

A local height-diameter model with mixed-effects for *Abies religiosa* in Tlaxcala, Mexico

Un modelo local altura - diámetro con efectos mixtos
para *Abies religiosa* en Tlaxcala, México

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ABSTRACT

Height-diameter models are fundamental for the inventory of timber, biomass and carbon. Located in the central region of Mexico, *Abies religiosa* is a conifer with high timber value that lacks models to estimate its height as a function of diameter. The objective of this study was to determine a local height-diameter model for *A. religiosa* trees under a mixed-effects model approach in the region of Tlaxco, Tlaxcala, Mexico. The first step consisted in evaluating the quality of fit of three growth models and one power model. We used height-diameter data of 1,539 trees measured in 197 circular plots of 1,000 m². The selected model was the Weibull, which was adjusted in a second step under the mixed-effects modelling approach. Our results showed that the most accurate predictive capacity was obtained when using the sub-basin covariate as a clustering factor and the random effect in the parameter corresponding to the asymptote. Under this approach, the goodness of fit of the model was superior to the traditional one adjusted by nonlinear least square. Comparatively the gains in fit statistics R², RSME and AIC were of 12.19 %, 47.99 % and 8.46 %, respectively. The proposed model is robust, reliable, and biologically coherent for its operational application in the forest management of *A. religiosa* in the study region.

Keywords: sub-basin covariate, random effects, Weibull model.

RESUMEN

Los modelos de altura - diámetro son una pieza fundamental para realizar inventarios maderables, de biomasa y carbono. En la región central de México, *Abies religiosa* es una conífera de gran importancia comercial maderable la cual carece de modelos que estimen la altura en función del diámetro. El objetivo de este estudio fue determinar un modelo local altura-diámetro para árboles de *A. religiosa* bajo el enfoque de modelos con efectos mixtos en la región de Tlaxco, Tlaxcala, México. En la primera fase se evaluó la calidad de ajuste de tres modelos de crecimiento y un modelo potencial. Se utilizaron 1.539 pares de datos de altura-diámetro de árboles medidos en 197 sitios circulares de muestreo de 1.000 m². El mejor modelo fue el de Weibull, mismo que en una segunda fase se ajustó mediante la técnica de modelos de efectos mixtos; en este caso, la mejor capacidad predictiva se obtuvo cuando se utilizó la covariable subcuenca como factor de agrupación y se incluyó un efecto aleatorio en el parámetro correspondiente a la asíntota. Bajo este enfoque el ajuste fue superior al ajuste tradicional por cuadrados mínimos no lineales. Comparativamente las ganancias en los estadísticos de ajuste R², RCME y AIC fueron de 12,19 %, 47,99 % y 8,46 %, respectivamente. El modelo propuesto es robusto, confiable y biológicamente coherente para su aplicación operativa en la gestión forestal de las diferentes condiciones en que *A. religiosa* se desarrolla en la región de estudio.

Palabras clave: covariable subcuenca, efectos aleatorios, modelo de Weibull.

INTRODUCTION

Given its utility for forest management, the height-diameter relationship of trees has been extensively studied under different statistical approaches, and height-diameter models have been generated for various species and growth conditions in both natural forests and plantations (Corral-Rivas *et al.* 2014, Ercanli 2015, Corral *et al.* 2019, Hofíco *et al.* 2020, Ordaz-Ruiz *et al.* 2020). From a silvicultural point of view, these relationships are fundamental when estimating stand growth and yield (Ferraz *et al.* 2018). In ecological studies, they are useful for understanding the effects of the physical environment on tree growth for different taxa under varying environmental conditions (Wang *et al.* 2017).

A recurrent problem when modelling the allometric relationship of height-diameter is that theoretical assumptions of statistical regression are not always fulfilled, therefore it is common that heteroscedasticity and autocorrelation of errors occur (Calama and Montero 2004). This is generally due to the fact that the data used to fit the models have a nested hierarchical structure, since trees are located within sampling sites or re-measurement plots, and because these are nested within different stands, measurements are not independent (Ferraz *et al.* 2018). When these problems are not properly addressed, the predictive power of the models is severely limited (Corral-Rivas *et al.* 2014).

An approach that has been widely shown to be useful in overcoming the aforementioned problems is the mixed-effects modelling technique. With mixed-effects modelling it is possible to incorporate random effects that correspond to one or more biophysical covariates, taken as grouping levels. These can reflect the diversity of site conditions, thereby eliminating or minimizing heteroscedasticity and autocorrelation (Salas-Eljatib *et al.* 2019). In addition, the mixed-effects modelling technique improves prediction and requires little sampling effort (Corral *et al.* 2019). It also allows for calibration of models under new mixed-effect conditions where additional data on the variables of interest are available, and where the calibrated model exhibits high predictive power (Salas-Eljatib *et al.* 2019). Likewise, the model can maintain a simple structure without requiring the inclusion of additional predictor variables (Trincado *et al.* 2007).

In such a context, the mixed-effects modelling approach is an adequate option when modelling height-diameter relations (Corral-Rivas *et al.* 2014, Salas-Eljatib *et al.* 2019). In Mexico, this technique was used to model the height-diameter relations of different conifer species from mixed forests in Durango (Corral-Rivas *et al.* 2014, Corral *et al.* 2019). In tropical forests of Quintana Roo, this approach was also used to model this relationship in *Lysiloma latisiliquum* (L) Benth. (Hernández-Ramos *et al.* 2020). However, in the central region of Mexico, there are no studies of this type for praying fir (*Abies religiosa* Kunth Schltdl. et Cham.) despite its remarkable ecological and silvicultural importance in Mexico (SEMARNAT 2020).

Within the geographic distribution of praying fir in Mexico, the region known as the Transmexican Volcanic Belt stands out. Here the species coexists with other conifers and broadleaf species such as *Pinus hartwegii* Lindl., *Pinus teocote* Schiede ex Schltdl., *Cupressus lusitanica* Endl., *Quercus laurina* Humb et Bonpl., *Arbutus xalapensis* Kunth and *Alnus jorullensis* Kunth, among others (Sanchez-González *et al.* 2005). After the genus *Pinus*, *Abies religiosa* is the second most important conifer species in Mexico in terms of timber production, with an average annual harvested volume of 225,688 m³, for which the states of Mexico, Puebla, Michoacán and Tlaxcala account for 84.3 % of the annual production volume of this species (SEMARNAT 2020).

In the region of Tlaxco, Tlaxcala, praying fir forests are widely represented in diverse physiographical and climatic conditions. In this sense, its study is essential as most of the forest areas where it develops have been subject to regulated harvesting for more than three decades. The objective of the present study was to determine a local height-diameter model for *Abies religiosa* trees under the mixed-effects modelling approach in the region of Tlaxco, Tlax. Our goal was to obtain a sufficiently robust height-diameter model for operative application under the varying conditions in which the species grows in the study region.

METHODS

The study site is located within the Tlaxco forest region in the northern part of the state of Tlaxcala, between 19° 34' 12" to 19° 40' 48" N and 98° 13' 12" to 98° 12" W, where the altitudinal range goes from 2,290 to 3,430 m a.s.l. The predominant vegetation types in the region are temperate coniferous and broadleaf forests such as *A. religiosa*, *Pinus patula* Schl. et Cham., *P. ayacahuite* Ehrenb. ex Schltdl., *P. teocote*, *Q. laurina* and *Alnus* sp. The climate is temperate sub-humid with summer rainfalls, and the range of average monthly temperatures is 10 °C in the cooler months to 16 °C in the warmer months, with an average annual rainfall of 710 mm (IMTA 2009).

Following a systematic sampling design, we established 197 circular plots of 1,000 m² in four sub-basins identified as Atotonilco, Fondon, Tlaxco and Peñon, which integrate the upper basin of the Zahuapan River (figure 1).

Average distance between sampling plots was 250 m, covering a wide range of physiographic conditions. We measured 1,539 *A. religiosa* trees whose diameter at 1.3 m height from the ground level was greater than 7.5 cm. Tree diameter (*d*) was measured with a diametric tape, and tree height (*h*) measurements were made with a Vertex® digital hypsometer aided by a transponder. Table 1 displays the descriptive statistics of these data.

The first step of data analysis consisted of regression fitting of three nonlinear growth models and one allometric potential-type model consigned in Burkhart and Tomé

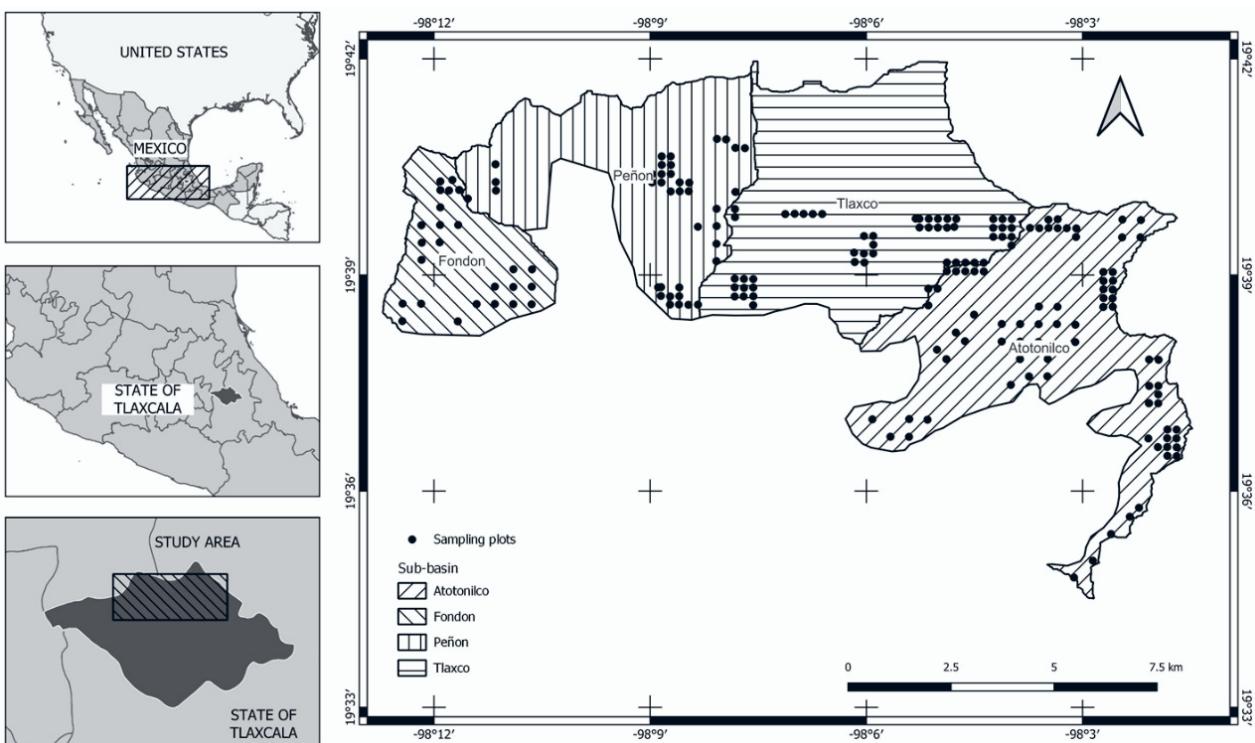


Figure 1. Study area with sub-basins and sampling plot locations in the state of Tlaxcala, Mexico.

Área de estudio con la ubicación de las sub-cuencas y parcelas de muestreo en el estado de Tlaxcala, México.

Table 1. Descriptive statistics of stand variables for *Abies religiosa* in Tlaxcala, Mexico.

Estadísticos descriptivos de variables de rodal para *Abies religiosa* en Tlaxcala, México.

Variable	Minimum	Mean	Maximum	SD	Asymmetry	Kurtosis
Diameter (<i>d</i> , cm)	7.5	24.6	71.5	12.2	0.8	0.3
Height (<i>h</i> , m)	3.0	19.41	38.0	7.5	0.1	-0.9
QMD (cm)	7.8	26.8	61.3	8.4	0.8	3.1
NT (trees ha ⁻¹)	10.0	199.9	750.0	162.8	1.1	1.3
BA (m ² ha ⁻¹)	0.05	11.8	51.1	10.2	1.3	2.1

SD: Standard deviation, QMD: quadratic mean diameter, NT: number of trees per ha, BA: basal area.

SD: Desviación estándar, QMD: diámetro cuadrático medio, NT: número de árboles/ha, BA: área basal.

(2012) and Panik (2014). These functions are commonly used to represent the allometric relationship of tree height as a function of diameter, assuming independence between observations (table 2).

These models were fitted to the data using the nonlinear least square technique (Bates and Chambers 1992). Selection criteria for the best model included the significance for all parameters ($P < 0.05$), the highest value of the coefficient of determination (R^2_{adj} [1]), the lowest values in the root square mean error ($RSME$ [2]), the standard error (Se) of parameters and the Akaike information criterion (AIC [3]) (Corral-Rivas *et al.* 2014, Guerra-De la Cruz *et al.* 2019).

$$R^2_{adj} = 1 - \left[\frac{\sum_{i=1}^n (Y_i - \hat{Y}_i)^2}{\sum_{i=1}^n (Y_i - \bar{Y}_i)^2} \right] \quad [1]$$

$$RSME = \sqrt{\frac{\sum_{i=1}^n (Y_i - \hat{Y}_i)^2}{n - p}} \quad [2]$$

$$AIC = 2 \cdot k - 2 \cdot \ln(\hat{L}) \quad [3]$$

Where: Y_i , \bar{Y}_i , \hat{Y}_i are the observed, mean and predicted values of the dependent variable, respectively; n is the num-

Table 2. Evaluated models for height-diameter relation of *Abies religiosa* in Tlaxcala, Mexico.

Modelos evaluados para la relación altura-diámetro de *Abies religiosa* en Tlaxcala, México.

Model	Expression	Reference
Schumacher	$h_i = 1.3 + \beta_0 \cdot e^{\frac{-\beta_1}{d_i}} + e_i$	Burkhart and Tome (2012)
Weibull	$h_i = 1.3 + \beta_0 \cdot (1 - e^{-\beta_1 \cdot d_i^{\beta_2}}) + e_i$	Panik (2014)
Chapman-Richards	$h_i = 1.3 + \beta_0 \cdot (1 - e^{-\beta_1 d_i})^{\beta_2} + e_i$	Panik (2014)
Stage	$h_i = 1.3 + \beta_0 \cdot d_i^{\beta_1} + e_i$	Burkhart and Tome (2012)

e : Exponential function; β_i : parameters to estimate; h_i : height; d_i : diameter

e : Función exponencial; β_i : parámetros a ser estimados; h_i : altura; d_i : diámetro

ber of observations; k is the number of estimated parameters in the model; \hat{L} = is the likelihood function.

Considering the importance of site factors in the modulation of height-diameter relationships (Temesgen *et al.* 2014), we investigated the effect of the covariate sub-basin as a grouping level, using an analysis of variance (ANOVA) under the generalized linear model (GLM). The existence of significant statistical differences at the 95 % confidence level ($\alpha = 0.05$) in the dependent variable height as a function of diameter was diagnosed. For this purpose, the null hypothesis H_0 stated that the dimensions in height between the different sub-basins are equal, while the alternative hypothesis H_a stated that the dimensions in total height are different in at least one of the sub-basins.

Using the aforementioned evidence, the second step of the analysis was performed based on Pinheiro and Bates (2000) and, Bronisz and Mehtätalo (2020), which consisted of fitting the best selected model using the mixed-effects modelling approach. The general structure of the height-diameter model under mixed-effects modelling has the following matrix form:

$$y_{ij} = f(\Phi_i, x_{ij}) + e_{ij} \quad [4]$$

Where: y_{ij} is the j -th observation of height taken from the i -th plot, x_{ij} is the j -th measurement from the predictor variable taken from the i -th plot or clustering level, Φ_i is a parameter vector, $r \times 1$ (where r is the number of parameters in the model), specific for each sampling unit, f is a nonlinear function of the predictor variables and the parameter vector, and e_{ij} is the term for residual noise.

Mixed-effects models allow parameter vectors to vary from plot to plot or clustering level; regression coefficients are broken down into a fixed part, common to the population, and random components, specific to each plot. The parameter vector, Φ_i , was defined as:

$$\Phi_i = A_i \lambda + B_i b_i \quad [5]$$

Where λ is the $p \times 1$ vector of fixed population parameters (where p is the number of fixed parameters in the model),

b_i is the $q \times 1$ vector of random-effects associated with the i -th plot or clustering level (where q is the number of random parameters in the model), A_i and B_i are design matrices of size $r \times p$ and $r \times q$, for the fixed and random-effects specific to each plot, respectively. It is assumed that errors e_{ij} are independently distributed as $N(0, R_i)$ and b_i as $N(0, \varphi^2)$, where R_i is the variance-covariance matrix of the error term and φ^2 is the variance-covariance matrix of the b_i random parameters; R_i matrix was expressed as:

$$R_i(\lambda, b_i, \rho) = \sigma^2 G_i^{0.5} \Gamma_i G_i^{0.5} \quad [6]$$

Where ρ is a set of common but unknown parameters, σ^2 is a scaling factor for the error dispersion given by the value of the residual variance of the model, $G_i^{0.5}$ is a $n_i \times n_i$ diagonal matrix describing the nonconstant variance, Γ_i is a $n_i \times n_i$ matrix showing the structure of the correlation among observations for plot i or clustering level, (can be the identity matrix I).

The variance-covariance matrix for the random-effects, φ^2 , common for all the plots, defines variability existing among plots or clustering level. For two random parameters u and v , the variance-covariance matrix was expressed as follows:

$$\varphi^2 = \begin{bmatrix} \sigma_u^2 & \sigma_{uv}^2 \\ \sigma_{uv}^2 & \sigma_v^2 \end{bmatrix} \quad [7]$$

Where σ_u^2 is the variance for the random-effect u , σ_v^2 is the variance for the random-effect v , and σ_{uv}^2 is the covariance among random-effects.

The random-effect was incorporated individually for each parameter (*i.e.* $h = 1.3 + (\beta_0 + \beta_{0i}) \cdot e^{\frac{-\beta_1}{d_i}}$) and in all possible combinations of these (*i.e.* $h = 1.3 + (\beta_0 + \beta_{0i}) \cdot d^{(\beta_1 + \beta_{1i})}$) where B_i indicates the position of the random-effect inclusion in the model (Pinheiro and Bates 2000, Gałecki and Burzykowski 2013).

Autocorrelation was removed by using an autoregressive moving average structure (ARMA) of order (p, q) , where p indicates the autoregressive order and q the moving average order. The autoregressive moving aver-

σ_v^2

age structure formulations, available in Pinheiro and Bates (2000), were fitted simultaneously with the height-diameter model. In this case, we performed the analysis by maximum likelihood with the NLME library of the free statistical program R version 2.6.0 (R-core Team 2020).

The estimation of specific parameters by clustering level given by the sub-basin covariate was performed using the procedure known as EBLUPs, through which more accurate estimations according to the nature of the information can be achieved (Gałecki and Burzykowski 2013, West *et al.* 2015). The selection criteria of the best model variant under the mixed-effects modelling technique were similar to those indicated for the first step. For the best model variant, we verified compliance with the assumptions of normality of the errors, where a straight-line trend is desirable. Homoscedasticity of the residuals was also checked (West *et al.* 2015). To quantify the gain in the quality of fit, verifiable by the goodness-of-fit statistics R^2_{adj} , SRME and AIC, we compared the fit of the best model with its best variant adjusted by mixed-effects modelling.

We performed a statistical validation of the best variant of the model adjusted under mixed-effects modelling using an additional sample of 182 pairs of height-diameter data from a neighbouring locality to the study area, one that

was independent of that used to fit the model. Predicted values were compared with the best variant of the selected model and those observed in the independent sample through a *t*-student test at 99 % confidence assuming equal means (R-core Team 2020).

RESULTS

In the first step of the analysis of the evaluated models, all parameters were statistically significant ($\alpha = 0.05$); however, the Weibull model explained 68.7 % of the sample variability, showed the smallest overall deviations (4.17 m) and the lowest likelihood value ($AIC = 8,770.1$) (table 3). Therefore, we selected the Weibull as the best height-diameter model for *A. religiosa* and proceeded with the adjustment by mixed-effects modelling in the second step.

The analysis of variance using the GLM to verify differences in the dimensions of height due to the sub-basin covariate yielded significant *F* probability values at a confidence level of 95 % ($F = 49.401$, $\alpha < 0.0001$). Therefore, we rejected the null hypothesis (H_0) and accepted the alternative hypothesis (H_a), that the dimensions of the total heights of *A. religiosa* trees are different in at least one of the sub-basins (table 4). In addition, when performing the means separation test by Tukey, it is observed that

Table 3. Parameter values and fit statistics of the evaluated height-diameter models.

Valores de parámetros y estadísticos de ajuste de modelos altura-diámetro evaluados.

Model	Parameter	Estimate	Se	t Value	Pr > t	R^2_{adj}	RMSE	AIC
Schumacher	β_0	37.22400	0.49610	75.030	***	0.6785	4.2258	8,809.55
	β_1	15.24920	0.32420	47.040	***			
Weibull	β_0	29.48681	0.73123	40.325	***	0.6870	4.1693	8,770.10
	β_1	0.01774	0.00204	8.702	***			
	β_2	1.29231	0.04872	26.523	***			
Chapman-Richards	β_0	30.53222	0.79484	38.410	***	0.6861	4.1755	8,774.67
	β_1	0.05542	0.00477	11.620	***			
	β_2	1.47071	0.10488	14.020	***			
Stage	β_0	2.39241	0.10584	22.600	***	0.6537	4.3853	8,923.56
	β_1	0.64180	0.01297	49.480	***			

Se: Standard error; R^2_{adj} : adjusted coefficient of determination; RMSE: root mean squared error; AIC: Akaike information criterion.

Ee: Error estándar; R^2_{adj} : coeficiente de determinación ajustado; RMSE: raíz del cuadrado medio del error; AIC: Criterio de información de Akaike.

Table 4. Analysis of variance by GLM for the sub-Basin classification variable.

Análisis de varianza por GLM para la variable de clasificación de sub-cuenca.

Variable	Degrees of freedom	Sum of squares	Mean square	F value	Pr > F	Coefficient of variation
Sub-basin	3	7,526	2,508.63	49.401	< 2.2e-16	***
Residuals	1,535	77,949	50.78			36.71541

the Peñon sub-basin presents the highest values, while Atotonilco presents the lowest (table 5).

The adjustment of six variants of the Weibull model, through the mixed-effects modelling technique, yielded sig-

nificant parameters in all cases ($\alpha = 0.05$). However, the best result was in variant 1, where the random-effect was incorporated in the parameter β_0 (table 6), corresponding to the maximum asymptotic value of height that is reachable by trees.

Table 5. Grouping by Tukey of the analysis of variance by sub-Basin level.

Agrupación por Tukey del análisis de varianza por nivel de sub-cuenca.

Sub-basin	Minimum value	Average height	Maximum value	Standard error	Tukey test
Atotonilco	3.0	17.4	31.0	6.170128	c
Fondón	6.0	18.8	30.0	8.032021	bc
Peñón	5.5	23.5	33.0	6.813830	a
Tlaxco	5.0	21.2	38.0	8.279006	b

Table 6. Parameter values and fit statistics of the six variants of the Weibull model fitted by the mixed-effects modelling technique.

Valores de parámetros y estadísticos de ajuste de las seis variantes del modelo Weibull ajustado por la técnica de modelación de efectos mixtos.

Variant	Mixed-effect parameters	Fixed parameter	Estimate	Se	t Value	Pr > t	R ²	RSME	AIC
1	β_0	β_0	29.16720	1.55412	18.7677	***	0.7708	2.1685	8,027.90
		β_1	0.01996	0.00190	10.5133	***			
		β_2	1.26761	0.03945	32.1349	***			
		<i>phi</i>	0.41470						
2	β_1	β_0	32.93720	0.98905	33.3017	***	0.7586	2.0694	8,111.04
		β_1	0.02643	0.00318	8.3195	***			
		β_2	1.10464	0.03668	30.1194	***			
		<i>phi</i>	0.41217						
3	β_2	β_0	32.42806	0.83056	39.0436	***	0.7652	2.0877	8,065.78
		β_1	0.02553	0.00202	12.6575	***			
		β_2	1.12359	0.04573	24.5686	***			
		<i>phi</i>	0.41420						
4	β_0 and β_1	β_0	29.17541	1.66191	17.5554	***	0.7709	2.1704	8,030.68
		β_1	0.02003	0.00190	10.5358	***			
		β_2	1.26787	0.03917	32.3711	***			
		<i>phi</i>	0.41452						
5	β_0 and β_2	β_0	29.15219	1.61261	18.0777	***	0.7708	2.1712	8,031.75
		β_1	0.01991	0.00190	10.5027	***			
		β_2	1.26926	0.03950	32.1297	***			
		<i>phi</i>	0.41461						
6	β_0 , β_1 and β_2	β_0	29.39049	1.23845	23.7316	***	0.7717	2.1744	8,031.28
		β_1	0.02144	0.00247	8.6890	***			
		β_2	1.24650	0.04945	25.2072	***			
		<i>phi</i>	0.41458						

Se: standard error; R²: coefficient of determination; RSME: root squared mean error; AIC: Akaike's information criterion; *phi*: structure parameter ARMA (1, 0). Ee: error estándar; R²: coeficiente de determinación; RCME: raíz del cuadrado medio del error; AIC: criterio de información de Akaike; *phi*: parámetro de la estructura ARMA (1, 0).

As an additional way to contrast the adjustments by mixed-effects modelling and ratify the selection system used, we performed an ANOVA with the results shown in table 3. It can be observed that the likelihood ratio test derived from the analysis of variance shows that variant 1 has the best values in the AIC and BIC fit statistics, and ranks fourth among values in the logLik statistic (table 7). Therefore, the choice of variant 1 for inclusion of the random-effects in the parameter β_0 is ratified.

Once the first variant was selected as the best fit with the random-effects model by sub-basin, we obtained the variance-covariance matrix (function vcov in the nlme library) of the global parameters, the error structure correlation parameter (which corrects autocorrelation) and the confidence intervals of the parameters. Based on those values all estimates are statistically equal (table 8).

In the mixed-effects modelling adjustment of variant 1 of the Weibull model, the assumptions of normality in the frequency of residuals (figure 2 A), homoscedasticity of residuals (figure 2 B) and non-correlated errors (figure 2 C) were also met. In addition, the random parameter in each sub-basin was found to be specific (figure 2 D) as evidenced by the performed ANOVA test.

Overall, the average trend of growth in height determined using the classical nonlinear least square approach

was similar to that determined using the mixed-effects modelling technique (figure 3), with the main differences shown in the values of the goodness of fit statistics (tables 5 and 6). Growth in height dimensions showed a different response in each sub-basin according to the specific values of the random parameter β_0 (figure 4) of variant 1 of the Weibull model. The height values were 25.68863 m for the Atotonilco sub-basin; 27.49261 m for Fondon; 30.68269 m for Peñon and 32.80487 m for Tlaxco, which implies asymptotic values with marked differences, where trees with the greatest heights are found in the Tlaxco sub-basin.

The contrast of fit statistics between nonlinear least square and mixed-effects modelling evidenced a statistical gain in the values of R^2 , SRME and AIC of 12.19 %, 47.99 % and 8.46 % respectively. This is attributed to the consideration of data variability in the adjustment by the grouping sub-basin covariate in the mixed-effects modelling technique.

When validating the estimates using variant 1 of the Weibull model by comparing it with the independent sample of height-diameter data, we obtained a statistical equality of the means ($t = -2.1303$, p -value = 0.03382), which indicates that the two populations are equal. However, the Shapiro-Wilk test revealed a failure to meet the assumption of normality ($W = 0.95947$, p -value = 4.193e-05).

Tables 7. Analysis of variance (ANOVA) for the selection between different fitting under the mixed-effects modelling approach.

Análisis de varianza (ANOVA) de selección entre los distintos ajustes bajo el enfoque de modelos de efectos mixtos (MEM).

Variante	Mixed-effects parameters	AIC	BIC	logLik	Test	L. Ratio	p-value
1	β_0	8,027.898	8,059.932	- 4,007.949			
2	β_1	8,111.035	8,143.068	- 4,049.518			
3	β_2	8,065.782	8,097.815	- 4,026.891			
4	$\beta_0 \wedge \beta_1$	8,030.676	8,073.387	- 4,007.338	3 vs 4	39.10591	< 0.0001
5	$\beta_0 \wedge \beta_2$	8,031.747	8,074.458	- 4,007.874			
6	$\beta_0, \beta_1 \wedge \beta_2$	8,031.281	8,090.009	- 4,004.641	5 vs 6	6.46592	0.0910

AIC: Akaike's information criterion, BIC: Bayesian information criterion, logLik: logarithm of maximum likelihood.

AIC: Criterio de información de Akaike, BIC: Criterio de información Bayesiano, logLik: logaritmo de máxima verosimilitud.

Table 8. Values of the variance-covariance matrix and range for each parameter for the best-fitted model.

Valores de la matriz de varianza-covarianza e intervalos para cada uno de los parámetros del modelo mejor ajustado.

Parámetros	vcov			Fixed parameter intervals		
	β_0	β_1	β_2	Lower	Estimate	upper
β_0	2.410568	0.000718	- 0.018368	26.12176	29.1672	32.2
β_1	0.000718	0.000004	- 0.000072	0.016236	0.019956	0.02
β_2	- 0.018368	- 0.000072	0.001553	1.190307	1.267606	1.34
phi	Correlation structure			0.367463	0.414697	0.46

vcov: variance-covariance matrix

vcov: matriz de varianza-covarianza.

For this reason and in accordance with McDonald (2014) regarding the absence of normality, the Levene's test was performed as two independent populations. The results indicated equality of variance ($F = 3.6031, p = 0.05847$) and a net difference observed between the groups, expressed

through the d -Cohen's value of 0.2688 with an interval of - 0.0749 and 0.6124. Therefore, we can infer equality between populations and ratify the validity of this variant for its operational use in the management of *Abies religiosa* forests in the study region.

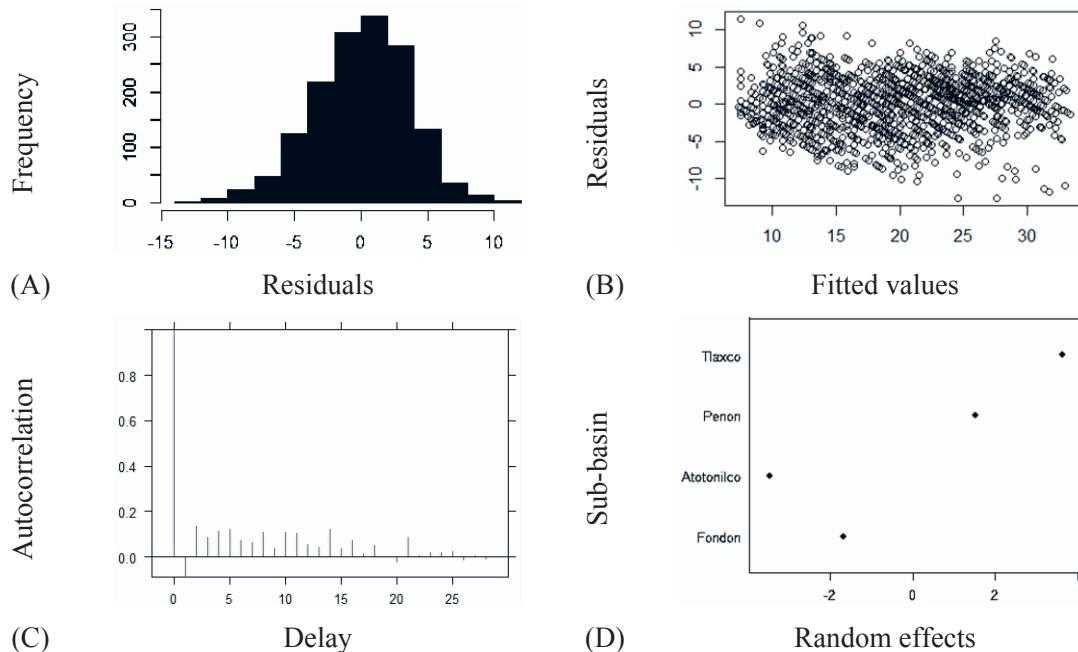


Figure 2. Graphics of normality tests (A), homoscedasticity (B) autocorrelation (C) and distribution of random effects by sub-basin (D) for variant 1 of Weibull model.

Gráficas de pruebas de normalidad (A), homocedasticidad (B), autocorrelación (C) y distribución de efectos aleatorios por subcuenca (D) para la variante 1 del Modelo Weibull.

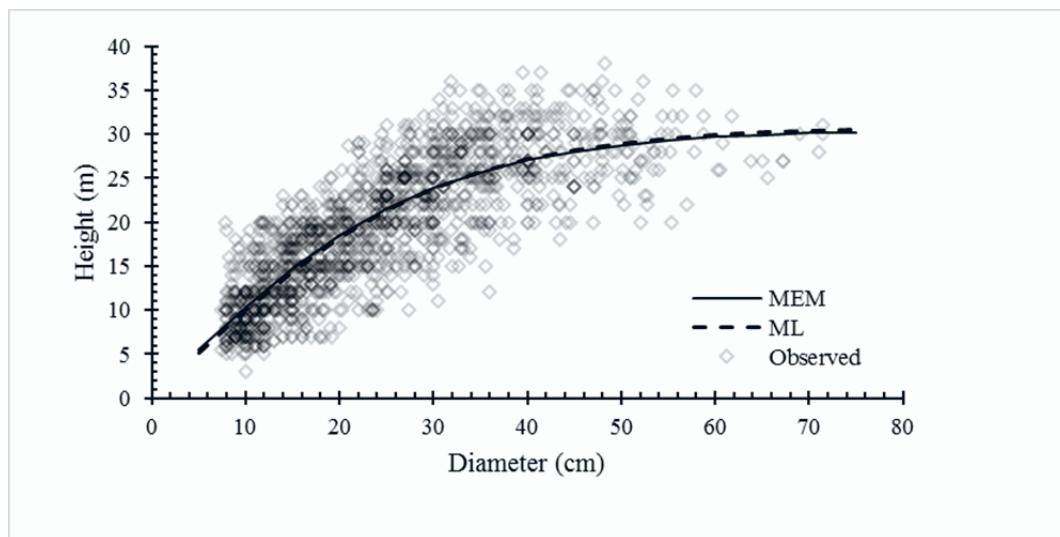


Figure 3. Height growth trends of *Abies religiosa* trees with the Weibull model, fitted by the classical nonlinear least square and the mixed-effects modelling approach.

Tendencias del crecimiento en altura de árboles de *Abies religiosa* con el modelo Weibull ajustado mediante el enfoque clásico de cuadrados mínimos no lineales y modelación de efectos mixtos.

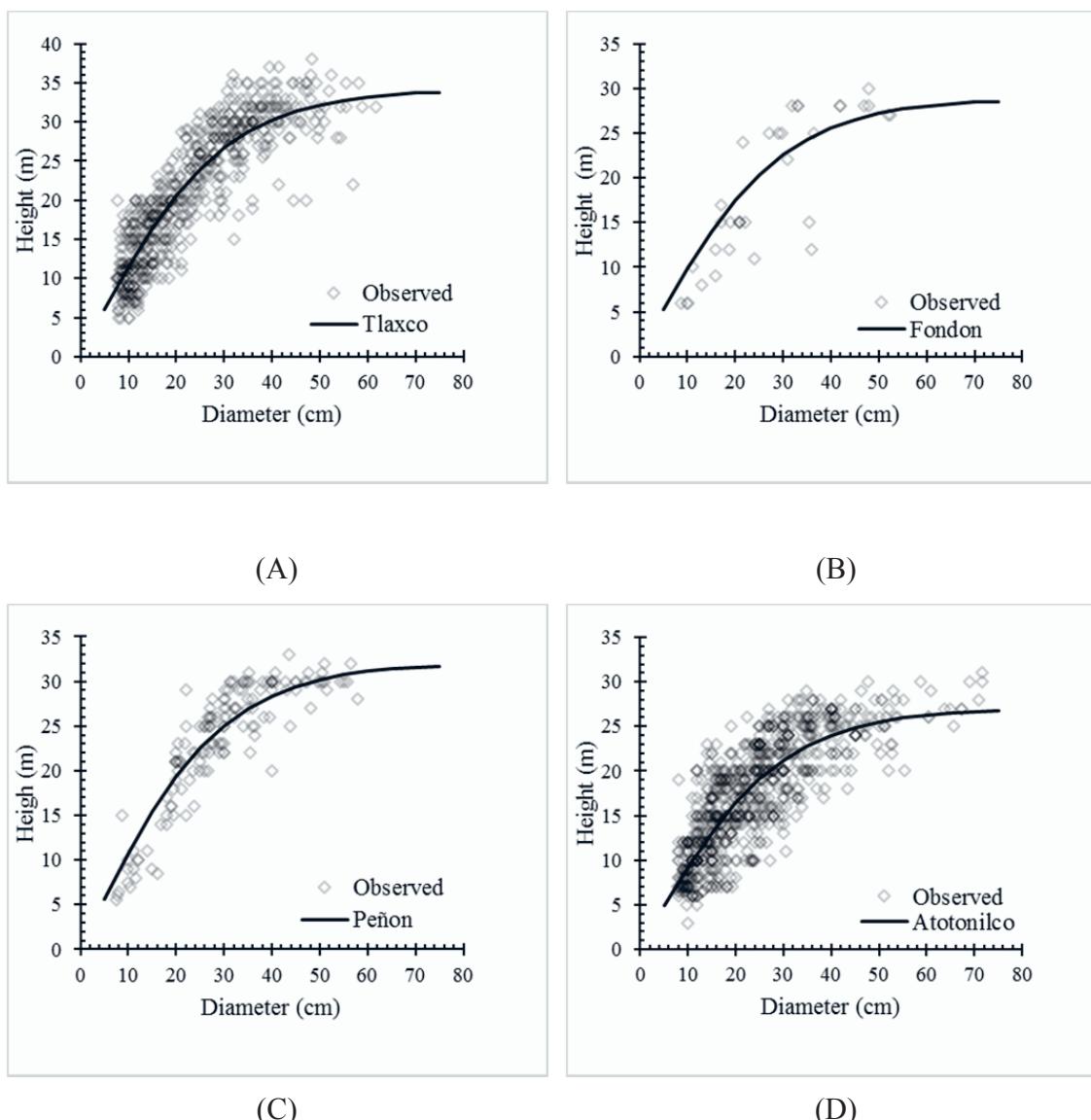


Figure 4. Average trend of total height growth provided by variant 1 of the Weibull model, fitted by the mixed effects modelling technique using the sub-basin as a covariate.

Tendencias promedio del crecimiento en altura proporcionados por la variante 1 del modelo Weibull ajustado par la técnica de modelación de efectos mixtos usando la subcuenca como covariante.

DISCUSSION

Modelling of the height-diameter relationship using the traditional nonlinear least square approach showed an R^2 value of 0.687 with the Weibull model, which is slightly higher than the values (R^2_{adj} 0.61 - 0.63) reported by Flores-Morales (2016), who fitted height-diameter models for *Pinus pseudostrobus* Lindl. Ordaz-Ruiz *et al.* (2020) also estimated R^2 values lower than 0.570 for this relationship in *Pinus patula* plantations; whereas Guerra-De la Cruz *et al.* (2019) fitted local height-diameter models for *Pinus montezumae* Lamb., and *P. teocote*, obtaining $R^2_{adj} = 0.91$, and 0.87 respectively, in western Tlaxcala, Mexico. With

these references, it is clear that the traditional fitting approach provides variable values for this statistic, which may be due in part to the high variability of tree heights at a given diameter for different species under varying conditions.

The use of refinement in the adjustment, such as the mixed-effects modelling technique incorporating the sub-basin as a grouping covariate, and the inclusion of a random effect in the asymptotic parameter of the height-diameter model, improved the goodness of fit statistics and the reliability of the estimates. In this regard, Salas-Eljatib *et al.* (2019) pointed out that with the mixed-effects modelling approach, the variance is reduced and becomes more homogeneous which indicates the efficiency of the covariate effect.

The improvement in R^2 value with the mixed-effects modelling was similar to those (0.6 - 0.8) reported by Corral-Rivas *et al.* (2014) for pine species in Durango; and slightly higher than that reported by Hernández-Ramos *et al.* (2020) ($R^2 = 0.7051$), who fitted the Hossfeld model for *Lysiloma latisiliquum* using clusters as a grouping covariate. Similarly, Arias (2004) reported R^2 values close to 0.64 in tropical species of Costa Rica when considering stand density as a covariate. In the present study, the SRME decreased from 4.16 to 2.6, representing a gain of 47.99 %, which is higher than that reported by Salas-Eljatib *et al.* (2019) for *Drimys winteri* J.R. et G. Forster (approximately 6 %) using stand and site as covariates.

In contrast, Hofiço *et al.* (2020) reported higher R^2 values (0.9183) and similar values in the SRME (0.558) for *Eucalyptus grandis* Hill ex. Maiden, when they incorporated basal area and quadratic diameter as covariates in a height-diameter model fitted with the mixed-effects modelling approach. Likewise, Ercanlı (2015) found higher R^2 values (0.82 to 0.86) in *Fagus orientalis* Lipsky in Turkey, although with a lower gain than that obtained in this study, while the SRME was greater than 2.04. For their analysis under mixed-effects modelling, they incorporated different sampling designs and sample sizes as covariates.

These differences show that when using the mixed-effects modelling approach, it is possible to incorporate and analyse different covariates (site, cluster, stand, among others) as grouping factors, achieving substantial statistical improvements. Usually, these covariates involve different site conditions given diverse physiographic, edapho-climatic and silvicultural management characteristics, which strongly influence height-diameter relationships (Temesgen *et al.* 2014). In the present study, the use of sub-basin as a grouping covariate under mixed-effects modelling implicitly incorporates the variety of site conditions (altitude, slope and aspect), thus accounting for the variability of growing conditions for *A. religiosa* at a regional scale.

Therefore, the biological congruence of the proposed model is noticeable since it adequately reflects the effects of growing conditions for species in the sub-basins. In Tlaxco and Peñon sub-basins (where the trees reached their greatest height values), the average elevations are lower than 3,000 m a.s.l., and the slope average is less than 37.4 % (data not shown). This implies that in these sub-basins, *A. religiosa* trees exhibit tapered growth because mild environmental conditions favour height growth over diameter growth. In contrast, the Atotonilco and Fondón sub-basins (with lowest asymptotic height values) have much steeper slopes, and Atotonilco has average elevations of higher than 3,000 m a.s.l., which apparently does not favour the growth in height of the species, resulting in stunted growth of praying fir trees. In this regard, Wang *et al.* (2017) has pointed out the limitations and effects, similar to those described above, that high elevation and associated low temperatures impose on the growth in height of temperate climate-species in altitudinal gradients. Thus, the statistical robustness of the model

and its biological congruence increase its operational utility in the management of *A. religiosa* forests in the study region.

CONCLUSIONS

The Weibull growth model was the best alternative to estimate the total height as a function of diameter of *A. religiosa* trees, explaining about 68 % of the variability in the observed total height. This value increased to 77 % when including the covariate sub-basin as a grouping factor and a random-effect in the asymptotic parameter.

Fitting of height-diameter models for *Abies religiosa* trees under the mixed-effects modelling approach allowed for statistical improvement and greater precision with respect to the traditional nonlinear least square technique, when estimating total height as a function of diameter in the region of Tlaxco, Tlaxcala, Mexico.

The proposed height-diameter model also allows for consistent biological interpretation of the total height growth of *A. religiosa* in accordance with growing conditions, which increases its usefulness in the forest management of the species in the four sub-basins that comprise the forest region of Tlaxco, Tlaxcala.

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AUTHORS' CONTRIBUTIONS

Vidal Guerra-De la Cruz, study design, field data collection and writing the manuscript; Jonathan Hernandez-Ramos, data analysis and writing the manuscript; Enrique Buendía-Rodríguez, field data collection and writing the manuscript; Juan Carlos Tamarit-Urias, data analysis and writing the manuscript; Fabian Islas-Gutierrez, field data collection and writing the manuscript.

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