



# Allometric tree biomass models of various species grown in short-rotation agroforestry systems

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**Abstract** Biomass equations for tree species and the early stages of growth used in short-rotation coppices and agroforestry systems are still lacking. Further, discussion about the structure and parameters of biomass equations are still ongoing. Yield estimations should be precise, while keeping efforts low. To determine the influence of tree species, farming system, and tree position (inner and outer row) on allometric relationships, we derived biomass equations for various tree species from organic and conventional silvoarable agroforestry systems with an alley-cropping configuration. The allometric equations were based on the power relationship between aboveground dry biomass and stem base diameter (SBD) as a single variable or in combination with tree height (H) and were calculated by log-linear mixed-effect regression. Equations span the third and fourth growth year of the first rotation and were validated on the fourth year. Neither farming system nor row position influenced allometric relationship, although biometric variables varied between trees from inner and outer rows. A general model across species explained 95% ( $R^2_{\text{cond}}$ ) of the variation for tree dry weight or 97% ( $R^2_{\text{cond}}$ ) with H as covariate. Yet, for the sake of precision, species-specific equations were necessary. The best fitting equation

with only SBD as predictor had species-specific allometric factors and a general exponent across species. However, predicted yields were biased by 8–31%. Thus, functions incorporating H are recommended, as compensation for variances in height-diameter relationships due to the ontogenetic stage, site differences, or social status of the tree reduced the bias of biomass estimation (<10%).

**Keywords** Aboveground biomass · Poplar · Locust · Alder · Willow

## Introduction

For the purpose of bioenergy production, short-rotation coppices (SRC) are gaining an increasing interest. In this context, yield potential plays a decisive role in economic viability and in ecological issues, e.g., nutrient and energy balances, carbon sequestration, and CO<sub>2</sub> mitigation (Al Afas et al. 2008; Karp and Shield 2008; Njakou Djomo et al. 2011). Short-rotation agroforestry systems (SRAFS), in which agricultural crop strips alternate with rows of short-rotation woody crops, are not widespread and less studied than SRC. However, their implementation is expected to result in various positive agroecological effects such as conservation of biodiversity, soil protection (Jose 2009), and an increase in biomass (Graves et al. 2007). This distinctive role and potential urges for special focus on SRAFS.

Besides biomass assessments at the end of rotation, knowledge of species-specific growth dynamics during rotation is crucial for identifying optimal harvest cycles and technologies (Böhm et al. 2011) and for assessing environmental influences (Arevalo et al. 2007) and the effects of different treatments (e.g., organic vs.

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conventional farming). Biomass estimation by harvesting is destructive and time-consuming (Al Afas et al. 2008), and therefore, the most common procedure is establishing biomass functions via regression analysis between the volume or biomass of a tree and easily measurable variables such as stem diameter and height (Muukkonen 2007). These relations can be expressed mathematically as allometric power models.

Biomass equations aim at gaining accurate estimates, while keeping a model as simple as possible to reduce sampling effort and assure biological plausibility and interpretability. In the recent literature, it is argued whether simple allometric models with diameter as single predictor should be preferred to more complex models with, for example, height as additional predictor (Sileshi 2014; Picard et al. 2015). A pivotal question is which allometric model holds across the whole ontogenetic development and, thus, across the whole range of tree size (Picard et al. 2015). In SRC trees span a limited tree size range and stand age, nevertheless there is uncertainty which effort (simple or complex allometry) assures accurate estimations and transferability to other stands.

Numerous allometric biomass equations have been developed for tree species grown in managed forest stands (Wirth et al. 2004; Zianis and Mencuccini 2004; Zianis et al. 2005; Fehrmann and Kleinn 2006; Muukkonen 2007), but fewer equations exist for woody species planted in short-rotation coppices in Europe. Only a few allometric studies have dealt with *Alnus glutinosa* (Hughes 1971; Verwijst and Telenius 1999; Johansson 1999, 2000) and *Robinia pseudoacacia* (Bongarten et al. 1992; Burner et al. 2006; Böhm et al. 2011); however, *Populus* (Laureysens et al. 2004; Zabek and Prescott 2006; Dillen et al. 2007; Al Afas et al. 2008) and *Salix* (Telenius and Verwijst 1995; Heinsoo et al. 2002; Nordh and Verwijst 2004; Sevel et al. 2012) species or clones have received more attention owing to their higher yields.

Furthermore, even fewer equations exist for small-diameter trees. Because biomass allocation patterns differ with tree age (Wirth et al. 2004), allometric equations generated from older trees are not applicable to trees whose diameter or height falls below the range of validity of a given model. In addition, functions using a standardized stem base diameter as predictor instead of the diameter at breast height (DBH, in 1.30 m above soil) must first be developed for trees shorter than 1.30 m. DBH might also be a poor biomass predictor for small trees taller than 1.30 m (Wirth et al. 2004), as it may be measured at any location in the crown. Here, the trunk is more tapered than that in the region below the crown (Sumida et al. 2013) or some species develop dichotomous branching.

In SRC or SRAFS, trees are densely planted. Under crowded condition, competition for sunlight leads to the

development of greater height growth relative to growth in diameter (Niklas 1995) and to suppression of lateral branches (Unruh Snyder et al. 2007) compared to open-grown trees. Thus, biomass equations developed for natural forests may not be adequate (Tumwebaze et al. 2013) and new functions applicable to dense short-rotation coppices are needed. In the special case of SRAFS with an alley-cropping configuration, trees are also highly influenced by edge effects, which may affect their allometry, resulting in equation parameters differing between those in border rows and those in interior rows (Verwijst and Telenius 1999).

Also fertilization was proposed to influence allometry by increasing tree height and reducing shoot dry weight (Heinsoo et al. 2002). Hence, distinctive conditions in organic farming (e.g., nutrient limitations, weed competition) may alter tree biomass allometry.

Shoots from tree species in their first rotation and soil properties of the investigated organic and conventional silvoarable agroforestry systems were measured in an attempt to fill the gaps described above. The main objective is to evaluate the influence of farming system, row position, and tree species on allometric biomass functions while putting them into the context of allometric theories.

## Materials and methods

### Study area and plant material

The study was performed in a long-term field experiment with short-rotation agroforestry systems at the Scheyern experimental farm (48°30'N, 11°21'E) in Bavaria, southern Germany. The farm is located 460–490 m above sea level in Tertiary hills. Most soils have a loamy texture and are classified (WRB soil classification) as either Cambisols or Eutrochrepts with a thin layer of loess, Cambisol with sand and gravel subsoil or small-scale clay soils (Scheinost et al. 1993; Schröder et al. 2002). Meteorological data were obtained from the nearby Altomünster-Maisbrunn weather station (48°24' N, 11°19'E) of the Deutscher Wetterdienst (DWD), 15 km from the experimental site. The climate is temperate, with annual average temperature of 8.7 °C and annual precipitation of 803 mm between 2009 and 2012. The long-term (1981–2010) average is 8.3 °C and 887 mm. Precipitation during the establishment phase in 2009 (May–July) was above average.

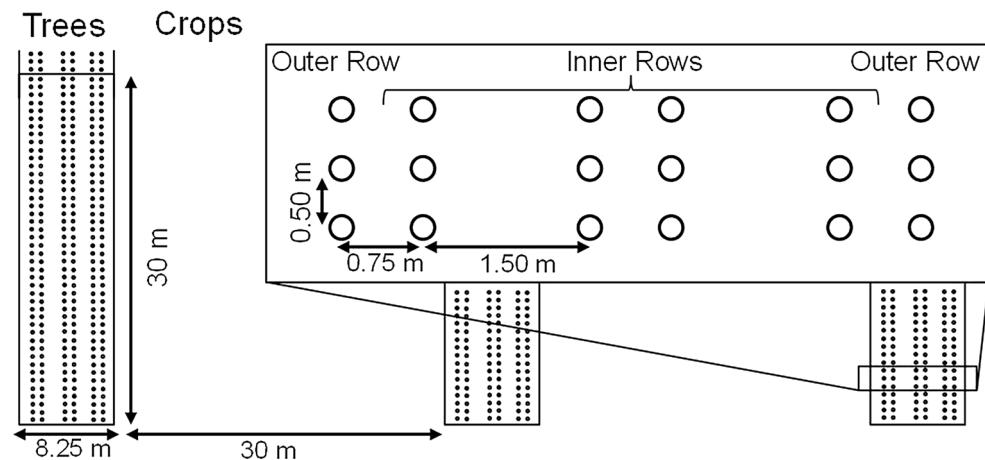
In 1992, the experimental farm had been subdivided into an organic (OS) and conventional farming systems (CS). OS is maintained as low-input system and since 2005 as organic arable farming without livestock. It is based on a seven-field crop rotation (with 29% grass-clover-alfalfa). Mineral nitrogen and chemico-synthetic plant protection products are omitted. Tillage is carried out with a

moldboard plow. In contrast, CS is a high-input system with chemico-synthetic plant protection use, mineral nitrogen input and a simple structured crop rotation with 50% wheat, 25% forage maize, and 25% potato. Here conservation tillage is applied (no plowing, crop residue incorporation with a grubber, mustard catch crop). System differences in structure and production features led to significantly higher agricultural crops yields in CS (Küstermann et al. 2008, 2010).

In April 2009, agroforestry systems were established in 4 fields, two for each farming system. Using a randomized block design, three strips of different fast-growing tree species were planted on every field with a spacing of 30 m for the field crops in between (Fig. 1). Each strip was divided into plots per species consisting of 360 trees, planted in three 30 m-long double rows (8.25 m wide) accommodating an overall planting density of 17,778 cuttings  $\text{ha}^{-1}$ . Inter-row spacing was 0.75 m within double rows and 1.50 m between double rows. Intra-row tree spacing was 0.50 m.

The species studied were black alder (*A. glutinosa*), black locust (*R. pseudoacacia*), poplar clone 'Max 3' (*Populus maximowiczii* × *P. nigra*), poplar clone 'Androscoggin' (*P. maximowiczii* × *P. trichocarpa*), and willow clone 'Inger' (*Salix triandra* × *S. viminalis*). All studied species belong to the functional group of pioneers with vigorous juvenile growth (Kauter et al. 2003). Poplar and willow cuttings, approximately 20 cm in length, were planted manually to a depth of 15 cm, leaving one or two buds above the soil surface. The other species, 70–90 cm in length, were planted manually as barerooted saplings. The tree strips were not manured, but weeds were controlled by herbicide application (CS) and mechanical weeding (OS) in the first year of establishment. No further weed control or fertilizer applications were provided.

**Fig. 1** Plant design of the agroforestry systems, showing the alternating tree and crop rows and the inner structure of the tree rows



## Measurement and harvest of trees

Two datasets were used for model building and validation. The first was used to develop allometric models, the second to validate them. All measurements were taken on 12 plots for each species (3 plots × 2 fields × 2 systems), with the exception of *S. 'Inger'*, planted only on one field of each system (in total 6 plots) and of *P. 'Androscoggin'*, planted only on one conventional field (in total 3 plots).

In both datasets, stem base diameter (SBD in cm, 10 cm above the soil) was measured in two perpendicular directions using a caliper, and the mean value was used in further calculations. Tree height (H in m) was measured using a Vertex hypsometer. No dead trees were sampled. Sampling numbers and variable ranges are given in Table 1.

First dataset: In winter 2011 and 2012, in each species plot, a total of 9 leafless single-shoot trees of the outer and inner rows were harvested (3 in 2011, 6 in 2012) (Fig. 1; Table 1). For each shoot SBD, H and biomass were measured. *P. 'Androscoggin'* was measured only in 2012. Due to the loss of some trees, sample numbers differed with tree species.

Second dataset: In winter 2012, in each species plot on areas different to dataset 1, all shoots of 10 trees of the middle double row (2.25 m × 2.5 m area) were measured (SBD and H, Table 1). Afterward, all shoots were cut manually 10 cm above soil surface. However, more trees than measured were harvested (40 trees of each species plot, 2.25 m × 10 m area). All shoots from one harvested species plot defined one sample. The fresh weight of these samples was measured on site using a load cell ( $\pm 50$  g) suspended from the fork of a tractor. Yield at stand level ( $\text{Mg ha}^{-1}$ ) was calculated.

All fresh biomass samples were shredded separately into wood chips and mixed thoroughly to get a representative

**Table 1** Summary statistics of the datasets used to develop (1) and to validate (2) allometric biomass equations

Tree species	Dataset	<i>n</i>	SBD (cm)			H (m)			HD (cm/cm)			M (kg or Mg)		
			Min	Max	Med	Min	Max	Med	Min	Max	Med	Min	Max	Med
<i>A. glutinosa</i>	1	91	1.7	7.6	4.5	1.3	7.2	4.6	67	153	104	0.1	5.3	1.2
	2	120	1.8	7.4	5.2	1.6	7.0	5.2	64	215	100	24.3	36.1	30.0
<i>R. pseudoacacia</i>	1	87	1.4	9.9	4.9	1.7	7.7	5.7	41	234	106	0.1	17.1	2.3
	2	120	1.1	9.3	4.1	0.5	8.9	4.7	46	217	119	28.3	52.3	32.8
<i>P. 'Androscoggin'</i>	1	18	2.9	7.9	4.9	5.9	8.7	7.9	106	203	159	0.4	5.3	2.7
	2	30	2.2	7.1	4.8	4.0	9.8	7.3	113	257	152	31.9	56.4	36.9
<i>P. 'Max 3'</i>	1	96	1.6	7.7	5.8	1.9	9.7	6.7	96	225	138	0.1	8.0	2.1
	2	120	1.0	7.0	5.0	3.1	9.1	7.5	96	232	159	29.0	50.5	35.8
<i>S. 'Inger'</i>	1	54	1.2	5.1	3.1	2.6	7.7	5.5	116	241	180	0.1	2.7	0.7
	2	60	1.7	5.8	3.9	3.5	7.3	6.1	117	224	161	11.5	28.1	20.7

Range of the variables stem base diameter (SBD), height (H), height:diameter ratio (HD) and aboveground (leafless) tree biomass (M), where *n* number of individual trees in the dataset, *Min* minimum, *Max* maximum, *Med* median. *M* in kg for dataset 1 (single tree level) and Mg for dataset 2 (stand level)

aliquot for the determination of dry matter content. Four 1 L subsamples were taken from each sample and dried in a forced air oven at 105 °C until constant mass was achieved. The mean dry matter content was used for the calculation. All biomass values are given as oven dry mass (*M* in kg or Mg).

### Analysis of factors influencing tree allometry

In order to decide on the inclusion of farming system in the allometric models, its influence on soil properties was analyzed. Therefore, at the beginning of the experiment in 2009, soil samples were taken of each species plot of each field at 0–30 cm depth (organic, *n* = 33; conventional, *n* = 36). Organic carbon (C<sub>org</sub>) and organic nitrogen (N<sub>org</sub>) were analyzed with the Dumas (1831) method, available phosphorus (P) and available potassium (K) with the calcium acetate lactate (CAL) method. The pH was also measured.

To decide on the inclusion of row position and tree species, their influence on biometric variables was also analyzed.

Mean differences of farming system, species, row position, as well as estimation method (harvested or by allometric models) were tested using generalized linear mixed-effect modeling to account for dependencies within the hierarchical dataset and for heteroscedasticity (Zuur et al. 2009). Including the random effect plot ID accounted for correlation of the row positions and for correlation of estimation methods for each species plot.

### Model building

On the basis of a power function commonly used in allometric biomass studies (Niklas 1994), a choice of two

model assumptions were applied to the dataset: (1) a simple allometric model with stem base diameter (SBD) as predictor of individual tree dry biomass and (2) one including tree height (H) as covariate:

$$M = \beta_0 \text{SBD}^{\beta_1} \quad (1)$$

$$M = \beta_0 \text{SBD}^{\beta_1} H^{\beta_2} \quad (2)$$

wherein *M* is the aboveground dry mass for a specific stem base diameter SBD and tree height *H*,  $\beta_0$  the intercept (allometric factor), and  $\beta_1$  and  $\beta_2$  the slopes (allometric exponent). Whereas  $\beta_0$  accounts for the basic morphological structure and for the initial offset of the tree,  $\beta_1$  and  $\beta_2$  describe the ratio of the relative growth rates between *M* and the explanatory variables (Pretzsch and Biber 2005). The allometric exponents reflect the actual size-dependent scaling of the organism and the necessary adjustment of biomass allocation for optimal physiological functioning (Pretzsch 2009).

Different equations for the inclusion of tree height were found in the literature (reviewed in Zianis et al. 2005), but the best description of our data (goodness of fit and likelihood ratio test, see ‘Model building’ section) was afforded by Eq. (2). As log-transformed SBD was moderate correlated with log-transformed height (Pearson’s correlation coefficient = 0.70) and, consequently, with a low variance inflation factor (VIF = 1.9), the inclusion of *H* was considered appropriate.

The error structure of the data was analyzed using the likelihood approach outlined by Xiao et al. (2011) and Ballantyne (2013). The information criteria of the normal (additive error) (AIC<sub>c-norm</sub>) and the lognormal (multiplicative error) (AIC<sub>c-logn</sub>) regression were computed. The AIC<sub>c</sub> (Burnham and Anderson 2002) is the small-sample-

size-corrected Akaike information criterion (AIC; Akaike 1973). The analysis revealed a multiplicative lognormal error structure ( $AIC_{c\text{-norm}} - AIC_{c\text{-logn}} = 467$ ) and required a linear regression on log-transformed data:

$$\ln M = \ln \beta_0 + \beta_1 \ln SBD \quad (3)$$

$$\ln M = \ln \beta_0 + \beta_1 \ln SBD + \beta_2 \ln H \quad (4)$$

The bias in the biomass estimation due to the retransformation into arithmetic units was corrected by multiplying the intercepts by a correction factor ( $CF = \exp^{\frac{RSE^2}{2}}$ ) calculated from the residual standard error of the estimate (RSE) of the regression slope (Sprugel 1983).

To accommodate the hierarchical and clustered dataset and to incorporate among-tree as well as among-plot variation, linear mixed-effects models were fitted (Zuur et al. 2009). Applying restricted maximum likelihood (REML) regression technique, different mixed models based on the fixed variables SBD and H were established. Illustrating only one level of hierarchy for the sake of clarity, the statistical models according to Eqs. (3) and (4) are expressed as:

$$\ln M_{ij} = (\ln \beta_0 + \ln b_{0i}) + (\beta_1 + b_{1i}) * \ln SBD_{ij} + \varepsilon_{ij} \quad (5)$$

$$\ln M_{ij} = (\ln \beta_0 + \ln b_{0i}) + (\beta_1 + b_{1i}) * \ln SBD_{ij} + (\beta_2 + b_{2i}) * \ln H_{ij} + \varepsilon_{ij} \quad (6)$$

where  $\beta_0$  (intercept),  $\beta_1$  (slope for SBD), and  $\beta_2$  (slope for H) are the coefficients associated with the fixed effects and  $b_0$ ,  $b_1$ , and  $b_2$  represent random effects. The residuals  $\varepsilon_{ij}$  are the remaining uncorrelated errors and were assumed to follow  $N(0, \sigma^2)$ . The additional indices  $i$  and  $j$  indicate that each observation  $j$  is nested within group  $i$ .

General allometric functions were fitted to identify a more general allometric pattern. Furthermore, farming system, row position and tree species were treated as fixed effects by adding dummy variables to evaluate differences in the coefficients.

In all steps described above, plot ID (to account for variance between plot means) and field were defined as random effects nested within each other. Each of the models was fitted separately for each combination of random effects on both intercept and slope.

## Model selection

The assumptions of homoscedasticity and normality were verified by visual evaluation of residual scatter plots (residual vs. predicted values). The goodness of fit of the models was evaluated by the AIC, the Bayesian information criterion (BIC; Schwarz 1978), the marginal as well as the conditional coefficient of determination ( $R^2_{\text{marg}}$ ,  $R^2_{\text{cond}}$ ;

Johnson 2014), the mean absolute percentage error ( $\text{MAPE} = \frac{100}{n} \sum_{i=1}^n \left( \frac{|M_{\text{observed}} - M_{\text{predicted}}|}{M_{\text{observed}}} \right)$ ; Sileshi 2014), and by the 95% confidence intervals of the linear regression of predicted against observed biomass values. AIC and BIC are both penalized-likelihood criteria, whereas BIC imposes a penalty for additional parameters.  $R^2_{\text{marg}}$  describes the proportion of variance explained by fixed factors and  $R^2_{\text{cond}}$  the proportion of variance explained by both fixed and random factors (Johnson 2014). Sileshi (2014) proposes a  $\text{MAPE} > 10\%$  as unreliable; however, a cut of point is not yet defined. In the regression of predicted against observed biomass values, prediction errors are not significant if the 95% confidence intervals cover 0 for the intercept and 1 for the slope (Sileshi 2014).

The fixed effects included in the final models were selected using likelihood ratio tests applying maximum likelihood, as comparisons using reduced maximum likelihood are not valid when the fixed effects change. To test whether the random intercept and/or slope were necessary, each in turn was omitted from the model and a likelihood ratio statistic was calculated, contrasting the refitted model with the original model.

All computations and statistical analyses were performed with R software (R Core Team 2015). Linear mixed-effects analyses were performed with the R package ‘nlme’ (Pinheiro et al. 2014), post hoc analyses (Tukey’s HSD test) with ‘multcomp’ (Hothorn et al. 2008).

## Results

### Factors influencing tree allometry

The two farming systems showed no significant difference in the initial nutrient status of the soil (Table 2; Appendix

**Table 2** Soil properties at 0–30 cm depth in organic and conventional farming systems from the beginning of the experiment in 2009

Component	Unit	Organic farming Mean ± SE	Conventional farming Mean ± SE
C <sub>org</sub>	%	1.17 ± 0.10 <sup>a</sup>	1.11 ± 0.07 <sup>a</sup>
N <sub>org</sub>	%	0.11 ± 0.01 <sup>a</sup>	0.11 ± 0.01 <sup>a</sup>
pH		5.5 ± 0.2 <sup>a</sup>	5.4 ± 0.1 <sup>a</sup>
P	kg ha <sup>-1</sup>	3.5 ± 1.9 <sup>a</sup>	5.2 ± 1.4 <sup>a</sup>
K	kg ha <sup>-1</sup>	9.6 ± 2.0 <sup>a</sup>	8.8 ± 1.4 <sup>a</sup>

Mean organic carbon (C<sub>org</sub>), organic nitrogen (N<sub>org</sub>), pH, available phosphorus (P), available potassium (K), and the respective standard errors (SE)

<sup>a</sup> Farming systems sharing the same letter are not significantly different from each other (Tukey HSD,  $p < 0.05$ )

Table 9), although they were managed differently for more than 20 years. Only soil organic carbon and potassium were slightly higher in the OS, whereas phosphorus was slightly higher in the CS.

The biometric parameters of the trees differed between species and positions (Tables 1, 3; Appendix Table 10). The values were always higher for trees in the outer rows. Also crown shapes were different, with *S. 'Inger'*, *P. 'Androscoggin'*, and *P. 'Max 3'* having more thin and elongated crowns with monopodial branching, and *A. glutinosa* and *R. pseudoacacia* often developing dichotomous branching and correspondingly greater crown widths.

HD was much greater for the *Salicaceae* family (*P. 'Androscoggin'*, *P. 'Max 3'*, and *S. 'Inger'*) than for *A. glutinosa* and *R. pseudoacacia* (Table 1). All species showed a decline in H increment with increasing SBD (Fig. 2).

### Allometric biomass models

By Eq. (5), which is based only on diameter, farming system did not have a significant influence on allometric relations. With the addition of H and tree species as covariates to the model (Eq. 6), farming system showed only a significant trend ( $p < 0.1$ ). Considering the standard level of significance ( $p < 0.05$ ), farming system was therefore not included as fixed effect. Accordingly, field and plot ID were chosen as random effects (Tables 4, 5) to account for the heterogeneity of the site (with respect to soil, nutritional status, and altitude) and the concomitant variance between the plots.

Tree position did not affect the allometric relations (Fig. 3), and its inclusion into the model revealed no significant improvement.

#### General models

The simplest allometric model with only SBD as explanatory variable and plot ID as random effect on the intercept (model 1, Table 4) exhibited much higher values

for AIC and BIC than all other well-fitting models considering species identity. SBD described 91% of the single-tree dry-weight variance ( $R^2_{\text{marg}} = 0.91$ ) and SBD plus random part explained 94% ( $R^2_{\text{cond}} = 0.94$ ). Adding H as a second predictor (model 5, Table 5), AIC and BIC were highly reduced and the coefficient of determination increased. However, tree height explained only additional 2% of the variance.

Despite the good performance of the general model based on diameter, the estimated biomass for *A. glutinosa* and *P. 'Androscoggin'* was overestimated and underestimated for *R. pseudoacacia*, *P. 'Max 3'*, and *S. 'Inger'* (Fig. 3; Table 6).

The less biased estimations were obtained for members of the *Salicaceae* family ( $\text{MAPE} \leq 19\%$ ), whereas for both *A. glutinosa* and *R. pseudoacacia*, they were biased by 35 and 20%, respectively (Table 7). The prediction error was significant only for *A. glutinosa* (Table 6).

Including H as second explanatory variable improved the biomass estimation of *A. glutinosa*, *P. 'Max 3'*, and *S. 'Inger'*, but impaired it for *R. pseudoacacia* and *P. 'Androscoggin'* (Table 7). The prediction error was significant for *R. pseudoacacia* (Table 6).

#### Species-specific models

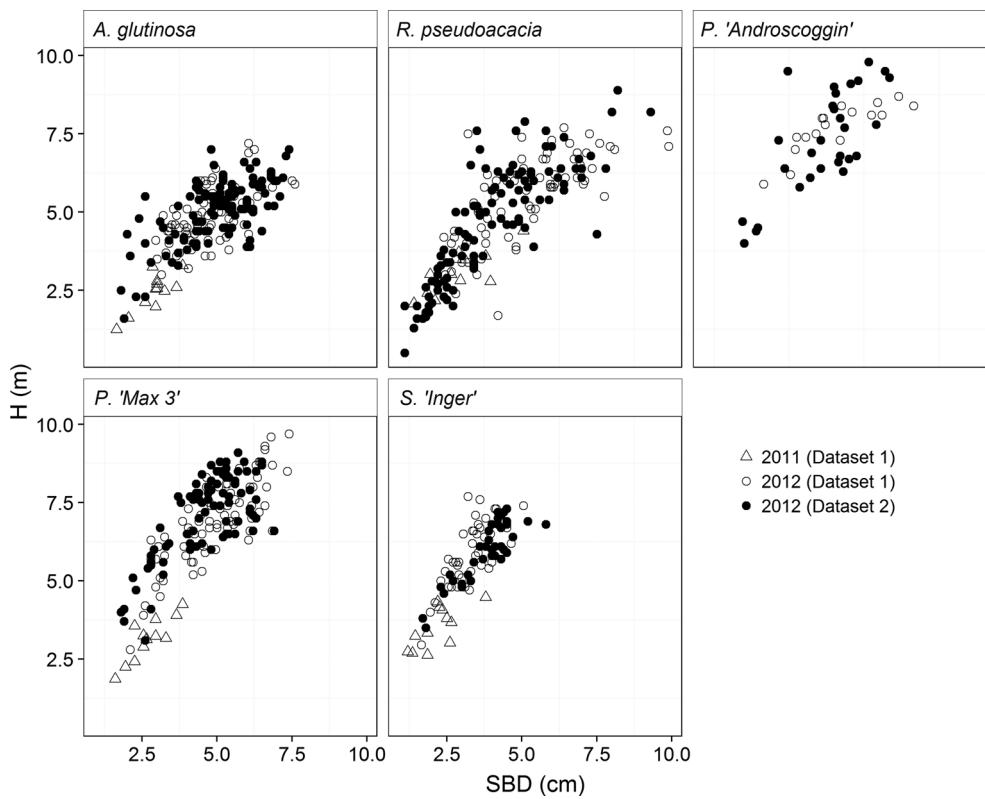
Adding tree species as a fixed effect on the intercept (model 2 and 6) led to a significant improvement in the general model performances (likelihood ratio test, Eq. 5:  $p < 0.001$ , Eq. 6:  $p < 0.001$ ), shown in higher  $R^2_{\text{marg}}$ , lower BIC and AIC (Tables 4, 5), and lower MAPE (Table 7). For the models with only SBD as explanatory variable, plot ID was the random effect that best explained the variance of the slope. This finding implicates that site differences perturbed the allometric exponent for each species more than the allometric factor. In contrast, when H was included, most variation due to site differences was explained by the intercept. This indicates that H explains part of the slope variance.

**Table 3** Difference between stem base diameter (SBD), height (H), and aboveground (leafless) biomass (M) of trees grown in the outer and inner rows of a tree strip

Tree species	Mean SBD (cm) $\pm$ SE		Mean H (m) $\pm$ SE		Mean M (kg) $\pm$ SE	
	Inner row	Outer row	Inner row	Outer row	Inner row	Outer row
<i>A. glutinosa</i>	4.5 $\pm$ 0.3 <sup>a</sup>	4.6 $\pm$ 0.3 <sup>a</sup>	4.9 $\pm$ 0.3 <sup>a</sup>	4.6 $\pm$ 0.3 <sup>a</sup>	1.4 $\pm$ 0.2 <sup>a</sup>	1.5 $\pm$ 0.2 <sup>a</sup>
<i>R. pseudoacacia</i>	4.6 $\pm$ 0.3 <sup>b</sup>	5.6 $\pm$ 0.5 <sup>a</sup>	5.0 $\pm$ 0.2 <sup>b</sup>	5.8 $\pm$ 0.4 <sup>a</sup>	2.8 $\pm$ 0.4 <sup>b</sup>	4.4 $\pm$ 0.7 <sup>a</sup>
<i>P. 'Androscoggin'</i>	4.8 $\pm$ 0.4 <sup>b</sup>	6.2 $\pm$ 0.7 <sup>a</sup>	7.6 $\pm$ 0.3 <sup>a</sup>	7.8 $\pm$ 0.5 <sup>a</sup>	2.2 $\pm$ 0.4 <sup>a</sup>	3.5 $\pm$ 0.7 <sup>a</sup>
<i>P. 'Max 3'</i>	4.5 $\pm$ 0.2 <sup>b</sup>	5.4 $\pm$ 0.4 <sup>a</sup>	6.3 $\pm$ 0.3 <sup>b</sup>	7.2 $\pm$ 0.5 <sup>a</sup>	2.2 $\pm$ 0.2 <sup>b</sup>	3.4 $\pm$ 0.5 <sup>a</sup>
<i>S. 'Inger'</i>	2.9 $\pm$ 0.2 <sup>b</sup>	3.5 $\pm$ 0.4 <sup>a</sup>	5.2 $\pm$ 0.3 <sup>a</sup>	5.9 $\pm$ 0.5 <sup>a</sup>	0.7 $\pm$ 0.2 <sup>b</sup>	1.1 $\pm$ 0.3 <sup>a</sup>

<sup>a,b</sup> Rows sharing the same letter are not significantly different from each other (Tukey HSD,  $p < 0.05$ )

**Fig. 2** Relationship between the stem base diameter (SBD) and the tree height (H) for the different tree species and clones of different years where dataset 1 refers to the data used for establishing the model, whereas dataset 2 was applied for model validation



For Eq. (5), the models with species-specific slopes (model 3) or species-specific intercepts and slopes (model 4) had a performance worse than the model with species-specific intercepts (model 2) (Table 4). For both models 2 and 3, the relative change in biomass in relation to the relative change in diameter was greatest in *R. pseudoacacia*, followed by *S. 'Inger'*, *P. 'Max 3'*, *P. 'Androscoggin'*, and *A. glutinosa*. Applying model 4 led to a change in the species order for biomass increment (in dependence on diameter increment) and favored *P. 'Max 3'* (Fig. 3).

For Eq. (6), different models with species-specific and fixed coefficients (for H, SBD, or both) were investigated. Only the two best models (model 6 and 7, Table 5) are presented in this study. SBD was the most important predictor, as it explained 95% of the single-tree dry-weights' variance, whereas tree height explained only additional 2% of the variance of M. However, the inclusion of H improved the model performance, as indicated by an overall reduction of RSE, a decrease in BIC and AIC, a higher  $R^2$  (Tables 4, 5), and a lower MAPE (Table 7). The model with species-specific slopes (model 7) had a performance worse than model 6, and for *A. glutinosa* it resulted in a significant prediction error (Table 6). In model 6, *R. pseudoacacia* again had the highest allometric factor and the ranking between *P. 'Max 3'* and *S. 'Inger'*, as well as between *P. 'Androscoggin'* and *A. glutinosa* changed. Model 6 revealed no significant prediction error.

## Model validation

For validation, the best fitting model of Eq. (5) (model 2) and 6 (model 6) was used (Table 8). Using model 2 revealed a bias  $\leq 15\%$  for all species, with the exception for *S. 'Inger'* (31%). For model 6, bias was  $\leq 10\%$ .

Except for *P. 'Androscoggin'*, biomass estimated by allometric functions was generally higher than biomass assessed by harvesting. The models are based on trees from the third and fourth growth year, but were applied on trees only from the fourth year. As H increment decreases with increasing diameter (Fig. 2), biomass was overestimated. Model 6, however, reduced this overestimation. In contrast, for *P. 'Androscoggin'* only the fourth year was used for function parametrization. Therewith, model 2 showed good results with low underestimation (4%). However, the use of the general slope for H in model 6 further reduced the estimated biomass (9%).

Overestimation of willow by model 2 was particularly high, although the previous fitting was highly precise (Table 7). This may be the result of the greater H for a given SBD of trees used for function parametrization than for validation (Fig. 2). Including H as predictor (model 6) corrected for varying biomass increments due to differences in H development. Similarly, estimations for *P. 'Max 3'* by model 6 are higher than by model 2, as H is on average higher in the validation dataset.

With the overestimation of *P. 'Max 3'* and underestimation of *P. 'Androscoggin'*, the ranking of the highest

**Table 4** Summary of mixed models predicting the aboveground (leafless) biomass across the tree species in dependence of the stem base diameter (SBD)

Model	Tree species	Coefficients fixed effect <sup>1,2</sup>		Random effect	SD random effect	RSE	df	AIC	BIC	$R^2_{\text{marg}}$	$R^2_{\text{cond}}$
		Antilog $\beta_0 \pm \text{SE}$	$\beta_1 \pm \text{SE}$								
1	$M = (\beta_0 + b_0) * \text{SBD}^{\beta_1} + \varepsilon_{ij}$	0.035 ± 0.002***	2.577 ± 0.037***	1 Plot ID	0.206	0.214	4	23.35	38.72	0.91	0.95
2	$M = \beta_0 * \text{SBD}^{(\beta_1+b_1)} + \text{Species} + \varepsilon_{ij}$	2.603 ± 0.036***	SBD-1 Plot ID	0.067	0.212	8	-12.58	18.05	0.95	0.95	
	<i>A. glutinosa</i>	0.025 ± 0.002 <sup>a</sup>									
	<i>R. pseudoacacia</i>	0.041 ± 0.006 <sup>c</sup>									
	<i>P. 'Androscoggin'</i>	0.032 ± 0.003 <sup>b</sup>									
	<i>P. 'Max3'</i>	0.036 ± 0.004 <sup>bc</sup>									
	<i>S. 'Willow'</i>	0.037 ± 0.004 <sup>bc</sup>									
3	$M = \beta_0 * \text{SBD}^{(\beta_1+b_1)} + \text{SBD} : \text{Species} + \varepsilon_{ij}$	0.035 ± 0.002***		SBD-1 Plot ID	0.064	0.215	8	-0.42	30.21	0.95	0.95
	<i>A. glutinosa</i>	2.377 ± 0.042 <sup>a</sup>									
	<i>R. pseudoacacia</i>	2.673 ± 0.034 <sup>c</sup>									
	<i>P. 'Androscoggin'</i>	2.533 ± 0.054 <sup>b</sup>									
	<i>P. 'Max3'</i>	2.631 ± 0.034 <sup>bc</sup>									
	<i>S. 'Willow'</i>	2.638 ± 0.046 <sup>bc</sup>									
4	$M = \beta_0 * \text{SBD}^{(\beta_1+b_1)} * \text{Species} + \varepsilon_{ij}$			SBD-1 Plot ID	0.067	0.211	12	-1.18	44.62	0.95	0.96
	<i>A. glutinosa</i>	0.026 ± 0.003 <sup>a</sup>									
	<i>R. pseudoacacia</i>	0.050 ± 0.017 <sup>b</sup>									
	<i>P. 'Androscoggin'</i>	0.037 ± 0.007 <sup>ab</sup>									
	<i>P. 'Max3'</i>	0.031 ± 0.007 <sup>a</sup>									
	<i>S. 'Willow'</i>	0.041 ± 0.010 <sup>ab</sup>									

$\beta_0, \beta_1$  = coefficient estimates of fixed effects, SD = standard deviation,  $b_0, b_1$  = random effects, SE = standard error, RSE = residual standard error, df = degrees of freedom, AIC = Akaike information criterion, BIC = Bayesian information criterion,  $R^2_{\text{marg}}$  = marginal and  $R^2_{\text{cond}}$  = conditional coefficient of determination

<sup>1</sup> Significance codes according to a p value: \*\*\* $p < 0.001$

<sup>2</sup> Values sharing the same letter are not significantly different from each other (Tukey HSD,  $p < 0.05$ )

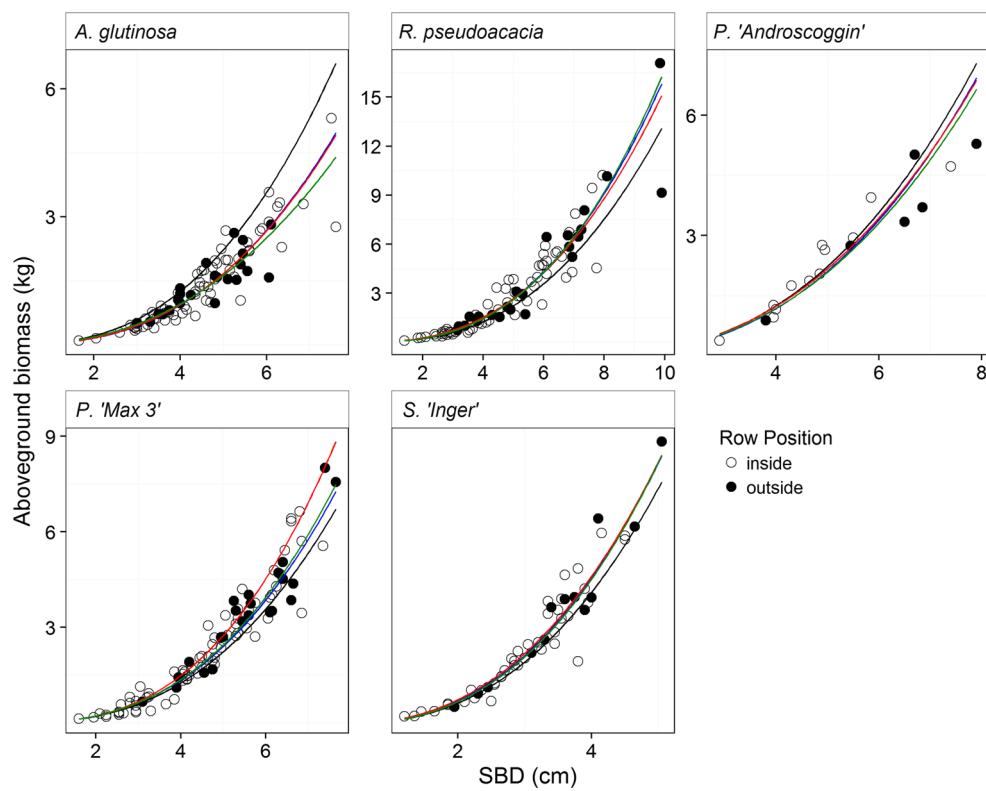
**Table 5** Summary of mixed models predicting the aboveground (leafless) biomass across the tree species in dependence of the stem base diameter (SBD) and the height (H), where  $\beta_0$ ,  $\beta_1$ ,  $\beta_2$  = coefficient estimates of fixed effects, SD = standard deviation,  $b_0$  = random effects, SE = standard error, RSE = residual standard error, AIC = Akaike information criterion, BIC = Bayesian information criterion,  $R^2_{\text{marg}}$  = marginal and  $R^2_{\text{cond}}$  = conditional coefficient of determination

Model	Tree species	Coefficients fixed effect <sup>1,2</sup>		Random effect $\beta_2 \pm \text{SE}$	SD random effect $b_0$	RSE	Df	AIC	BIC	$R^2_{\text{marg}}$	$R^2_{\text{cond}}$
		Antilog $\beta_0 \pm \text{SE}$	$\beta_1 \pm \text{SE}$								
5	$M = (\beta_0 + b_0) * \text{SBD}^{\beta_1} * H^{\beta_2} + \varepsilon_{ij}$	0.024 ± 0.002***	2.107 ± 0.051***	0.631 ± 0.055***	1 Plot ID	0.183	0.179	5	-87.02	-67.89	0.93
6	$M = (\beta_0 + b_0) * \text{SBD}^{\beta_1} * H^{\beta_2} + \text{Species} + \varepsilon_{ij}$	2.087 ± 0.053***	0.657 ± 0.057***	1 Field/ Plot ID	0.049 0.071	0.179	9	-119.80	-81.65	0.96	0.97
A. <i>glutinosa</i>	0.020 ± 0.001 <sup>a</sup>										
<i>R. pseudoacacia</i>	0.030 ± 0.003 <sup>c</sup>										
<i>P. 'Androscoggin'</i>	0.019 ± 0.002 <sup>a</sup>										
<i>P. 'Max3'</i>	0.024 ± 0.003 <sup>b</sup>										
S. 'Willow'	0.022 ± 0.002 <sup>ab</sup>										
7	$M = (\beta_0 + b_0) * \text{SBD}^{\beta_1} * H^{\beta_2} + \text{SBD} : \text{Species} + \varepsilon_{ij}$	0.024 ± 0.002***	0.652 ± 0.056***	1 Field/ Plot ID	0.049 0.071	0.181	9	-110.23	-72.08	0.96	0.97
A. <i>glutinosa</i>	1.963 ± 0.050 <sup>a</sup>										
<i>R. pseudoacacia</i>	2.218 ± 0.026 <sup>c</sup>										
<i>P. 'Androscoggin'</i>	1.964 ± 0.043 <sup>a</sup>										
<i>P. 'Max3'</i>	2.082 ± 0.029 <sup>b</sup>										
S. 'Willow'	2.000 ± 0.043 <sup>ab</sup>										

<sup>1</sup> Significance codes according to a  $p$  value: \*\*\*  $p < 0.001$

<sup>2</sup> Values sharing the same letter are not significantly different from each other (Tukey HSD,  $p < 0.05$ )

**Fig. 3** Relationship between the stem base diameter (SBD) and the aboveground biomass of different species with marked row positions. The models were fitted across species (black, model 1), with species-specific intercept (blue, model 2), slope (green, model 3), and slope and intercept (red, model 4). (Color figure online)



**Table 6** Test of significance of the intercept ( $a$ ) and slope ( $b$ ) of the regression of predicted against observed aboveground (leafless) tree biomass values

Model	Coefficient	Coefficient mean and 95% confidence interval				
		<i>A. glutinosa</i>	<i>R. pseudoacacia</i>	<i>P. 'Androscoggin'</i>	<i>P. 'Max 3'</i>	<i>S. 'Inger'</i>
1	$a$	0.17 (-0.06, 0.40)	0.17 (-0.36, 0.69)	-0.33 (-1.18, 0.53)	0.18 (-0.36, 0.72)	0.06 (-0.53, 0.66)
	$b$	<b>1.21 (1.07, 1.34)</b>	0.79 (0.51, 1.06)	1.21 (0.84, 1.58)	0.81 (0.53, 1.10)	0.82 (0.36, 1.27)
2	$a$	0.12 (-0.13, 0.37)	0.19 (-0.39, 0.76)	-0.32 (-1.26, 0.62)	0.19 (-0.40, 0.78)	0.07 (-0.58, 0.72)
	$b$	0.91 (0.76, 1.06)	0.95 (0.65, 1.25)	1.15 (0.74, 1.55)	0.88 (0.56, 1.19)	0.90 (0.41, 1.40)
3	$a$	0.22 (-0.31, 0.47)	0.11 (-0.48, 0.69)	-0.24 (-1.19, 0.71)	0.17 (-0.43, 0.77)	0.06 (-0.60, 0.72)
	$b$	<b>0.66 (0.81, 0.96)</b>	0.97 (0.66, 1.28)	1.10 (0.69, 1.51)	0.91 (0.59, 1.23)	0.91 (0.41, 1.41)
4	$a$	0.13 (-0.11, 0.37)	0.26 (-0.30, 0.87)	-0.23 (-1.14, 0.68)	0.09 (-0.48, 0.66)	0.08 (-0.55, 0.71)
	$b$	0.90 (0.75, 1.04)	0.90 (0.60, 1.19)	1.10 (0.70, 1.49)	0.96 (0.66, 1.26)	0.87 (0.40, 1.35)
5	$a$	0.14 (-0.03, 0.32)	0.26 (-0.14, 0.66)	0.00 (-0.66, 0.64)	0.20 (-0.22, 0.61)	0.09 (-0.37, 0.54)
	$b$	1.06 (0.96, 1.17)	<b>0.68 (0.46, 0.89)</b>	1.19 (0.91, 1.48)	0.88 (0.66, 1.10)	0.95 (0.60, 1.29)
6	$a$	0.13 (-0.07, 0.32)	0.34 (-0.11, 0.79)	0.02 (-0.72, 0.75)	0.20 (-0.27, 0.66)	0.08 (-0.43, 0.59)
	$b$	0.90 (0.79, 1.02)	0.86 (0.62, 1.10)	1.00 (0.68, 1.32)	0.88 (0.64, 1.13)	0.89 (0.50, 1.28)
7	$a$	0.18 (-0.02, 0.39)	0.21 (-0.26, 0.68)	0.14 (-0.63, 0.90)	0.21 (-0.27, 0.69)	0.10 (-0.43, 0.63)
	$b$	<b>0.84 (0.72, 0.96)</b>	0.91 (0.67, 1.16)	0.96 (0.63, 1.30)	0.89 (0.63, 1.14)	0.86 (0.46, 1.26)

If the 95% confidence intervals (figures in parenthesis) of  $a$  cover 0 and of  $b$  cover 1, then prediction errors are not significant. Significant errors are in bold. Coefficient mean indicates overestimation ( $b > 1$ ) or underestimation ( $b < 1$ )

**Table 7** Bias of the model prediction, calculated by the mean absolute percentage error (MAPE)

Tree species	MAPE (%)						
	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
<i>A. glutinosa</i>	35.0	16.7	17.9	16.8	20.1	14.1	13.8
<i>R. pseudoacacia</i>	20.2	18.2	18.0	18.3	20.7	15.5	15.5
<i>P. 'Androscoggins'</i>	3.2	3.1	3.1	3.1	4.7	2.9	3.2
<i>P. 'Max 3'</i>	18.7	17.8	17.9	17.3	13.8	13.7	13.9
<i>S. 'Inger'</i>	7.9	7.5	7.4	7.5	7.7	6.6	6.8

**Table 8** Comparison between estimated aboveground (leafless) biomasses (harvested and calculated by model 2 and 6) and the respective standard errors (SE) for different tree species

Tree species	Biomass ( $Mg\ ha^{-1}$ ) $\pm$ SE		
	Harvested	Model 2	Model 6
<i>A. glutinosa</i>	$30.0 \pm 2.6^b, A$	$33.7 \pm 1.5^{ab}, B$	$32.2 \pm 1.5^{ab}, AB$
<i>R. pseudoacacia</i>	$35.4 \pm 4.0^{bc}, A$	$40.8 \pm 3.5^{ab}, B$	$37.1 \pm 3.6^{ab}, AB$
<i>P. 'Androscoggins'</i>	$41.8 \pm 5.3^c, B$	$40.1 \pm 2.2^{ab}, AB$	$37.9 \pm 2.2^{ab}, A$
<i>P. 'Max 3'</i>	$38.8 \pm 3.4^{bc}, A$	$41.2 \pm 2.2^b, AB$	$42.7 \pm 2.3^b, B$
<i>S. 'Inger'</i>	$20.7 \pm 4.1^a, A$	$27.1 \pm 2.0^a, B$	$21.1 \pm 2.1^a, AB$

<sup>a,b,c</sup> Species sharing the same letter are not significantly different from each other (Tukey HSD,  $p < 0.05$ )

<sup>A,B</sup> Method sharing the same letter are not significantly different from each other (Tukey HSD,  $p < 0.05$ )

yielding species changed and potentially led to misleading conclusions about the species yield potential.

to distinguish between management and site effects. Other organic farms with depleted nutrients may, however, show a different allometry.

## Discussion

### Influence of alley structure and farming system

In a linear simultaneous agroforestry system with alternating crop strips, trees are exposed to differing growth conditions. This situation makes it worthwhile to distinguish between biomass equations for trees of outer and inner rows. On row borders, trees may be more open-grown, and thereby, more exposed to sunlight and wind-loading regimes than inner row trees. Verwijst and Teleijus (1999) detected differences in the allometry of trees from border and inner rows. In our case, the mean values of the biometric variables (SBD, H, and M) differed significantly between the inner and the border trees, but no differences in the allometric relations could be found.

The nutritional status of the forest or plantation site was also proposed to influence allometry. Heinsoo et al. (2002) showed that fertilization with N, P, and K led to an increase in shoot height but also reduced shoot dry weight compared to unfertilized shoots. Here, the tree strips were not fertilized and the nutritional status was not different between the systems, even though the previous long-term cultivation differed. No difference between the allometry of the trees in organic and conventional fields was found. Furthermore, large between- and within-field variations made it difficult

### Tree species differences

General allometric models across species show good model performances and explain a general pattern of a size-dependent shift of aboveground biomass in dependence on tree diameter and height. The good performance of these models agrees with theories of generalized interspecific allometric scaling relationships in biology and forestry (Niklas 1994; West 1997; Enquist et al. 1998; West et al. 1999; Enquist and Niklas 2001, 2002; Niklas 2004), where it is assumed that all plants share the same basic body plan and processes that govern the transport of essential materials to support cellular metabolism. To achieve more precise biomass predictions across species than provided by the theoretical models, several studies have empirically developed general biomass regression models mainly for tropical forests (Brown et al. 1989, 1995; Ketterings et al. 2001; Malhi et al. 2004; Segura 2005) or forests spanning the globe (Zianis and Mencuccini 2004; Pilli et al. 2006). Such mixed-species models satisfactorily explain the biomass of trees for a wide range of different species. Thus, they are flexible and particularly practical in forest systems with a large number of different tree species, where enormous efforts are needed to develop species-specific equations (Ketterings et al. 2001). For accurate biomass estimation, however, functions with species-specific

allometric coefficients are necessary. They can account for varying tree architectures, wood densities, annual growth dynamics, and reaction to environmental factors (Telenius and Verwijst 1995; Heinsoo et al. 2002; Sevel et al. 2012).

In this study, the differences in the allometric factor and thereby in the initial aboveground biomass at a given diameter are probably accounted for by a combination of different wood densities, tree shapes, and species-specific height growth. Although the willow and poplar clones shared the greatest HD, their allometric factor was still lower than that of *R. pseudoacacia*. The latter adopts a shape well distinguished from the more tightly packed, vertical and pyramidal shoot architecture of poplar and willow. Furthermore, it has the highest wood density ( $\rho = 0.60 \text{ g cm}^{-3}$ ; Klašnja et al. 2013). *A. glutinosa* also has higher wood density ( $\rho = 0.40 \text{ g cm}^{-3}$ ; Kiaei 2013) than *Populus* ( $\rho = 0.34$ ; Klašnja et al. 2013) and *Salix* clones ( $\rho = 0.34 \text{ g cm}^{-3}$ ; Klašnja et al. 2013). It also has a stouter crown and has the lowest allometric factor among the species, a result that may be explained by the modest height development.

A species-specific allometric factor, accounting for the initial species-specific state, was more important for predicting biomass than a quantified change in shape expressed by the specific allometric exponent. However, this is valid only for trees within the given diameter range and may change for different ontogenetic stages or ecological settings (Niklas 1995; Weiner 2004). Furthermore, tree growth is expected to be higher in the next rotation and more shoots per plant are presumed to resprout. This could lead to deviations in parameters used for estimation, such as relative lower wood density and greater height increase.

### Corrective potential of the parameter height

Although fitting the data very well, our allometric functions with SBD only were restricted to specific SBD-H relations. Overall estimation accuracy was enhanced considerably by including H, although the effect on  $R^2$  was small, which is concordant with previous studies (Joosten et al. 2004; Cienciala et al. 2005). However, for *P. 'Max 3'*, the general exponent of model 2 alters the corrective effect of model 6.

Even for young trees, ontogenetic differences between two years can lead to changes in the allometric coefficients. Although trees were just 4 years old, H increment already decreased with increasing SBD (Fig. 2). Picard et al. (2015) proved that exponents of power models with only

SBD as predictor do not remain constant along the complete ontogenetic development of the plant. By the inclusion of small-diameter trees into the function parameterization, the allometric factor trends to decrease, whereas the allometric exponent increases (Picard et al. 2015). With this, high-diameter trees are overestimated, while small-diameter trees are underestimated. Consequently, when functions are developed across different years but applied to only one year, like in our validation, bias in biomass estimations may appear. This makes them less transferable to other stand ages.

At our study area, an appreciable plot variance was detected, reflecting the small-scale variation in edaphic conditions and slope typical of the Tertiary hills of Germany. In model 2, those site differences influenced the allometric exponent. This indicates a higher sensitivity of tree shape, height growth, or wood density to site effects. When height was included in the model, most variation due to site differences was explained by the intercept, indicating that H already reflected site characteristics. With height growth being highly sensitive to site quality (Joosten et al. 2004; Kobal et al. 2015) and also to competition or the social status of the tree (Vanninen and Mäkelä 2000), the incorporation of H may be important when the equation is applied to varying site conditions or different environments as also suggested by Ketterings et al. (2001). However, whether the developed equations are adequate for estimating biomass of other stands or rotations and therefore serve as a practical tool for farmers remains to be tested.

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### Appendix

See Tables 9, 10, 11 and 12.

**Table 9** Comparison of the effect of farming system (organic and conventional) on different soil properties (organic carbon (C org), organic nitrogen (N org), pH, available phosphorus (P), available potassium (K)) using ANOVA

Traits	Units	Fixed effect Farming system	Random effects variance		Residual variance				
			Field						
C org	[%]	$F_2 = 0.352$ ns	0.091 <sup>2</sup>						0.155 <sup>2</sup>
N org	[%]	$F_2 = 0.154$ ns	0.011 <sup>2</sup>						0.015 <sup>2</sup>
pH		$F_2 = 0.253$ ns	0.190 <sup>2</sup>						0.232 <sup>2</sup>
P	[kg ha <sup>-1</sup> ]	$F_2 = 0.738$ ns	1.852 <sup>2</sup>						1.094 <sup>2</sup>
K	[kg ha <sup>-1</sup> ]	$F_2 = 0.169$ ns	1.913 <sup>2</sup>						2.405 <sup>2</sup>

The F values of fixed effects with the corresponding degrees of freedom as subscripts are listed

Level of significance of the effects is indicated by asterisks: ns = nonsignificant

**Table 10** Comparison of the effect of row position (Ou = outer, In = inner) and species on stem base diameter (SBD), height (H), and aboveground (leafless) tree biomass (M) using ANOVA

Traits	Units	Fixed effects			Random effects variance		Residual variance	Variance factor				
		Row position	Species	Row position x Species	Field	Plot ID		Alder	Locust	Andro	Max	Inger
SBD	[cm]	$F_1 = 19.457$ ***	$F_4 = 22.793$ ***	$F_4 = 1.719$ ns	0.453 <sup>2</sup>	0.007 <sup>2</sup>	1.092 <sup>2</sup>	1.00	1.60	1.13	1.19	0.77
H	[m]	$F_1 = 8.900$ **	$F_4 = 40.865$ ***	$F_4 = 1.260$ ns	0.544	0.163 <sup>2</sup>	1.150 <sup>2</sup>	1.00	1.23	0.69	1.43	1.19
M	[kg ha <sup>-1</sup> ]	$F_1 = 12.093$ ***	$F_4 = 26.180$ ***	$F_4 = 2.823$ *	0.342	0.111 <sup>2</sup>	0.908 <sup>2</sup>	1.00	3.13	1.52	1.85	0.60

The F values of fixed effects with the corresponding degrees of freedom as subscripts and the variance factors for each species are listed. Level of significance of the effects is indicated by asterisks: ns = nonsignificant; \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ **Table 11** Comparison of the effect of species on aboveground (leafless) tree biomass (M) harvested and calculated by model 2, 4, and 6 using ANOVA

Traits	Units	Fixed effects		Random effects variance		Residual variance	Variance factor				
		Species	Field	Plot ID	Alder	Locust	Andro	Max	Inger		
M <sub>Harv</sub>	[Mg ha <sup>-1</sup> ]	$F_5 = 9.357$ ***	–	–	4.130 <sup>2</sup>	1.00	1.75	3.14	1.81	1.47	
M <sub>Mod2</sub>	[Mg ha <sup>-1</sup> ]	$F_4 = 2.911$ ***	–	–	5.887 <sup>2</sup>	1.00	2.27	1.86	1.89	1.57	
M <sub>Mod6</sub>	[Mg ha <sup>-1</sup> ]	$F_4 = 4.502$ **	–	–	6.090 <sup>2</sup>	1.00	2.31	1.85	1.80	1.30	

The F values of fixed effects with the corresponding degrees of freedom as subscripts and the variance factors for each species are listed. Level of significance of the effects is indicated by asterisks: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ **Table 12** Comparison of the effect of estimation method (harvested and calculated by model 2, 4, and 6) and species on the aboveground (leafless) tree biomass (M) using ANOVA

Traits	Units	Fixed effects			Random effects variance		Residual variance	Variance factor				
		Method	Species	Method x Species	Field	Plot ID		Alder	Locust	Andro	Max	Inger
M	[Mg ha <sup>-1</sup> ]	$F_2 = 10.571$ ***	$F_4 = 5.780$ **	$F_8 = 3.087$ **	2.524 <sup>2</sup>	8.345 <sup>2</sup>	3.248 <sup>2</sup>	1.00	2.21	0.55	1.13	0.64

The F values of fixed effects with the corresponding degrees of freedom as subscripts and the variance factors for each species are listed. Level of significance of the effects is indicated by asterisks: \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$

## References

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