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Allometry and biomass dynamics in temperate mixed and monospecific stands: Contrasting response of Scots pine (*Pinus sylvestris* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.)

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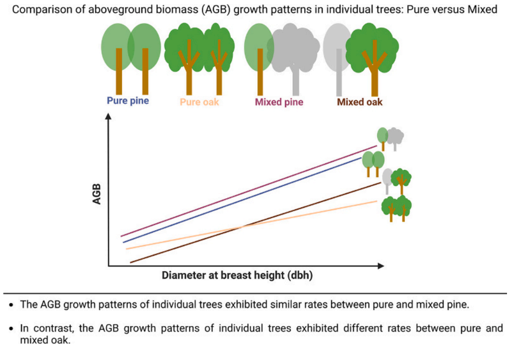
HIGHLIGHTS

- Mixing influenced the aboveground biomass of sessile oak, but that of Scots pine remained unchanged.
- The biomass of sessile oak trees in mixed settings eventually surpassed that of monocultures as diameter increased.
- Biomass models were developed separately for mixed and pure sessile oak stands; however, the Scots pine models were applied to both.
- Nonlinear mixed-effects models produced a better fit than logarithmic regression in predicting aboveground biomass.
- Considering tree species mixing in biomass modeling is important for accurate estimations.

GRAPHICAL ABSTRACT


Comparison of aboveground biomass (AGB) growth patterns in individual trees: Pure versus Mixed

- The AGB growth patterns of individual trees exhibited similar rates between pure and mixed pine.
- In contrast, the AGB growth patterns of individual trees exhibited different rates between pure and mixed oak.

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ABSTRACT

Mixed forests generally outperform monospecific forests in terms of productivity, stability, and resilience and are becoming increasingly important for sustainable forest management. However, accurate estimates of tree biomass allocation, as well as aboveground and component biomass in mixed forests, remain scarce. Our study addressed three different objectives to identify differences in biomass between mixed and monocultures and develop biomass models: (1) identification of biomass growth patterns in mixed and monoculture stands using analysis of covariance (ANCOVA), (2) investigation of the best fitting approach to modeling aboveground biomass using logarithmic regression and nonlinear mixed-effects models, and (3) fitting compartment biomass proportion models by Dirichlet regression, considering the additivity property. We analyzed 52 harvested trees from six plots within an experimental triplet in northern Spain, consisting of mixed and single-species stands of Scots pine (*Pinus sylvestris* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.). Moreover, diameter at breast height and tree height were used as covariate variables to determine the most accurate and unbiased models. The research findings showed that (i) allometric patterns of individual-tree biomass in mixed stands significantly differed from those in monospecific stands for sessile oak, while those in Scots pine did not change; (ii) nonlinear

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mixed-effect models demonstrated a better fit – indicated by lower Furnival index values – than logarithmic regression models in predicting aboveground biomass; and (iii) the fitted biomass equations provided good performance and accurate estimates of biomass component proportions compared to those of existing models. Consequently, our results offer a better understanding of biomass and carbon storage within mixed and monoculture forests in the context of climate change.

1. Introduction

Tree allometry is affected by species mixtures in temperate forests (Poudel et al., 2019), impacting biomass and carbon allocation within individual trees (Osada, 2011). This connection has triggered increasing interest in the use of component biomass for bioenergy production in the context of the global effort to calculate the carbon balance in forest ecosystems (Poudel et al., 2019). Precise and unbiased tree biomass estimations are essential for estimating the aboveground biomass (AGB) and component biomass of trees (Næsset, 2004) to account for global carbon budgets (Litton and Kauffman, 2008). In forestry, fitting biomass models requires data that can be obtained through destructive or non-destructive methods (Zianis, 2008). Although some researchers posit that destructive measurements are more accurate and reliable for estimating tree biomass (Henry et al., 2011; Melson et al., 2011), this method is insufficient for large geographical areas. Carbon-related research has focused primarily on AGB due to the difficulty in estimating belowground biomass (BGB), particularly the complexities associated with root systems (Yuen et al., 2016).

The Scots pine (*Pinus sylvestris* L.), a widely distributed and important timber species across Eurasia (Stanners and Bourdeau, 1995) due to its ability to thrive on various substrates, in poor soils, in cool wet climates, and in extremely cold continental climates (Cañellas et al., 2000). According to Stanners and Bourdeau (1995), Scots pine forests contribute substantially to Europe's carbon sequestration efforts, covering 24 % of the total forested area (75 million km^2). Meanwhile, sessile oak (*Quercus petraea* (Matt.) Liebl.), a deciduous broadleaved tree species found across Europe (Eaton et al., 2016), provides high-quality timber, firewood, acorns, and tree bark. Scots pine and sessile oak commonly coexist in mixed European forests, although they exhibit different shade tolerance temperaments. Scots pine species are intolerant of shade, whereas sessile oak species display a moderate level of shade tolerance (Niinemets and Valladares, 2006). Additionally, their rooting patterns vary, which allows them to use resources in mixed environments more efficiently. As a result of this ecological diversity, mixed-species forests may grow faster and increase in biomass, highlighting the importance of understanding the effects of mixtures of these two species in forest ecosystems.

Single-species stand management and dynamics have been well researched and developed in Europe since the early 18th and 19th centuries (Griess and Knoke, 2011). However, due to climate change and improved resource management, mixed-species stands have gained considerable attention in recent years (for instance, Bravo-Oviedo et al., 2014; Hulvey et al., 2013; Pretzsch and Schütze, 2016; Steckel et al., 2020). European forest managers have gradually shifted their focus from monocultures to mixed forests (Bravo-Oviedo et al., 2014). Some scientific literature provides evidence that mixed forests offer greater productivity, stability, and ecosystem services than monocultures (Bauhus et al., 2017; del Río et al., 2017; Gamfeldt et al., 2013). In mixed-species stands, different species can exhibit significant variations in growth patterns, crown architecture, and wood density (Bravo et al., 2019; del Río et al., 2017). As a result of these variations, certain effects are observed such as overyielding (Pretzsch and Forrester, 2017) and changes in tree allometry (Forrester et al., 2018; Pretzsch, 2019). In contrast, Frivold and Frank (2002) examined mixtures of birch and conifers in southeast Norway, while del Río and Sterba (2009) studied a mix of *Pinus sylvestris* and *Quercus pyrenaica* in Spain. Interestingly, both studies revealed that tree mixing had neither positive nor negative effects. In the last decade, there has been growing interest in how forest composition – whether mixed or monospecific – influences both forest dynamics and biomass production (Lu et al., 2016). This influence could be attributed to how these species utilize and adapt to available resources such as low light and specific rooting patterns. Zhang et al. (2020) emphasized that tree allometry differs depending on factors such as tree architecture and silvicultural management.

Despite mixed-species forests accounting for a large proportion of global forested areas and their ecological importance, tree biomass estimation models usually focus on monospecific forests, with mixed-species forests receiving very little attention, with a few relevant exceptions (Bravo et al., 2019; Briseño-Reyes et al., 2020; Pretzsch et al., 2015). This leads to a substantial research gap. This limitation may be due to the complexity of mixed forests and the absence of standardized methods to estimate their biomass. Therefore, models developed for monospecific forests are often employed for mixed forests (Forrester and Pretzsch, 2015), potentially resulting in biases and inaccuracies in estimating tree biomass in mixed stands (Bravo et al., 2019; Dutcă et al., 2018). Hence, it becomes necessary to either validate the accuracy of the models before applying them in mixed forests or modify the models to incorporate the influence of mixed forests in the biomass equations. In cases where monospecific models are unsuitable for mixed forests, new biomass models should be developed and fitted. The use of biomass data from mixed forests and adequate modeling approaches are needed (Weiskittel et al., 2015). The use of classical linear and nonlinear regression methods to fit biomass models is the standard method in forestry, with diameter at breast height (dbh), either alone or in combination with tree height (ht), as the main independent variable. Independent fitting by biomass compartments leads to incompatible estimations of biomass fractions and AGB. Methods such as seemingly unrelated regressions (SUR) (Parresol, 1999), nonlinear seemingly unrelated regression (NSUR) (Dong et al., 2014), and Dirichlet regression (Eker et al., 2017) employ simultaneous equations to ensure additivity and predict biomass proportions for different tree components (Wharton and Cunia, 1987). In our present study, we developed compatible equations to estimate the single-tree aboveground and component biomasses of mixed pine-oak stands and pure stands of each species. The aim of this study was to understand the effects of species composition on tree biomass allometry in mixed and pure stands of Scots pine and sessile oak. A comprehensive evaluation of the hypothesis posited the following: (1) the allometric patterns of individual-tree biomass for Scots pine and sessile oak do not differ between mixed stands and monospecific stands; (2) the AGB equations for both species are not affected by forest composition (mixed versus monospecific); and (3) the percentage of biomass in different tree components of Scots pine and sessile oak is not affected by mixture versus monoculture. Subsequently, we compared our fitted models with those available for the study area developed by Ruiz-Peinado et al. (2011) for Scots pine (*Pinus sylvestris* L.) and Balboa-Murias et al. (2006) for pedunculate oak (*Quercus robur* L.), both of which use SUR fitting for tree components. The comparison used models for *Q. robur* because there was no existing biomass model for *Q. petraea* in Spain. Additionally, our fitted models were also compared to those of Menéndez-Miguélez et al. (2021), who fitted with a slightly different approach using the crown ratio proportion for crown biomass estimation, observing additivity using SUR.

2. Materials and methods

2.1. Study area

In our study, we used the triplet-based approach as detailed by Pretzsch et al. (2020). This method consists of an observational site with three different types of plots located within the same place in order to ensure uniform growth conditions such as site quality, soil type, elevation, slope, environmental conditions, silvicultural practices, stand age and tree density. The triplet includes a monospecific Scots pine (*Pinus sylvestris* L.) plot, a monospecific sessile oak (*Quercus petraea* (Matt.) Liebl.) plot, and a mixed plot where both tree species are grown together at the same place. This allows the comparison of biomass accumulation and growth dynamics under the same environmental conditions between mixed-species stands and corresponding pure stands. The triplets were found in two locations in the Cantabrian Mountains of the Castilla y León region in northern Spain. The first location was Busnela, which is in Burgos province (03°47′19 W, 43°02′52 N), and the second location was Valberzoso, which is in Palencia province (04°14′32 W, 42°53′41 N) (see Fig. 1). Table 1 provides information on the forest stands investigated in this study. The triplets are rectangular in shape and range in size from 580 to 890 m^2. The forest stands in Busnela were initially planted with Scots pine 58 years ago, which was accompanied by natural regeneration of sessile oak. The stands in Valberzoso, however, have naturally regenerated with both Scots pine and sessile oak, averaging 60 years.

2.2. Data collection and measurements

The surveys and biomass sampling took place in April 2018 at the Busnela site and in March 2020 at the Valberzoso site. Within each plot, the diameter at breast height (dbh) and tree height (ht) were recorded for all the standing trees. This procedure was crucial for determining the distribution of tree sizes within the study sites. We ensured that species size variability was represented while considering resource and time constraints by adhering to the following criteria: (a) 5 to 8 trees per species from each plot were selected across the observed dbh range to enable more accurate biomass estimation; (b) suppressed trees, trees showing signs of disease and structural deformity trees, were ignored in all stands; (c) dead trees and trees with dead tops were neglected in the selection; and (d) in the mixed forests, the sample trees selected were those that grew under different species competition conditions to capture diverse interspecific competition conditions.

The dataset included 52 trees obtained across 6 plots (2 triplets). In Busnela, 8 trees were sampled in each monospecific plot and 16 were sampled in the mixed plot (8 of each species), while in Valberzoso, 5 trees were sampled in each monospecific plot, and 10 were sampled in the mixed plot (5 of each species). Trees were meticulously allocated to ensure a representative sample across the plots, taking into account the specific composition of each plot. A direct measurement technique was used to estimate the individual tree AGB based on the methodologies described by Ruiz-Peinado et al. (2012, 2011). As part of the destructive biomass sampling method, trees designated for harvesting were selected through a random selection process across the observed dbh range following established criteria. The tree biomass was divided into four

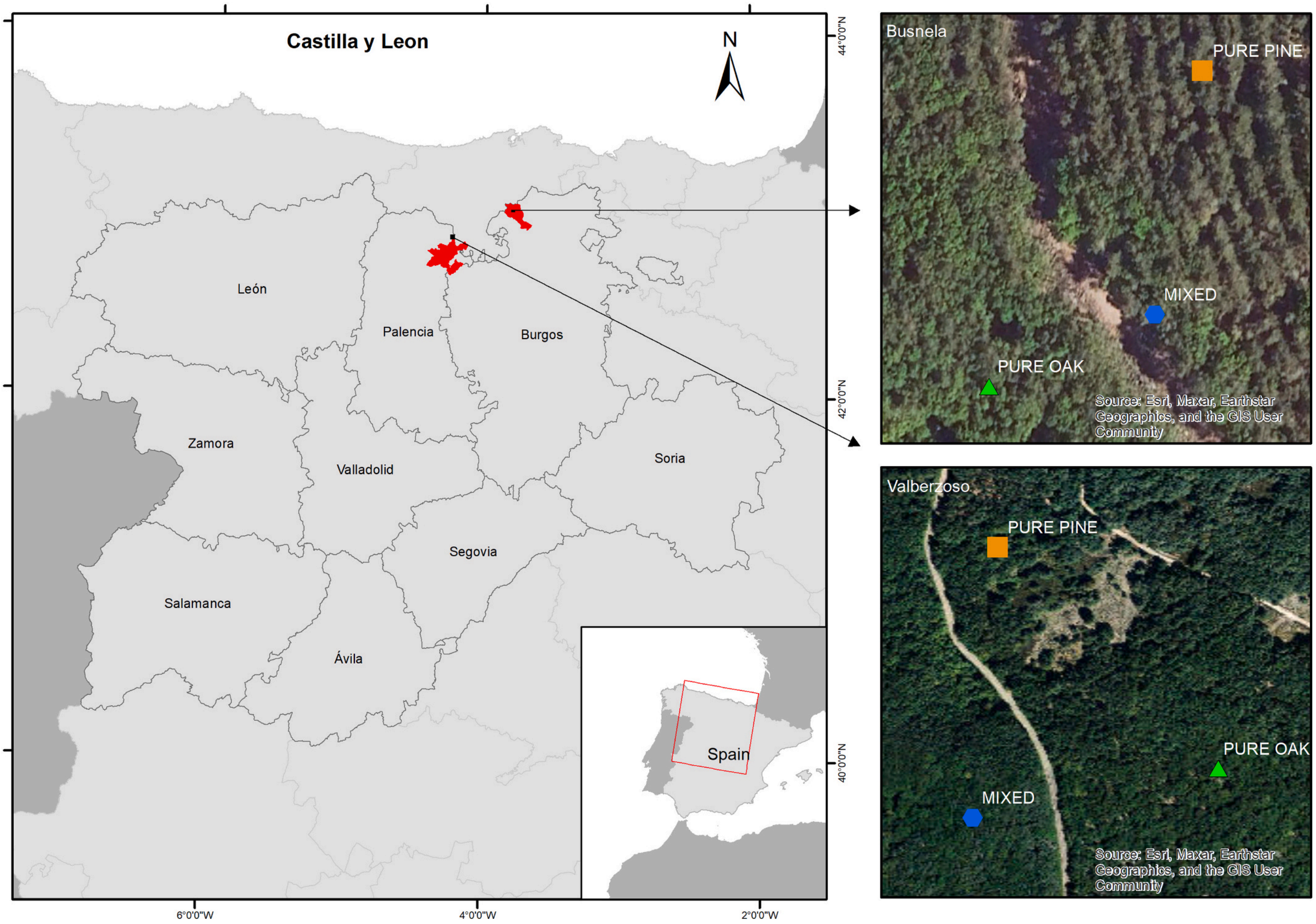

Fig. 1. Map of the study area in the Cantabrian Mountains of the Castilla y León region in Spain, with triplet locations.

Table 1
General characteristics of the studied locations (Busnela and Valberzoso, Spain).

Location	Plot	Longitude (°W)	Latitude (°N)	Altitude (m)	Slope (%)	Area (ha)	Number of trees (tree ha^{-1})	Basal area (m^2 ha^{-1})
Busnela	Pure pine	03° 47′19”	43°02′55”	810	22	0.062	1102	66.17
	Pure oak	03° 47′21”	43°02′51”	760	34	0.058	1461	47.65
	Mixed	03° 47′19”	43°02′52”	785	28	0.089	1203	52.65
Valberzoso	Pure pine	04°14′31”	42°53′52”	897	16	0.062	1134	71.30
	Pure oak	04°14′22”	42°53′43”	880	10	0.062	1240	58.70
	Mixed	04°14′32”	42°53′41”	810	11	0.089	1165	54.20

The longitude and latitude are presented in degrees (°), minutes (‘), and seconds (“); the altitude is measured in meters (m); the slope is indicated as a percentage (%); the plot area is measured in hectares (ha); the number of trees is reported per hectare (trees ha^{-1}); and the basal area is expressed in square meters per hectare (m^2 ha^{-1}).

primary categories: i) stem with bark, ii) thick branches (diameter > 2 cm), iii) thin branches (diameter < 2 cm), and iv) foliage (oak leaves were not present at the time of sampling). Table 2 provides the summary statistics of the harvested trees for the estimation of individual tree AGB and its various components. The fresh biomass of each component in the field was weighed using a digital hanging balance (accuracy 50 g) with a maximum working load of 50 kg. The dry weight of each component of the AGB was determined by bringing a representative subsample (between 2000 g and 4000 g) to the laboratory in a sealed plastic bag. All the collected subsamples were reweighed before being oven-dried at a suitable temperature of 102 °C (Williamson and Wiemann, 2010) until a constant mass was reached. As it was not possible to weigh the stem directly in the field, the stem diameter was recorded every 1 m from the base up to a minimum diameter of 7 cm (merchantable volume). Afterwards, the volume was calculated using Smalian's formula. Wood disks, approximately 1–3 cm in width, were harvested from each tree at the base, breast height, and top to accurately ascertain the average wood density to estimate the stem biomass. Water displacement was used to determine the fresh volume of these disks in a graduated cylinder suitable for their size. The disks were then oven-dried after recording their fresh volume. We calculated the wood density for each tree by dividing the dry mass of each disk by its fresh volume. The approach of sampling wood disks at three different heights along the stem, accurately captures the variations in wood density (Demol et al., 2021). The calculated wood density was multiplied by the stem volume to estimate the biomass dry weight. The total dry weight of the AGB and the biomasses of the different components (stems with bark, thick branches, thin branches, and foliage) were finally calculated with the aid of the following Eqs. (1)–(3):

$$\text{Biomass}_{\text{stem}} = \text{volume}_{\text{stem}} * \text{wood density} \tag{1}$$

$$\text{Biomass}_{\text{component}} = \text{FW}_{\text{component}} * \frac{\text{SDW}_{\text{component}}}{\text{SFW}_{\text{component}}} \tag{2}$$

$$\text{AGB} = \text{Biomass}_{\text{stem}} + \text{Biomass}_{\text{branches}} + \text{Biomass}_{\text{foliage}} \tag{3}$$

where volume$_{\text{stem}}$ is the stem volume, and wood density is the wood density. FW$_{\text{component}}$ is the fresh weight of each component, SDW$_{\text{component}}$ is the subsample dry weight of the component, and SFW$_{\text{component}}$ is the subsample fresh weight of the component. Biomass$_{\text{stem}}$, Biomass$_{\text{branches}}$, and Biomass$_{\text{foliage}}$ are the biomasses of the stem, branches, and foliage, respectively.

2.3. Data analysis

The common data assumptions were checked to confirm normality, homogeneity of variance, independence, and linearity. Our data analysis followed a five-step sequential process. ANCOVA was first applied to determine the differences between mixtures and monocultures. The second step involved fitting both logarithmic regression and nonlinear mixed-effect (NLME) models to AGB. In the third step, the proportions of biomass components were fitted via Dirichlet regression (Douma and Weedon, 2019). In the fourth step, we evaluated and ranked all the models to determine the most appropriate model for providing insight into biomass allocation and accurate estimates of biomass use. As a final step, the best-performing models chosen from the pool of candidate models were compared with previously published models to evaluate their performance. Each of these steps is explained in the following sections.

Table 2
Summary of tree characteristics for the sampled trees in pure and mixed forest stands.

Variables	n	Min	Mean	Max	sd	Variables	n	Min	Mean	Max	sd
Scots pine sampled trees in pure stands						Scots pine sampled trees in mixed stands					
dbh (cm)	13	15.1	25.7	38.0	7.2	dbh (cm)	13	17.2	24.9	33.3	4.6
ht (m)	13	15.0	17.2	21.3	2.1	ht (m)	13	14.9	18.8	21.6	2.4
Volume (m^3)	13	0.12	0.45	1.14	0.32	Volume (m^3)	13	0.15	0.42	0.77	0.19
Stem biomass (kg)	13	55.7	212.7	538.0	150.4	Stem biomass (kg)	13	72.3	195.7	374.9	84.7
Thick branch biomass (kg)	13	3.4	26.2	69.1	24.3	Thick branch biomass (kg)	13	4.4	17.4	39.7	12.7
Thin branch biomass (kg)	13	3.7	15.4	31.0	9.3	Thin branch biomass (kg)	13	1.3	9.0	27.1	7.7
Foliage biomass (kg)	13	1.9	8.7	27.3	8.0	Foliage biomass (kg)	13	1.7	5.8	23.4	6.2
AGB-tree (kg)	13	66.0	263.0	665.2	189.4	AGB-tree (kg)	13	80.0	227.9	448.2	102.5
Sessile oak sampled trees in pure stands						Sessile oak sampled trees in mixed stands					
dbh (cm)	13	7.6	14.8	22.0	4.7	dbh (cm)	13	8.3	15.6	25.0	5.4
ht (m)	13	6.7	15.5	20.9	3.7	ht (m)	13	9.8	16.4	20.8	3.3
Volume (m^3)	13	0.02	0.17	0.39	0.11	Volume (m^3)	13	0.02	0.18	0.50	0.16
Stem biomass (kg)	13	2.1	121.9	277.4	77.4	Stem biomass (kg)	13	14.1	123.8	297.3	97.6
Thick branch biomass (kg)	13	0.5	10.2	36.8	10.3	Thick branch biomass (kg)	13	7.5	20.9	47.4	14.2
Thin branch biomass (kg)	13	0.5	2.2	8.2	2.4	Thin branch biomass (kg)	13	0.8	6.4	26.4	7.2
AGB-tree (kg)	13	23.9	134.3	322.4	85.2	AGB-tree (kg)	13	22.7	151.1	360.1	114.6

dbh: diameter at breast height; ht: tree height; AGB-tree: aboveground biomass per tree; n: number of sampled trees; Min: minimum value; Max: maximum value; sd: standard deviation.

2.3.1. *Differences in aboveground and component biomasses between mixed and monospecific stands*

As a preliminary analysis, the Spearman correlation test (using Spearman's rank correlation coefficient) was conducted to analyze the degree of correlation between AGB and other variables namely dbh and ht. During this initial step, we were able to understand how our data were related. We subsequently used analysis of covariance (ANCOVA) to determine the primary focus of the study, which was to examine the significant variations in aboveground and component biomasses in mixed versus monospecific stands. Log-transformation of variables was needed, with dbh used as a covariate for the regression models. For our analysis to be valid, we ensured that all the models satisfied the ANCOVA assumptions. The Johnson-Neyman procedure was applied, as implemented in the R package 'JNplots' (Toyama, 2023), to identify regions with significant slope differences when the homogeneity of slope conditions was not met.

2.3.2. *Fitting biomass models*

Subsequently, biomass models were fitted separately for trees in mixed stands and those in monospecific stands when the mixture had a statistically significant difference. Whenever there were no significant differences between the mixed and monospecific stands, the same biomass models were applied to the whole species-specific dataset. The fitting of the biomass models involved two procedures. First, we fitted the AGB biomass models and then performed simultaneous fitting of the biomass proportions for the different tree compartments through the Dirichlet regression technique. The selection of the appropriate method for fitting AGB models has long been debated (Packard, 2013). However, the AGB and component biomass of each species have incorporated diverse model forms documented in the literature. In particular, we adapted models as outlined by Menéndez-Miguélez et al. (2022) and Ruiz-Peinado et al. (2012) which were related to dbh and total height as independent variables, applying them to fit the data for individual species. We used two different methods grounded in a power-law distribution (Eq. (4)). The first approach was linear regression on log-transformed data with additive error (Eq. (5)), which addresses heteroscedasticity problems in biomass data. The second approach was nonlinear regression on original data with multiplicative error (Eq. (6)) (Huy et al., 2019; Picard et al., 2012). The tested models comprised linear regression forms with log-transformed equations (Eqs. (7)–(13)), as well as the NLME models (Eqs. (11)–(14)). These methods ensure that the models follow the regression assumptions while also producing the most promising results (Addo-Fordjour and Rahmad, 2013). When converting logarithmic transformations back to biomass weight units, a correction factor (CF) is needed. The value of the CF can be calculated using the formula CF = $\exp.[SEE^2/2]$, as suggested by Baskerville (1972), where SEE is the standard error of the estimate. Within the framework of the NLME models, dbh and ht served as fixed effects that captured the main predictors for predicting AGB. We included the 'plot' variable as a random effect, which accounted for individual differences across the different study plots. In these models, weights based on a variance function are applied to account for heteroscedasticity and residual distributions, ensuring that variance across observations is appropriately managed, thereby improving model fit and accuracy (Balboa-Murias et al., 2006; Parresol, 2001). By employing these strategies, we overcame any concerns about data dispersion and improved the trustworthiness of our results.

$$Y = \beta_0 X^{\beta 1} * \varepsilon \tag{4}$$

$$\mathit{log}Y = \mathit{log}\beta_0 + \beta_1 \mathit{log}X + \varepsilon \tag{5}$$

$$Y = \beta_0 X^{\beta 1} + \varepsilon \tag{6}$$

where Y = aboveground dry biomass, X = tree dimension variable (e.g., dbh or ht), and ε = residual error term. β_0, and β_1 = model parameters or fitted coefficients.

Next, the Dirichlet regression approach was used to fit the biomass proportions for the following tree compartments: stems, thick branches, thin branches, and foliage (specifically for pine trees) using the 'DirichReg' package (Maier, 2014). This approach ensures the additivity property so that the prediction of the different components sums to the aboveground biomass. The predicted proportions were subsequently applied to the predicted AGB to obtain the predicted biomass estimates for the tree components. The Dirichlet regression presented the predicted proportions for each component of biomass (i.e., pstem, pthick branch, pthin branch, and pfoliage). These predicted proportions were then multiplied by the predicted AGB to calculate the predicted biomass estimates for the various components. Refer to the Supplementary Methods for comprehensive procedures for calculating biomass proportions. In recent years, the use of this method for calculating biomass has significantly increased (e.g., Eker et al., 2017; Poudel et al., 2019; Poudel and Temesgen, 2016). Dirichlet regression outperforms other fitting algorithms (Poudel and Temesgen, 2016). Furthermore, we fitted the most commonly used biomass estimation models with logarithmic transformations (Eqs. (7)–(10)), but alternatively, we fitted their counterparts using nonlinear approaches through NLME models. To ensure a thorough and correct assessment of the aboveground biomass distribution in our study, these customized models played a crucial role in accurately predicting the percentage of biomass for different tree components.

$$\mathrm{logAGB} = \beta_0 + \beta_1 \mathrm{logdbh} \tag{7}$$

$$\mathrm{logAGB} = \beta_0 + \beta_1 \mathrm{loght} \tag{8}$$

$$\mathrm{logAGB} = \beta_0 + \beta_1 \mathit{log}\mathrm{dbh}^2 + \beta_2 \mathrm{loght} \tag{9}$$

$$\mathrm{logAGB} = \beta_0 + \beta_1 \mathit{log}\left(\mathrm{dbh}^2\mathrm{ht}\right) \tag{10}$$

$$\mathrm{AGB} = \beta_0 \mathrm{dbh}^{\beta 1} \tag{11}$$

$$\mathrm{AGB} = \beta_0 \mathrm{ht}^{\beta 1} \tag{12}$$

$$\mathrm{AGB} = \beta_0 \left(\mathrm{dbh}^2\right)^{\beta 1} \mathrm{ht}^{\beta 2} \tag{13}$$

$$\mathrm{AGB} = \beta_0 \left(\mathrm{dbh}^2\mathrm{ht}\right)^{\beta 1} \tag{14}$$

2.3.3. *Model evaluation*

The most accurate model was chosen for each species, considering the proposed model structure (Cao and Li, 2019; Xiao et al., 2011). The models were compared based on a combination of criteria comprising the Akaike information criterion (AIC) and root mean square error (RMSE) (Eq. (15)). Additionally, observed versus predicted plots and the biological behavior of the models were used to evaluate the biological significance and reliability of the models. However, applying the same methodology to compare models with different dependent variables could lead to misleading findings (Parresol, 1999). Furnival's index (FI), as delineated in Eq. (16), was used to compare the logarithmic versus NLME models. This index was tailored to models with different dependent variables (Furnival, 1961).

$$\mathrm{RMSE} = \sqrt{\frac{\sum_{i=1}^{n} \left(y_i - \widehat{y}_i\right)^2}{n - p}} \tag{15}$$

$$\mathrm{FI} = \frac{1}{[f'(Y)]} \sqrt{\mathrm{MSE}} \tag{16}$$

$$\mathrm{Bias} = \frac{\sum_{i=1}^{n} \left(y_i - \widehat{y}_i\right)}{n} \tag{17}$$

$$\text{Bias }(\%) = 100 \times \frac{\text{Bias}}{\overline{\text{Y}}}\% \tag{18}$$

where n is the total number of trees, y_i and $\hat{y}_i$ are the observed and predicted values of AGB or its component, respectively, p is the number of parameters of the equation, and $\overline{Y}$ is the mean aboveground or component biomass. Additionally, f'(Y) represents the derivative of the dependent variable concerning biomass, and MSE represents the mean square error of the fitted equation. The geometric mean is denoted by the square bracket symbol ([]). The analysis was carried out with Statistical R software 3.6.3 (R Core Team, 2020) coupled with the 'performance' package. The package 'nlme' (Pinheiro and Bates, 2017) was used for the NLME models.

2.3.4. Comparing the developed models to existing models for performance analysis

A comparison of the developed models for each species in this study (denoted Model I) was carried out with two commonly used models in Spain to evaluate model performance. Model II included the representative of Ruiz-Peinado et al. (2011) for Scots pine and Balboa-Murias et al. (2006) for pedunculate oak, both of which were fitted through SUR. Given that there is no biomass model for sessile oak in Spain, the model for pedunculated oak was used. Both Quercus species could be considered very similar in terms of their traits and growth patterns, and volume estimations are usually developed together in Spain. Model III (Menéndez-Miguélez et al., 2021) incorporates an equation used for estimating tree biomass with a novel approach that includes stem biomass and crown ratio estimations through SUR fitting for both species. Both authors fitted models (models II and III) using data from monospecific stands. Among the criteria used in evaluating newly developed biomass models against earlier models, particularly in the prediction of AGB, stem biomass, and crown biomass, were bias percentage (Eqs. (17)–(18)) and RMSE. We used this methodology to ensure a rigorous analysis of the effectiveness of our newly developed biomass models against established models in Spain.

3. Results

3.1. Descriptive and analytical differences in forest types (mixture versus monoculture)

We assessed the distribution of biomass in stands with different tree species, including trees growing in mixed pine-oak stands, monospecific pine stands, and monospecific oak stands. Within the observed dataset, 80.9 %, 10.0 %, 5.8 %, and 3.3 % of the trees sampled from the monospecific pine stands had mean dry biomass distributions in the stems, thick branches, thin branches, and needles, respectively, of the mean AGB. Moreover, in the mixed pine stands, the mean dry biomass in the stems, thick branches, thin branches, and needles accounted for 85.9 %, 7.6 %, 3.9 %, and 2.6 %, respectively, of the mean AGB. For the pure oak stands, the mean aboveground dry biomasses represented by the stem, thick branches, and thin branches were 90.8 %, 7.6 %, and 1.6 %, respectively. Additionally, the oak-mixed stands exhibited different distributions of aboveground dry biomass, with 82.0 % aboveground dry biomass in stems, 13.8 % in thick branches, and 4.2 % in thin branches (see Table 2). The AGB and dbh were positively correlated in both mixed and pure stands of pine and oak trees. The correlation between AGB and ht. for pines was moderately positive. However, the correlation for oak trees varied between mixed oak trees and pure oak trees (see Supplementary Table S1).

3.2. Differences between AGB and tree components (stem, branches, and foliage) between mixed and monospecific stands

The ANCOVA analysis revealed that, for the pine trees, no statistically significant differences were detected in the interaction effect when comparing mixed versus monospecific trees for all biomass categories, including AGB, thick branches, thin branches, and needle biomass compartments (Fig. 2). However, in the case of oak trees, the significant effect of the interaction term for AGB and stem biomass suggested that the growth patterns of trees in the mixed settings were different from those in the monocultures. Notably, the significant differences in AGB between mixed and monospecific oak trees were due to substantial differences in stem biomass. The Johnson-Neyman procedure identified dbh ranges where slope differences in mixtures versus monocultures were significant. Among the specific dbh ranges, including 11.0 to 26.9 cm for AGB and 12.6 to 33.5 cm for stem biomass, the slope differences were not significant. In this way, when the trees were small (early stages), the oak trees in the mixed stands had significantly lower AGB than those in the monospecific stands. In contrast, as the trees grew, the oak trees in the mixed stands eventually surpassed the oak trees in the monospecific stands in terms of AGB (as illustrated in Fig. 2).

3.3. Estimation of aboveground biomass (AGB)

From the logarithmic fitting, the best model for predicting the AGB of Scots pine trees was the Eq. (9), which depended jointly on dbh and ht as independent variables. This model showed the highest goodness of fit among all the tested models (Table 3). Upon shifting our focus to oak trees, we found that the best models varied with forest composition. For monospecific oak stands, Eq. (9), which depends on dbh and ht., again emerged as the best model. Conversely, for mixed oak stands, Eq. (7), which relies exclusively on dbh, performs best. The fitting of the NLME models revealed that Eq. (13), which depended on dbh and ht, notably produced the lowest AIC value when predicting the AGB of Scots pine (Table 4). Eq. (13) also performed best in pure oak settings. However, for mixed oak trees, Eq. (11) relies solely on a single variable (dbh) and yields the lowest AIC value. After examining Furnival's index values in detail, the comparative analysis clearly confirmed that NLME models were unequivocally superior to the logarithmic models. Conclusively, Eqs. (13), (13), and (11) demonstrated the lowest FI values (0.033, 0.300, and 0.075, respectively, for pine, pure oak, and mixed oak). The models were found to be highly accurate in predicting AGB variations, with residual variations measured between the observed and predicted values quantified at 0.004 kg tree^{-1}, 0.008 kg tree^{-1}, and 0.005 kg tree^{-1}, respectively. Despite the residual variations not presented in the tables, these contributions illustrate the effectiveness of the models in capturing subtle dynamics in AGB. We observed that the selected models had superior fitting statistics and did not exhibit any problems with heteroscedasticity in AGB.

3.4. Estimation of biomass proportions using the Dirichlet method

The results obtained from fitting the Dirichlet regression models, showing the parameter estimates and the efficacy of the models, are presented in Table 5. We observed changes in biomass proportions across the dbh and ht gradients in Scots pine, pure oak, and mixed oak, as depicted in Fig. 3. In the Scots pine trees, an increase in dbh was associated with a decrease in stem biomass, while the biomass of thick branches, thin branches, and foliage simultaneously increased. Nevertheless, as ht increased, the trend reversed, with the stem proportion increasing and the other compartments decreasing (Fig. 3a,b). For both mixed and pure sessile oaks, the proportion of stem biomass increased, whereas the biomass of thick branches and thin branches decreased as dbh and ht increased (Fig. 3c-f). From the tested biomass Eqs. (11)–(14), Eq. (13), which includes both dbh and ht., provided the most accurate predictions for pine species in our candidate models. This selected equation showed strong statistical fit and had the lowest AIC value, as shown in Table 5. In particular, Eq. (12), which relies solely on ht as the predictor variable, performed the best for both pure oak species and

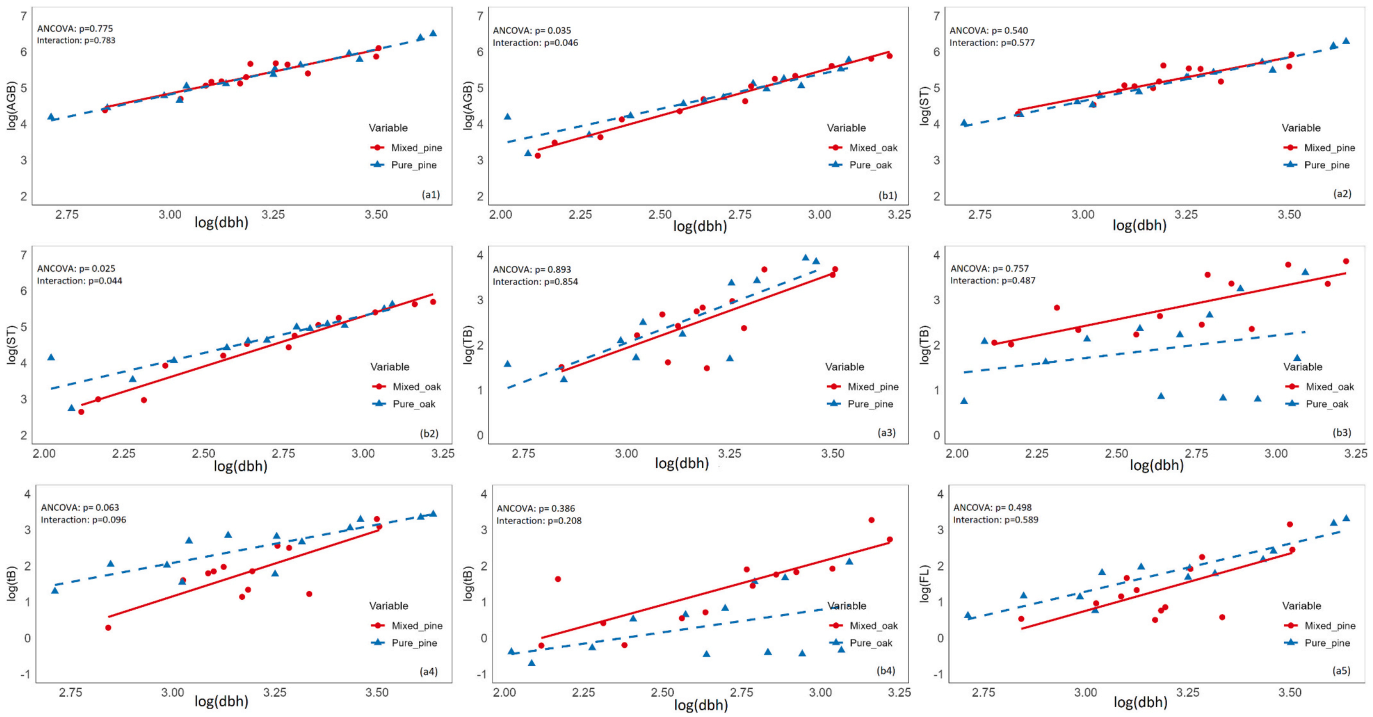

Fig. 2. Biomass allometry for mixed and pure stand trees (pine spans a1 to a5 and oak depicts from b1 to b4). log(dbh) represents the covariate, and log(AGB), log (ST), log(TB), log(tB), and log(FL) represent the dependent variable (ST: stem, TB: thick branches, tB: thin branches, FL: foliage, respectively). Solid red lines and dots represent mixed trees and dashed blue lines and triangles represent monospecific trees.

mixed oak species. While Eq. (12) had the lowest AIC value, it did not exhibit the smallest deviance compared to the other equations for both species. The model predicted that the mean biomass proportion of stems with respect to the AGB was 81.99 %, whereas that of thick branches was 8.70 %, that of thin branches was 5.61 % and that of needles was 3.69 % in Scots pine. Stems accounted for 83.34 % of the AGB in pure sessile oak, while thick branches and thin branches accounted for 11.36 % and 5.30 %, respectively. On the other hand, in mixed sessile oak, stem accounted for 74.00 % of the AGB, whereas thick branches accounted for 19.27 % and thin branches accounted for 6.74 %. Based on the Dirichlet regression method for both pine and oak species, unbiased predictions of component proportions could be made, as well as more precise estimates of component biomass, as shown in Table 5.

3.5. Unraveling the performance of fitted models: a comparative analysis of new biomass equations versus previously developed models

In terms of bias, Models II and III performed worse than the models fitted in this study (Model I) across the AGB, stem, and crown components of the pine and oak species (see Fig. 4). Model I overestimated the AGB and crown biomass and underestimated the stem biomass for all the species. A greater bias was evident in models II and III, indicating a limited ability to capture the true variability in mixed oak biomass. Model II showed an RMSE slightly greater than that of Model I for all the species, with Model II showing the highest RMSE values, especially for the AGB and crown compartments. Therefore, the statistics for Model I indicated more accurate estimations and superior predictive accuracy across pine and oak species than did the existing models, indicating that Model I is preferable for estimating ABG, stem, and crown components.

4. Discussion

4.1. Assessing biomass allometry in mixed-stand and pure-stand forests: comparative study and implications

Our results provide compelling evidence that the biomass growth patterns of Scots pine are similar in mixed and monospecific environments. In contrast, sessile oak biomass development, particularly the AGB and stem biomass, differed in both environments. Previous findings by Pretzsch (2020) suggested that oaks in mixed settings would have wider crowns. However, our study indicated that oak trees with wider crowns may not necessarily have greater crown biomass. Both mixed and monoculture forests produced similar crown biomasses for oak trees. The reason for this difference may be that oak trees in mixed forests have a lower ratio of woody biomass to crown area than monocultures. Furthermore, as pine trees grow quickly in the early stages, there may be less interspecific competition among species in mixed stands for light. Similarly, intraspecific competition within monocultures is equally important. In contrast, the AGB and stem biomass of oak trees exhibited different biomass patterns but there was no significant impact on branch development, resulting in sessile oak crown biomass being equally affected by both intra- and interspecific competition. In other mixtures, it was observed that Norway spruce growing with European beech showed a reduction in branches and needle biomass, which was attributed to increased crown competition (Dutcă et al., 2018). We found that oak trees in mixtures had lower AGB and stem biomass at smaller dbh ranges than oak trees in monocultures. This suggests that there may be competition or limited resources in mixed environments that affect the early stages of oak development (Forrester et al., 2018). However, as the dbh range increases, there is a noticeable change in the trend. Oak trees in mixtures gradually catch up to, and eventually exceed, oak trees in monocultures, reaching equal or greater AGB and stem biomass at the end of the range that was sampled. This increase in the biomass growth of the oaks in the mixed stands could be attributed to the search for sunlight. When light cannot pass through

Table 3
Parameter estimates, standard errors, and goodness-of-fit statistics for logarithmic models developed to predict AGB in forest stands.

No.	Parameter	Scots pine						Pure sessile oak						Mixed sessile oak					
		Estimate	SE	AIC	RMSE	FI	CF	Estimate	SE	AIC	RMSE	FI	CF	Estimate	SE	AIC	RMSE	FI	CF
7	β0	−2.601	0.394	−23.251	0.138	0.186	1.074	−0.397	0.623	8.094	0.262	0.266	1.153	−1.948	0.306	**−10.056**	0.130	0.146	1.074
	β1	2.477	0.123					1.926	0.234					2.471	0.113				
8	β0	−2.561	2.121	39.988	0.465	0.341	1.274	0.319	1.557	26.585	0.534	0.453	1.337	−5.227	1.732	21.288	0.436	0.185	1.267
	β1	2.742	0.736					1.612	0.572					3.569	0.622				
9	β0	−3.873	0.552	**−29.560**	0.118	0.114	1.064	0.587	0.599	**2.450**	0.195	0.350	1.118	−1.894	0.636	−8.068	0.130	0.290	1.077
	β1	1.144	0.062					1.369	0.170					1.246	0.124				
	β2	0.651	0.221					−1.155	0.408					−0.040	0.408				
10	β0	−4.543	0.448	−27.759	0.126	0.178	1.068	−0.605	0.893	14.890	0.341	0.881	1.203	−3.156	0.461	−3.856	0.166	0.423	1.094
	β1	1.064	0.048					0.662	0.111					0.963	0.056				

Note: SE = standard error, AIC = Akaike Information Criterion, RMSE = root mean square error, FI = Furnival index, CF = log-bias correction factor. The bolded values indicate the best model for each species type, based on the AIC. All regression coefficients were statistically significant at the 5 % significance level ($p < 0.05$).

Table 4
Parameter estimates, standard errors, and goodness of fit statistics for weighted models developed to predict AGB in forest stands.

No.	Parameter	Scots pine					Pure sessile oak					Mixed sessile oak				
		Estimate	SE	AIC	RMSE	FI	Estimate	SE	AIC	RMSE	FI	Estimate	SE	AIC	RMSE	FI
11	β0	0.073	0.029	259.363	35.982	0.028	0.124	0.054	123.371	16.888	0.150	0.126	0.044	**114.358**	13.39	0.075
	β1	2.483	0.124				2.513	0.141				2.515	0.119			
12	β0	0.094	0.198	326.659	118.176	0.008	0.069	0.180	150.576	54.674	0.249	0.003	0.005	146.368	54.906	0.018
	β1	2.710	0.729				2.717	0.907				3.843	0.698			
13	β0	0.022	0.012	**251.940**	30.198	0.033	0.047	0.021	**119.602**	16.962	0.300	0.199	0.101	115.487	19.786	0.051
	β1	1.142	0.063				1.048	0.079				1.295	0.126			
	β2	0.646	0.225				0.764	0.243				−0.233	0.383			
14	β0	0.011	0.005	253.499	32.288	0.031	0.032	0.012	119.974	17.771	0.334	0.016	0.008	119.868	13.068	0.077
	β1	1.063	0.05				0.996	0.040				1.079	0.058			

Note: SE = standard error, AIC = Akaike Information Criterion, RMSE = root mean square error, FI = Furnival index. Bolded values indicate the best model for each species type, based on the lowest AIC value. All regression coefficients were statistically significant at the 5 % significance level ($p < 0.05$).

Table 5
Parameter estimates (standard errors in parenthesis), bias and root mean square error (RMSE) for the component biomass models (proportions) for Scots pine, pure sessile oak, and mixed sessile oak trees using Dirichlet regression.

Species type	Biomass component	Parameter estimates			Evaluation metrics	
		Intercept	dbh^2	ht	Bias (%)	RMSE (kg)
Scots pine	Stem	2.1618 (1.2376)	0.0005 (0.0007)	0.1340 (0.0754)	0.0006	0.0013
	Thick branches	1.8751 (1.2443)	0.0018 (0.0007)	−0.0248 (0.0762)	−0.2249	0.0153
	Thin branches	0.6925 (1.2692)	0.0011 (0.0007)	0.0456 (0.0757)	−0.6563	0.0229
	Foliage	−0.6412 (1.2625)	0.0012 (0.0007)	0.0928 (0.0741)	−1.1669	0.0299
Pure sessile oak	Stem	−0.7114 (1.4473)	-*	0.2945 (0.0899)	0.0004	0.0067
	Thick branches	−0.6007 (0.1535)	-*	1.1489 (0.0720)	−5.5239	0.1390
	Thin branches	−1.8812 (1.2779)	-*	0.1900 (0.0803)	−45.3049	0.3241
Mixed sessile oak	Stem	−0.1714 (1.5568)	-*	0.2388 (0.0939)	−0.0045	0.0068
	Thick branches	0.7843 (1.4812)	-*	0.0952 (0.0894)	−0.1921	0.0312
	Thin branches	−1.8675 (1.9046)	-*	0.1974 (0.1139)	−6.1474	0.1053

* Denotes dbh^2 was not included in the best models for pure and mixed sessile oak. Bias is expressed as a percentage (%) and RMSE values are in kilograms (kg). The 5 % level of significance ($p < 0.05$) was reached by all regression coefficients.

pine crowns, oaks are forced to grow more as they adjust to the available light (Amoroso and Turnblom, 2006). This explains why trees encounter less competition or even facilitation in interspecific competition than in intraspecific competition (Ngo Bieng et al., 2013; Strieder and Vospernik, 2021). These findings are consistent with those of Toïgo et al. (2015), who reported that sessile oak overyielded when mixed with Scots pine. In mixed and monospecific stands, sessile oak exhibits distinct growth patterns and biomass allocation strategies.

4.2. *Differences in the AGB equation between mixed and monospecific stands*

Our study contributes to the ongoing debate regarding the most effective modeling approaches for addressing data heterogeneity in biomass studies (Huy et al., 2021; Jabłońska, 2018; Zeng and Tang, 2011). NLME models are considered to be more effective than traditional models in forestry research due to their ability to handle data heterogeneity better than traditional models (Bravo et al., 2019; Porté et al., 2002; Pretzsch et al., 2015). The findings presented in this paper aligned with the conclusions of Bronisz and Mehtatalo (2020), who advocated for mixed-effect models in the estimation of AGB. Our results revealed that the NLME models performed better than logarithmic regressions, reinforcing the preference for this fitting approach. These convergences challenge conventional practices and support more effective methodological decisions and greater research effectiveness. Generally, NLME models display minimal downward bias, suggesting their accuracy in predicting data. NLME models are ideal for analyzing data involving repeated observations and spatial dependencies. As demonstrated in our study, these models create a variance-covariance architecture that effectively mitigates the effects of random variables, such as plots. A common challenge when applying NLME models is the identification of mixed parameters and the calculation of random effects (Xu et al., 2014). Different biomass patterns were identified for sessile oak but not for Scots pine trees. Hence, species-specific biomass estimation models must be developed to accurately reflect species dynamics. Moreover, the inclusion of ht and dbh as an independent variable for predicting AGB in Scots pine and pure sessile oak is consistent with the findings of previous studies (Dong et al., 2014; Litton and Kauffman, 2008; Moore, 2010; Ruiz-Peinado et al., 2011). We found that using both dbh and ht. yielded more accurate AGB estimates due to the robustness of these estimates, as demonstrated by the superior goodness of fit of these models compared to that of the other models tested. The addition of ht. included some information about stand site quality and tree competitive status. For oak trees in mixed-species stands, the AGB biomass model depended only on dbh, indicating that less complex models are sufficient (Wang et al., 2018). This decision emphasizes the suitability of diverse models for different tree species and types, highlighting that a one-size-fits-all approach may not be appropriate. The differences in the models may reflect variations in stand structure, tree density, or other species-specific factors. Few published studies have developed general biomass equations, especially for pine species (Brown et al., 2018; Johnson et al., 2016) and oak species (Forrester et al., 2017; Menéndez-Miguélez et al., 2022). It may not be useful to apply such general equations in sessile oak mixed stands. The differential response of oaks in mixed stands suggests that separate biomass equations should be developed specifically for mixed and monoculture oak stands to accurately estimate their biomass. Sessile oak trees exhibit different biomass patterns between mixed and monocultures. This observation is consistent with the findings of a previous study revealing the unique competitive advantage and resource acquisition ability of oaks (Abrams, 1998). Our study underscores the importance of selecting appropriate regression models tailored to tree species composition, such as mixed and pure models, when estimating AGB.

4.3. *Estimation of tree components (stem, branches, and foliage) in mixed and pure stands*

We stated that modeling proportions are more suitable for addressing some problems associated with biomass models. Thus, the models may be used outside the range that they were fitted, avoiding great biomass overestimation due to the poor behavior of the models. It is well established that dbh, ht. and biomass are closely related. However, there is some disagreement about the inclusion of height in biomass equations, as it is strongly correlated with dbh and generally results in limited predictive accuracy when combined (Johansson, 1999; Porté et al., 2002). In fact, some studies have suggested that tree height alone can serve as a sufficient parameter for certain species (Annighöfer et al., 2016; Juan-Ovejero et al., 2023; Menéndez-Miguélez et al., 2022). The biomass prediction model for Scots pine performed best when both dbh and ht. were considered. Conversely, when dealing with both mixed and pure oak stands, the biomass proportion models were exclusively related to tree height, suggesting that interspecific interactions strongly influence growth rates. The dominance of stem biomass suggested that pine trees may prioritize vertical growth and stem biomass production as key strategies for light acquisition and structural support (Pretzsch et al., 2020). Increasing tree size alters the distribution of biomass among various tree components (Forrester et al., 2017; Menéndez-Miguélez et al., 2021) Similarly, as dbh increases, the proportion of biomass allocated to the stem decreases, whereas the proportion assigned to crown biomass (branches and needles) increases. This decrease may be attributed to the heightened lateral competition pressure (Pretzsch et al., 2010). Pine trees appear to shift their focus away from vertical growth as they grow older, perhaps to prioritize canopy development and lateral growth (Harper et al., 2009). The presence of oak trees growing with conifer species likely introduces competition for resources

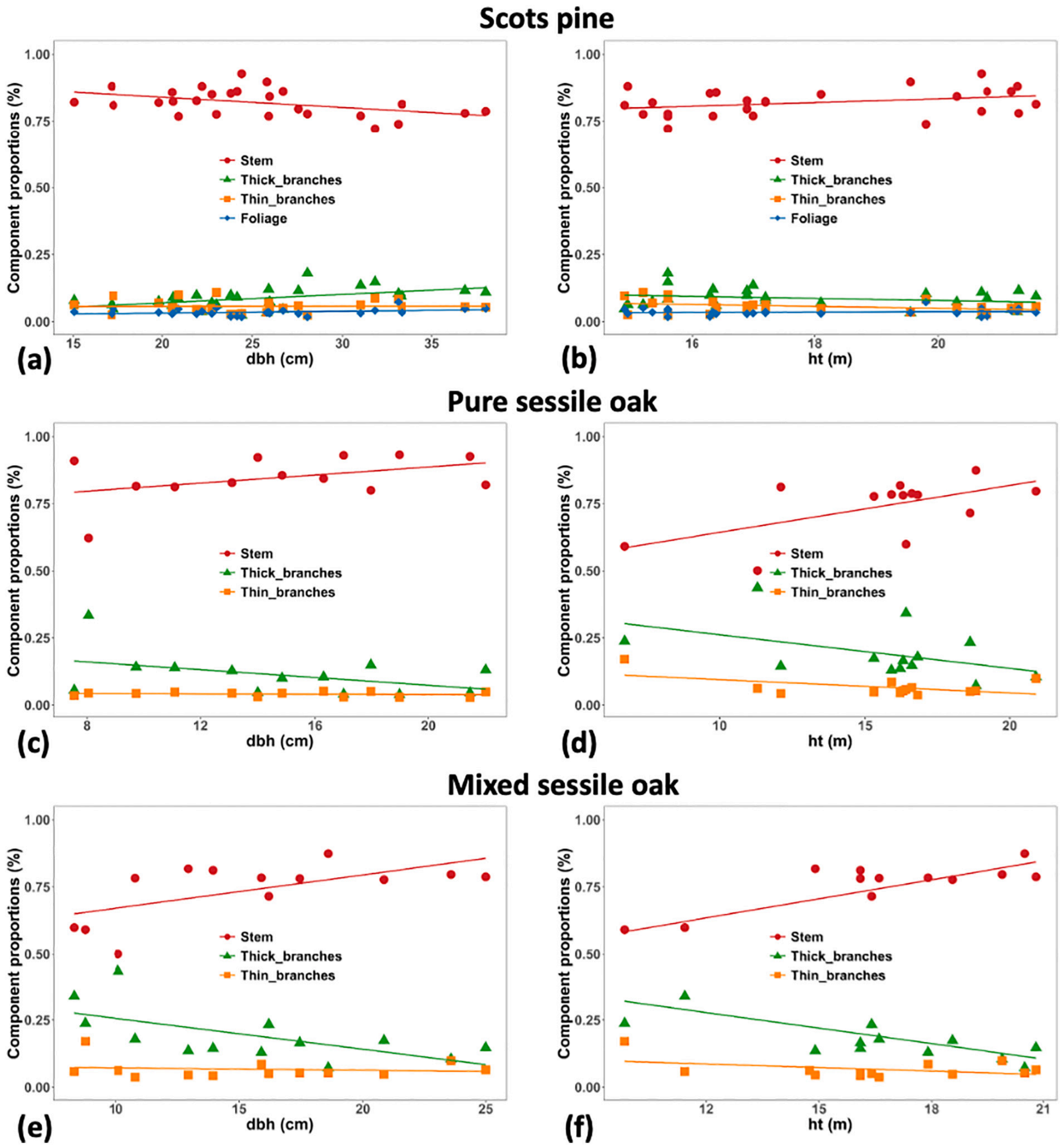

Fig. 3. The trend in predicted biomass component proportions for Scots pine ((a) and (b)), pure sessile oak ((c) and (d)), and mixed sessile oak ((e) and (f)) as functions of diameter at breast height (dbh) and tree height (ht). Dots, triangles, and squares are observed values for stem, thick branches, and thin branches biomass proportions, respectively, while diamond shapes indicate foliage biomass (but only for Scots pine).

such as light, water, and nutrients (Tilman et al., 2014), although these species exhibit a complementary niche – for example, rooting space, water use, and light requirements – to a lesser extent (Pretzsch et al., 2020). In forestry practices, these findings suggest the need for nuanced and species-specific management strategies that allow for more informed decision making about tree selection, thinning, and stand management.

The species-specific biomass equations developed in this paper were compared to established models in the literature (Balboa-Murias et al., 2006; Menéndez-Miguélez et al., 2021; Ruiz-Peinado et al., 2011). As expected, our equations demonstrated minimal prediction bias and good predictive accuracy (Forrester et al., 2017). The fitted models for Scots pine were consistent with the estimations put forth by Ruiz-Peinado et al. (2011) whose sampled data covered a wide range of areas and tree sizes – dbh and ht. variations – contributing to the robustness of our results. According to Balboa-Murias et al. (2006), the oak species model performed well, particularly in distinguishing between mixed-species stands and monocultures. However, the models introduced by Menéndez-Miguélez et al. (2021) produced fewer consistent results, especially when accounting for the proportion of crown biomass. This variance in model performance may be attributed to the dataset used in our study, which was not as large and was centered on a reduced dbh and ht range of medium-aged forest stands. Thus, the model effectiveness might differ depending on the dataset. Past research has suggested that accuracy is particularly evident when site-specific factors such as geographical location and environmental conditions are considered (Rademacher et al., 2009). Considering our findings, mixed oak forests require specific biomass equations, which have significant implications for the

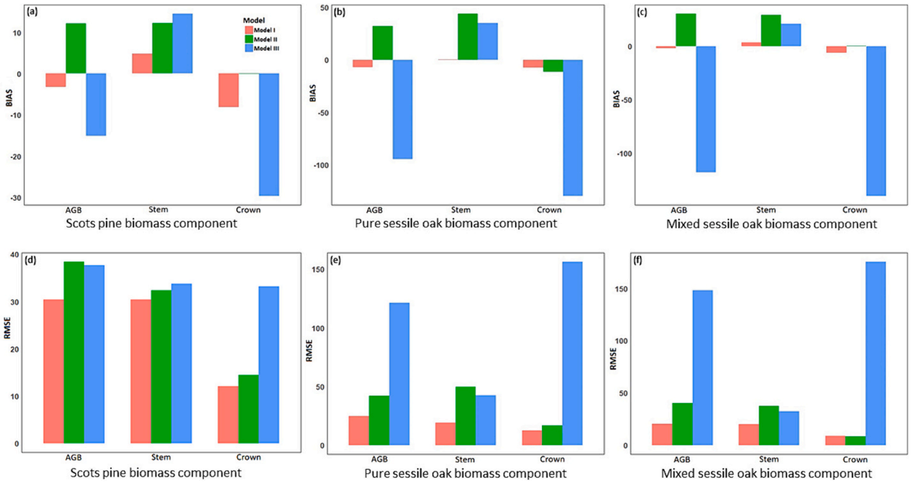

Fig. 4. Comparative evaluation of bias and root mean square error (RMSE) metrics for predicting AGB, stem, and crown components, across three distinct forest compositions: Scots pine ((a) and (d)), pure sessile oak ((b) and (e)), and mixed sessile oak ((c) and (f)). The evaluation shows the performance of three models: the study's newly developed models, denoted as Model I (orange bars), Ruiz-Peinado et al. (2011) for Scots pine, and Balboa-Murias et al. (2006) for pedunculate oak as Model II (green bars), and Model III (Menéndez-Miguélez et al. (2021) (blue bars).

assessment of carbon sequestration (Ruiz-Peinado et al., 2017), reforestation strategies, and policy decisions (Luyssaert et al., 2018). Addressing biases through refined modeling techniques and incorporating competition conditions, such as species composition can enhance the reliability of biomass predictions, providing informed and effective forest management strategies.

4.4. Study limitations

Despite the limitations of this study, several factors may affect its generalizability and interpretability. First, the number of triplets was reduced because it was quite difficult to find sites where both species were growing in monoculture and mixed, with the same age and management conditions. Despite this challenge, the triplet approach provides greater validity to our findings since the differences observed could be largely due to species mixing. Second, the number of trees sampled was relatively small due to logistical and resource constraints associated with detailed, destructive sampling for precise biomass estimation. The results of our study are likely to be more robust and more applicable if more trees representative of a wider range of stand ages, densities, and site qualities, are used. For a better understanding of biomass dynamics in temperate forests, future research should integrate a wider range of forest environments. Finally, we excluded oak foliage biomass from our analysis due to practical limitations and to the timing of our fieldwork, which coincided with the leaf shedding season. Foliage, however, plays a crucial role in the carbon cycling and biomass of forest ecosystems. The inclusion of foliage biomass in future analyses is crucial for better estimates of biomass allocation and carbon stocks, especially in mixed and monospecific stands. Additionally, further research and model refinement are necessary to address the observed discrepancies and improve the precision of biomass estimation for different tree species and compositions.

5. Conclusion

In our research, we developed new models to accurately estimate the aboveground and component biomasses in mixed and monoculture stands of Scots pine and sessile oak in temperate forests. We discovered that the AGB and stem biomass of sessile oak vary significantly across stand types, necessitating separate models for mixed and pure stands, while Scots pine does not exhibit such variability, so a universal model should be used for both. Modeling biomass proportions through Dirichlet regression has emerged as a suitable approach to observe the additivity property and to obtain reliable estimates of component biomass proportions. Therefore, compared with the existing models, the fitted biomass models performed well in terms of AGB and component biomass estimation. The use of these biomass equations may be pivotal for obtaining accurate biomass estimates and enhancing our understanding of tree species mixing in biomass estimation. Additionally, they also offer a more precise tool for forest managers and provide valuable insights for the future management of forests in the context of climate change.

CRediT authorship contribution statement

Eric Cudjoe: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Felipe Bravo:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing. **Ricardo Ruiz-Peinado:** Conceptualization, Formal analysis, Methodology, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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