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EARLY PERFORMANCE AND GENETIC GAIN OF *CEDRELA ODORATA* FAMILIES FROM WIDE-RANGING SITES IN MEXICO

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HERNÁNDEZ-MÁXIMO E, LÓPEZ-UPTON J, SÁNCHEZ-MONSALVO V, VARGAS-HERNÁNDEZ JJ & SALAZAR-GARCÍA JG. 2016. Early performance and genetic gain of *Cedrela odorata* families from wide-ranging sites in Mexico. *Cedrela odorata* is a tree of utmost importance. Thus a progeny trial was established in Veracruz, Mexico, with 168 families from 19 provenances of southeast Mexico. Significant differences among provenances and families were found at 3, 5, 7 and 11 years of age for height, diameter at breast height [dbh] and volume, and stem straightness and branch thickness at 11 years of age. Individual heritability (h^2_i) fluctuated between years from 0.16 to 0.29, improving with age. For straightness and branch thickness, $h^2_i = 0.12$ and 0.10 respectively. Growth traits showed a genetic correlation ($r_g \geq 0.99$) among them. Genetic correlation (r_g) of straightness with height, dbh, volume and branch thickness were -0.24, -0.13, -0.18 and 0.56 respectively, and r_g of branch thickness with height, dbh and volume were 0.04, 0.11 and 0.13 respectively. Age-age genetic correlations were ≥ 0.93 for growth traits. A 56% gain in volume was obtained by using this variable as the selection criterion, leaving 20% of the best trees standing. Early selection at three years old, based on dbh was efficient to improve volume at 11 years with 37.3% gain, whereas at seven years the volume gain was 54%. None of the options dramatically altered form variables.

Keywords: Breeding, genetic correlation, heritability, DBH, height, volume

INTRODUCTION

The goal behind intensive cultivation of commercial forest plantations is to obtain maximum timber production of the highest quality at the lowest possible cost. Proper site selection, silvicultural practices and seed sources are important tools for increasing plantation yields (Ward et al. 2008). It is therefore necessary to have germplasm that generates plants of superior genetic quality, with the most common way being through seed orchards of genetically-selected trees developed in the plantation area. To establish these germplasm sources it is necessary to select trees based on economically important traits. To determine whether a parent tree has superior genetic quality, the performance of its progeny must be compared in field trials against that of other parents whose appearance was also outstanding. These trials help determine the breeding value of the selected trees and estimate genetic parameters such as heritability and genetic correlations among different traits (Falconer & Mackay 1996, White et al. 2007). These parameters are important for estimating the benefits that can be obtained from selection and cross-breeding programs (Zobel & Talbert 1984).

Cedrela odorata (Spanish cedar) is a forest species of great economic importance in Mexico because its wood is in great demand. It is aromatic, moderately lightweight, easy to work and resistant to termites and rot, thus making it very durable. It is used to make furniture, musical instruments and handicrafts, and also used in construction (Cintrón 1990, Santiago-Trinidad et al. 2007). Despite this, Spanish cedar plantations face the constant threat of attack by the shoot borer moth, *Hypsipyla grandella*. The larva of this lepidopteran causes severe damage that deforms the tree, reduces growth in the first three years and limits the success of commercial plantations (Navarro et al. 2004). It is a specific plague of the family Meliacea, with the Spanish cedar being the most susceptible species because it has lower resistance to attack by the insect (Cornelius & Watt 2003). Damage can be reduced through integrated pest management with insecticides and breeding techniques using genotypes resistant to the pest (Cornelius & Watt 2003, Sánchez-Monsalvo et al. 2003).

Studies on *C. odorata* have involved monitoring and development of *H. grandella* control methods, and the evaluation of trials in pure plantations and agroforestry systems (Sánchez-Monsalvo & Velázquez-Estrada 1998, Martínez-Vento et al. 2010). Few authors have studied the behavior of the genetic parameters of *C. odorata* growth traits. Navarro et al. (2004) examined the genetic variation among Mesoamerican provenances and families of Spanish cedar grown in association with coffee, and determined the heritability for height and diameter at breast height (dbh) at 25 months of age. In Mexico, few genetic evaluations have been established. Among them, Sánchez-Monsalvo et al. (2003), in a study of 42 open-pollinated families at five years of age, estimated the expected response to selection under two scenarios and found high heritability values for growth traits, which gave a genetic gain in volume up to 50%. In genetic trials at Noh Bec and Bacalar in Yucatan Peninsula, Ward et al. (2008) reported individual heritability of 0.16 and 0.09 for height at two years, respectively, and by selecting 20% of the best individuals, the genetic gain was estimated as 9.2 and 5.4% at both sites, respectively. The authors recommended provenance selection over multiple trials, as well as early selection to attain rapid growth, avoiding damage by the insect. Accelerated growth at a young age enables the tree to escape attack by the shoot borer moth and avoid deformities in the stem, or tolerate the attack by recovering the straight shape of the stem (Speight & Wainhouse 1989). These should be evaluated in conjunction with growth variables.

The aim of this study was (1) to estimate the genetic parameters for growth and form traits in a provenance-progeny trial of 168 families of 11-year-old *C. odorata* trees established in Tezonapa, Veracruz and (2) to estimate the response to selected 20% of the best trees for the purpose of establishing a seed orchard.

MATERIALS AND METHODS

Area description, design and establishment of provenance-progeny trial

The trial was established at El Palmar Experimental Station operated by the National Institute of Forestry, Agriculture and Livestock (INIFAP), Tezonapa, Veracruz, located at 18º 32' N latitude and 96º 47' W longitude, at elevation 180 masl. The climate is hot and humid with summer rains. The mean annual temperature is 24.4 °C, with a minimum of 16.1 and a maximum of 35.5 °C. The soil is acrisol, deep and well-drained, with a sandy-clay loam texture, pH 6.0. In the period 2009–2014, 11,390 mm of rainfall, equivalent to 1,898 mm annually, was recorded, and in the winter, average rainfall of 43 mm was observed (INIFAP 2015).

The trial was established with a randomised complete block design from July to September 2003. Between the first block and the last there was a difference of about ten weeks. The experiment consisted of 12 replications, where the experimental plot was one tree per family. In total, 168 families from 19 provenances obtained of the Mexican states of Veracruz, Tabasco, Chiapas, Oaxaca and Quintana Roo were established (Table 1). The parent trees were selected based on height, dbh and stem form. A systematic layout with spacing of 3 × 3 m and a total of 2016 individuals was used. Site preparation consisted of weeding, mechanised harrowing and marking, and creating 30 × 30 cm planting holes. In addition, a row of Spanish cedar trees was planted around the plantation to ensure that all individuals would grow under full competition. Weed control was done manually. No fertilisers, neither insecticides were applied to control *H. grandella* or other pests.

Evaluated variables

Measurements were made at the age of 3, 5, 7 and 11 years (2014) in the winter when trees halt their growth. Survival was evaluated as total height

Table 1 Geographical location of the provenances and number of families per each origin of *Cedrela odorata* established in the provenance-progeny trial

Provenance	State	North latitude	West longitude	Elevation masl	Number of families
Martínez	Veracruz	20° 02' 07.6''	97° 01' 49.0''	90.5	15
Tlapacoyan	Veracruz	19° 56' 37.0''	97° 12' 57.6''	576.4	4
Misantla	Veracruz	19° 54' 17.7''	96° 48' 39.8''	427.5	6
Papantla	Veracruz	19° 48' 08.9''	96° 08' 04.4''	166.9	22
Cardel	Veracruz	19° 15' 45.9''	96° 16' 17.7''	37.4	10
Veracruz	Veracruz	18° 53' 20.7''	96° 09' 01.5''	36.0	3
Yanga	Veracruz	18° 47' 24.0''	96° 47' 30.1''	734.0	6
Tinaja	Veracruz	18° 44' 34.9''	96° 29' 04.6''	280.2	5
Omealca	Veracruz	18° 40' 39.4''	96° 45' 38.9''	323.0	3
Tierra Blanca	Veracruz	18° 30' 41.7''	96° 23' 51.6''	117.0	6
Tezonapa	Veracruz	18° 26' 31.8''	96° 04' 24.4''	134.0	24
Tuxtlas	Veracruz	18° 09' 43.7''	95° 08' 13.6''	148.6	15
Acayucan	Veracruz	17° 53' 13.3''	94° 50' 07.8''	73.5	5
Tuxtepec	Oaxaca	17° 56' 53.9''	96° 08' 04.4''	38.5	9
Cárdenas	Tabasco	17° 56' 57.0''	93° 12' 38.0''	17.8	21
Teapa	Tabasco	17° 31' 40.0''	92° 55' 46.0''	56.8	6
Balancán	Tabasco	17° 48' 16.0''	91° 33' 48.0''	9.0	1
Palenque	Chiapas	17° 28' 51.4''	91° 58' 01.5''	52.0	4
Bacalar	Q. Roo	18° 33' 20.0''	88° 28' 35.0''	33.5	3

Q. Roo = state of Quintana Roo

(HT), using a measuring rod, and dbh, measured at 1.3 m above ground level using a diameter tape. In individuals presenting bifurcation under breast height, the diameter of both trunks was measured and then averaged. Stem volume was estimated using the formula by Sánchez-Monsalvo & García-Cuevas, 2009:

$$\text{Volume} = (0.000065659) * (\text{dbh})^{1.768431077} * (\text{HT})^{1.137733502}$$

where dbh = diameter at breast height and HT = total height. At 11 years old, stem straightness was assessed using a scale of 1–4, (1) = straight without bifurcating, (2) = slightly crooked without bifurcating, (3) = crooked or straight bifurcating and (4) = very crooked or crooked bifurcating. Bifurcation was quantified up to 4.0 m (Salazar & Boshier 1989). Branch thickness was evaluated on a scale of 1–3, (1) = thin, (2) = medium and (3) = thick branches (approximately < 3, 3–5 and > 5 cm in diameter, respectively). Likewise, branch angle was evaluated on a scale of 1–3, (1) = straight, (2) = normal and (3) = acute angle, right insertion angles being the best. However, since no significant differences were found at the family level for branch angle, it was omitted from further analysis.

Statistical analysis and estimation of genetic parameters

To determine differences among families and the average trait values and obtain the variance components, an analysis of variance was performed with the MIXED procedure of Statistical Analysis System (SAS) package (Littell et al. 1996). The statistical model used was:

$$Y_{ijk} = \mu + B_i + P_j + BP_{ij} + F_{k(j)} + e_{ijk},$$

where Y_{ijk} = value of tree observation of k family belonging to the j provenance in the i block, μ = mean of population, B_i = fixed effect of block, P_j = fixed effect of provenance, BP_{ij} = fixed effect of block and provenance interaction, $F_{k(j)}$ = random effect of family k nested in provenance j and e_{ijk} = random effect (error) of the tree from family k in provenance j in block i. Provenance was considered as a random effect only to compare variance components of provenances and families. To compare differences among provenances least-square means and pairwise comparisons of means were obtained by piecewise differentiable (PDIFF) option on least-square means (LSMEANS) statement. In order to have normality in branch thickness and straightness, the data was square root transformed (Sokal & Rohlf 1969, Little & Hills 1989):

$$(\sqrt{(Y_i + 1/2)}) \qquad (1)$$

where Y_i = value of tree observation. To avoid overestimation (Squillace 1974), a coefficient of genetic determination of 3 was used to calculate the additive genetic variance, assuming that the genetic correlation between siblings obtained by open pollination is ⅓ (Sorensen & White 1988). Other researchers have also assumed partial inbreeding and used a coefficient of determination of 3 (Sotelo-Montes et al. 2006, Weber et al. 2011). So, the genetic and phenotypic variances and the narrow sense heritability, both at individual (h^2_i) and family (h^2_f) mean levels, were estimated for all variables with the equations:

$$h_i^2 = \frac{3\sigma^2{}_f}{\sigma^2{}_f + \sigma^2{}_e} \quad h_f^2 = \frac{{}^1\!/_4\ 3\,\sigma^2{}_f}{[\sigma^2{}_f + \sigma^2{}_e/n]} \qquad (2)$$

where h^2_i = individual heritability, h^2_f = family heritability, σ^2_f = variance of families, σ^2_e = error variance and n= harmonic mean number of plants per family in the trial. The standard error for heritability [$EE(h^2_i)$] was calculated using the following formula (Dickerson 1969):

$$EE(h^2{}_i) = \sqrt{\frac{3^2(\sigma^2{}_f)}{(\sigma^2{}_f + \sigma^2{}_e)^2}} \qquad (3)$$

where EE = standard error, (h^2_i) = individual heritability, σ^2_f = variance of families and σ^2_e = error variance. Genetic and phenotypic correlations among variables observed at the same age and trait, recorded at different ages (age-age correlation), were determined. Phenotypic correlations were estimated using SAS correlation procedure (SAS Institute 1996). Genetic correlations (r_{gxy}) between pairs of variables were obtained by the following formula (Falconer & Mackay 1996):

$$r_{gxy} = \sigma_{fxy} / (\sigma_{fx}\ \sigma_{fy}) \qquad (4)$$

where σ_{fxy} = covariance of families between variables x and y, and σ_{fx} & σ_{fy} = standard deviations of families of the variables x and y.

In this case:

$$\sigma_{fxy} = ½[\ \sigma^2{}_{f\ (x+y)} - (\sigma^2{}_{fx} + \sigma^2{}_{fy})\ ] \qquad (5)$$

where $\sigma^2_{f\ (x+y)}$ = variance of families of the variable x + y and σ^2_{fx} & σ^2_{fy} = variance of families of the variable x and y, respectively. The analysis of genetic correlation between ages requires that both variables have the same number of observations, so information from trees with data across all measurement ages was used.

The standard error for the genetic correlations was calculated using the following formula (Falconer & Mackay 1996):

$$EE(r_g) = 1 - r_g^2 \sqrt{\frac{EE(h^2{}_x)\ EE(h^2{}_y)}{2(h^2{}_x\ h^2{}_y)}} \qquad (6)$$

where EE = standard error, r_g = genetic correlation and h^2_x & h^2_y = narrow sense heritability of the trait x and y.

The expected response to selection (R_y) or genetic gain was estimated by using the following formula (Falconer & Mackay 1996):

$$R_y = 2\ i\ h^2{}_y\ \sigma_{py} \qquad (7)$$

where i = selection intensity; h^2_y = narrow sense heritability of the trait *y* and σ_{py} = standard phenotypic deviation of y. This equation assumes that the selected trees will either remain in a seed orchard or be cloned and established in a clonal seed orchard, where seed for the establishment of plantations will be obtained. The selection intensity (i) was 1.4, equivalent to selecting 20% of the best trees within the population for the desired trait (Falconer & Mackay 1996). The expected response was also obtained as a percentage by dividing the absolute value of R_y by the mean of the original population.

Indirect response to selection (R_{Cy}) was calculated by the following formula (Falconer & Mackay 1996):

$$R_{Cy} = 2\ i\ h_x\ h_y\ r_{Gxy}\ \sigma_{Py} \qquad (8)$$

where i = selection intensity, h_x and h_y = square root of the heritability of the variable x and y; r_{Gxy} = genetic correlation between the variables x and y and σ_{Py} = phenotypic standard deviation of the variable y.

RESULTS AND DISCUSSION

At three years old, the *C. odorata* trees had an average HT of 4.61 m and dbh of 5.53 cm (Table 2). The values were lower than those of Cornelius & Watt (2003) for a clonal trial established in Costa Rica, with averages of 5.8 m in height and 6.2 cm in dbh at 34 months of age. These differences could be due to the genetic quality of the trial materials, the pruning regimes, pest control received by the clones and the application of fertiliser when establishing them. In our study, trees at 11 years old had an average HT of 10.65 m, dbh of 14.0 cm and stem volume of 120 dm^3.

The results obtained at age five in the present study were higher than those reported by Sánchez-Monsalvo et al. (2003) for *C. odorata* in a five-year progeny trial in the same experimental field and those of Márquez-Ramírez et al. (2009) in an eight-year provenance-progeny trial in the state of Veracruz. The mean annual increase in volume during the assessment years ranged from 3.3 to 10.9 dm^3 (Table 2). The reduced height growth could be attributed to the damage caused by *H. grandella* in the terminal buds, as the insect destroys existing stem growth (Cibrián-Tovar et al. 1995, Cornelius & Watt 2003). On the other hand, increased competition for space among trees with age decreases diameter growth (Ignacio-Sánchez et al. 2005).

Significant differences among provenances and families were found at 3, 5, 7 and 11 years old in height, dbh, volume, straightness ($p < 0.0001$) and branch thickness ($p < 0.05$). The variance of families was greater at 11 years in dbh and volume than for the rest of the traits. The greatest variability was in the error, between 83.7 and 98.3% of the total variation estimated, indicating a large degree of variation among trees within families, which allowed selection within them. Provenances contributed 0.0 to 8.3% (Table 2), values similar to those obtained in other forest

Table 2 Mean values, standard error and variance components of the variables evaluated by age in a provenance-progeny test of *Cedrela odorata* in Tezonapa, Veracruz

Trait	Age (years)	Average	Standard error	Variance components (%)			
				σ^2_p	σ^2_{bp}	$\sigma^2_{f(p)}$	σ^2_e
Total height (m)	3	4.61	0.03	4.74	1.10	5.28**	88.88
	5	7.33	0.04	5.57	0.98	6.89**	86.56
	7	8.51	0.05	6.63	1.44	7.96**	83.97
	11	10.65	0.05	8.27	1.26	6.80**	83.67
Diameter at breast height (cm)	3	5.53	0.05	3.64	0.00	5.26**	91.10
	5	9.71	0.08	4.63	0.77	6.75**	87.85
	7	10.89	0.08	4.89	0.85	8.58**	85.68
	11	14.00	0.11	5.84	0.48	8.62**	85.06
Volume (dm^3)	3	9.82	0.22	3.39	0.06	4.01**	92.54
	5	41.68	0.76	4.63	0.63	5.89**	88.85
	7	59.83	1.04	5.13	0.77	8.67**	85.43
	11	119.81	2.09	5.59	0.65	9.14**	84.62
Stem straightness	11	3.08	0.01	3.69	0.79	4.01**	91.51
Branch thickness	11	2.20	0.01	0.00	0.00	2.83*	97.17

σ^2_p = variance of provenance, σ^2_{bp} = variance of block by provenance, $\sigma^2_{f(p)}$ = family variance, σ^2_e = error variance (*$p \le 0.05$, ** $p \le 0.0001$)

species (Riemenschneider 1988, Magnussen & Yeatman 1990, Farfán-Vázquez et al. 2002, Sotelo-Montes et al. 2006, Sotelo-Montes & Weber 2009, Weber et al. 2011) and for the same species at five-years age (Sánchez-Monsalvo et al. 2003).

No significant differences among provenances and families were found in the four evaluations of survival. Survival at three years was 80% and decreased to 77.5% at 11 years, although the provenances ranged from 67 to 87.5%. Sánchez-Monsalvo et al. (2003) reported 95% survival in a Spanish cedar trial at this site. Tree mortality could be attributed to the damage caused by natural weakness of some individuals, shoot borer moth and poor management received by the trial (only weed control), which was conducted in order to determine which genotypes exhibited resistance to borer attacks.

The Cárdenas and Tuxtepec provenances had the best growth in the four evaluations, while Bacalar showed the lowest values. These results may be due to adaptation of provenances to different environments since the rainfall in Bacalar is less than the annual average recorded in El Palmar, Tezonapa, and it is the farthest geographically from the trial site. The differences among provenances were detected from age three onwards.

The average value recorded for stem straightness and branch thickness was relatively high (Table 3), indicating that in general the population has crooked or bifurcated stems and thick branches. At least 13% of the trees showed form values between 1 and 2, corresponding to straight stems with little crookedness. These individuals could be selected for future use if they have outstanding volume. For other tropical tree species, similar behavior in terms of stem form were reported (Balcorta-Martínez & Vargas-Hernández 2004, Mesén et al. 2007, Mesén & Vásquez 2009, Weber et al. 2011). The Balancán, Cárdenas and Palenque provenances recorded the lowest average values, corresponding to

Table 3 Comparison of means of total height, diameter at breast height, volume, stem straightness and branch thickness by provenances of *Cedrela odorata* at 11 years

Provenance*	Total height (m)	Diameter at breast height (cm)	Volume (dm^3)	Stem straightness**	Branch thickness+
Cárdenas	11.35 a	15.55 a	151.93 a	2.83 a	2.20 a
Tuxtepec	11.29 ab	15.41 ab	148.67 ab	3.02 ab	2.16 a
Teapa	10.90 abc	14.83 abc	137.08 abc	2.93 ab	2.19 a
Misantla	11.00 abc	14.90 abc	133.95 abc	3.11 abc	2.12 a
Acayucan	10.95 abc	14.83 abc	128.65 abc	3.05 abc	2.26 a
Martínez	10.69 bc	14.22 bcd	121.05 bc	3.13 abc	2.19 a
T. Blanca	10.65 bcd	14.24 abcd	119.67 bc	3.19 bc	2.21 a
Balancán	10.47 bcdef	12.96 cdef	117.47 bcd	2.70 a	2.17 a
Omealca	10.51 bcde	13.91 bcde	116.17 bcd	3.08 abc	2.33 a
Tinaja	10.27 cdef	13.78 cde	115.56 bcd	3.06 abc	2.18 a
Palenque	10.11 cdef	13.56 cde	114.63 bcd	2.93 ab	2.11 a
Papantla	10.40 cdef	13.89 cde	114.60 bcd	3.13 abc	2.20 a
Tuxtla	10.61 bcd	13.81 cde	112.50 cd	2.99 ab	2.20 a
Tezonapa	10.46 cdef	13.50 cde	109.29 cd	3.20 c	2.17 a
Yanga	9.97 def	13.13 cde	100.84 cd	3.31 c	2.23 a
Veracruz	10.00 cdef	12.52 cdef	91.09 cd	3.22 c	2.32 a
Cardel	9.38 f	11.97 ef	80.49 d	3.26 c	2.24 a
Tlapacoyan	9.61 ef	12.09 def	79.74 d	3.31 c	2.19 a
Bacalar	8.80 f	9.85 f	55.27 d	3.25 c	2.13 a

Means were ordered with reference to volume, * = provenances with the same letter are not statistically different ($p \leq 0.05$), ** = straightness in a scale of 1–4, where 1 = straight, 2 = slightly crooked, 3 = crooked or straight bifurcated and 4 = very crooked or slightly crooked bifurcated, + = branch thickness in a scale of 1–3, where 1 = thin, 2 = medium-thick and 3 = thick branches, with no significant differences among provenances fewer bifurcated or crooked trees with thinner branches (Table 3).

Individual and family heritability

Height had eliminate lower coefficient of genetic variation (CV_G) than dbh and volume, the average CV_G for dbh and volume were 9 and 20%, respectively (Table 4). Form variables had values lower than 4% for CV_G. Thus, the *C. odorata* growth traits showed moderate genetic control. During the assessment period, individual heritability (h^2_i) was 0.16–0.25 for height, 0.16–0.27 for dbh and eliminate 0.12–0.29 for volume. The family heritability value (h^2_f) was slightly higher, showing an increase in values with increasing tree age, except for height, whose h^2_f remained relatively constant across measurement ages.

Heritability obtained at both individual and family levels were low for stem straightness and branch thickness (Table 4). According to Zobel & Talbert (1984), stem form (straightness) is under strong genetic control and higher heritability values would be expected for this variable. In another study, Mesén & Vásquez (2009) attributed the low h^2_i value for straightness to either high mortality or the rating scale used for the evaluation. In addition, among provenances and families there were no obvious differences in straightness and branch thickness.

Heritability at individual level (h^2_i) for both height and dbh were greater than those reported by Ward et al. (2008). However, they were lower at the family level (h^2_f) than those reported by these same authors for a genetic trial of three-year-old *C. odorata* (h^2_i= 0.12, 0.13 and h^2_f= 0.26, 0.28 for height and diameter). In a five-year progeny trial, Sánchez-Monsalvo et al. (2003), using a coefficient of 3, reported individual heritability of 0.38, 0.65 and 0.54 for dbh, height and volume, and family heritability of 0.62, 0.53 and 0.59 for the same variables, respectively.

Using a coefficient of 3, Navarro et al. (2004) determined individual heritability of 0.12 for dbh and 0.20 for height in young *C. odorata* individuals (aged 25 months). The trial was established under different climatic conditions and in association with coffee agroforestry system. It had management practices such as fertilisation, which makes plants bigger, causes families to differentiate at a younger age and increases the heritability value (López-Upton et al. 1999). Higher heritability for growth has also been observed in other species, in zones with higher rainfall and more fertile soils in the Peruvian Amazon (Sotelo-Montes et al. 2006, Weber et al. 2011).

Phenotypic and genetic correlations

The genetic correlations estimated for growth traits at 11 years of age were higher than the phenotypic correlations; both were high and positive (Table 5). Sánchez-Monsalvo et al. (2003) found at five years that these traits had high genetic correlation values, ranging from 0.91 to 0.95.

The coefficients of phenotypic and genotypic correlation between height, dbh and volume with stem straightness were relatively low and negative, indicating that selecting trees just for superior quality of their straight stems had virtually no impact in terms of improved growth

Table 4 Coefficient of genetic variation (CV_G) and heritability at individual (h^2_i) and family (h^2_f) level in a provenance-progeny trial of 11-year-old *Cedrela odorata*

Trait	3 years			5 years			7 years			11 years		
	CV_G (%)	h^2_i	h^2_f	CV_G (%)	h^2_i	h^2_f	CV_G (%)	h^2_i	h^2_f	CV_G (%)	h^2_i	h^2_f
Total height	5.64	0.16	0.23	4.86	0.22	0.29	5.13	0.25	0.32	4.58	0.22	0.31
Diameter at breast height	7.60	0.16	0.25	7.32	0.21	0.29	8.04	0.27	0.34	8.81	0.27	0.35
Volume	16.2	0.12	0.22	15.8	0.18	0.28	18.9	0.27	0.36	19.95	0.29	0.37
Stem straightness	—	—	—	—	—	—	—	—	—	3.87	0.12	0.21
Branch thickness	—	—	—	—	—	—	—	—	—	3.11	0.10	0.17

$CV_G = (\sigma f/\bar{x})100$

Table 5 Genetic (below the diagonal) and phenotypic (above the diagonal) correlations between the variables evaluated in a provenance-progeny trial of 11-year-old *Cedrela odorata* established in Tezonapa, Veracruz

Age/trait		11 years old				
		Total height	Diameter at breast height	Volume	Stem straightness	Branch thickness
11 years	Total height		0.81	0.81	-0.29	0.13
	Diameter at breast height	0.99(0.01)†		0.96	-0.22	0-12
	Volume	0.99(0.004)	0.99(0.002)		-0.24	0.14
	Stem straightness	-0.24(2.75)	-0.13(1.81)	-0.18(0.40)		0.07
	Branch thickness	0.04(3.86)	0.11(2.40)	0.13(0.54)	0.56(5.39)	

† = Standard error of the genetic correlations

in height, dbh or volume of the progeny. On the other hand, neither will selecting on the basis of volume alone improve stem straightness. However, selecting parent trees on the basis of volume alone would tend to increase branch thickness, but large trees with thin branches should be sought. The value of the genetic correlations between straightness and branch thickness indicated that the selection of straight trees would produce thin-branched offspring.

The age-age genetic correlations obtained for height, dbh and volume evaluated at 11 years of age, compared to the measurements made at 3, 5 and 7 years of age were high (Table 6). Thus, for the three traits considered, the selection of trees or families could be made at three years of age.

The age-age genetic correlations were high, so the breeding cycle could be significantly shortened (Lambeth 1980), since there is a strong genetic correlation between growth at young age and growth at 11 years old. There is great interest in reducing the duration of genetic trials by experimenting with intensive management techniques (López-Upton et al. 1999), aimed at reducing the spacing in the plantation to accelerate canopy closure and competition among genotypes (Li et al. 1992, Woods et al. 1995).

Expected response to selection

If 20% of the trees were selected based on height at 11 years old, an 11.8% increase in average height of 11 year old trees in the next generation would be expected. Also, an increase of almost

Table 6 Estimated genetic (age-age) and phenotypic correlation between total height, diameter at breast height and volume between age 11 and different ages in a provenance-progeny trial of *Cedrela odorata*

Trait y	Variable x-age	Genetic correlation r_{gxy}	Phenotypic correlation r_p
Total height 11	height 3	0.94 (0.21) †	0.74
	height 5	1.00 (0.001)	0.86
	height 7	0.99 (0.04)	0.91
Diameter at breast height 11	DBH 3	0.93 (0.13)	0.77
	DBH 5	1.00 (0.02)	0.89
	DBH 7	1.00 (0.002)	0.94
Volume 11	Volume 3	1.00 (0.001)	0.77
	Volume 5	1.00 (0.002)	0.89
	Volume 7	1.00 (0.002)	0.94

† = error estándar de las correlaciones genéticas

Table 7 Expected direct and indirect response in absolute (R) and relative (%) values in a trial of 11-year-old *Cedrela odorata*

Selection criteria	Age	Expected response at 11 years old*									
		Height		Diameter at breast height		Volume		Stem straightness		Branch thickness	
		R (m)	%	R (cm)	%	R (dm^3)	%	R	%	R	%
Height	11	1.26	11.81	2.92	20.87	57.60	48.08	-0.12	-4.01	0.01	0.65
	3	1.03	9.67	2.13	15.22	42.62	35.58	-	-	-	-
	5	1.26	11.81	2.64	18.84	52.39	43.73	-	-	-	-
	7	1.33	12.50	3.00	21.42	60.15	50.21	-	-	-	-
Diameter at breast height	11	1.39	13.04	3.27	23.37	64.18	53.57	-0.07	-2.38	0.05	2.13
	3	0.99	9.27	2.34	16.72	44.74	37.34	-	-	-	-
	5	1.23	11.53	2.89	20.66	55.63	46.43	-	-	-	-
	7	1.34	12.61	3.23	23.07	62.83	52.44	-	-	-	-
Volume	11	1.43	13.43	3.35	23.95	67.01	55.93	-0.11	-3.46	0.06	2.65
	3	0.96	9.06	2.24	15.97	43.89	36.64	-	-	-	-
	5	1.20	11.29	2.75	19.61	54.25	45.28	-	-	-	-
	7	1.38	12.97	3.27	23.33	65.17	54.40	-	-	-	-
Stem straightness	11	-0.23	-2.17	-0.29	-2.07	-8.04	-6.71	0.60	19.48	0.16	7.19
Branch thickness	11	0.03	0.30	0.22	1.56	5.21	4.35	0.19	6.09	0.40	18.37

* = expected response to selecting 20% (I = 1.4) of the best individuals in the population

21% in dbh and 48% in volume of trees at this age would be expected (Table 7). If dbh was used as the selection criterion, a slightly greater response in height (13.4%), dbh (23.3%) and volume (53.5%) at 11 years eliminate would be expected. Since stem volume is a function of tree height and dbh, an increase in volume would be expected in a population selected on the basis of both criteria. The maximum response would be given using eliminate volume at age 11 with 55.9% gain, and with a slight improvement in tree straightness (3.46%) but an increase in branch thickness eliminate, due to the fact that larger trees tend to have thicker branches. If the straightest trees were selected, a 6.7% improvement in volume, based on the inverse straightness assessment scale would be expected.

Early selection at 3, 5 or 7 years old, whether based on height, dbh or volume, would be quite efficient to improve these traits at age 11. For example, selecting on the basis of DBH at three years would produce in the next generation an increase of 9.3% in average height, 16.7% in dbh and 37.3% in volume at 11 years, whereas selecting dbh at seven years would result in a 52.4% gain in volume (Table 7). Early selection efficiency was slightly better when using volume as the selection criterion. In the study conducted by Sánchez-Monsalvo et al. (2003) in *C. odorata*, it was found that the expected responses to selection in growth traits were high compared to the results obtained in other woody plants, both conifers and broadleaf trees, using similar selection intensity. Often it is found that the genetic gains at a young age are highly correlated with the gains obtained at the rotation age (White et al. 1993, Gwaze et al. 1997, Wu 1999). If the material from genetic trials or seed orchards were combined with silvicultural activities and sanitation pruning, it would be possible to increase the growth and stem straightness values. Similarly, moderate insecticide application could improve growth values and genetic control, as well as the value of the trees.

CONCLUSIONS

Highly significant differences in growth traits among the 19 provenances and families tested in the trial were found. In most of the growth traits evaluated, both individual and family heritability increased with age, attaining moderate values for height, dbh and stem volume. However, heritability for stem form variables was low. Overall, genetic and phenotypic correlations were high and positive among growth-related variables, i.e. height, dbh and volume. Considering heritability values, selection of trees could be based on volume, considering elimination of malformed trees, to establish a seed orchard.

The high age-age correlations between age 11 years and those at 3, 5 and 7 years would make it feasible to select at an early age, with a reduced risk of eliminating individuals with superior performance at age 11. The results obtained for the expected response to selection suggests that it is feasible to make the selection at three years, although it is better at seven years of age. Gain percentages were closer to those that would be obtained if selection were made at 11 years. In addition, at a younger age it is possible to reduce the costs generated by data collection.

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