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Individual Tree Diameter and Height Growth Models for 30 Tree Species in Mixed-Species and Uneven-Aged Forests of Mexico

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Abstract: Lack of knowledge of individual tree growth in species-rich, mixed forest ecosystems impedes their sustainable management. In this study, species-specific models for predicting individual diameter at breast height (dbh) and total tree height (h) growth were developed for 30 tree species growing in mixed and uneven-aged forest stands in Durango, Mexico. Growth models were also developed for all pine, all oaks, and all other species of the genus *Arbutus* (strawberry trees). A database of 55,158 trees with remeasurements of dbh and h of a 5-year growth period was used to develop the models. The data were collected from 217 stem-mapped plots located in the Sierra Madre Occidental (Mexico). Weighted regression was used to remove heteroscedasticity from the species-specific dbh and h growth models using a power function of the tree size independent variables. The final models developed in the present study to predict dbh and total tree height growth included size variables, site factors, and competition variables in their formulation. The developed models fitted the data well and explained between 98 and 99% and of the observed variation of dbh, and between 77 and 98% of the observed variation of total tree height for the studied species and groups of species. The developed models can be used for estimating the individual dbh and h growth for the analyzed species and can be integrated in decision support tools for management planning in these mixed forest ecosystems.

Keywords: dbh; total tree height; individual tree growth; species-rich forests

1. Introduction

Accurate estimates of both current resource levels and the expected resource changes from implementing selected management alternatives are needed to develop tools to support forest management informed decision-making (e.g., [1]). Forest growth models describe the change in size of a tree or another tree attribute or stand-level variable with age. They are used to analyze and estimate different relationships in forest stand development such as species composition, site characteristics, tree competitive status, and silvicultural management (e.g., [2–4]). Such models, together with stand regeneration, harvesting, and mortality models, are important tools in long-term forest management systems because they can simulate stand development and production under various management alternatives (e.g., [3,5–7]).

Empirical forest tree growth models predict growth as a function of tree attributes (such as tree size, crown ratio, vigor and tree competition) and plot or stand level variables (such as age site index and stand density) [8–12]. In particular, individual-tree diameter and height growth models are a fundamental component of forest growth and yield frameworks and constitute very important tools for sustainable forest management planning [5,7]. Although many factors such as tree size, neighborhood competition and environmental variables, have been proposed as being important in explaining patterns of tree growth, their relative contribution for different species and ecosystems are still subject to debate (e.g., [5,13–15]). Improving our knowledge of the controls influencing tree growth is central to better understand forest community organization and dynamics [15], and is also important to the development of sustainable management of forest ecosystems [16].

Understanding the factors that should be included into growth models to explain patterns in mixed-species forest with high species richness is critical for modeling ecological dynamics in such stands [16]. In uneven-aged, mixed-species natural forests, tree-to-tree variation in growth can be considerable within and among species, as well as spatially within a stand (e.g., [17]). This variability results from the structural and compositional complexity that often characterize these forests (e.g., [13,17–19]). In this context, an improved understanding of the factors regulating variability in growth rates can lead to better anticipation of individual tree success and community dynamics [17]. Such understanding can help in developing biometric tools to support forest management decision-making in mixed-species stands, including the development of management strategies based on natural stand dynamics (e.g., [18,20,21]). Nevertheless, factors influencing tree growth in structurally complex forests remain poorly understood [18]. Most previous studies of competition and tree growth have focused on plantations, managed forests, and even-aged, relatively young natural forests (e.g., [22,23]). In contrast, studies analyzing individual tree growth in mixed forest ecosystems are relatively more scarce (e.g., [13,17,18,24]), but have received increased attention in the last decades due to a worldwide trend in managing such forests to improve the biodiversity and ecosystems services and to assure long-term sustainable forest resources [3,25].

The Sierra Madre Occidental in the Mexican State of Durango constitutes a hotspot of forest biodiversity, being home to about five million hectares of species-rich and uneven-aged forest stands [26]. It is the first forest reserve in Mexico with an estimate of 422.1 million m³ of timber volume, and represents 22.4% of the total estimated production at the national level [27,28]. In 2015, Durango produced 28.5% of the total timber volume harvested in Mexico [3]. These forests are dominated by irregular and multispecies stands [29], and have been subject to selective harvesting for more than a century to provide a mix of services to local communities [30]. Although the main objective of forestry in Durango has been timber production, increased emphasis is being given to the concepts of ecological sustainability and biodiversity. Consequently, the development of forest growth models for mixed and uneven-aged stands is imperative to be used as important tools to support the informed decision-making in this type of forest ecosystems. To date in Durango, forest growth studies have been conducted on site quality [31–33], stand density management [28], dbh growth models [3], tree competition [34,35], tree volume and biomass equations [27,36,37] and tree diameter-height relationships [38]. However, most of the previous studies dealt with only one or a few tree species and

there have been very limited efforts to develop individual-tree dbh or height growth models for most of the commercial tree species in mixed-species forests. Definitely, we are not aware of studies that have developed individual-tree height growth models for the main tree species in Durango using data of stem-mapped and re-measured plots. In this situation, more research and studies become necessary to better understand stand growth and predict the effect of silvicultural practices in these species-rich and uneven-aged forests that are among the richest in the country. Therefore, the objective of this study was to develop new species-specific models for predicting individual-tree dbh and total tree height growth for 30 commercial species growing in the mixed and uneven-aged stands in Durango, Mexico. Some generic growth equations were also developed for all pines, all oaks, and all strawberry species. Such generic group equations can provide useful estimates for a few remaining tree species with still not enough re-measurements of dbh and total tree height in the area of study.

2. Materials and Methods

2.1. Study Area and Data

The data used in this study were collected in the Sierra Madre Occidental in the State of Durango, Northwestern Mexico, located between the geographic coordinates 22°20' and 26°46' N latitude and from 103°46' to 107°11' W longitude. The data are part of a network of stem-mapped re-measured plots, which were established to monitor the stand dynamics of Durango's forests [38]. Plot establishment began in 2007 and re-measurements started in 2012, after a five-year interval. Each plot covers an area of 50 × 50 m. The plots are generally distributed systematically, with a variable grid ranging from 3 to 5 km (Figure 1). The tree number, genus, species, dbh outside bark (*dbh*; cm), total tree height (*h*; m), and other variables of all trees with $dbh \geq 7.5$ cm were recorded. The installation and re-measurement of the plots followed the methodology developed by Corral-Rivas et al. [39]. Only undisturbed plots without intermediate harvesting between measurements were selected and considered for this study. A total of 217 re-measured plots were available for the development of the individual-tree dbh and total tree height growth models. The research plots included a variety of stand site conditions, tree sizes and competition levels. A description of the main plot-level variables for the re-measured plots is summarized in Table 1.

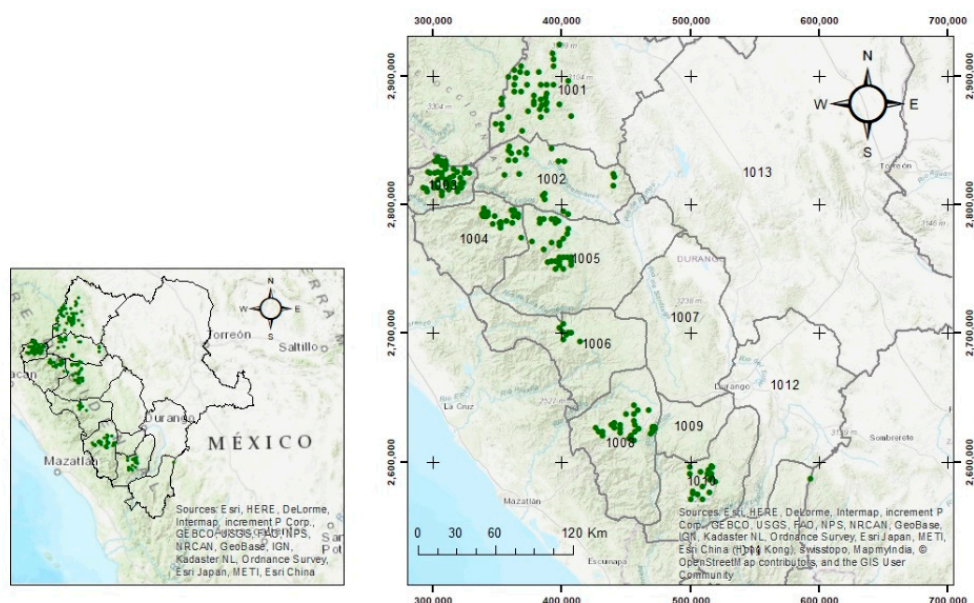


Figure 1. Study area, and location of 217 stem-mapped plots in Durango, Mexico (plot size is of 50 × 50 m).

Table 1. Summary statistics of the 217 re-measured plots used in this study.

Variable	2007				2012			
	Mean	Max	Min	SD	Mean	Max	Min	SD
<i>N</i>	623.78	2264.00	120.00	281.30	624.18	2152.00	144.00	275.91
<i>G</i>	21.16	53.63	3.15	8.20	23.31	58.52	3.92	8.98
<i>QMD</i>	21.32	34.10	12.40	4.28	22.34	36.00	13.40	4.44
<i>H₀</i>	16.82	29.50	5.20	4.80	18.18	31.60	5.80	5.19
<i>V</i>	188.55	604.21	12.04	106.19	221.04	709.20	16.57	124.28
<i>dbh</i>	17.98	72.52	6.75	9.96	19.19	74.58	7.16	10.26
<i>S</i>	8	15	1	2	8	16	1	2
<i>PAI</i>					6.50	21.66	0.24	4.40

N = number of trees per hectare, *G* = basal area (m²ha⁻¹), *QMD* = quadratic mean diameter (cm), *H₀* = dominant height, the mean height of the 100 largest-dbh trees per hectare (m), *V* = timber volume (m³ha⁻¹), *dbh* = diameter at breast height (cm), *S* = number of tree species in plot; *PAI* = periodic annual volume increment (m³ha⁻¹yr⁻¹), SD = standard deviation.

The re-measured *dbh* (*dbh₂*) and total tree height (*h₂*) after a 5-year period were obtained from 55,158 sampled trees of 30 species (each species included more than 100 trees for both variables). The considered species were: *Abies durangensis* Martínez, *Alnus firmifolia* Fernald, *Arbutus arizonica* Sargent, *A. bicolor* González Elizondo, *A. madrensis* González Elizondo, *A. tessellata* Sørensen, *A. xalapensis* Kunth, *Cupressus lusitanica* Mill., *Juniperus deppeana* Steud, *Pinus arizonica* Engelm., *P. cooperi* C.E. Blanco, *P. durangensis* Martínez, *P. engelmannii* Martínez, *P. herrerae* Martínez Martínez, *P. leiophylla* Schiede, *P. lumholtzii* B.L. Rob., *P. strobiformis* Engelm., *P. teocote* Schltdl., *Quercus arizonica* Sarg., *Q. crassifolia* Bonpl., *Q. durifolia* Seemen, *Q. emoryi* Porter & J.M. Coult., *Q. fulva* Liebmann, *Q. jonesii* Trelease, *Q. laeta* Liebm., *Q. mcvaughii* Spellenberg, *Q. radiata* Trelease, *Q. rugosa* Née, *Q. sideroxylla* Bonpl., *Q. urbanii* Trel. The information for studied tree species is summarized in Table 2.

2.2. Procedures for Developing the Species-Specific Individual-Tree Growth Equations

We used the following empirical model form as starting point of the model selection (1). The equation can be also considered a form of the growth equation proposed by Wykoff [40] for mixed conifer stands in the Northern Rocky Mountains. It predicts the observed *dbh* and total tree height for a growth period (5-year in our study) as a function of tree initial size (*dbh* or height), stand level variables and tree competition as predictor variables.

$$y = \alpha T^{\beta} \exp(\gamma S + \delta C) + \varepsilon \quad (1)$$

where *y* is the dependent variable (*dbh* —in cm— or total tree height —in m—) re-measured in 2012; *T* are initial tree size variables (*dbh* or total tree height) measured in 2007; *S* represents the effect of stand variables that commonly include stand density and dominant height; *C* represents the effect of tree competition; α , β , γ and δ are the regression coefficients of the equation; and ε is the model error term.

Table 2. Summary statistics of the tree species and species groups used to develop the diameter and height growth equations.

Species	n	2007				2012							
		Mean		SD		Mean				SD			
		dbh ₁	h ₁	dbh ₁	h ₁	dbh ₂	h ₂	AAI-dbh	AAI-h	dbh ₂	h ₂	AAI-dbh	AAI-h
<i>Abies durangensis</i>	134	25.16	16.16	15.05	7.90	26.45	17.74	1.29	1.58	15.25	8.20	0.94	1.65
<i>Alnus firmifolia</i>	425	15.05	9.27	8.32	4.01	16.49	10.86	1.44	1.59	8.63	4.40	1.01	1.50
<i>Arbutus arizonica</i>	592	14.84	5.57	8.09	2.16	15.92	6.32	1.08	0.75	8.34	2.38	0.81	0.87
<i>Arbutus bicolor</i>	698	14.91	5.69	8.24	2.16	16.15	6.61	1.23	0.93	8.69	2.57	0.92	1.05
<i>Arbutus madrensis</i>	846	15.60	5.73	8.14	2.09	16.82	6.62	1.22	0.89	8.56	2.50	0.92	1.06
<i>Arbutus tessellata</i>	387	15.60	5.64	7.96	2.17	16.76	6.51	1.16	0.87	8.18	2.56	0.89	1.24
<i>Arbutus xalapensis</i>	947	14.76	5.90	7.71	2.40	15.81	6.78	1.05	0.88	8.03	2.81	0.91	1.02
<i>Cupressus lusitánica</i>	315	23.78	13.16	19.67	7.95	25.09	14.35	1.32	1.19	20.43	8.47	1.23	1.19
<i>Juniperus deppeana</i>	2896	15.52	7.00	9.02	2.87	16.77	7.82	1.26	0.82	9.29	3.02	0.91	0.87
<i>Pinus arizonica</i>	7618	17.99	10.74	9.27	4.88	19.12	11.95	1.13	1.22	9.59	5.18	0.84	1.07
<i>Pinus cooperi</i>	2770	20.49	13.11	10.25	5.67	22.32	14.52	1.82	1.41	10.79	5.74	1.24	1.18
<i>Pinus durangensis</i>	11,760	18.92	13.23	10.80	5.61	20.33	14.68	1.41	1.45	11.25	5.94	1.06	1.32
<i>Pinus engelmannii</i>	751	23.24	14.56	11.77	6.17	24.65	15.66	1.41	1.10	11.99	6.26	1.14	1.19
<i>Pinus herrerae</i>	1766	25.01	16.62	14.09	6.62	26.54	18.43	1.53	1.81	14.49	6.85	1.23	1.65
<i>Pinus leiophylla</i>	2161	21.09	12.89	10.37	5.54	22.51	14.04	1.43	1.15	10.78	5.80	1.02	1.15
<i>Pinus lumholtzii</i>	1458	16.95	10.50	7.68	4.28	17.98	11.54	1.03	1.04	7.77	4.41	0.77	1.14
<i>Pinus strobiformis</i>	2550	17.74	11.54	9.33	4.72	19.29	12.91	1.54	1.37	9.66	4.92	0.99	1.17
<i>Pinus teocote</i>	3953	19.00	11.95	10.36	5.11	20.43	13.14	1.43	1.18	10.68	5.40	1.00	1.25
<i>Quercus arizonica</i>	179	19.15	9.47	7.79	3.94	20.07	10.91	0.92	1.44	7.95	4.37	0.76	1.58
<i>Quercus crassifolia</i>	2186	17.47	8.14	10.33	3.85	18.46	9.07	0.99	0.93	10.65	4.20	0.87	1.04
<i>Quercus durifolia</i>	255	18.50	7.75	11.02	3.70	19.70	8.44	1.21	0.69	11.18	3.84	0.96	0.91
<i>Quercus emoryi</i>	171	14.54	8.28	8.49	2.63	15.67	9.40	1.13	1.12	8.45	3.01	0.75	1.09
<i>Quercus fulva</i>	327	18.76	9.38	8.58	3.92	19.72	10.42	0.96	1.04	8.65	4.20	0.93	1.25
<i>Quercus jonesii</i>	222	16.19	6.76	8.52	3.74	17.24	7.62	1.04	0.86	8.82	3.98	0.76	0.84
<i>Quercus laeta</i>	389	17.67	9.19	9.64	3.88	18.57	10.28	0.90	1.10	9.82	4.28	0.77	1.31
<i>Quercus mcvaughii</i>	870	14.67	5.96	6.93	2.02	15.72	6.69	1.05	0.73	7.01	2.17	0.73	0.73
<i>Quercus radiata</i>	158	15.65	7.78	8.72	4.04	16.90	8.48	1.25	0.70	9.06	4.25	0.83	0.80
<i>Quercus rugosa</i>	896	18.60	8.78	11.29	3.56	19.97	9.58	1.37	0.80	11.75	3.82	1.05	0.95
<i>Quercus sideroxyla</i>	7373	19.30	9.50	12.26	4.33	20.60	10.56	1.30	1.05	12.65	4.65	1.04	1.20
<i>Quercus urbanii</i>	105	18.97	6.11	8.41	1.79	20.38	6.59	1.41	0.48	8.73	1.92	1.03	0.40
All pines	34,885	19.21	12.45	10.51	5.56	20.59	13.79	1.38	1.33	10.90	5.85	1.03	1.25
All oaks	13,228	18.36	8.82	11.27	4.12	19.56	9.80	1.20	0.98	11.62	4.44	0.98	1.13
All strawberries	3470	15.10	5.73	8.02	2.21	16.25	6.60	1.15	0.87	8.37	2.59	0.90	1.04

n = number of trees, Mean = mean variable values, SD = standard deviation, AAI = average annual increment of dbh (cm) and total tree height (m) observed between 2007 and 2012.

Initially, a regression procedure was used to select the definitive tree and stand variables for the individual tree dbh and height growth models. The significance level of 5% was used for the selection of candidate predictive variables in the model. These predictive variables were the measurements at the beginning of the selected 5-year growth period. They included initial tree dbh (*dbh*₁, cm); initial tree total height (*h*₁, m); the sum of the basal area of the trees larger than the subject tree (BAL, proposed by Wykoff et al. [41]), a modified BAL (BALMOD, proposed by Schröder and Gadow [42]) which includes the relative spacing index (i.e., BALMOD = (1 - (1 - (BAL/G)))/IH, where IH = 100/H₀N^{1/2}); the stand quadratic mean diameter (QMD, cm); stand density (N, number of trees per hectare); the total basal area of the plot (G, m²ha⁻¹); stand dominant height (H₀, m); and crown competition factor (CCF) [43]. H₀ was calculated from the proportion of the 100 thickest trees of pines per hectare. Data from trees with broken or dead tops were not used to calculate H₀. These predictive variables, along with their various combinations were tested separately by each species or species group using the *lm* and *nls* functions of R software environment [44]. In order to avoid problems related to multicollinearity, the value of the variance inflation factor (VIF) was computed for the groups of variables that best predicted the dependent variables. Candidate variables with a VIF larger than 10 were excluded, as suggested by Myers [45]. Non-significant parameters at 5% were also removed in the modeling process (i.e., they were fixed at 1 in the final model fitting). Therefore, a little bit different models were used for such species, resulting in the following two dbh and height models as the best candidate model formulations for describing both dbh and height growth in general among the models tested:

$$dbh_2 = a_0 dbh_1^{a_1} \exp(a_2 H_0 + a_3 BAL) + \epsilon \tag{2}$$

$$h_2 = b_0 h_1^{b_1} \exp(b_2 H_0 + b_3 \text{BAL}) + \varepsilon \quad (3)$$

where dbh_2 is the diameter at breast height after the selected 5-year growth period (cm), dbh_1 is the initial tree diameter (cm), H_0 is the stand dominant height (m), BAL is the sum of the basal area of the trees larger than the subject tree proposed by Wykoff et al. [41], h_2 is the total tree height after a 5-year growth period (m), h_1 is the initial total tree height (m), a_0 – b_3 are the regression coefficients, and ε is the model error term.

The models were first fitted under the assumption that the errors within equation were independent and identically distributed [46]. As only two measurements were available for each tree in the dataset, autocorrelation among measurements within a tree was not considered in the present study. However, residual analysis revealed the presence of heteroscedasticity in most species-specific dbh and total tree height growth equations. To deal with this problem weighted regression was used, modelling the error variances as a power function of the independent size variables (e.g., [46,47]). For the diameter growth model, the error variance was modelled with a power function of dbh_1 as independent variable (i.e., $\sigma_i^2 = dbh_1^k$). Using the method suggested by Park [48], squared residuals ($\hat{\varepsilon}_i^2$) were regressed against dbh_1 to obtain an estimate of k as follows: $\hat{\varepsilon}_i^2 = \gamma x dbh_1^k$, this expression was linearized by the use of the natural logarithm: $\ln \hat{\varepsilon}_i^2 = \ln \gamma + k \ln dbh_1$ and parameters were then estimated by linear least squares regression; the species-specific k value was subsequently included in the weighting factor ($w_i = 1/dbh_1^k$). The same was done for the species-specific height growth models (3), but using h_1 as the independent variable.

2.3. Model Comparison

Evaluation of the performance of the dbh and height growth equations was based on numerical and graphical analysis of the residuals. Two goodness-of-fit statistics were calculated: the root mean square error (RMSE) and the coefficient of determination (R^2). These statistics were computed on the basis of the unweighted residuals because these are the values of most interest by users of the equations. The expressions of these statistics are:

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{n - p}} \quad (4)$$

$$R^2 = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2} \quad (5)$$

where y_i , \hat{y}_i and \bar{y} are the observed, predicted, and mean values of the dependent variable, respectively; and n and p are the total number of observations and the number of parameters used to fit the models, respectively.

Plots of studentized residuals against predicted values of the dependent variables were used for visual evaluation of the models [49,50]. These graphs are very important for indicating areas for which the equations provide especially poor or good predictions.

3. Results

3.1. Diameter Growth Equations

The parameter estimates and the goodness-of-fit statistics for predicting dbh after a 5-year growth period with model 2 for each analyzed tree species are presented in Table 3. Most of the parameter estimates were significant at $\alpha = 0.05$. All non-significant parameters were dropped from model 2. The initial tree diameter was the most significant and important predictor of dbh_2 . In all cases the coefficients a_0 and a_1 were positive, and a_1 was less than 1.0 in all cases, indicating that dbh_1 limits diameter growth by itself. The term H_0 was positive in all species except for *Pinus engelmannii* and

Quercus arizonica (see a_2 in Table 3), resulting in increasing diameter with increasing stand dominant height. On the other hand, coefficient a_3 multiplying the BAL competition index was negative in all species except for *Pinus engelmannii* and *P. herrerae*, indicating a decrease in diameter growth as individual tree competition increases.

Table 3. Parameter estimates and goodness-of-fit statistics of the individual tree dbh growth equations developed.

Species	n	Estimated Parameters				RMSE (cm)	R ²
		a_0	a_1	a_2	a_3		
<i>Abies durangensis</i>	134	1.2745	0.9422	ns	−0.0013	0.88	0.997
<i>Alnus firmifolia</i>	425	1.3368	0.9453	ns	−0.002	0.97	0.987
<i>Arbutus arizonica</i>	592	1.2053	0.9589	ns	ns	0.79	0.991
<i>Arbutus bicolor</i>	698	1.2017	0.9619	ns	−0.001	0.83	0.991
<i>Arbutus madrensis</i>	846	1.1737	0.9658	0.0013	ns	0.85	0.99
<i>Arbutus tessellata</i>	387	1.2073	0.9626	ns	ns	0.87	0.989
<i>Arbutus xalapensis</i>	947	1.1680	0.9721	ns	ns	0.87	0.988
<i>Cupressus lusitanica</i>	315	1.1516	0.9735	ns	−0.0007	0.98	0.998
<i>Juniperus deppeana</i>	2896	1.2959	0.9421	0.0008	−0.0017	0.87	0.991
<i>Pinus arizonica</i>	7618	1.1711	0.9618	0.0018	−0.0007	0.78	0.993
<i>Pinus cooperi</i>	2770	1.3175	0.9251	0.0045	−0.0027	1.11	0.99
<i>Pinus durangensis</i>	11,760	1.2015	0.9567	0.002	−0.001	0.96	0.993
<i>Pinus engelmannii</i>	751	1.2143	0.9689	−0.0026	0.001	1.12	0.991
<i>Pinus herrerae</i>	1766	1.1624	0.9729	ns	0.0005	1.16	0.994
<i>Pinus leiophylla</i>	2161	1.222	0.9509	0.0021	−0.0014	0.95	0.992
<i>Pinus lumholtzii</i>	1458	1.2734	0.9320	0.0025	−0.0019	0.77	0.99
<i>Pinus strobiformis</i>	2550	1.2577	0.9402	0.0027	−0.0009	0.93	0.991
<i>Pinus teocote</i>	3953	1.2358	0.9431	0.0031	−0.0012	0.94	0.992
<i>Quercus arizonica</i>	179	1.1084	0.9931	−0.003	0.0014	0.75	0.991
<i>Quercus crassifolia</i>	2186	1.1858	0.9598	0.0012	−0.001	0.83	0.994
<i>Quercus durifolia</i>	255	1.3001	0.9386	ns	−0.0017	0.94	0.993
<i>Quercus emoryi</i>	171	1.5079	0.882	0.0048	−0.0066	0.62	0.995
<i>Quercus fulva</i>	327	1.3912	0.9165	0.0013	−0.0037	0.91	0.989
<i>Quercus jonesii</i>	222	1.1978	0.9526	ns	−0.0026	0.71	0.994
<i>Quercus laeta</i>	389	1.2017	0.9593	ns	−0.0011	0.75	0.994
<i>Quercus mcvaughii</i>	870	1.2704	0.9333	0.0023	−0.0012	0.73	0.989
<i>Quercus radiata</i>	158	1.2433	0.9278	0.0069	−0.0026	0.74	0.993
<i>Quercus rugosa</i>	896	1.2257	0.954	0.0015	−0.0013	0.96	0.993
<i>Quercus sideroxyla</i>	7373	1.258	0.9438	0.0022	−0.0018	0.97	0.994
<i>Quercus urbanii</i>	105	1.2524	0.9547	ns	ns	0.99	0.987
All pines	34,885	1.2085	0.9516	0.0025	−0.0010	0.96	0.992
All oaks	13,228	1.2328	0.9495	0.0018	−0.0015	0.93	0.994
All strawberries	3470	1.1875	0.9659	ns	−0.0004	0.85	0.990

n = number of trees used in model fitting, a_1 – a_3 = parameter estimates, ns = these parameters were not significant at $p < 0.05$, and were therefore fixed at 1 in the final model fitting, resulting in a little different model for these species, RMSE = root mean square error, R² = coefficient of determination.

The developed equations fitted the data well and generally explained between 98 and 99% of the observed variation of dbh_2 for all studied tree species. Average RMSE values for pines, other conifers (*Abies durangensis*, *Cupressus lusitanica*, and *Juniperus deppeana*), oaks, and other broadleaf species were 0.93 cm ±0.17 cm, 0.83 cm ±0.12 cm, 0.84 cm ±0.03 cm, and 0.92 cm ±0.06 cm, respectively. The RMSE values estimated for all pines, all oaks, and all strawberries species groups were 0.96, 0.93 and 0.85 cm, respectively.

The graphs of studentized residuals against predicted dbh values showed no evidence of heterogeneous variance over the full range of predicted values for all species after fitting the models with weighted regression.

In accordance with Huang et al. [50], plots of RMSE were obtained across tree sizes to evaluate the accuracy and precision of diameter predictions of model 2 for the developed equations. Figure 2 shows the plots for the three generic equations developed in this paper (species groups: all pines, all oaks, and all strawberries). It can be inferred that the final equations performed quite well for all sampled diameter classes. All strawberries model produced larger prediction errors for large-sized trees in comparison with all oaks and all pines models.

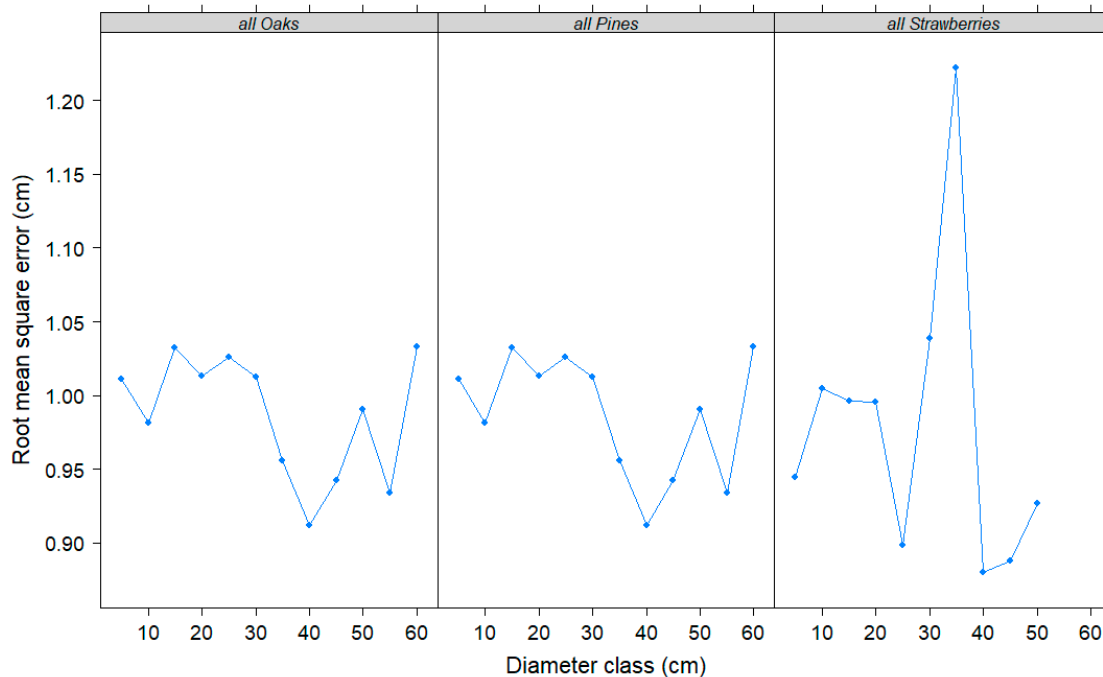


Figure 2. Root mean square error averaged over 5-cm dbh classes for three generic individual diameter growth equations developed in this study.

3.2. Height Growth Equations

The parameter estimates and the goodness-of-fit statistics for predicting total tree height after a 5-year growth period with model 3 for each species are presented in Table 4. Most of the parameter estimates were significant at $\alpha = 0.05$. All non-significant parameters were removed from model 3. The initial total tree height was the most significant and important predictor of height after a 5-year growth period. In all cases, the coefficients b_0 and b_1 were positive, b_1 was less than 1.0 in all cases (except for *Quercus urbanii*), indicating that h_1 limits height growth by itself. The term H_0 was positive in all species except for *Quercus urbanii* and *Cupressus lusitanica* (see b_2 in Table 3), resulting in increasing height growth with increasing stand dominant height. On the other hand, coefficient a_3 multiplying the BAL competition index was negative in all species except for *Cupressus lusitanica*, indicating a decrease in height growth as individual tree competition increases.

The developed equations fitted the data well and generally explained between 77 and 98% of the observed variation of the total tree height for all studied species. Average RMSE values of total tree height of pines, other conifers, oaks, and other broadleaf species were 1.16 m \pm 0.25 m, 0.99 m \pm 0.29 m, 1.03 m \pm 0.12 m, and 1.41 m \pm 0.26 m, respectively. The RMSE values estimated for all pine, all oak, and all strawberries species groups were 1.23, 1.10 and 1.03 m, respectively.

Table 4. Parameter estimates and goodness-of-fit statistics of the total individual tree height growth equations developed.

Species	n	Estimated Parameters				RMSE (m)	R ²
		b ₀	b ₁	b ₂	b ₃		
<i>Abies durangensis</i>	134	1.3983	0.8883	0.0054	ns	1.64	0.960
<i>Alnus firmifolia</i>	425	1.6787	0.8847	ns	−0.0019	1.48	0.887
<i>Arbutus arizonica</i>	592	1.2969	0.8920	0.0049	ns	0.87	0.867
<i>Arbutus bicolor</i>	698	1.2665	0.9044	0.0082	−0.0022	1.03	0.840
<i>Arbutus madrensis</i>	846	1.2893	0.9273	ns	ns	1.05	0.824
<i>Arbutus tessellata</i>	387	1.5365	0.8387	0.0087	−0.0090	1.22	0.773
<i>Arbutus xalapensis</i>	947	1.2214	0.9441	0.0041	ns	0.99	0.876
<i>Cupressus lusitanica</i>	315	1.2178	0.9759	−0.0018	0.0002	1.10	0.983
<i>Juniperus depeana</i>	2896	1.3426	0.8885	0.0047	−0.0023	0.87	0.918
<i>Pinus arizonica</i>	7618	1.3660	0.8813	0.0072	−0.0017	1.03	0.961
<i>Pinus cooperi</i>	2770	1.5429	0.8528	0.0049	−0.0021	1.16	0.959
<i>Pinus durangensis</i>	11,760	1.3379	0.9096	0.0034	−0.0006	1.31	0.952
<i>Pinus engelmannii</i>	751	1.3622	0.8881	0.0054	−0.0018	1.19	0.964
<i>Pinus herrerae</i>	1766	1.6105	0.8488	0.0047	−0.0022	1.64	0.943
<i>Pinus leiophylla</i>	2161	1.3041	0.9095	0.0042	−0.0013	1.14	0.962
<i>Pinus lumholtzii</i>	1458	1.3825	0.8874	0.0041	−0.0012	1.15	0.932
<i>Pinus strobiformis</i>	2550	1.3900	0.8924	0.0038	−0.0009	1.16	0.944
<i>Pinus teocote</i>	3953	1.2745	0.9115	0.0051	ns	1.23	0.948
<i>Quercus arizonica</i>	179	1.4913	0.8536	0.0081	−0.0045	1.56	0.872
<i>Quercus crassifolia</i>	2186	1.2162	0.9275	0.0044	ns	1.01	0.943
<i>Quercus durifolia</i>	255	1.2883	0.9023	0.0049	−0.0030	0.90	0.945
<i>Quercus emoryi</i>	171	1.2861	0.9079	0.0078	−0.0039	1.06	0.875
<i>Quercus fulva</i>	327	1.2640	0.8933	0.0074	ns	1.23	0.914
<i>Quercus jonesii</i>	222	1.2470	0.9241	ns	ns	0.83	0.956
<i>Quercus laeta</i>	389	1.2588	0.9217	0.0048	ns	1.29	0.909
<i>Quercus mcvaughii</i>	870	1.2981	0.8996	0.0035	ns	0.73	0.887
<i>Quercus radiata</i>	158	1.2473	0.9186	ns	−0.0029	0.79	0.966
<i>Quercus rugosa</i>	896	1.2068	0.9290	0.0048	−0.0015	0.93	0.940
<i>Quercus sideroxyla</i>	7373	1.2952	0.9087	0.0046	−0.0014	1.18	0.935
<i>Quercus urbanii</i>	105	1.3727	1.0010	−0.0190	ns	0.37	0.962
All pines	34,885	1.3512	0.8957	0.0050	−0.0010	1.23	0.956
All oaks	13,228	1.2560	0.9156	0.0050	−0.0013	1.10	0.938
All strawberries	3470	1.2800	0.9207	0.0043	−0.0018	1.03	0.843

n = number of trees used in model fitting, b₀–b₃ = parameter estimates, ns = these parameters were not significant at p < 0.05, and were therefore fixed at 1 in the final model fitting, resulting in a little different model for these species, RMSE = root mean square error, R² = coefficient of determination.

The graphs of studentized residuals against predicted total height values showed no evidence of heterogeneous variance over the full range of predicted values for all species after fitting the models with weighted regression.

Figure 3 shows the plots of RMSE obtained across tree height classes for the three generic equations developed in this paper to predict total tree height after a 5-year growth period with model 3. It can be seen that the final models performed quite well for all sampled height classes. The prediction errors for the all strawberries equation can be only evaluated for trees less than 25 m in height due to these tree species occupy always the subdominant vertical layers when mature and are small-sized trees [51].

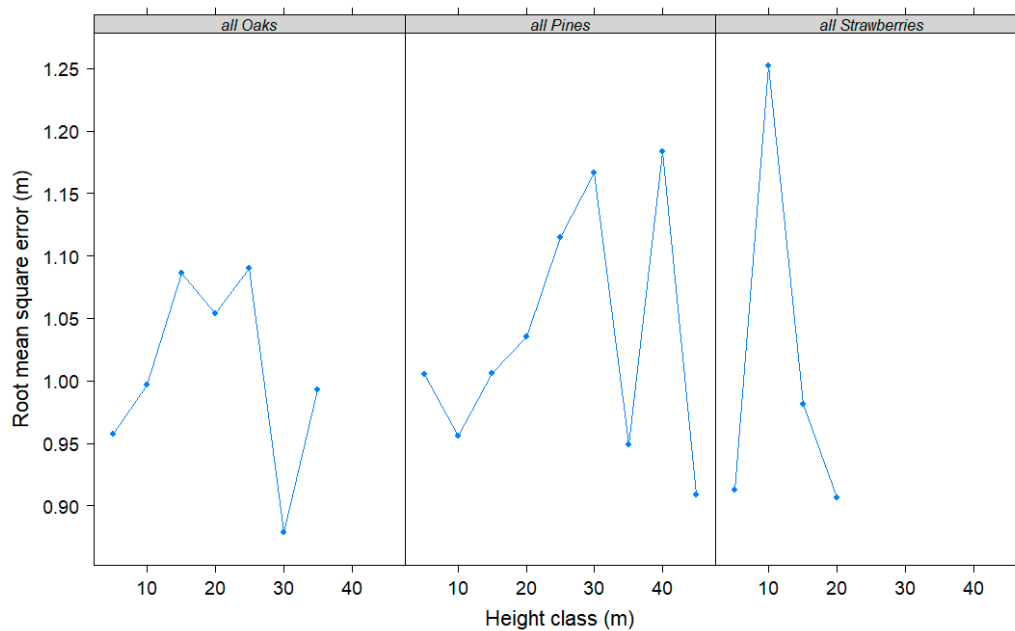


Figure 3. Root mean square error averaged over 5-m height classes for three generic individual height growth equations developed in this study.

4. Discussion

The species-specific growth models developed in the present study to predict dbh and total tree height of individual trees after a 5-year growth period included size variables (dbh_1 , h_1), site factors (i.e., H_0), and competition variables (BAL) in their formulation. In our study, the most important contribution of the variance explained by equations 2 and 3 came from size variables, followed by competition and site factors, respectively. These variables have also been selected by other authors for individual dbh, basal area and height increment models (e.g., [11,15,40,47,52,53]), although the most important variable has largely varied between ecosystems and species (e.g., [5,15,54,55]).

Our observed significant positive role of tree size on tree growth for all species agrees with studies that have observed that larger trees tend to grow faster (e.g., [15,17,56]). For example Stephenson et al. [57] presented a global analysis showing that larger trees had higher growth rates than smaller trees. Higher growth rates of larger trees are likely associated with increased access to resources; for example, larger trees generally have prominent position in the canopy, greater leaf area, and therefore have more access to light and other resources (e.g., [17]). In contrast, other studies have reported that growth rates increase to a maximum with tree size and then either levels off or decreases for the largest trees, as a result of reduced efficiency, accumulated stress, or senescence [16,17,55,58–60]. We did not observe a decrease in tree growth for the largest trees for our observed diameter range, which included diameters of up to 50–70 cm for most of the species. Some authors have found declines above this diameter range, sometimes at ages above 50 years (e.g [55,61]). Such very mature and larger trees are relatively scarce in most forests under management schemes and our sample was not big enough to find them.

Significant competition and site effects associated with BAL and H_0 were observed for most of the studied tree species both for individual dbh and height growth models. For dbh growth models, only five tree species showed no competition effect, while a non-significant site effect was found for thirteen tree species. In contrast, for height growth models a non-significant competition effect associated with BAL was found for eleven tree species, and only four of the studied species showed non-significant site factor effects. This appears to indicate that competition is a more important key driving factor for individual dbh growth in the study area than site factor (i.e., H_0), while the latter appears to be more appropriate for predicting height growth, as it significantly contributes to describing this variable. This

higher sensitivity of diameter growth to competitive stress is probably explained because of a higher dependence of this process on light interception, whereas height growth is less affected (e.g., [62–64]).

Our results agree with previous studies that have shown improvements in diameter growth prediction for different species when a competition index was included (e.g., [36,55,65–68]). Competition is an important driver of tree growth since the degree of shadowing emanating from competing neighbors substantially determines the amount and quality of solar radiation that is available for the target tree [64,69], together with the role of neighboring plants in competing for growing space and resources including water, and soil nutrients [17,70]. The consideration of competition after tree size for explaining diameter growth in our study agrees with previous studies that have also found that competition indices were the second most important variables, after tree size, in explaining individual tree diameter growth, for a variety of tree species. For example, in the studies of Wykoff [40], Monserud and Sterba [11] or Crecente-Campo et al. [46], the main variables in explaining growth were size variables (dbh or crown ratio), followed by the BAL competition index. In contrast, other studies have found competitive position, measured by BAL or modifications of BAL, to be the strongest individual predictor of diameter growth in both even-aged and uneven-aged stands [5,58,71,72].

In our study, BAL index explained a higher variance of tree growth than BALMOD or CCF indices. These results are similar to the findings of Crecente-Campo et al. [46], who found that BAL showed better results than BALMOD in terms of predicting basal area growth of Scots pine in NW Spain, unlike results from other studies where the latter has outperformed BAL (e.g., [43,73]), including a previous study in even-aged *Pinus cooperi* stands in the area of study by Corral-Rivas et al. [36] where BALMOD was selected.

In this study, significant site effects associated with H_0 were found for seven out of the eight developed individual dbh growth models for the pine species. Also, a significant H_0 effect was observed for the height growth models in all pine species, and indeed in almost all the studied tree species. Thus, H_0 appears to be an appropriate variable for predicting individual dbh and height growth for the study area, as it significantly contributes to describe individual tree growth within different stands. This finding is very interesting because more than 80% of Durango's forests are covered by mixed and uneven-aged stands, for which the most traditional growth modeling variables such as site index and age which appear to be important in describing the growth of individual trees within different stands, at least in even-aged forests [47]) are generally not available [74]. H_0 has also previously been included in generalized $h-d$ models developed for some of the tree species studied in this paper in the same study area (e.g., [38,75]). Therefore, the inclusion of H_0 in the models might be used to indicate the stage of development of a stand, thus compensating better sites with lower age [11,76]. Nevertheless, the effect of dominant height on growth varied between species, similar to previous studies that have documented that the effect of site quality on tree growth was not consistent across species (e.g., [5]).

Individual tree species in forests have adapted to specific site conditions and are capable of responding to a range of complex environmental challenges to improve their chances of survival, reproduction, and growth. Some species are shade tolerant, others are light demanding. Some require high humidity and others are adapted to dry conditions [26]. In our study some trees species did not show significant competition or site factor effects, and therefore it is interesting to examine the possible reasons for the observed lack of sensitivity to those factors.

The species *Quercus urbanii*, *Arbutus arizonica*, *A. tessellata*, *A. xalapensis* and *A. madrensis* showed a non-significant effect of tree competition on dbh growth. According to Lujan-Soto et al. [51], these tree species occupy always the subdominant vertical layer when are mature, and consequently are shade-tolerant and possibly less sensitive to competition for light. In addition, *Quercus crassifolia*, *Q. fulva*, *Q. laeta*, *Q. mcvaughii*, *Q. urbanii*, *Abies durangensis*, *Arbutus arizonica* and *A. xalapensis* showed non-significant competition effects (i.e., BAL) on height growth, also being species adapted to the subdominant strata [51]. Similarly, in the area of study, the previous study by Quiñonez et al. [3] found that oak species seemed to have an advantageous competition in the mixed-species stands, since their

growth was not significantly influenced by competition from other species. These results agree with observations from other studies in mixed-species conifer forests that have noted a lower sensitivity to competition for the more shade-tolerant species (e.g., [13,15,55,64]).

Non-significant site factor effects (i.e., H_0) on diameter growth were observed for *Pinus herrerae*, *Quercus durifolia*, *Q. jonesii*, *Q. laeta*, *Arbutus bicolor* and the group of *Arbutus* spp., which are tree species that are found growing in a vast geographic area of contrasting soils and site conditions [26]. The large plasticity of these tree species may suggest that such variation in dbh growth was not possible to be explained with dominant height [77,78], given their successful capacity of adaptation to very varied site quality conditions. On the other hand, the species *Abies durangensis*, *Alnus firmifolia*, and *Cupressus lusitanica*, which are species found in a very limited range of site conditions, also showed no significant competition effects on diameter growth. These are the most shade-tolerant species considered in our study which are growing only in a few plots with high humidity [26]. Similarly, *Quercus radiata* and *Alnus firmifolia*, which occurred on a very limited range of site conditions [26], showed no significant effects of site quality on tree height growth. The fact that these tree species occur on a very limited range of site conditions, possibly limited the inclusion of dominant height as a diameter growth predictor variable, given the low variability in this variable covered by the natural distribution of these species in our study area.

Future studies expanding the range of observed environmental conditions should also analyze the role of climatic and edaphic variables on tree growth, allowing to integrate the role of climatic or soil limitations on tree growth predictions (e.g., [16,17,58,79,80]) for improving our decision making capacity under climatic or management scenarios.

Although individual-tree dbh and height growth models as the ones developed in this paper are key components in many forest growth and yield prediction systems, their use would have restricted applicability without other model components such as ingrowth and mortality [11]. Hopefully, these model components will be developed for the studied tree species in the future. Thus, a reliable prediction system will be available for managing these natural species-rich and irregular forests in Durango, Mexico. However, the growth models developed in our study represent useful operational tools to support decision making for a comprehensive variety of tree species in Durango's forests. They may provide good simulation of growth (diameter, height, volume) for short term projections, provide detailed information about stand structure development (diameter and height distribution), calculate biomass and carbon stocks projection, and allow considerations of a wide variety of silvicultural treatments/prescriptions, among others.

5. Conclusions

The predictive variables used in the models to predict dbh and total tree height after a 5-year growth period were tree initial dbh and total tree height, respectively, the dominant height as a site factor (H_0), and the sum of the basal area in trees larger than the subject tree as a competition index (BAL). Some of the studied trees species did not show significant competition or site factor effects in the developed models, being the species-specific shade-tolerance and plasticity, respectively, the main reasons for the observed lack of sensitivity to those factors. Because these new species-specific growth models were developed with a large and unique dataset provided by an extensive network of stem-mapped and re-measured plots that covers a large variation of individual tree growth, they can be recommended not only for the forests of Durango but also for the surrounding regions with similar growth conditions. For other tree species that exist in the study area, but that were not considered in the study due to the lack of enough data, the generic models fitted on the combined data sets could be used for dbh and total tree height growth prediction. It is recommended that further studies on individual-tree growth for the studied species and species groups are continued with the aim to develop a reliable prediction system for managing these natural species-rich forests. Future models should analyze the role of species-specific ecological aspects on individual tree growth, once this knowledge has been generated.

Author Contributions: J.B.-R. designing the research, analyzing the data and wrote the manuscript; J.J.C.-R. contributed with the data, in designing the research, in analyzing the data and in revising the manuscript; R.S.-M. participated in revising the manuscript; J.R.P.-M. participated in analyzing the data and in revising the manuscript; D.J.V.-N. participated in revising the manuscript; P.M.L.-S. participated in revising the manuscript; B.V.-L. participated in revising the manuscript, U.D.-A. assisted in analysis of the results and revised the manuscript; G.Q.-B. participated in revising the manuscript and C.A.L.-S. assisted in revising the manuscript. All authors have read and agreed to the published version of the manuscript.

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