116 For the general model fit, different tree-level variables were tested as regressor [ $D$  (1),  $H$  (2),  $DH$  (3),  $DN$  (4),  
 117  $DHN$  (5)], and the different stages of development according to the root age (R) or the stem age (S) were also  
 118 evaluated [ $DR$  (6),  $DS$  (7)] (Table 3).

119 In all the proposed models, parameter  $b$  is the power of the basal diameter ( $D_b$ ), parameter  $c$  is the total height  
 120 ( $H_t$ ), parameter  $d$  is the number of shoots (N), parameter  $e$  is the root age (R) and parameter  $f$  is the stem age (S).

121 To evaluate the performance of the models, we used the proportion of variance explained by the weighted models  
 122 (pseudo-coefficient of determination,  $pse-R^2$ ), the root of weighted mean square error ( $RMSE_\psi$ ), the error sum of  
 123 squares ( $SSE_\psi$ ) and the total sum of squares ( $SST_\psi$ ):

**Table 1** Locations and characteristics of the experimental sites

Sites	Coordinates		Altitude, masl	TM <sup>a</sup>	pH	OM <sup>b</sup>	Köppen climate classification
	Latitude	Longitude					
E1	41° 28' 18.6"N	2° 32' 51"W	947	11.2	8.42	2.08	Temperate oceanic climate
E2	41° 41' 42.6"N	2° 40' 22.3"E	65	16.1	6.31	0.3	Warm Mediterranean climate
E3	42° 37' 25"N	6° 38' 54"W	556	12.7	6.21	0.85	Temperate Mediterranean climate
E4	39° 11' 40.22"N	4° 16' 57.86"W	670	15.0	6.1		Cold semi-arid climate
E5	42° 9' 6.24"N	5° 33' 42.37"W	254	11.8	6.84	0.62	Temperate Mediterranean climate
E6	41° 35' 58.3"N	2° 30' 23.7"W	1097	10.2	6.4	0.57	Temperate oceanic climate
E7	39° 15' 39.81"N	4° 13' 46.6"W	670	14.6	6.08	1.11	Warm Mediterranean climate
E8	41° 35' 29.65"N	4° 10' 20.48"W	770	11.9	8.27	1.78	Temperate Mediterranean climate
E9	41° 50' 11"N	5° 54' 36.1"W	716	12.1	5.41	1.51	Temperate Mediterranean climate
E10	39° 14' 53.99"N	4° 13' 44.13"W	670	14.6	6.2	0.93	Cold semi-arid climate
E11	42° 04' 47.2"N	3° 3' 56.3"E	12	15.7	8.43	0.66	Warm Mediterranean climate
E12	37° 11' 43.1"N	3° 46' 3.7"W	554	15.3	8.45	1.43	Warm Mediterranean climate
E13	41° 19' 29.94"N	4° 32' 4.34"W	756	12.3	9.04	0.89	Temperate Mediterranean climate
E14	42° 3' 21.9"N	5° 35' 12.4"W	715	11.8	8.26	1.04	Temperate Mediterranean climate
E15	40° 30' 47.4"N	3° 18' 39.6"W	593	13.7	8.4	0.49	Warm Mediterranean climate
E16	42° 36' 45.7"N	6° 39' 52.6"W	531	12.8	6.01	1.02	Temperate Mediterranean climate
E17	39° 14' 42.75"N	4° 13' 21.88"W	670	14.7	6.29	1.25	Cold semi-arid climate
E18	39° 13' 3.45"N	4° 11' 38.83"W	670	14.7	6.18	0.94	Cold semi-arid climate
E19	39° 15' 24.74"N	4° 13' 36.87"W	670	14.6			Warm Mediterranean climate
E20	39° 50' 56.82"N	5° 39' 32.79"W	258	16.7	7.05	0.93	Cold semi-arid climate
E21	42° 21' 4.78"N	5° 4' 11.07"W	838	11.9	7.54	1.18	Temperate oceanic climate
E22	41° 56' 59.47"N	0° 47' 15.98"W	279	14.5	8.26	1.15	Warm oceanic climate

<sup>a</sup> TM is the average annual mean temperature (°C)

<sup>b</sup> OM is the soil organic matter (%)

$$SSE_{\Psi} = \sum_{i=1}^n (\Psi_i * (W_{si} - \hat{W}_{si})^2) \quad (1)$$

$$SST_{\Psi} = \sum_{i=1}^n \left( \Psi_i * \left( W_{si} - \frac{\sum_{j=1}^n (\Psi_j * W_{sj})}{\sum_{j=1}^n \Psi_j} \right)^2 \right) \quad (2)$$

$$pse - R^2 = r_{w_i \hat{w}_i}^2 \quad (3)$$

$$RMSE_{\Psi} = \sqrt{\frac{SSE_{\Psi}}{n-p}} \quad (4)$$

125

126 where  $r_{w_i \hat{w}_i}^2$  is the correlation coefficient for a linear regression between the observed and the predicted values of  
 127 the dependent variable [23],  $W_{si}$  is the observed biomass,  $\hat{W}_{si}$  is the predicted biomass,  $\Psi_i$  is the weighted factor,  
 128  $n$  is the number of data used in the fitting and  $p$  is the number of parameters to be estimated.

129 The genotype- and taxonomic group-level models were fitted by considering only the basal diameter ( $Db$ ) as  
 130 regressor variable, as this is the most common model formulation used in biomass prediction and was the model  
 131 which explained the highest variability at the general level.

#### 132 *Evaluation of the Similarity in Biomass Allometry Among Genotypes*

133 The similarity in biomass allometry among genotypes was evaluated by cross-predicting with the genotype-level  
 134 models and comparing the predictions at the genotype level with the observed values. Two genotypes are assumed  
 135 to share allometry when the biomass model fitted for a given genotype produces non-deviated predictions over  
 136 the other. Four non-parametric validation tests were used for evaluating the similarity in biomass allometry among  
 137 genotypes [24]. All these tests showed similar performance, and the mean p-values were computed pairwise for  
 138 all genotypes. The null hypothesis for all tests is that both samples belong to the same population, so small p-  
 139 values lead us to reject the null hypothesis that both samples share the same allometric model. To plot the model  
 140 suitability of each genotype, a radial chart was used, which is a useful graphical tool for data comparison on a  
 141 two-dimensional chart. It is also known as a radar chart or kiviati diagram [25–27].

**Table 2** Genotypes and taxonomic groups considered in this study. Information obtained from the International Register of Cultivars of *Populus L.* 2016 [18]

Genotype	Parentage		Section	Origin	Breeder	Number of sites where present
'2000 verde'	<i>P. × canadensis</i>	D × N	Aigeiros	-	Italy, 1982	1
'A2A'	Mönch	D × N	Aigeiros	-	Italy, 1993	1
'A4A'		D × N	Aigeiros	(Illinois USA) × (Piemonte, Italy)	Italy, 1986	6
'AF2'		D × N	Aigeiros	(Illinois USA) × (Italy)	Italy, 1994	10
'B-1 M'		D × N	Aigeiros	-	Italy, 1960s	1
'Ballottino'		D × N	Aigeiros	-	Italy	11
'Dorskamp'		D × N	Aigeiros	(Missouri USA) × (Italy)	Netherlands, 1952	4
'Guardi'		D × N	Aigeiros	(Stoneville USA) × (Spain)	Italy, 1960s	5
'I-214'		D × N	Aigeiros	('Canadesi bianco') × (Italy)	Italy, 1929	17
'Luisa Avanzo'		D × N	Aigeiros	-	Italy, 1968	1
'MC'		D × N	Aigeiros	Italy	Italy, 1954	4
'Muur'		D × N	Aigeiros	(Iowa USA × Illinois USA) × (Italy × Belgium)	Belgium, 1978	1
'Orion'		D × N	Aigeiros	(Texas USA) × (Italy)	Italy, 1983	4
'Oudenberg'		D × N	Aigeiros	(Iowa US × Illinois USA) × (Italy × Belgium)	Belgium, 1978	14
'Triplo'		D × N	Aigeiros	(Mississippi USA) × (Italy)	Italy, 1961	2
'Vesten'		D × N	Aigeiros	(Iowa USA × Illinois USA) × (Italy × Belgium)	Belgium, 1978	6
'Beaupre'	<i>P. × generosa</i> Henry	T × D	Tacamahaca × Aigeiros	(USA) × (Iowa USA × Missouri USA)	Belgium	1
'Hoogvorst'		T × D	Tacamahaca × Aigeiros	(USA) × (Michigan USA)	Belgium, 1969	1
'Raspalje'		T × D	Tacamahaca × Aigeiros	(USA) × (Iowa USA × Missouri USA)	Belgium	3
'Unal'		T × D	Tacamahaca × Aigeiros	(USA) × (Iowa USA × Missouri USA)	Belgium, 1960	5
'AF8'		(D × T) × T	(Aigeiros × Tacamahaca) × Tacamahaca	(Iowa USA × Oregon USA) × (Wash. USA)	Italy, 1993	8
'Grimminge'		D × (T × D)	Aigeiros × (Tacamahaca × Aigeiros)	(Michigan USA × Conn. USA) × (Wash. USA × (Iowa USA × Missouri USA))	Belgium, 1976	3
'AF6'	<i>P. × generosa</i> Henry × <i>P. nigra L.</i>	(T × D) × N	(Tacamahaca × Aigeiros) × Aigeiros	-	Italy	1
'Monviso'		(D × T) × N	(Aigeiros × Tacamahaca) × Aigeiros	(Iowa USA × Oregon USA) × (Piemonte Italy × Umbria Italy)	Italy, 1991	9
'Baldo'	<i>P. deltoides W.</i>	D	Aigeiros	-	Italy, 1985	4
'Viriato'	Bartram ex Marshall	D	Aigeiros	(Hardvard, USA) × (Stoneville, USA)	Portugal, 1986	5
'Gazi'	<i>P. nigra L.</i>	N	Aigeiros	-	Turkey	1
'Lombardo leones'		N	Aigeiros	León, Spain	Spain, 1970	1
'Bruhl 7'	<i>P. trichocarpa</i> Torr. & A. Gray	T	Tacamahaca	Oregon, USA	USA, 1950	1

142

**Table 3** Model formulations

Equation	Nomenclature	Model
1	<i>D</i>	$Ws = a * D_b^b$
2	<i>H</i>	$Ws = a * H_t^c$
3	<i>DH</i>	$Ws = a * D_b^b * H_t^c$
4	<i>DN</i>	$Ws = a * D_b^b * N^d$
5	<i>DHN</i>	$Ws = a * D_b^b * H_t^c * N^d$
6	<i>DR</i>	$Ws = a * D_b^b * R^e$
7	<i>DS</i>	$Ws = a * D_b^b * S^f$

143

144 *Ws* total above-ground woody dry biomass (g dry matter [DM]); *D<sub>b</sub>* diameter over bark at 10 cm of dominant  
 145 shoots per stool (mm); *H<sub>t</sub>* total height of the highest shoot per stool (cm); *N* number of shoots per stool; *R* root  
 146 age (years); *S* stem age (years)

147

## 148 Results

### 149 Allometric Above-Ground Biomass Models

#### 150 *General Weighted Fit*

151 First, a general model was fitted which included all sites, genotypes and management variability (stand density  
152 and rotation length), and which used different combinations of regressor variables including basal diameter,  
153 dominant shoot height, number of shoots and age (represented by root age and stem age). The parameter  
154 estimations and fitting statistics are shown in Table 4.

155 All the parameter estimates simultaneously contributed to statistically significant improvements in the quality of  
156 the fit of the model to the data ( $p < 0.0001$ ), and the models accounted for more than 72% of the total variability  
157 in biomass yield, except for the model that included only height as a predictor, which accounted for only 38% of  
158 the total variability. Model 1 ( $D$ ) accounted for 87% of the total variability, which is the highest variability  
159 explained by any of the tested general models. This model had the smallest sum of squares error and  $RMSE_y$ , and  
160 the highest  $pse-R^2$ . The sum of the weighted residual was similar when the number of shoots was included in the  
161 model, but this is not the case where only height is used as a predictor.

#### 162 *Genotype Weighted Fit*

163 Tables 5 and 6 show the parameter estimates and fitting statistics for the models fitted at the taxonomic group and  
164 genotype levels, respectively. The singularity of these equations is that they include the site variability. The  
165 number of sites where each genotype is present is shown in Table 2.

166 All the equations considered achieved convergence, and the parameter estimates significantly improved the  
167 quality of the model fit to the data at  $p = 0.05$ , with the exception of parameter  $a$  for the genotype ‘Baldo’ (Table  
168 6). It is known that the numerical value of the parameter  $a$  depends on the value of the  $b$  parameter, as well as on  
169 the units of the response and regressor variables, which implies that the  $a$  parameter has no biological meaning,  
170 and therefore there is no serious implication as regards the non-significance of this parameter [28].

171 The general model accounts for only 87% of the variability in biomass estimations, whereas the taxonomic group-  
172 level models account for 86 to 92% of the total variability. The genotype-level models accounted for 82–95% of  
173 the total production variability.

### 174 Similarity in Biomass Allometry Among Different Genotypes

175 The  $p$ -values of the validation tests used to explore the similarity in biomass allometry among the different poplar  
176 genotypes are presented in Fig. 2. Only those cases where the tests detected differences in biomass allometry  
177 among genotypes ( $p > 0.05$ ) are included. The genotypes in Fig. 2 are grouped in circular sectors according to the  
178 different taxonomic groups to which they belong, represented in different colors. The distribution of the colors  
179 for the different taxonomic groups indicates that the clusters were not dependent on the taxonomic group to which  
180 they belonged, as all colors are distributed over the four circular sections considered. In addition, for the genotypes  
181 within the same taxonomic group (e.g., the dots in blue), the  $p$ -values in the outermost positions are located in  
182 circular sections belonging to different taxonomic groups, meaning that the closest allometries were more  
183 frequently observed for genotypes belonging to different taxonomic groups.

## 184 Discussion

### 185 Allometric Above-Ground Biomass Models

186 The need for an accurate biomass estimation tool for poplar cultivation in SRC is an issue which has been  
187 discussed extensively [6, 17, 29, 30]. However, due to the specificity of these equations, which are often  
188 constructed using data from a very small area, their applicability in large areas is limited [31]. In addition to the  
189 inherent limitations due to the genetic specificity [32], it is important to consider the genotype  $\times$  environment  
190 interaction ( $G \times E$ ), both in the development of the equation and when applying it [33].

191 The general model proposed in this study may provide a useful tool for poplar biomass estimations, as the data  
 192 used for its development cover a wide range of environments and genotypes, ensuring its applicability in  
 193 Mediterranean conditions. A total of 22 different environments and 29 different genotypes belonging to 7 different  
 194 taxonomic groups were used to develop the equation, attaining 87% of explained variability using model D (1)  
 195 (which includes only the basal diameter of the dominant shoot as predictor). Even though the model we propose  
 196 explains less variability than that developed by Ben Brahim et al. [17] (94%), our model was fitted using a larger  
 197 dataset and a broader range of genotypes sites and rotation length.

**Table 4** Parameter estimates and goodness-of-fit statistics for the general models, testing different combinations of regressor variables

No.	Model	Estimate	SE	<i>t</i> value	Pr(>  <i>t</i>  )	RMSE pond	pse- R <sup>2</sup>	SSE	SST	DF	
1	D	$\hat{a}$	0.1351	0.0053	25.6999	<0.0001	15.11	0.87	2, 571, 247	19, 346, 661	11, 263
		$\hat{b}$	2.4577	0.0092	266.9371	<0.0001					
2	DH	$\hat{a}$	0.0093	0.0005	18.5732	<0.0001	18.12	0.81	3, 697, 895	19, 346, 661	11, 262
		$\hat{b}$	1.8020	0.0126	142.7784	<0.0001					
		$\hat{c}$	0.8149	0.0126	64.4689	<0.0001					
3	H	$\hat{a}$	0.0005	0.0000	11.0285	<0.0001	32.62	0.38	11, 982, 596	19, 346, 661	11, 263
		$\hat{c}$	2.3581	0.0135	175.2047	<0.0001					
4	DN	$\hat{a}$	0.1287	0.0050	25.7229	<0.0001	15.64	0.86	2, 754, 025	19, 346, 661	11, 262
		$\hat{b}$	2.4630	0.0092	268.8941	<0.0001					
		$\hat{d}$	0.0853	0.0059	14.5741	<0.0001					
5	DHN	$\hat{a}$	0.0086	0.0005	18.6787	<0.0001	18.04	0.81	3, 665, 854	19, 346, 661	11, 261
		$\hat{b}$	1.8043	0.0125	144.8650	<0.0001					
		$\hat{c}$	0.8200	0.0125	65.6383	<0.0001					
		$\hat{d}$	0.0897	0.0049	18.2734	<0.0001					
6	DR	$\hat{a}$	0.0905	0.0039	23.2819	<0.0001	22.10	0.72	5, 501, 217	19, 346, 661	11, 262
		$\hat{b}$	2.4302	0.0096	254.2441	<0.0001					
		$\hat{f}$	0.4495	0.0249	18.0194	<0.0001					
7	DS	$\hat{a}$	0.0905	0.0039	23.2819	<0.0001	22.10	0.72	5, 501, 217	19, 346, 661	11, 262
		$\hat{b}$	2.4302	0.0096	254.2441	<0.0001					
		$\hat{e}$	0.4495	0.0249	18.0194	<0.0001					

198

199  $W_s$  total above-ground woody dry biomass (g dry matter [DM]);  $D_b$  diameter over bark at 10 cm of dominant  
 200 shoots per stool (mm); Ht total height of the highest shoot per stool (cm);  $N$  number of shoots per stool;  $R$  root  
 201 age (years);  $S$  stem age (years);  $SE$  standard error

**Table 5** Parameter estimates and goodness-of-fit statistics for the taxonomic group-level models with the formulation  $W_s = a * D_b^b$

Taxonomic group	Estimate	SE	<i>t</i> value	Pr(>  <i>t</i>  )	RMSE pond	pse- R <sup>2</sup>	SSE	SST	DF	
<i>P. × canadensis</i> Mönch	$\hat{a}$	0.1435	0.0062	22.9121	<0.0001	14.34	0.87	1, 785, 955	13, 350, 259	8688
	$\hat{b}$	2.4394	0.0104	234.7719	<0.0001					
<i>P. × generosa</i> Henry	$\hat{a}$	0.1054	0.0135	7.8377	<0.0001	18.12	0.87	408, 389.3	3, 168, 968	1244
	$\hat{b}$	2.5182	0.0294	85.7138	<0.0001					
<i>P. deltoides</i>	$\hat{a}$	0.0496	0.0149	3.3341	0.0010	17.32	0.86	86, 103	609, 394	287
	$\hat{b}$	2.6940	0.0700	38.4895	<0.0001					

202

203  $W_s$  total above-ground woody dry biomass (g dry matter [DM]);  $D_b$  diameter over bark at 10 cm of dominant  
 204 shoots per stool (mm);  $SE$  standard error

**Table 6** Parameter estimates and goodness-of-fit statistics for the genotype-level models with the formulation  $Ws = a * Db^b$ 

Genotype		Estimate	SE	<i>t</i> value	Pr(>  <i>t</i>  )	RMSE pond	pse- R <sup>2</sup>	SSE	SST	DF
'Guardi'	$\hat{a}$	0.1251	0.0252	4.9737	<0.0001	9.40	0.91	24, 232	250, 858	274
	$\hat{b}$	2.4925	0.0501	49.7590	<0.0001					
'Oudenberg'	$\hat{a}$	0.1942	0.0195	9.9478	<0.0001	11.34	0.87	203, 304	1, 604, 185	1580
	$\hat{b}$	2.3877	0.0249	95.8349	<0.0001					
'Vesten'	$\hat{a}$	0.1865	0.0271	6.8909	<0.0001	8.71	0.93	26, 613	378, 115	351
	$\hat{b}$	2.3788	0.0354	67.1952	<0.0001					
'Triplo'	$\hat{a}$	0.1404	0.0653	2.1494	0.0334	15.89	0.91	33, 573	364, 686	133
	$\hat{b}$	2.4126	0.1055	22.8632	<0.0001					
'I-214'	$\hat{a}$	0.0920	0.0079	11.6919	<0.0001	14.19	0.89	458, 511	4, 059, 415	2278
	$\hat{b}$	2.5453	0.0201	126.4736	<0.0001					
'AF2'	$\hat{a}$	0.0758	0.0130	5.8334	<0.0001	20.50	0.84	358, 168	2, 216, 374	852
	$\hat{b}$	2.5787	0.0389	66.3466	<0.0001					
'Ballottino'	$\hat{a}$	0.1619	0.0186	8.6926	<0.0001	10.44	0.90	126, 820	1, 236, 377	1163
	$\hat{b}$	2.3804	0.0279	85.2810	<0.0001					
'A4A'	$\hat{a}$	0.1875	0.0446	4.2019	<0.0001	16.46	0.89	70, 960	615, 059	262
	$\hat{b}$	2.3869	0.0556	42.9665	<0.0001					
'Dorskamp'	$\hat{a}$	0.3048	0.0752	4.0558	0.0001	17.21	0.85	86, 195	562, 713	291
	$\hat{b}$	2.2766	0.0588	38.7374	<0.0001					
'MC'	$\hat{a}$	0.1915	0.0351	5.4527	<0.0001	11.13	0.88	70, 847	563, 988	572
	$\hat{b}$	2.3583	0.0447	52.7246	<0.0001					
'Orion'	$\hat{a}$	0.1114	0.0464	2.4013	0.0181	19.12	0.89	38, 003	325, 625	104
	$\hat{b}$	2.5631	0.0968	26.4910	<0.0001					
'Unal'	$\hat{a}$	0.1166	0.0176	6.6204	<0.0001	9.42	0.95	22, 710	434, 365	256
	$\hat{b}$	2.5004	0.0355	70.4094	<0.0001					
'Raspalje'	$\hat{a}$	0.1546	0.0319	4.8490	<0.0001	18.20	0.94	63, 951	1, 026, 973	193
	$\hat{b}$	2.4903	0.0463	53.7515	<0.0001					
'AF8'	$\hat{a}$	0.1952	0.0426	4.5795	<0.0001	15.82	0.86	125, 672	900, 930	502
	$\hat{b}$	2.3317	0.0506	46.0501	<0.0001					
'Monviso'	$\hat{a}$	0.1729	0.0231	7.4882	<0.0001	15.66	0.90	205, 267	1, 939, 761	837
	$\hat{b}$	2.4257	0.0315	76.9794	<0.0001					
'Grimminge'	$\hat{a}$	0.3257	0.0775	4.2022	<0.0001	8.88	0.90	16, 012	151, 701	203
	$\hat{b}$	2.2301	0.0598	37.3135	<0.0001					
'Baldo'	$\hat{a}$	0.0291	0.0186	1.5652	0.1206	23.86	0.82	59,189	314,277	104
	$\hat{b}$	2.8152	0.1463	19.2396	<0.0001					

**Table 6** (continued)

Genotype		Estimate	SE	<i>t</i> value	Pr(>  <i>t</i>  )	RMSE pond	pse- R <sup>2</sup>	SSE	SST	DF
'Viriato'	$\hat{a}$	0.0677	0.0194	3.4946	0.0006	12.07	0.90	26,353	249,441	181
	$\hat{b}$	2.6221	0.0685	38.2790	<0.0001					

205

206

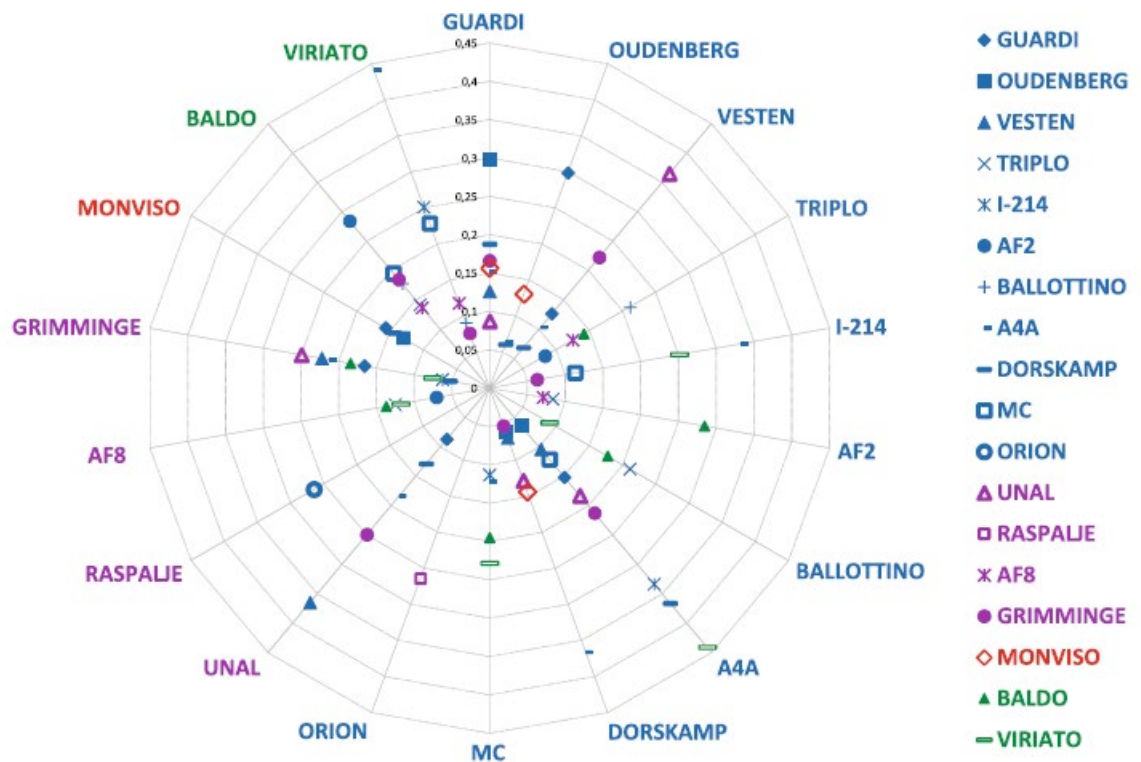
207 *Ws* total above-ground woody dry biomass (g dry matter [DM]); *Db* diameter over bark at 10 cm of dominant  
 208 shoots per stool (mm)

209 The main grouping criteria considered in biomass production is clearly related to the genetic background of the  
 210 genotypic plant materials [30], and previous studies have suggested that a single equation for tree dry weight  
 211 might be applied at the taxonomic group level irrespective of the environmental conditions [8]. Hence, we provide  
 212 taxonomic group-level models for cases where we have sufficient data (*P. × canadensis*, *P. × generosa* and *P.*  
 213 *deltooides*). The variability explained at the taxonomic group level is within the range found by Dillen et al. [8],  
 214 from 0.74 to 0.99. Although these equations are expected to be more accurate than the generalized equation, this

215 is not so in all cases. This evidences the fact that taxonomic group affinity is not a suitable clustering factor to  
 216 explain individual tree biomass allometry. When a specific equation for a particular genotype is not available or  
 217 where there are several different genotypes in a given plantation, the use of general equations simplifies the  
 218 estimation of biomass stocks, despite some loss of precision. The greatest precision is achieved using genotype-  
 219 level models, so when this information is available, the use of such models is preferable over any of the general  
 220 models. Although the genotype-level models provided in this study are specific in terms of genotype, data were  
 221 collected from different environments, so  $G \times E$  are included and can be considered suitable for Mediterranean  
 222 conditions.

### 223 Similarity in Biomass Allometry Among Different Genotypes

224 In contrast to what might be expected, the similarities or differences with respect to the biomass allometry among  
 225 genotypes do not appear to bear any relation to the taxonomic group [8]. In fact, the results highlight that genotypes  
 226 belonging to the same taxonomic group exhibit a wide range of biomass allometry. This may be evidence that the  
 227 typical procedure of clustering in taxonomically close groups does not always yield efficient results in biomass  
 228 modelling under SRC. This is also a common procedure in biomass estimation in highly diverse forests, where  
 229 attributes at genus, family or higher taxonomic-levels are averaged when species-specific values are missing [34–  
 230 36]. It could be expected that the geographical origin of the progenitor species for similar crossing could imply  
 231 that the biomass prediction models based on allometry can transcend taxonomic barriers. However, there are  
 232 no similarities in allometry that allow common models for genotypes in which the geographical origin seems  
 233 similar (e.g., ‘Oudenberg’ and ‘Vesten’ or ‘A4A’ and ‘AF2’).



234  
 235 **Fig. 2** Radial chart of the average p-values from the four tests applied [24] (showing only the results with a p-  
 236 value > 0.05). The vertices are the genotype-level model, and the symbols in each line represent the genotypes for  
 237 which these models can be applied as a result of considering the average *p*-value

238 Given that individual tree biomass allometry is driven by volume allometry and the variability in specific wood  
 239 density [37], it is possible that different genotype traits linked to factors such as architecture patterns, wood-  
 240 specific gravity and carbon assimilation rates interact with one another. This makes it difficult to identify which  
 241 factor is causing the dissimilarities in biomass allometry within genotypes of the same taxonomic group. It would  
 242 therefore be interesting in future studies to determine the specific factors underlying the allometric similarities

243 found between genotypes. This will enable the development of generalized allometric equations which depend on  
244 specific variables based on similarities between the genotypes and which would be more accurate than those based  
245 on the taxonomic group.

## 246 **Conclusions**

247 This study evaluated similarities in biomass allometry among genotypes belonging to different taxonomic groups.  
248 The results showed that genetic origin did not explain such similarities. This is a particularly important finding,  
249 since taxonomic grouping is a common procedure in biomass modeling in short-rotation woody crops as well as  
250 other forest monitoring exercises.

251 Biomass models at different hierarchical levels (general, taxonomic group and genotype) are provided for a wide  
252 range of site and environmental conditions under a Mediterranean climate. These models were developed based  
253 on a robust and extensive database covering the geographical variability of SRC under Mediterranean conditions.  
254 The genotype-level biomass models cover the main poplar genotypes used in SRC in this area. We observed that  
255 the taxonomic group levels did not always perform better than the general model, which confirms the  
256 dissimilarities in biomass allometry among the genotypes of the same taxonomic group.

257 **Acknowledgements** This research was funded by MINECO (Spain) through the RTA2014-00007-C03-01, the  
258 PSE-On Cultivos and Lignocrop projects, and the fellowships FPI-SGIT-2015-04 and IICI- 2014-20614. We  
259 thank M.J. Hernandez, E. Viscasillas and P. de la Iglesia for their technical support. We are also grateful to Adam  
260 Collins for his English language review of the manuscript.

## 261 **References**

- 262 1. Tallis MJ, Casella E, Henshall PA, Aylott MJ, Randle TJ, Morison JIL, Taylor G (2013) Development and  
263 evaluation of ForestGrowth-SRC a process-based model for short rotation coppice yield and spatial sup-  
264 ply reveals poplar uses water more efficiently than willow. *GCB Bioenergy* 5(1):53–66.  
265 <https://doi.org/10.1111/j.1757-1707.2012.01191.x>
- 266 2. Mareschi L, Paris P, Sabatti M, Nardin F, Giovanardi R, Manazzone S, Mugnozza G (2005) The new varieties  
267 of poplar biomass guarantee interesting yield. *Informatore Agrario* 6(18):49–53
- 268 3. Sixto H, Cañellas I, van Arendonk J, Ciria P, Camps F, Sánchez M, Sánchez-González M (2015) Growth  
269 potential of different species and genotypes for biomass production in short rotation in Mediterranean  
270 environments. *For Ecol Manag* 354:291–299. <https://doi.org/10.1016/j.foreco.2015.05.038>
- 271 4. Yemshanov D, McKenney D (2008) Fast-growing poplar plantations as a bioenergy supply source for Canada.  
272 *Biomass Bioenergy* 32:185–197
- 273 5. Sixto H, Salvia J, Barrio M, Ciria MP, Cañellas I (2011) Genetic variation and genotype-environment  
274 interactions in short rotation *Populus* plantations in southern Europe. *New For* 42(2):163–177.  
275 <https://doi.org/10.1007/s11056-010-9244-6>
- 276 6. Paris P, Mareschi L, Sabatti M, Pisanelli A, Ecosse A, Nardin F, Scarascia-Mugnozza G (2011) Comparing  
277 hybrid *Populus* clones for SRF across northern Italy after two biennial rotations: survival, growth and  
278 yield. *Biomass Bioenergy* 35(4):1524–1532. <https://doi.org/10.1016/j.biombioe.2010.12.050>
- 279 7. Sixto H, Gil P, Ciria P, Camps F, Sánchez M, Cañellas I, Voltas J (2014) Performance of hybrid poplar clones  
280 in short rotation coppice in Mediterranean environments: analysis of genotypic stability. *GCB Bioenergy*  
281 6(6):661–671. <https://doi.org/10.1111/gcbb.12079>
- 282 8. Dillen SY, Marron N, Bastien C, Ricciotti L, Salani F, Sabatti M, Pinel MPC, Rae AM, Taylor G, Ceulemans  
283 R (2007) Effects of environment and progeny on biomass estimations of five hybrid poplar families  
284 grown at three contrasting sites across Europe. *For Ecol Manag* 252(1–3):12–23.  
285 <https://doi.org/10.1016/j.foreco.2007.06.003>

- 286 9. Pérez-Cruzado C, Sanchez-Ron D, Rodríguez-Soalleiro R, Hernández M, Sánchez-Martín M, Cañellas I, Sixto  
287 H (2013) Biomass production assessment from *Populus* spp. short-rotation irrigated crops in Spain. GCB  
288 Bioenergy. <https://doi.org/10.1111/gcbb.12061>
- 289 10. Tumwebaze SB, Bevilacqua E, Briggs R, Volk T (2013) Allometric biomass equations for tree species used  
290 in agroforestry systems in Uganda. Agrofor Syst 87(4):781–795. [https://doi.org/10.1007/s10457-013-  
9596-y](https://doi.org/10.1007/s10457-013-<br/>291 9596-y)
- 292 11. Flores O, Coomes DA (2011) Estimating the wood density of species for carbon stock assessments. Methods  
293 Ecol Evol 2(2):214–220
- 294 12. Shaiek O, Loustau D, Trichet P, Meredieu C, Bachtobji B, Garchi S, Aouni MHE (2011) Generalized biomass  
295 equations for the main aboveground biomass components of maritime pine across contrasting  
296 environments. Ann For Sci 68(3):443–452
- 297 13. Muukkonen P (2007) Generalized allometric volume and biomass equations for some tree species in Europe.  
298 Eur J For Res 126(2): 157–166
- 299 14. Barrio-Anta M, Sixto-Blanco H, Viñas IC-RD, Castedo-Dorado F (2008) Dynamic growth model for I-214  
300 poplar plantations in the northern and central plateaux in Spain. For Ecol Manag 255(3–4): 1167–1178.  
301 <https://doi.org/10.1016/j.foreco.2007.10.022>
- 302 15. Mosseler A, Major J, Labrecque M, Larocque G (2014) Allometric relationships in coppice biomass production  
303 for two North American willows (*Salix* spp.) across three different sites. For Ecol Manag 320:190–196
- 304 16. Verwijst T, Telenius B (1999) Biomass estimation procedures in short rotation forestry. For Ecol Manag  
305 121(1–2):137–146. [https://doi.org/10.1016/s0378-1127\(98\)00562-3](https://doi.org/10.1016/s0378-1127(98)00562-3)
- 306 17. Ben Brahim M, Gavaland A, Cabanettes A (2000) Generalized allometric regression to estimate biomass of  
307 *Populus* in shortrotation coppice. Scand J For Res 15(2):171–176.  
308 <https://doi.org/10.1080/028275800750014975>
- 309 18. FAO (2016) International Register of *Populus* Cultivars. <http://www.fao.org/forestry/ipc/69637/en/>.  
310 Accessed 30 Dec 2016
- 311 19. Sixto H, Hernández MJ, de Miguel J, Cañellas I (2013) Red de parcelas de cultivos leñosos en alta densidad  
312 y turno corto. Monografías INIA: Serie Forestal, Madrid
- 313 20. Willebrand E, Verwijst T (1993) Population dynamics of willow coppice systems and their implications for  
314 management of shortrotation forests. For Chron 69(6):699–704
- 315 21. Kopp R, Abrahamson L, White E, Volk T, Nowak C, Fillhart R (2001) Willow biomass production during ten  
316 successive annual harvests. Biomass Bioenergy 20(1):1–7
- 317 22. Parresol BR (1999) Assessing tree and stand biomass: a review with examples and critical comparisons. For  
318 Sci 45(4):573–593
- 319 23. Ryan TP (1997) Modern regression methods. Wiley, New York
- 320 24. Pérez-Cruzado C, Fehrmann L, Magdon P, Cañellas I, Sixto H, Kleinn C (2015) On the site-level suitability  
321 of biomass models. Environ Model Softw 73(C):14–26. <https://doi.org/10.1016/j.envsoft.2015.07.019>
- 322 25. Howse J, Molina F, Taylor J (2000) On the completeness and expressiveness of spider diagram systems. In:  
323 Anderson M, Cheng P, Haarslev V (eds) Theory and application of diagrams, vol 1889. Springer, Berlin  
324 Heidelberg, pp 26–41. [https://doi.org/10.1007/3-540-44590-0\\_8](https://doi.org/10.1007/3-540-44590-0_8), Lecture Notes in Computer Science

- 325 26. Gil J, Howse J, Kent S Formalizing spider diagrams. Visual Languages, 1999. Proceedings. 1999 I.E.  
326 Symposium on, ate 1999. IEEE, pp 130–137
- 327 27. Chambers J, Cleveland W, Kleiner B, Tukey P (1983) Graphical techniques for data analysis. Duxbury Press,  
328 Belmont
- 329 28. Antonio N, Tome M, Tome J, Soares P, Fontes L (2007) Effect of tree, stand, and site variables on the  
330 allometry of *Eucalyptus globulus* tree biomass. Can J For Res 37(5):895–906. [https://doi.org/10.1139](https://doi.org/10.1139/x06-276)  
331 [/x06-276](https://doi.org/10.1139/x06-276)
- 332 29. Laureysens I, Pellis A, Willems J, Ceulemans R (2005) Growth and production of a short rotation coppice  
333 culture of poplar. III. Second rotation results. Biomass Bioenergy 29(1):10–21. [https://doi.org/10.1016/j.](https://doi.org/10.1016/j.biombioe.2005.02.005)  
334 [biombioe.2005.02.005](https://doi.org/10.1016/j.biombioe.2005.02.005)
- 335 30. Verlinden MS, Broeckx LS, Van den Bulcke J, Van Acker J, Ceulemans R (2013) Comparative study of  
336 biomass determinants of 12 poplar (*Populus*) genotypes in a high-density short-rotation culture. For Ecol  
337 Manag 307:101–111. <https://doi.org/10.1016/j.foreco.2013.06.062>
- 338 31. Ketterings QM, Coe R, van Noordwijk M, Ambagau Y, Palm CA (2001) Reducing uncertainty in the use of  
339 allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests. For  
340 Ecol Manag 146(1–3):199–209. [https://doi.org/10.1016/S0378-1127\(00\)00460-6](https://doi.org/10.1016/S0378-1127(00)00460-6)
- 341 32. Wang C (2006) Biomass allometric equations for 10 co-occurring tree species in Chinese temperate forests.  
342 For Ecol Manag 222(1–3):9–16. <https://doi.org/10.1016/j.foreco.2005.10.074>
- 343 33. Yang Y, Monserud RA, Huang S (2004) An evaluation of diagnostic tests and their roles in validating forest  
344 biometric models. Can J For Res 34(3):619–629. <https://doi.org/10.1139/x03-230>
- 345 34. Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Killeen TJ, Laurance SG,  
346 Laurance WF (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass.  
347 Glob Chang Biol 10(5):545–562
- 348 35. Swenson NG, Enquist BJ (2007) Ecological and evolutionary determinants of a key plant functional trait:  
349 wood density and its community-wide variation across latitude and elevation. Am J Bot 94(3):451–459
- 350 36. Phillips OL, Aragão LEOC, Lewis SL, Fisher JB, Lloyd J, López- González G, Malhi Y, Monteagudo A,  
351 Peacock J, Quesada CA, van der Heijden G, Almeida S, Amaral I, Arroyo L, Aymard G, Baker TR,  
352 Bánki O, Blanc L, Bonal D, Brando P, Chave J, de Oliveira ÁCA, Cardozo ND, Czimczik CI, Feldpausch  
353 TR, Freitas MA, Gloor E, Higuchi N, Jiménez E, Lloyd G, Meir P, Mendoza C, Morel A, Neill DA,  
354 Nepstad D, Patiño S, Peñuela MC, Prieto A, Ramírez F, Schwarz M, Silva J, Silveira M, Thomas AS,  
355 Steege H, Stropp J, Vásquez R, Zelazowski P, Dávila EA, Andelman S, Andrade A, Chao K-J, Erwin T,  
356 Di Fiore A, Eurídice Honorio C, Keeling H, Killeen TJ, Laurance WF, Cruz AP, Pitman NCA, Vargas  
357 PN, Ramírez-Angulo H, Rudas A, Salamão R, Silva N, Terborgh J, Torres-Lezama A (2009) Drought  
358 sensitivity of the Amazon Rainforest. Science 323(5919):1344–1347.  
359 <https://doi.org/10.1126/science.1164033>
- 360 37. Nogueira EM, Fearnside PM, Nelson BW (2008) Normalization of wood density in biomass estimates of  
361 Amazon forests. For Ecol Manag 256(5):990–996. <https://doi.org/10.1016/j.foreco.2008.06.001>