

A mixed nonlinear height–diameter model for pyrenean oak (*Quercus pyrenaica* Willd.)

Patricia Adame*, Miren del Río, Isabel Cañellas

Forest Research Centre (CIFOR-INIA), Ctra La Coruña km 7.5, Madrid 28040, Spain

ARTICLE INFO

Article history:

Received 24 October 2007

Received in revised form 28 March 2008

Accepted 3 April 2008

Keywords:

Individual tree model

Random model

Rebollo oak

Height–diameter relationship

ABSTRACT

A nonlinear mixed-effects modelling approach was used to model the individual tree height–diameter relationship in pyrenean oak (*Quercus pyrenaica* Willd.). A set of 24,627 pairs of height–diameter measurements were used to fit the model. These were taken at 950 Spanish National Forest Inventory plots embracing six different biogeoclimatic strata. Eleven biparametric nonlinear height–diameter equations were evaluated to find a local model, which only includes the dimensions of the tree as explanatory variables. After selecting the local model, a regional or generalized model was studied. The following stand variables were tested for inclusion in the model as fixed effects: stand density, quadratic mean diameter, arithmetic mean diameter, dominant diameter, arithmetic mean height, dominant height and basal area. Dominant height and basal area of the stand were found to produce the most satisfactory fits in the stand model. Interregional variability was studied by including strata effects as dummy categorical variables and was analysed using the non-linear extra sum of squares method and the Lakkis–Jones test. Height–diameter models were found to be similar for the six biogeoclimatic strata. Finally, a mixed nonlinear model technique was applied to fit the definitive model. By calibrating the model it is possible to predict random components of definitive model from height measurements previously taken from a subsample of trees. The different alternatives tested reveal that only two or three trees are necessary to calibrate the model.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

The tree variables most frequently used in management plans and measured in inventories are diameter and height. Measuring tree height can be time consuming and costly, therefore either subsamples are taken or no measurements are taken at all, whereas tree diameter can be easily measured at little cost. Where both height and diameter measurements are available for a sample of trees, a height–diameter model can be used to predict heights from the rest of tree belonging to the same plot, thus reducing data acquisition costs in regional inventories.

A substantial amount of data exists regarding height–diameter relationships in different species and different forest regions. Height–diameter models have been used to assess tree volume (Larsen and Hann, 1987; Jayaraman and Lappi, 2001), to determine the social position of the tree within the stand (Colbert, 2002), to find the dominant height and from this, calculate the index of stand productivity (Huang and Titus, 1993; Vanclay, 1994; Jayaraman and Lappi, 2001) and finally, to describe stand growth dynamics

and succession (Curtis, 1967; Peng et al., 2001). Many growth and yield-projection systems also use height and diameter as the two basic input variables, with all or part of the tree heights predicted from measured diameters (Arney, 1985; Huang et al., 2000). Yuancai and Parresol (2001) recommended the Schnute function (Schnute, 1981) and Bertalanffy–Richards (Richards, 1959) as probably the most flexible and versatile functions available for modelling height–diameter relationships, but no particular function has been identified as superior (Mehtätalo, 2004).

Certain characteristics should be considered to selecting the height–diameter curve (Yuancai and Parresol, 2001): (i) monotonic increment, (ii) inflection point, and (iii) asymptote. According to these authors, S-shaped curves are more appropriate for describing a realistic height–diameter relationship which exhibits an S-shaped biological growth pattern. However, if a dataset includes only larger or older trees beyond the inflection point, then a model generating a concave curve will probably work best. Other important characteristics that should be taken into account to the selection of a height–diameter curve are flexibility (expressed by the number of parameters) and biological interpretation of the parameters.

Height–diameter equations can be for local application or can have a more generalized use (Soares and Tomé, 2002). The local

* Corresponding author.

E-mail address: adame.patricia@inia.es (P. Adame).

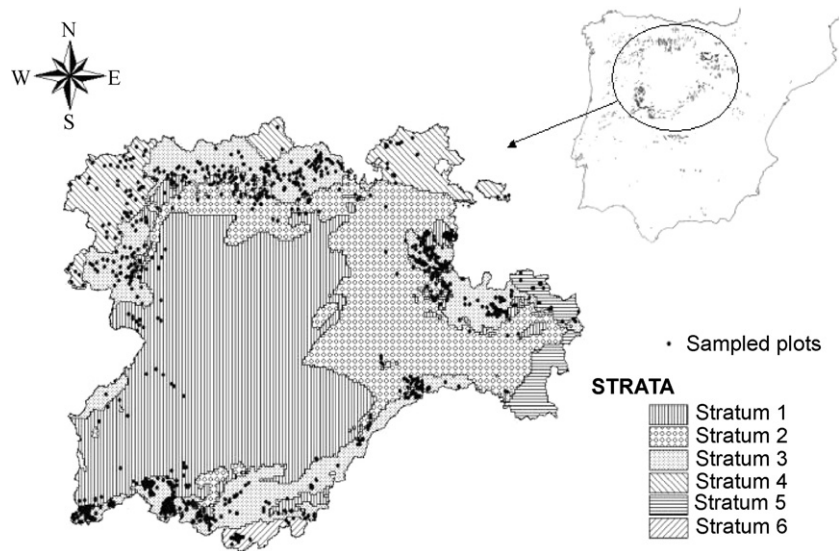


Fig. 1. Map of sample locations and biogeoclimatic strata.

height–diameter curves, which only depend on tree diameter, do not adapt well to all possible situations that can be found within a forest, so different regressions may be necessary for each stand. Generalized height–diameter equations, however, are function of tree and stand variables and can be applied at regional level. Further development of ecoregion-based individual tree height–diameter models is important for the improvement of accurate models on which to base forest management decisions. The relationship between growth and yield often varies from one ecoregion to another (Huang et al., 2000; Peng et al., 2001).

Datasets used in height–diameter models often show a lack of independence among measurements. This situation can result from different observations being taken at the same sampling unit, i.e. nested stochastic structure – trees within plots (West et al., 1984; Gregoire, 1987). Furthermore, the same plots are measured in successive inventories. Mixed modelling methodologies are increasingly being used for incorporating nested stochastic structure in individual-tree growth models (Lappi, 1991; Hökkä, 1997; Mehtätalo, 2004). Moreover, mixed effects reasonably explain the individual random variation commonly associated with repeated measurement data from permanent plots.

Mixed models allow fixed and random parameters to be estimated simultaneously, therefore local and generalized models can be combined in the fixed model structure and nested variability can be defined using random parameters. Stochastic individual tree models allow the preservation of observed spatial, temporal, or nested dependencies in predictions (Fox et al., 2001). In this way, it is possible to estimate the value of the random parameters for a location not present in the original estimation data. This approach is known as localization or calibration and can be applied if supplementary observations of the dependent variable (total tree height) are available.

The purpose of the present work was to develop a height–diameter model for pyrenean oak (*Quercus pyrenaica* Willd.), a deciduous oak which is mainly found in the mountain ranges of north-west Spain (Fig. 1) (Costa et al., 2001), covering a total surface area of 340,000 ha (DGCN, 1996). Low productivity, a decrease in the use of firewood and charcoal as an energy source and rural emigration to the cities led to any management practices in these coppice oak forests being abandoned. As a consequence, very little research has been carried out into the development of growth and yield models for this species, or even into height–

diameter relationships. The significant surface area compels us to have an in-depth knowledge of the species that allow us to look for new purposes (biomass, wine barrels) or to establish a sustainable forest management plan. A first step towards fulfilling this research requirement involved the study of stand variables and ecoregional differences. Taking into account the nested structure of the dataset, the nonlinear mixed approach was used to fit the data. Secondly, the predictive ability of the model was evaluated by predicting random parameters using data taken from a small sample of heights in a plot.

2. Materials and methods

2.1. Data used

Data from the Second (DGCN, 1996) and Third (DGCN, 2006) Spanish National Forest Inventory (SNFI) located in northwest Spain (Castilla y León region) were used to develop the height–diameter model. SNFI is a systematic sample of permanent plots of variable radii distributed on a square grid of 1 km, with a re-measurement interval of 10 years. The plots, which are circular in shape, are composed of four sub-plots with radii of 5, 10, 15 and 25 m, and a minimum diameter at breast height threshold of 75, 125, 225 and 425 mm, respectively. At each measurement, the data recorded for each sample tree are, among others: species, diameter at breast height and total height.

An initial selection of suitable plots was made from all the SNFI plots located in the Castilla y León region, selecting those plots in which *Q. pyrenaica* was the dominant species (basal area proportion over 90%). Because of the wide variety of silvicultural treatments applied, the different ecological characteristics of the pyrenean stands and the lack of past management information in the SNFI, a second selection was made according to the stand typology classification (Roig et al., 2007). Impoverished stands and excessively open stands were left out, so that those selected were characterized by medium to high densities (stand density index over 200 trees per hectare) and regular diameter distributions. Only measurements from live trees without top damage were included in the statistical analysis.

A total of 24,627 pairs of height–diameter measurements, 9328 from the second SNFI and 15299 from the third SNFI, taken in 950 permanent plots were used to fit the height–diameter model. Elena

Table 1
Characteristics (average, standard deviation (S.D.), minimum (min) and maximum (max)) of the both samples trees used to fit the height–diameter model and test dataset used to calibrate the model

Stratum	Plots	Trees	Average <i>D</i> (cm)	S.D. <i>D</i> (cm)	<i>D</i> min– <i>D</i> max (cm)	Average <i>H</i> (m)	S.D. <i>H</i> (m)	<i>H</i> min– <i>H</i> max (m)
Fitting dataset								
1	152	3805	18.6	9.6	7.5–101.5	10.1	3.3	2–24.5
2	122	2436	17.4	10.5	7.5–102.8	8.5	2.5	1.5–18.5
3	570	15690	18.6	12.0	7.5–147	9.8	3.2	2–27.5
4	73	1855	20.6	11.5	7.5–87.9	10.8	3.9	2–22.5
5	14	365	15.9	9.1	7.5–70	9.1	2.6	3–18.5
6	19	476	18.7	7.1	7.5–55.5	10.8	3.4	2.5–19.1
All	950	24627	18.6	11.5	7.5–147	9.8	3.3	1.5–27.5
Test dataset								
1	5	35	19.2	9.9	9.2–46.8	11.1	3.2	5.6–17.0
2	3	19	20.5	10.0	8.4–39.2	9.3	2.3	5.5–14.8
3	18	124	24.0	13.8	8.0–94.5	12.5	3.5	4.6–20.8
All	26	178	22.7	12.9	94.5–8.0	11.9	3.5	20.8–4.6

D, breast height–diameter; *H*, total height; min, minimum value; max, maximum value; S.D., standard deviation.

Roselló (1997) defined two ecoregions within this study area and six strata according to biogeoclimatic characteristics and these are taken into account in the development of the height–diameter model (Fig. 1). Summary statistics, including the average, minimum, maximum, and standard deviation for total tree height and diameter at breast height according to biogeoclimatic stratum are shown in Table 1. Stand variables for the sample plots by stratum are given in Table 2. Dominant height was defined as average height of the thickest 100 stems per hectare.

The test dataset was taken from 26 independent plots (Tables 1 and 2), different from fitting dataset, which had been used to study the autoecology and the growth of pyrenean oak in Castilla y León region. Measurements were taken and data collected at these sample plots in 2004 using a procedure similar to that which was used in the modelling dataset. In these plots, a few trees (5–8 per plot) were randomly sampled. Diameter at breast height and total height were measured on a total of 178 trees.

2.2. Model development

2.2.1. Selection of the basic nonlinear height–diameter model

Eleven biparametric nonlinear growth functions selected from the 27 models proposed by Huang et al. (2000) were considered for evaluation in this study (Table 3). Besides their capacity to predict the height–diameter relationships, the number of parameters (two parameters as against three parameters of the rest 16 models) and their biological interpretation also had to be taken into account (Peng et al., 2001). All these functions can be written in the following general form:

$$H_i = f(D_i, \phi) + \varepsilon_i \quad (1)$$

where H_i is the i th observation of the dependent variable tree height (m), D_i the i th observation of the independent variable diameter at breast height (cm), ϕ a vector of parameters to be estimated and ε_i the random error term, and i is the i th observation with $i = 1, 2, \dots, n$.

Each regression model was fitted separately to the data from each of the sample plots (Fang and Bailey, 1998). Nonlinear regressions using ordinary nonlinear least squares (ONLS) techniques were carried out using the SAS NLIN procedure (SAS/STAT, 2000). To ensure a global rather than local least squares solution, different initial values for the model parameters were provided for the fits.

The models were evaluated quantitatively by examining the magnitude and distribution of residuals to detect any obvious

patterns and systematic discrepancies, and by testing for bias and precision to determine the accuracy of model predictions (Vanclay, 1994; Soares et al., 1995; Gadow and Hui, 1998). Comparison of the estimates among the different functions was based on numerical analyses, as shown in Table 4 (Amaro et al., 1998).

2.2.2. Inclusion of stand variables in the model

It should be possible to use the measured stand variables when predicting the H – D curve in order to express the variability detected among plots (Pinheiro and Bates, 1995; Hökkä, 1997) when up-scaling from a local model to a generalized model. In the case of re-measured permanent plot data, serial correlation and spatial correlation might be expected. However, the large number of trees in comparison to the number of re-measurements for the same individual (measured twice maximum), makes it reasonable to assume an absence of serial correlation (Vanclay et al., 1995; Zhao, 2003; Castedo Dorado et al., 2006). Therefore, it is assumed that both measurements occasions have different curves and they are treated as different plots. With regard to spatial correlation, as the plots were widely spaced (more than 1 km), the between-plot correlation should also be minimal and as such, not worth considering in the model (Zhao et al., 2004).

The parameters defined in selected local model were expanded with stand variables using graphical and linear regression analysis over the stand variables for each plot. The following stand variables were tested for inclusion in the model: stand density (N , stems/ha), mean square diameter (DG, cm), mean diameter (Dm, cm), dominant diameter (Do, cm), dominant height (Ho, m) and basal area (BA, m²/ha). In the analysis, different combinations of these variables and their logarithmic transformations were tested. Linear models including different stand variables were fitted to explain the variation in the model parameters (a and b in Table 3) calculated for each plot. This linear modelling was performed using SAS REG procedure (SAS/STAT, 2001). The model selected was that which showed the maximum coefficient of determination R^2 .

2.2.3. Comparison of height–diameter models among the different biogeoclimatic strata

As the plots are located in six biogeoclimatic strata, the differences in the height–diameter relationship for the different strata were compared using both the full and the reduced models (Huang et al., 2000). The full model employs completely different sets of parameters for each stratum and is obtained by expanding each parameter, including an associated parameter as well as a dummy variable to differentiate the strata. The reduced model uses the same set of parameters for all the strata combined.

Table 2
Stand characteristics values of both the sample plots used to fit the model and test plots used to calibrate the model

	Stratum	1	2	3	4	5	6	All
Fitting dataset								
N (trees/ha)	Average	1048.6	1011.1	1246.8	1046.5	1387.2	797.0	1171.2
	S.D.	710.2	602.7	760.4	607	782.6	380.5	731.3
	Min–max	201.6–3055.8	205.1–2928.4	201.6–3947	216.9–3119.4	220–2833	212.2–1559.7	201.6–3947
Dm (cm)	Average	15.6	13.8	15	16.5	13.5	16.3	16.0
	S.D.	5.6	4.4	6.1	5.4	4.8	4.26	6.3
	Min–max	8.5–37.2	8.6–35.4	8.5–65.7	9.4–34.8	8.9–30	9.8–26.4	8.5–65.7
DG (cm)	Average	16.4	14.7	15.9	17.7	14.1	16.9	15.06
	S.D.	5.9	5	6.7	5.9	5.5	4.3	5.8
	Min–max	8.4–36.8	8.4–32.7	8.5–64.6	9.3–33.3	8.8–28.2	9.5–25.9	8.4–64.6
Hm (m)	Average	9	7.6	8.8	9.4	8.5	10.1	8.8
	S.D.	2.7	1.6	2.3	2.5	1.7	3	2.4
	Min–max	3.1–20.5	4.3–13.4	2.2–20.4	4.4–15.7	5.3–12.8	4.6–15.7	2.2–20.5
Ho (m)	Average	11.1	9.5	11.11	12.3	10	12	11.0
	S.D.	3	2.1	2.81	3.2	2.3	3.3	2.9
	Min–max	4.9–21.4	4.5–14.2	3.2–23.2	5.3–18.3	6.3–13.5	5.5–16.9	4.5–23.2
BA (m ² /ha)	Average	17.8	14.4	20.0	21.4	16.9	16.3	19.1
	S.D.	8.8	6.5	9.8	8.7	5.9	6.7	9.4
	Min–max	2.3–38.8	3–35.9	2–72.5	3.8–40.2	7.7–27.9	2.5–26.8	2–72.5
Test dataset								
N (trees/ha)	Average	821.6	390.0	800.9	–	–	–	761.1
	S.D.	458.8	192.1	702.6	–	–	–	636.9
	Min–max	359–1513.7	113.2–569	131.6–2833	–	–	–	113.2–2833
Dm (cm)	Average	15.7	19.7	17.2	–	–	–	17.1
	S.D.	6.2	5.9	6.6	–	–	–	6.5
	Min–max	8.5–24.4	15–28.4	9.8–32.7	–	–	–	8.5–32.7
DG (cm)	Average	17.5	20.6	18.8	–	–	–	18.7
	S.D.	8.6	5.5	7.4	–	–	–	7.5
	Min–max	8.6–31.4	15.9–28.6	9.9–35.5	–	–	–	8.6–35.5
Do (cm)	Average	25.8	26.1	28.2	–	–	–	27.5
	S.D.	13.9	3.5	11.7	–	–	–	11.6
	Min–max	11.3–48.9	21.5–29.2	12.1–53.7	–	–	–	11.3–53.7
Hm (m)	Average	8.8	8.2	9.2	–	–	–	9.0
	S.D.	2.3	1.8	2.1	–	–	–	2.2
	Min–max	5.6–12.3	6.1–10.6	6.7–15.7	–	–	–	5.6–15.7
Ho (m)	Average	10.4	9.6	11.8	–	–	–	11.3
	S.D.	2.7	0.9	2.9	–	–	–	2.9
	Min–max	5.5–13.6	8.6–10.8	7.8–16.9	–	–	–	5.5–16.9
BA (m ² /ha)	Average	16.4	10.3	16.7	–	–	–	16.0
	S.D.	8.7	3.0	9.1	–	–	–	8.8
	Min–max	3.7–27.8	7.3–14.5	2.8–38.4	–	–	–	2.8–38.4

N, density; Dm, mean diameter; DG, mean square diameter; Do, dominant diameter; Hm, mean height; Ho, dominant height; BA, basal area. S.D., standard deviation; Min–max, minimum and maximum value.

Besides, two tests for detecting simultaneous homogeneity among parameters were used: the Bates and Watts non-linear extra sum of squares *F* test (Huang, 1997; Huang et al., 2000) and the test proposed by Lakkis and Jones, in Khattree and Naik (1995), to check the differences in height–diameter models between strata. These tests are frequently applied to analyse differences among different geographic regions (Huang et al., 2000; Álvarez González et al., 2005).

2.2.4. Nonlinear mixed modelling

Eq. (1) presented is assumed to be common to all plots, but the parameter estimates may vary across the plots. Therefore, regression coefficients can be broken down into a fixed part, common to the population, and random components, specific to each plot. Nonlinear mixed models entertain unobserved mean-zero random variables known as random effects, conditional upon which the observed data are assumed to have a Gaussian distribution with some general nonlinear mean function and unknown variance–covariance parameters. In these types of models, it is possible for

both fixed and random effects to have a nonlinear relationship with the parameters.

The general expression for mixed model defined by Lindstrom and Bates (1990) and the parameter vector for the nonlinear mixed

Table 3
Height–diameter functions selected for evaluation (Huang et al., 2000)

Function number	Function form
F1	$H = 1.3 + aD^b$
F2	$H = 1.3 + e^{a+b/(D+1)}$
F3	$H = 1.3 + aD/(b + D)$
F4	$H = 1.3 + a(1 - e^{-bD})$
F5	$H = 1.3 + D^2/(a + bD)^2$
F6	$H = 1.3 + ae^{b/D}$
F7	$H = 1.3 + aD/(D + 1) + bD$
F8	$H = 1.3 + a[D/(1 + D)]^b$
F9	$H = 1.3 + e^{aD^b}$
F10	$H = 1.3 + aDe^{-bD}$
F11	$H = 1.3 + aD + bD^2$

H, total height (m); *D*, diameter at breast height (cm); *a* and *b*, parameters.

Table 4
Model performance evaluation criteria

Performance criterion	Symbol	Formula	Ideal
Mean residual	Mres	$\sum_{i=1}^n \frac{\text{est}_i - \text{obs}_i}{n}$	0
Variance ratio	VR	$\frac{\sum_{i=1}^n (\text{est}_i - \text{est})^2}{\sum_{i=1}^n (\text{obs}_i - \text{obs})^2}$	1
Root mean square error	RMSE	$\sqrt{\frac{\sum_{i=1}^n (\text{est}_i - \text{obs}_i)^2}{n - p}}$	0
Absolute mean error	AME	$\frac{\sum_{i=1}^n \text{est}_i - \text{obs}_i }{n}$	0
Coefficient of determination R^2		$1 - \frac{\sum_{i=1}^n (\text{est}_i - \text{obs}_i)^2}{\sum_{i=1}^n (\text{obs}_i - \text{obs})^2}$	1
Linear regression	α, β and R_{adj}^2	$\text{obs}_i = \alpha + \beta \text{est}_i + \varepsilon_i, \alpha = 0, \beta = 1, R_{\text{adj}}^2 = 1$	

est_i , i th estimated value; obs_i , i th observed value; n , number of observations; p , number of parameters of the model; R_{adj}^2 , coefficient of determination based on the linear regression.

models defined by Pinheiro and Bates (1995) were used. Model specification (nature of the parameters, within-plot and among-plot variance–covariance structures) was made following the structure laid down by Castedo Dorado et al. (2006).

Parameter estimation for nonlinear mixed-effects models requires numerical integration of random effects in the model, which often enter it nonlinearly. Traditional approaches for fitting nonlinear mixed models are based on a linear approximation to the marginal likelihood function by expanding it with Taylor series to be linear on the vector of random parameters. The Taylor expansion can be either at 0 (best linear unbiased predictor, BLUP) or at the empirical best linear unbiased predictor (EBLUP) of the random effects. The first approach is cheaper in terms of computing time, but the second approach can be more accurate although possibly more unstable (Wolfinger and Lin, 1997).

The variance components, along with the parameters of fixed predictors, were estimated using the REML method, since it results in lower biases (Littel et al., 1996), procedure available in the NLMIXED procedure of SAS/STAT[®] (2001). The maximization of the marginal likelihood function was achieved using the best linear unbiased predictor (BLUP) approximation (Beal and Sheiner, 1982).

2.2.5. Height prediction

For the purposes of forest management, yield predictions are important, and previous height observations may or may not be available for the studied plot. The nonlinear mixed-effects model can distinguish these two situations, and the correlation between the observations from the same plot provides an opportunity to improve the precision of the individual prediction (Fang et al., 2001; Hall and Bailey, 2001).

If no tree heights have been measured, the prediction of the fixed part is obtained simply by inserting the measured values of the predictors, and the expected value 0 is used for all random parameters. This case defines the mean behaviour of the pattern of variation in height versus diameter for given stand and regional conditions. If tree heights have been measured, calibration of the height–diameter model can carry out predicting the random effect (best linear unbiased predictor).

To evaluate the predictive ability of the model, data included in the test dataset are used. For this calibrated response pattern, different alternatives of sampling size within each plot were evaluated, measuring stand variables and the height of, respectively, 1, 2, 3 and 4 trees, randomly selected in each case. The calibrated height–diameter equations were applied to the remaining trees for which height measurements were available in the same plot. These alternatives were evaluated and compared with the estimation obtained with ONLS

techniques in the individual fit of the selected function for the evaluation plots and with a typical fixed-effects response pattern.

Evaluation is carried out by testing for bias and precision to determine the accuracy of model precision (Vanclay, 1994; Soares et al., 1995; Gadow and Hui, 1998). Mean residual or bias, residual mean of squares and coefficient of determination were calculated as in Table 4. Because the subsample of the height measurements is randomly selected, the results of the statistics are estimated as the mean value after 500 realizations.

3. Results

3.1. Selection of the basic nonlinear height–diameter model

The statistics used for the selection of basic model are shown in Table 5. The values of the statistics used to compare the models indicate that all the models performed reasonably and the majority of the chosen models produced very similar results with the considered criteria. This is not surprising as any nonlinear function which may be expressed as a Taylor series expansion of a polynomial, truncated after terms, becomes inconsequentially small (Fang and Bailey, 1998).

Functions F2, F6 and F8 provided the best results for the goodness-of-fit statistics calculated, with low values of Mres, RMSE and AME and both VR and R^2 values closer to 1. The results were slightly better with F6, so this function was selected as the basic nonlinear height–diameter model:

$$h_{ij} = 1.3 + ae^{b/d_{ij}} + e_{ij} \quad (2)$$

where h_{ij} is the height (m) of the j th tree in the i th plot; d_{ij} is the diameter at breast height (cm) of the same tree and e_{ij} represents the estimation error for the j th observation in the i th plot.

3.2. Inclusion of stand covariates

The parameters defined in Eq. (2) (a and b) were expanded with stand variables using graphical and linear regression analysis over the stand variables for each plot (Figs. 2 and 3). Different combinations of stand variables (inverse and logarithmical included) were tested. The influence of more than one variable in the parameters was evaluated using the RSQUARE selection method, procedure available in the REG procedure of SAS/STAT[®] (2001).

The best results, taking into account number of variables and coefficient of determination, were provided by the following combination:

$$\begin{aligned} a &= a_1 + a_2 \text{BA} + a_3 \text{Ho} \\ b &= b_1 \end{aligned} \quad (3)$$

where a_2 and a_3 are fixed parameters for basal area (BA) and dominant height (Ho) respectively; and a_1 and b_1 are fixed parameters indicating the intercept of the model.

Thus, the height of tree j in plot i can be estimated by the model:

$$h_{ij} = 1.3 + \left[(a_1 + a_2 \text{BA} + a_3 \text{Ho}) \exp\left(\frac{b_1}{d_{ij}}\right) \right] + e_{ij} \quad (4)$$

The value of the asymptote when d_{ij} tends to infinite is 24 m.

3.3. Comparison of height–diameter models among the different strata

Using the indicator variable approach (Bates and Watts, 1988), the full model of the height–diameter function (Eq. (4)) for six

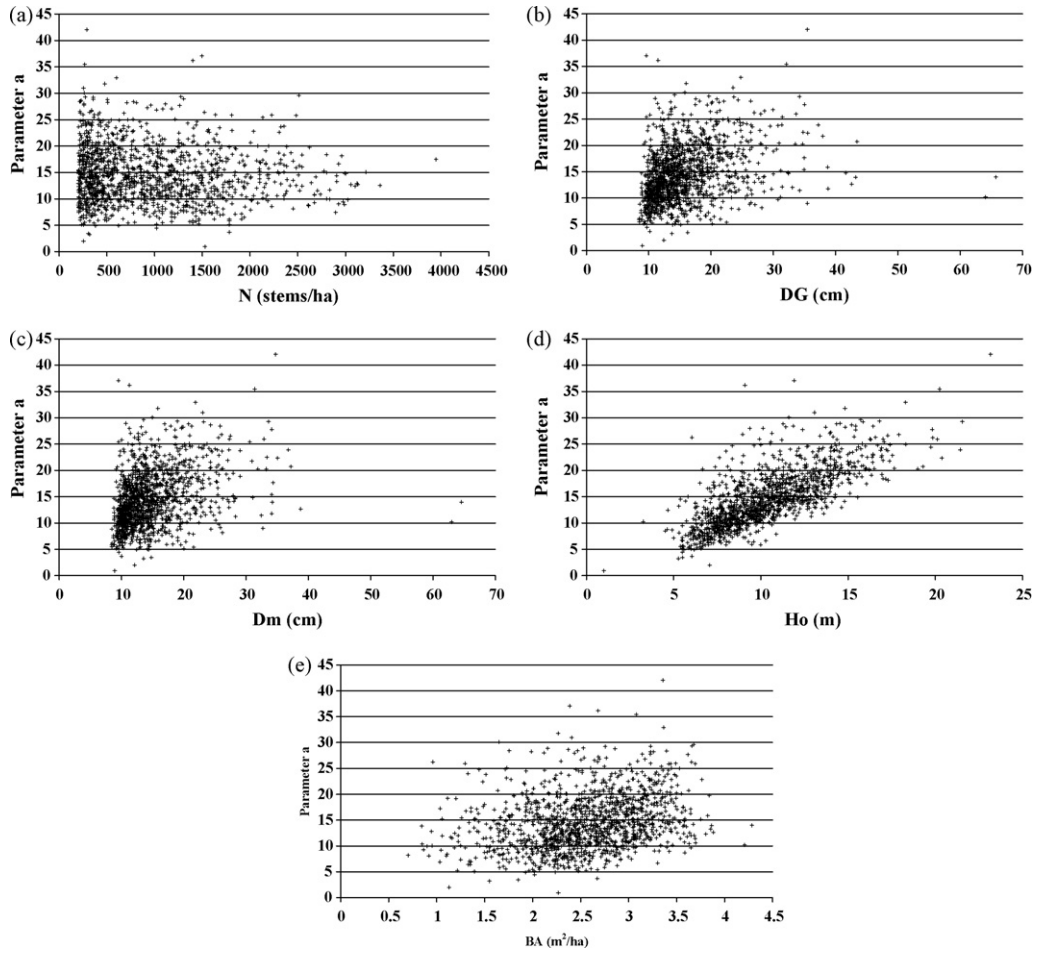


Fig. 2. Scatter plot of estimated parameter *a* obtained from individual fit to each plot, against potential stand variables *N* (2a), *DG* (2b), *Dm* (2c), *Ho* (2d) and *BA* (2e).

biogeoclimatic strata can be written as:

$$h_{ij} = 1.3 + \left[(a_1 + \Delta_1 x_1 + \Delta_2 x_2 + \Delta_3 x_3 + \Delta_4 x_4 + \Delta_5 x_5 + a_2 BA + a_3 Ho) \exp\left(\frac{(b_1 + \Phi_1 x_1 + \Phi_2 x_2 + \Phi_3 x_3 + \Phi_4 x_4 + \Phi_5 x_5)}{d_{ij}}\right) \right] + e_{ij} \quad (5)$$

where x_i is a dummy variable whose value is equal to 1 for stratum i and 0 for the other strata.

Parameters belonging to stratum 1, 2, 3 and 4 ($\Delta_1, \Delta_2, \Delta_3, \Delta_4, \Phi_1, \Phi_2, \Phi_3, \Phi_4$) are not significantly different from zero and as such can be removed from the model. On the other hand, both parameters Δ_5

and Φ_5 are significant, so a different model might be required for stratum 5. Fig. 4 represents Eq. (5) adjusted for each stratum where $BA = 20 \text{ m}^2/\text{ha}$ and $Ho = 12 \text{ m}$. No significant differences are identified between strata 1, 2, 3 and 4, but stratum 5 shows a slightly different pattern.

Table 5
Performance criteria for tested basic height–diameter models

Function	Mres	VR	RMSE	AME	R^2	Linear regression		
						α	β	R^2_{adj}
F1	-0.0048	0.5035	1.3633	0.9246	0.5188	-0.1872	1.0182	0.5191
F2	-0.0005	0.5332	1.3214	0.8965	0.5369	-0.0664	1.0062	0.5370
F3	0.0098	0.5560	1.3929	0.9264	0.4604	-0.2861	1.0289	0.5304
F4	0.0204	0.6126	1.4066	0.9378	0.4279	-0.4818	1.0508	0.5355
F5	-0.0028	0.5255	1.3248	0.8987	0.5354	-0.1453	1.0139	0.5361
F6	0.0002	0.5360	1.3201	0.8956	0.5377	-0.0491	1.0045	0.5378
F7	-0.0026	0.4976	1.3902	0.9414	0.5077	-0.7725	1.0979	0.5091
F8	-0.0002	0.5347	1.3207	0.8960	0.5373	-0.0579	1.0053	0.5374
F9	-0.0048	0.5035	1.3633	0.9246	0.5188	-0.1872	1.0182	0.5191
F10	0.0011	0.5556	1.3310	0.9029	0.5236	-0.0290	1.0081	0.5440
F11	0.0285	0.6622	1.3847	0.9347	0.4728	0.5749	0.9459	0.5445

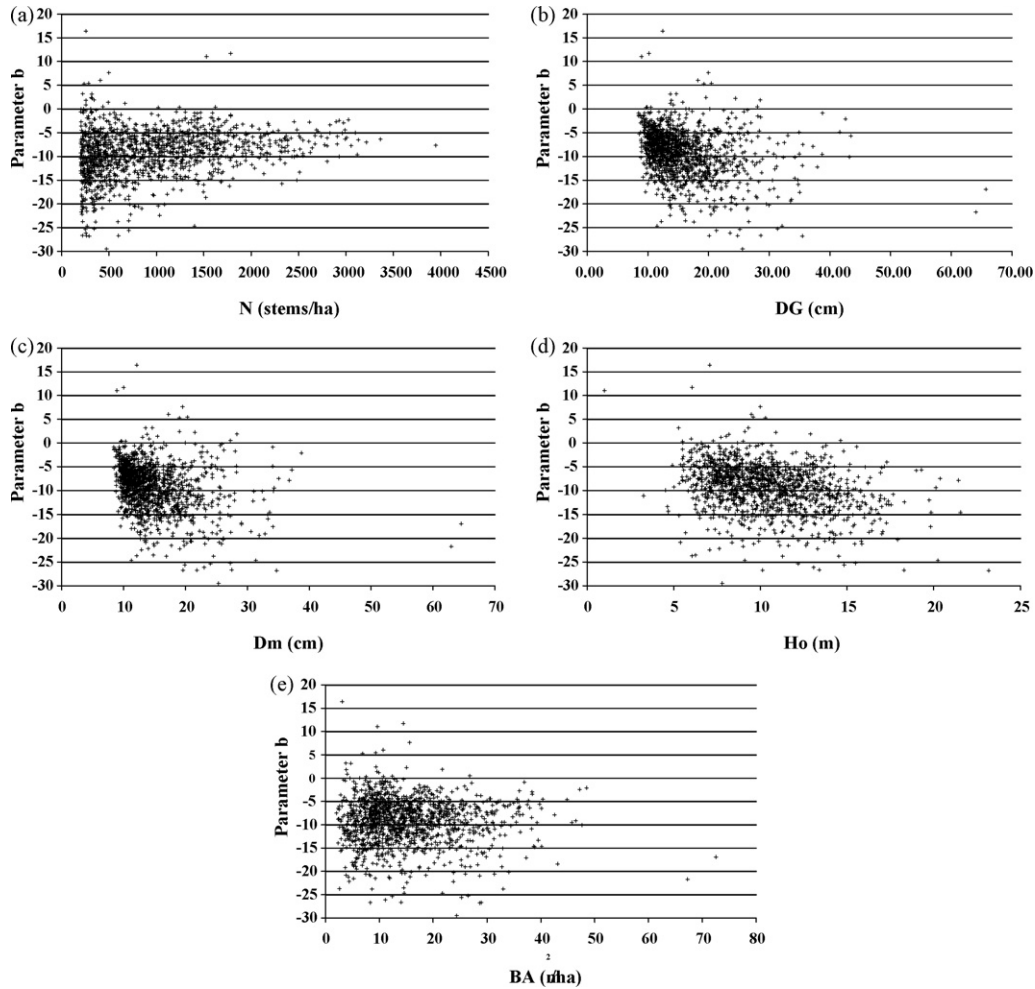


Fig. 3. Scatter plot of estimated parameter *b* obtained from individual fit to each plot, against potential stand variables *N* (3a), *DG* (3b), *Dm* (3c), *Ho* (3d) and *BA* (3e).

Due to statistics differences between model that included only stand variables and model that included regional and stand variables are slight (Table 6), and stratum 5 is represented by the smallest number of plots (14 plots in Table 1), both *F* test and Lakkis–Jones test were calculated. The values for the *F* test (0.396) and Lakkis–Jones test (0.1356) were nonsignificant, revealing in both cases that the null hypothesis of parameter homogeneity was acceptable in the reduced model (single model for all strata). According to these results, the total reduced model (all strata together) should be selected (Eq. (4)). In this model, all the parameters are significantly different from zero and the number of parameters to be estimated is smaller.

3.4. Model specification

Both parameters *a*₁ and *b*₁ were considered as mixed (both random and fixed) and the general expression for the model can be defined as:

$$h_{ij} = 1.3 + \left[(a_1 + u_i + a_2BA + a_3Ho) \exp\left(\frac{(b_1 + v_i)}{d_{ij}}\right) \right] + e_{ij} \quad (6)$$

$$\begin{bmatrix} u_i \\ v_i \end{bmatrix} \sim N(0, \mathbf{D}) \\ e_i \sim N[0, \mathbf{R}_i]$$

where *a*₁, *a*₂, *a*₃ and *b*₁ are considered fixed parameters, common to every plot; *u*_{*i*} and *v*_{*i*} are random parameters, specific to the *i*th plot.

A plot of the residuals versus predicted height (obtained by fitting the nonlinear mixed height–diameter model (Eq. (6)) to dataset) is presented in Fig. 5. The variation of the residuals revealed systematic pattern and the variance over the full range of the predicted values was not homogeneous, so the inclusion of weighting factors to balance the error variance was necessary. The variance of the residual error can then be expressed as a function of the diameter using the following function:

$$\text{Var}(e_{ij}) = q_1[\min(d_{ij}, 50)]^2 + q_2[\min(d_{ij}, 50)] + q_3 \quad (7)$$

where *q*_{*i*} are parameters and *d*_{*ij*} is diameter at breast height (cm). Values obtained using GLM procedure of SAS/STAT® (2001) were 0.00017104, 0.06662 and 0.60481 for *q*₁, *q*₂ and *q*₃ respectively.

Hence, the expression for the within-plot variance–covariance matrix is constructed as follows (Calama and Montero, 2004):

$$\mathbf{R}_i(\boldsymbol{\lambda}, b_i, \boldsymbol{\rho}) = \sigma^2 \mathbf{G}_i \mathbf{I}_{n_i} \quad (8)$$

where σ^2 is a scaling factor for the residual variance of the model; \mathbf{G}_i is a *n*_{*i*} × *n*_{*i*} diagonal matrix describing the no constant variance; \mathbf{I}_{n_i} is the identity matrix with a range equal to the number of observations in the plot (*n*_{*i*}).

Table 6
Fitting parameters and comparison of mixed model effects performance for different alternatives of fixed effects inclusion

	Parameters	Basic nonlinear model (Eq. (2))	Stand covariates inclusion (Eq. (4))	Regional and Stand covariates inclusion (Eq. (5))	Regional and stand nonlinear model (Eq. (5))	Nonlinear mixed model (Eq. (9))
Fixed parameters	a_1	15.9206 (0.0681)	2.7314 (0.0766)	3.0716 (0.3730)	4.0729 (0.0903)	3.099 (0.1680)
Stand fixed parameters	a_2	–	–0.0018 (0.0021)	–0.00173 (0.0021)	–0.1424 (0.00409)	–0.00203 (0.0054)
	a_3	–	0.9304 (0.00646)	0.9298 (0.00656)	1.1049 (0.00765)	1.0249 (0.0158)
	b_1	–9.8024 (0.0723)	–6.7146 (0.0554)	–6.9816 (0.4502)	–7.9281 (0.0637)	–8.5052 (0.1139)
Regional fixed parameters	Δ_1	–	–	–0.4797 (0.3863)*	–	–
	Δ_2	–	–	–0.6826 (0.3942)*	–	–
	Δ_3	–	–	–0.2835 (0.3736)*	–	–
	Δ_4	–	–	0.2335 (0.4025)*	–	–
	Δ_5	–	–	–1.9792 (0.5050)	–1.3474 (0.3500)	–
	Φ_1	–	–	0.6416 (0.4731)*	–	–
	Φ_2	–	–	0.4343 (0.4869)*	–	–
	Φ_3	–	–	0.2263 (0.4552)*	–	–
	Φ_4	–	–	–0.8162 (0.4911)*	–	–
	Φ_5	–	–	2.9231 (0.6386)	2.1505 (0.4100)	–
Variance components	σ_u^2	–	–	–	–	4.4864
	σ_v^2	–	–	–	–	10.7130
	σ_{uv}^2	–	–	–	–	–5.9088
	σ^2	–	–	–	–	1.0479
Model performance	Mres	–0.0003	0.0044	0.0041	0.0065	–0.0156
	VR	0.4584	0.7313	0.7322	0.7500	0.79284
	RMSE	2.4201	1.7172	1.6874	1.6688	1.37788
	AME	1.8530	1.3027	1.2992	1.2592	1.01130
	R^2	0.4590	0.7243	0.7257	0.7396	0.8225
	α	–0.0058	0.0512	0.0476	0.0741	–0.2
	β	1.0006	0.9952	0.9956	0.9931	1.0187
	R_{adj}^2	0.4590	0.7243	0.7257	0.7397	0.8228

Standard deviation in brackets.
Indicates a not statistically significant estimate.

Based on the above considerations, the resulting height–diameter model was:

$$h_{ij} = 1.3 + \left[(3.099 + u_i - 0.00203BA + 1.02491Ho) \exp\left(\frac{(-8.5052 + v_i)}{d_{ij}}\right) \right] + e_{ij} \quad (9)$$

$$\begin{bmatrix} u_i \\ v_i \end{bmatrix} \sim N(0, \mathbf{D}) \quad \mathbf{D} = \begin{bmatrix} 4.4864 & -5.9088 \\ -5.9088 & 10.713 \end{bmatrix}$$

$$e_i \sim N[0, \mathbf{R}_i(\boldsymbol{\lambda}, b_i, \boldsymbol{\rho})] \quad \mathbf{R}_i = 1.0479\mathbf{G}_i$$

The estimates and standard errors for the basic nonlinear model (Eq. (2)), stand model (Eq. (4)), regional and stand model (Eq. (5)) and the mixed-effects model (Eq. (9)), along with the variances

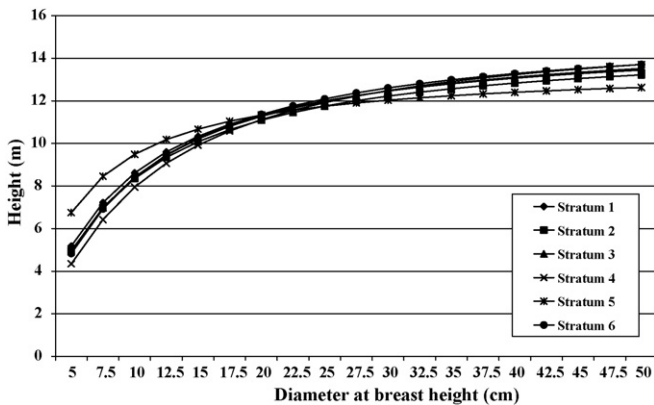


Fig. 4. Stratum height–diameter curves according to Eq. (5) and values BA = 20 m²/ha and Ho = 12 m.

and covariances for the random parameters in Eq. (9) and the goodness-of-fit statistics are shown in Table 6.

3.5. Height prediction for new observations

Values for a single tree height h_{ij} from a new experimental plot can be obtained either by using fixed parameters common to all the plots alone or by adding random parameters specific to each plot to these common parameters calculated from prior observations. The calibrated responses data included in the test dataset were used to examine different sample sizes from additional observations and evaluate their statistical performance (Table 7). The predictive ability of any calibrated model is better than that of the fixed-effect model and, logically, worse than that obtained by using an individual fit to data of each plot (ONLS).

A notable improvement is attained by including just one random tree measurement; reducing the bias and RMSE of the predictions by over 38% and 14% respectively, and increasing R^2 by more than 25%. As opposed to one random tree measurement, two random tree measurements improve bias, RMSE and R^2 by 16%, 5% and 3% respectively. If more than two trees are measured for calibration purposes, the results are slightly better, although the increase in sampling costs needs to be evaluated.

To demonstrate the predictive ability of the mixed model, an example with calibration was developed for two plots from the evaluation dataset (Fig. 6).

Table 7
Comparison of model performance for different alternatives of subsample size in calibration

Alternatives	Mres	% Mres reduction	RMSE	% RMSE reduction	R ²
(1) Only stand variables are measured	1.1684	–	2.3251	–	0.4231
(2) Stand variables + 1 height random tree	0.7202	–38.3644	1.9820	–14.7559	0.6744
(3) Stand variables + 2 height random trees	0.5320	–54.4698	1.8643	–19.8207	0.7099
(4) Stand variables + 3 height random trees	0.4280	–63.3706	1.8027	–22.4666	0.7248
(5) Stand variables + 4 height random trees	0.3572	–69.4267	1.7628	–24.1854	0.7317
(6) Individual fit to data from each plot (ONLS)	0.2012	–82.7810	1.3549	–41.7260	0.8486

Mres, mean residual; RMSE, root mean square error; R², coefficient of determination. For alternatives 2–5, the statistics are obtained as the average after 500 realizations.

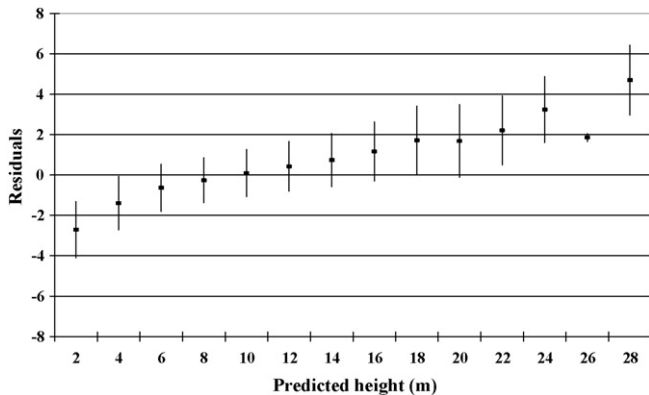


Fig. 5. Plot of class means residuals with standard errors against predicted values of height for the nonlinear mixed height-diameter model (Eq. (6)) fitted to the data.

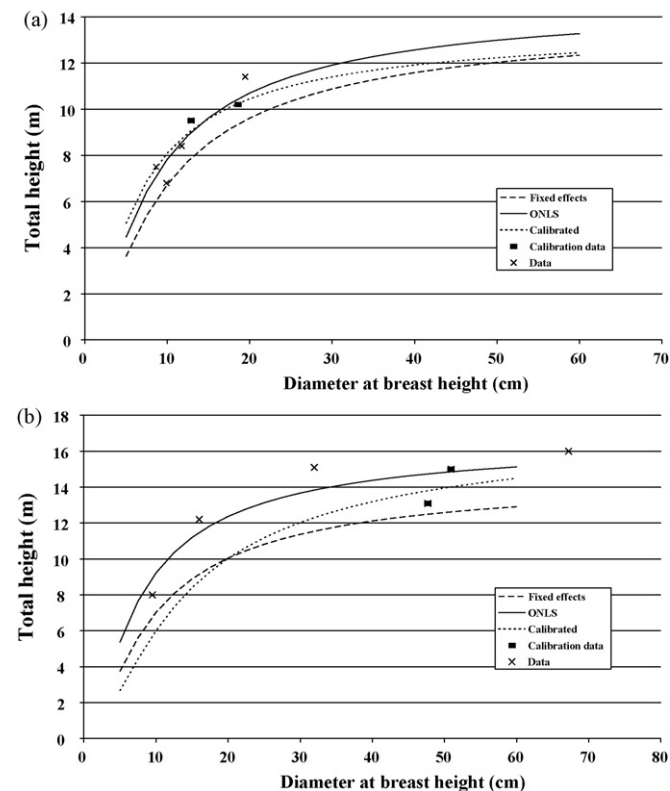


Fig. 6. Height-diameter performance of typical (fixed-effects only) and calibrated with two random trees (including random parameters), compared with individual ordinary nonlinear least squares (ONLS) for plot 1 (a) and plot 8 (b) in the test dataset.

4. Discussion and conclusions

The aim of this study was to develop a model capable of predicting the height-diameter pattern of *Quercus pyrenaica* stands in Castilla y León (northwest Spain) for application in yield simulators and basic calculation of forest inventories. Tree height is an important variable which is used for estimating stand volume, site quality and for describing stand structure.

Eleven asymptotic and nonlinear biparametric equations from Huang et al. (2000) were proposed as possible candidates for a basic nonlinear height-diameter model (Table 3). This type of height-diameter equation is consistent with the biological growth curves characteristics. Models with the same number of parameters, fitted to the same set of data and where the same nonlinear least-square criteria for convergence are applied, should produce similar fit statistics (Fang and Bailey, 1998).

In general, the inclusion of stand variables in a local height-diameter model reduces bias and increases the precision of the model (Soares and Tomé, 2002; Calama and Montero, 2004). Measurements from at least one sample of trees are required for the practical application of the equation, although the stand measurements used in this study are available in most growth and yield models. The relationship between diameter and height is influenced by the competition of the rest of trees as well as by age and site index. With this in mind, various relevant model forms were evaluated. Both dominant height (H₀) and basal area (BA) seem to have significant influence on the performance of the height-diameter model (Figs. 2 and 3). The use of dominant height in height-diameter models was previously proposed by Eerikäinen (2003), Calama and Montero (2004) and Castedo Dorado et al. (2005). The use of the basal area as a covariate in height-diameter models was proposed by Pascoa (1987), Hökkä (1997) and Schröder and Álvarez González (2001).

In most growth modelling studies, both tree and stand development are linked to the development of dominant height (Borders, 1989; Hynynen, 1995). This is justified because the dominant height is a measurable stand characteristic and it indicates the site quality in terms of the stand growth and yield capacity (Eerikäinen, 2003). Regarding basal area as density indicator, the height of a tree of the same diameter varies as a function of the stand stocking (Hökkä, 1997).

Analysis of the ecoregion-based height-diameter model for pyrenean oak in the forests of Castilla y León shows that all the stratum variables are not significantly different from zero, except for stratum 5 (Fig. 4). Stratum 5 has a slightly different pattern, but as the sample size and the mean diameter are the smallest in the dataset (Tables 1 and 2), the use of a different model was not considered justifiable. The establishment of a single diameter-height model is supported by Adame et al. (2006), who found that for the same strata considered in this study, the dominant height growth pattern between strata was not significantly different.

Once the fixed parameters have been considered, among-plot variability is modelled by including random effects specific to each

plot. There are several studies in which the modelling of the height–diameter relationship is based on mixed models, with random and fixed parameters (Hökkä, 1997; Lappi, 1997; Calama and Montero, 2004; Castedo Dorado et al., 2006). Using a mixed-effect modelling approach allows for the quantification of these multiple sources of variances and complex patterns of correlation and thus is more flexible. If additional observations are available, the random effects corresponding to a specified individual can be estimated and therefore, more precise predictions can be obtained.

After the estimation phase, the random parameters for a given stand could be predicted with the empirical best linear unbiased predictor (EBLUP) using the height and diameter measurements from sample trees in the same stand. This ‘localizing’ (calibration) can be done without the need for a representative sample as the measurements from just one tree of any diameter taken at any point in time will suffice. Furthermore, the calibration procedure assures that the within-stand and among-stand variation observed in the modelling data are used in a statistically correct and well-grounded manner. There is also a possibility that when trees are randomly chosen for height measurement, a random component might (in rare cases) change the sign of the slope of the height–diameter curve, making it inappropriate.

The random parameter model was tested using a validation dataset with a different number of randomly selected sample trees from each stand. Both the bias and the root mean square of residuals are lower in the random parameter model, and both of them decrease with the number of sample trees used for calibration purposes. Height measurements from two random trees significantly improve the height–diameter mixed model. This result is very similar to that obtained by Calama and Montero (2004), and Castedo Dorado et al. (2006) for different types of pinus. Calama and Montero (2004) proposed the use of height measurements from four random trees, Krumland and Wensel (1988) suggested that the height measurements should be for four dominant trees and Castedo Dorado et al. (2006) found the height of three trees per plot to be adequate. In all cases, the improvement detected between the fixed model and the mixed model using the height measurement from just one random tree was less than that detected in the present study. Therefore, it appears that the influence of the stand component is stronger for *Quercus pyrenaica* than for *Pinus* species.

Due to the wide range of silvicultural and ecological conditions, the same height–diameter model may not be appropriate for all stand types in the study area. This study is restricted to coppices characterized by medium to high densities (stand density index over 200 trees per hectare), regular diameter distributions and where *Q. pyrenaica* is the dominant species (basal area proportion over 90%). The open woodlands and impoverished stands have not been considered in this study.

Hasenauer and Monserud (1997) demonstrated that fit statistics measuring deviations about smoothed data (data predicted from a heuristic function of diameter) are misleading and strongly biased, and the resulting models produce biased predictions. So, the application of the height predicted from this model has to be careful if they are used for estimating volume or other variables.

The suggested model improves the accuracy of height prediction, ensures compatibility among the various estimates in a growth and yield model, and maintains projections within reasonable biological limits. Together with diameter growth models and models for ingrowth and self-thinning, stand development predictions can provide a basis for making management decisions.

Acknowledgements

This work forms part of the project titled “Estudio autoecológico y modelos de gestión de los rebollares (*Quercus pyrenaica* Willd.) y normas selvícolas para *Pinus pinea* L. y *Pinus sylvestris* L. en Castilla y León”, involving the collaboration of the INIA and the government of Castilla-León. The author would like to thank Dr. R. Calama, Dr. M. Barrio and the anonymous reviewers for their constructive comments on the manuscript.

References

- Adame, P., Cañellas, I., Roig, S., del Rio, M., 2006. Modelling dominant height growth and site index curves for rebollo oak (*Quercus pyrenaica* Willd.). *Ann. For. Sci.* 63, 929–940.
- Álvarez González, J.G., Ruíz González, A.D., Rodríguez Soalleiro, R., Barrio Anta, M., 2005. Ecoregional site index models for *Pinus pinaster* in Galicia (northwestern Spain). *Ann. For. Sci.* 62, 115–127.
- Amaro, A., Reed, D., Tomé, M., Themido, I., 1998. Modeling dominant height growth: eucalyptus plantations in Portugal. *Forest Sci.* 44, 37–46.
- Arney, J.D., 1985. A modeling strategy for the growth projection of managed stands. *Can. J. Forest Res.* 15, 511–518.
- Bates, D.M., Watts, D.G., 1988. *Nonlinear Regression Analysis And Its Applications*. John Wiley & Sons, New York.
- Beal, S.L., Sheiner, L.B., 1982. Estimating population kinetics. *CRC Crit. Rev. Biomed. Eng.* 8, 195–222.
- Borders, B.E., 1989. System of equations in forest stand modelling. *Forest Sci.* 35, 548–556.
- Calama, R., Montero, G., 2004. Interregional nonlinear height–diameter model with random coefficient for stone pine in Spain. *Can. J. Forest Res.* 34, 150–163.
- Castedo Dorado, F., Barrio Anta, M., Parresol, B.R., Álvarez González, J.G., 2005. A stochastic height–diameter model for maritime pine ecoregions in Galicia (northwestern Spain). *Ann. Forest Sci.* 62, 455–465.
- Castedo Dorado, F., Diéguez-Aranda, U., Barrio Anta, M., Sánchez Rodríguez, M., von Gadow, K., 2006. A generalized height–diameter model including random components for radiata pine plantations in northwestern Spain. *Forest Ecol. Manage.* 229, 202–213.
- Colbert, K.C., 2002. Height–diameter equations for thirteen Midwestern bottom-land hardwoods species. *North. J. Appl. For.* 19, 171–176.
- Costa, M., Morla, C., Sainz, H., (Eds.), 2001. *Los Bosques Ibéricos. Una Interpretación Geobotánica*. Ed. Planeta.
- Curtis, R.O., 1967. Height–diameter and height–diameter–age equations for second-growth Douglas-Fir. *Forest Sci.* 13, 365–375.
- DGCN, 1996. II Inventario Forestal Nacional 1986–1996. Dirección General de Conservación de la Naturaleza, Ministerio de Medio Ambiente, Madrid.
- DGCN, 2006. III Inventario Forestal Nacional 1996–2006. Dirección General de Conservación de la Naturaleza, Ministerio de Medio Ambiente, Madrid.
- Eerikäinen, K., 2003. Predicting the height–diameter pattern of planted *Pinus kesiya* stands in Zambia and Zimbabwe. *Forest Ecol. Manage.* 175, 355–366.
- Elena Roselló, R., 1997. *Clasificación Biogeoclimática de España Peninsular y Balear*. MAPA, Madrid.
- Fang, Z., Bailey, R.L., 1998. Height–diameter models for tropical forest on Hainan Island in southern China. *Forest Ecol. Manage.* 110, 315–327.
- Fang, Z., Bailey, R.L., Shiver, B.D., 2001. A multivariate simultaneous prediction system for stand growth and yield with fixed and random effects. *Forest Sci.* 47, 550–562.
- Fox, J.C., Ades, P.K., Bi, H., 2001. Stochastic structure and individual-tree growth models. *Forest Ecol. Manage.* 154, 261–276.
- Gadow, K.v., Hui, G., 1998. *Modelling Forest Development*. Kluwer Academic Publishers, The Netherlands.
- Gregoire, T.G., 1987. Generalized error structure for forestry yield models. *Forest Sci.* 33, 423–444.
- Hall, D.B., Bailey, R.L., 2001. Modeling and prediction of forest growth variables based on multilevel nonlinear mixed models. *Forest Sci.* 47, 311–321.
- Hasenauer, H., Monserud, R.A., 1997. Biased prediction for tree height increment models developed from smoothed ‘data’. *Ecol. model.* 98, 13–22.
- Hökkä, H., 1997. Height–diameter curves with random intercepts and slopes for trees growing on drained peatlands. *Forest Ecol. Manage.* 97, 63–72.
- Huang, S., 1997. Development of compatible height and site index models for young and mature stands within an ecosystem-based management framework. In: Amaro, A., Tomé, M., (Eds.), *Empirical and Process Based Models for Forest Tree and Stand Growth Simulation*. Oeiras, Portugal, pp. 61–98.
- Huang, S., Price, D., Titus, S.J., 2000. Development of ecoregion-based height–diameter models for white spruce in boreal forests. *Forest Ecol. Manage.* 129, 125–141.
- Huang, S., Titus, S.J., 1993. An index of site productivity for uneven-aged and mixed-species stands. *Can. J. Forest Res.* 23, 558–562.
- Hynynen, J., 1995. Predicting the growth response to thinning for Scots Pine stands using individual-tree growth models. *Silva Fenn.* 29, 225–246.

- Jayaraman, K., Lappi, J., 2001. Estimation of height–diameter curves through multi-level models with special reference to even-aged teak stands. *Forest Ecol. Manage.* 142, 155–162.
- Khattree, R., Naik, D.N., 1995. *Applied Multivariate Statistics With SAS Software*. SAS Institute Inc., Cary, NC.
- Krumland, B.E., Wensel, L.C., 1988. A generalized height–diameter equation for coastal California species. *West. J. Appl. For.* 3, 113–115.
- Lappi, J., 1991. Calibration of height and volume equations with random parameters. *Forest Sci.* 37, 781–801.
- Lappi, J., 1997. A longitudinal analysis of height/diameter curves. *Forest Sci.* 43, 555–570.
- Larsen, D.R., Hann, D.W., 1987. Height–diameter equations for seventeen tree species in southwest Oregon. Research paper 49. Forest Research Laboratory, Oregon State University, Corvallis.
- Lindstrom, M.J., Bates, D.M., 1990. Nonlinear mixed effects for repeated measures data. *Biometrics* 46, 673–687.
- Littel, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., 1996. *SAS system for Mixed Models*. SAS Institute Inc., Cary, NC.
- Mehtätalo, L., 2004. A longitudinal height–diameter model for Norway spruce in Finland. *Can. J. Forest Res.* 34, 131–140.
- Pascoa, F., 1987. *Estrutura, crescimento e produção em povoamentos de pinheiro bravo. Um modelo de simulação*. Universidade Técnica de Lisboa, Lisboa.
- Peng, C., Zhang, L., Huang, S., Zhou, X., Parton, J., Woods, M., 2001. Developing ecoregion-based height–diameter models for jack pine and black spruce in Ontario. Forest Research Report 159. Ministry of Natural Resources. Ontario Forest Research Institute, Ontario, Canada.
- Pinheiro, J.C., Bates, D.M., 1995. Model building for nonlinear mixed effects model. Technical Report 91. Department of Biostatistics, University of Wisconsin, Madison, WI.
- Richards, F.J., 1959. A flexible growth function for empirical use. *J. Exp. Bot.* 10, 290–300.
- Roig, S., del Río, M., Ruíz-Peinado, R., Cañellas, I., 2007. Tipología dasométrica de los rebollares (*Quercus pyrenaica* Willd.) de la zona centro de la Península Ibérica. In: *Los sistemas forrajeros: entre la producción y el paisaje*. Actas de la XLVI Reunión Científica de la Sociedad Española para el Estudio de los Pastos, Vitoria, pp. 535–542.
- SAS/STAT, 2000. *SAS/STAT user's guide, version 8*. In: SAS Institute Inc., Cary, NC.
- SAS/STAT, 2001. *The SAS System for Windows Release 6.12*. In: SAS Institute Inc., Cary, NC.
- Schnute, J., 1981. A versatile growth model with statistically stable parameters. *Can. J. Fish. Aquat. Sci.* 38, 1128–1140.
- Schröder, J., Álvarez González, J.G., 2001. Developing a generalized diameter–height model for maritime pine in Northwestern Spain. *Forstwissenschaftliches Centralblatt* 120, 18–23.
- Soares, P., Tomé, M., 2002. Height–diameter equation for first rotation eucalypt plantations in Portugal. *Forest Ecol. Manage.* 166, 99–109.
- Soares, P., Tomé, M., Skovsgaard, J.P., Vanclay, J.K., 1995. Evaluating a growth model for forest management using continuous forest inventory data. *Forest Ecol. Manage.* 71, 251–265.
- Vanclay, J.K., 1994. *Modelling Forest Growth and Yield – Application to Mixed Tropical Forests*. CAB Internat., UK.
- Vanclay, J.K., Skovsgaard, J.P., Pilegaard Hansen, C., 1995. Assessing the quality of permanent sample plot databases for growth modelling in forest plantations. *Forest Ecol. Manage.* 71, 177–186.
- West, P.W., Ratkowsky, D.A., Davis, A.W., 1984. Problems of hypothesis testing of regressions with multiple measurements from individual sampling units. *Forest Ecol. Manage.* 7, 207–224.
- Wolfinger, R.D., Lin, X., 1997. Two Taylor-series approximation methods for nonlinear mixed models. *Comput. Stat. Data Anal.* 25, 465–490.
- Yuancai, L., Parresol, B.R., 2001. Remarks on height–diameter modeling. Research Note SE-10. U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, NC.
- Zhao, D., 2003. *Modeling mixed species forest stands*. Ph.D. dissertation, University of Georgia, Athens, Georgia, USA.
- Zhao, D., Borders, B., Wilson, M., 2004. Individual-tree diameter growth and mortality models for bottomland mixed-species hardwood stands in the lower Mississippi alluvial valley. *Forest Ecol. Manage.* 199, 307–322.