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Genetic parameters of growth, and resistance to the shoot borer, in young clones of the tree *Cedrela odorata* (Meliaceae)

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Abstract: Damage by *Hypsipyla grandella* Zeller restricts the success of plantations of *Cedrela odorata*. The most critical and vulnerable infection period by *H. grandella* is during the first three years. The aim was to estimate the expected genetic gain for the selection of clones of fast growth and resistant to the attack by this insect. A trial with 40 clones produced by grafting was planted in Veracruz, Mexico. Heritability, genetic correlations and genetic gain of clones were estimated with data at two years-old. The survival rate of the trial was of 97 % (466 living ramets in total), 2.84 m in total high and 2.32 cm of average normal diameter. Aditionally, 9.9 % of the ramets did not present attacks, indication of evasion, and 0.6 percent without response to attack. With response to attack 89.5 % of the ramets (several degrees of tolerance): 29 % with a single shoot, 14.2 % with several shoots and 46.3 % with a dominant shoot of several shoots formed. The clonal heritability of normal diameter, height, volume, stem taper index, number of attacks and response to the attack was H^2c = 0.81, 0.80, 0.81, 0.61, 0.34, and 0.26. The genetic correlations between height, diameter and volume were ≥ 0.95, and the correlation of the volume with the incidence and the response to the attack was r_g = -0.31 and r_g = 0.62, that is a decrease in number of attacks and moderate increase in tolerance. With a selection intensity of 10 %, selecting the four clones with higher volume will produce a genetic gain of 82 % for volume, a decrease of 10.9 % of number of attacks and 6.3 % of better recovery from damage; this is more tolerance to the insect attack. The genetic gain justifies the use of the best clones in commercial plantations in Veracruz, Mexico.

Key words: *Cedrela odorata*; genetic correlations; genetic gain; heritability; shoot borer; insect resistance.

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Cedrela odorata L. (Spanish cedar) grows in the humid and seasonally dry American tropics and subtropics, its adaptability, fast growth and valuable timber make a species well suited to commercial plantation (Cornelius & Watt, 2003). In México is the tree species more planted, with 20.5 % of the total surface established (CONAFOR, 2015), it has an attractive economic return and good social acceptance (Ramírez-García, Vera-Castillo, Carrillo-Anzures, & Magaña-Torres, 2008). However, commercial plantation are highly affected by larvae of *Hypsipyla grandella* Zeller, Lepidoptera, which damage the apical meristem of *C. odorata* individuals, causing increased branching and slowing down growth, 100 % of the trees may be stroked (Cornelius & Watt, 2003). *Cedrela odorata* is the Mealiceae species more susceptible with severe damage mainly during the first three years after planting (Navarro, Montagnini, & Hernández, 2004).

It is possible to decrease effects of pests through use of biological and chemical control, pruning and genetic improvement using resistant genotypes (Cornelius & Watt, 2003; Sánchez-Monsalvo, Salazar-García, Vargas-Hernández, López-Upton, & Jasso-Mata, 2003; Cunningham, Floyd, Griffiths, & Wylie, 2005). To accelerate the process, measurements are taken at early ages. The selected material can be cloned to increase genetic gain and frequency of superior trees (Kumar, 2007; White, Adams, & Neale, 2007). Newton, Cornelius, Mesén, and Leakey (1995) pointed out that genetic improvement would be greatly accelerated if, at an early age, genotypes capable of recovering from attack due to strong apical growth could be identified.

Estimation of genetic parameters is crucial to defining breeding strategies and estimating the genetic value of progenitors (Osorio, White, & Huber, 2001). When characteristics of resistance to pests is included in genetic breeding programs, greater gains in growth are obtained (Swedjemark & Karlsson, 2004). The objective was to estimate expected genetic gain when clones resistant to attack by *Hypsipyla grandella* were selected by calculating heritability and genetic correlations of diameter at breast height, tree height, volume and trunk taper index, number of attacks and clone recovery from damage by *H. grandella.*

MATERIALS AND METHODS

Study site: The clonal trial was located in Tezonapa, Veracruz, México, at the Research Station "El Palmar" of the Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias, situated at (18°32' N & 96°47' W), at 180 m. The climate is hot humid with rains in summer, with an average annual rainfall of 2 888 mm and average annual temperature of 24.4 °C. The soils are of the acrisol type, deep, good drainage, silty clay-loam texture and pH of 5 (Sánchez-Monsalvo & Velázquez-Estrada, 1998).

Plant material and experimental design: The clones in evaluation come from the clonal bank of the Research Station, formed by bud grafts. The clones are superior genotypes due to their growth and resistance to the attack of *H. grandella*, whose value was determined in three provenance-progeny trials in the area. The trial was established in 2011 with 40 clones. The experimental layout used was a complete random blocks design, with single-tree plots and 12 replications, at a spacing of 3 x 3 m.

Evaluated traits: The evaluation of the trial was carried out two years after being established, survival was 97 %. Total height and diameter were measured. The trunk diameter was determined at three heights: at 0.30 m, at 1.30 m (DBH) and at 2 m. The volume (in dm^3) was estimated as $0.065659\ (DN)^{1.768431077}\ (AT)^{1.137733502}$, equation for young trees in plantations of *C. odorata* (Sánchez-Monsalvo & García-Cuevas, 2009). A taper index of the first log of the tree was calculated as the ratio of the trunk area calculated by sections using the diameters at 0.30, 1.30 and 2 m divided by the product area of the diameter at 0.30 m x 2 m (Sánchez-Monsalvo et al., 2003). A higher value indicates a more cylindrical shape.

The number of attacks of *H. grandella* (intensity) in each ramet was evaluated. Tolerance was then evaluated as the ability to recover from damage (Newton et al., 1995; Ward, Wightman, & Rodríguez-Santiago, 2008). Five categories were defined in response to the attack: 0) without shoots; 1) several shoots but without apical dominance; 2) several shoots but one took apical dominance; 3) a single shoot and 4) ramet without attack (equivalent to evasion to damage).

Finally, for comparative purposes the vigor of the ramets was estimated according to Ramírez-García et al. (2008) as: 1) poor vigor = yellowish, thin, incomplete and twisted foliage or inclined stem; 2) regular vigor = dull to yellowish green foliage, medium dense foliage, and fissured stem; 3) adequate vigor = dense foliage, intense green foliage and straight stem. The evaluation was conducted in the second year during the summer, season of mating and damage by *H. grandella,* when the cedar plants have tender and turgid foliage and buds (Ward et al., 2008). Being this variable of categorical type, it was only used as a classifier for comparison purposes of the clones. An analysis of variance was performing for vigor categories.

The components of variance were estimated using the SAS "Mixed" procedure (Littell, Milliken, Stroup, & Wolfinger, 1996), with the model: $Y_{ij} = \mu + B_i + C_j + \varepsilon_{ij}$, where Y_{ij} *is the observed trait value of the j-th clone in the i-th block*, μ is the overall mean, B_i *is the effect of the i-th block* C_j is the random effect of the j-th clone ~ NID $(0, \sigma^2_c)$ and ε_{ij} is the random error ~ NID $(0, \sigma^2_e)$; i = 1, 2,…, 12; j = 1, 2,…, 40. For the variables of growth, stem taper index, number of attacks and response to damage, broad-sense heritability was estimated for ramets $(H^2_i = \sigma^2_c / \sigma^2_c + \sigma^2_e)$ and clone mean $(H^2_C = \sigma^2_c / \sigma^2_c + [\sigma^2_e / i])$, i value was of 11.64, the average living ramets by block. The estimation of H^2_C is of practical use since selection is commonly performed on the basis of the average value of the clones, that is, a clone is selected as such and not a copy of the clone. H^2_C is affected by the number of replications (i), it is also necessary to estimate H^2_i to compare the level of existing genetic variation (Ignacio-Sánchez, Vargas-Hernández, López-Upton, & Borja-de la Rosa, 2005).

Phenotypic correlations were calculated as Pearson product-moment coefficients of correlation (Ignacio-Sánchez et al., 2005). Genetic correlations were estimated using $r_{gxy} = (Cov_{(x,y)} / [\sigma^2_{Cx} * \sigma^2_{Cy}]^{-2})$ (Falconer & Mackay, 1996), where $Cov_{(x,y)} = (\sigma^2_{C(x+y)} - [\sigma^2_{Cx} + \sigma^2_{Cy}]) / 2$ (White & Hodge, 1988), $\sigma^2_{C(x+y)}$ is the genetic variation of the variable x+y, obtained from the sum of the two traits involved; and σ^2_{Cx} and σ^2_{Cy} genetic variation in each trait.

The expected genetic gain was estimated as $Gg = i\, H^2_c \sqrt{\sigma^2_P}$ (Falconer & Mackay, 1996), where σ^2_P is the phenotypic variance of the clone means and i is the selection intensity. It was considered the propagation of four best clones in volume (the trait of greater genetic gain) for the selection (10 % of the clones), thus i = 1.76 (Mullin & Park, 1992; Falconer & Mackay, 1996). In addition, the genetic gain was obtained as a percentage over the mean without selection. In order to determine the effect on the other characteristics by selecting the best clones based on the volume, the correlated response to the selection was calculated with $CR_y = i_x H_x H_y r_{gxy} \sigma_{Py}$ (Falconer & Mackay, 1996). Where $i_x = 1.76$, H_x is the square root of the volume's heritability; H_y is the square root of the heritability for the character that will experience the correlated response; r_{gxy} is the genetic correlation between both variables, and σ_{Py} is the square root of the phenotypic variance of the clone means of the character that will be modified by the correlated response. This procedure was done in the opposite way, which is, selecting the other variables to determine their effect on the volume.

RESULTS

Mean values of growth traits and response to attack by *Hypsipyla grandella*: The clone trial after two years had a survival of 97 %. Of the 15 dead ramets, 10 were from clone 85, suggesting incompatibility. The ramets of the assay were 2.87 SE = 0.04 m average height, 2.35 SE = 0.05 cm in diameter at breast height, and 1.1312 SE = 0.0529 dm^3 average volume.

Vigor of 32.8 % of the ramets was adequate, that of 32.0 % was regular and that of 35.2 % was poor. The most vigorous clones were those less attacked (0.95 *vs* 1.14 attacks on average, P = 0.016). They had greater growth (vigorous trees were 1.24 dm^3 volume, *vs*. 0.93 dm^3 of the weaker trees, P = 0.02) and better generation of sprouts (P = 0.001).

The average number of *H. grandella* attacks recorded was 1.08 ranging from 0 to 3 attacks per ramet in 2 years. Thirty-eight clones had 1 to 5 ramets that were not attacked and eight clones were not attacked on more than 50 % of their ramets; 9.9 % of the ramets were not damaged, indicating that they evaded attack (category 4). The most common response to *H. grandella* attack was generating several sprouts, 282 ramets (14.2 % category 1 and 46.3 % category 2). Most of the ramets produced one early dominating sprout; 29 % of the ramets had a single apical sprout (category 3), that is, high tolerance to damage. Only 0.6 % of the ramets had no response to damage by the insect.

Heritability: Growth variables had high genetic control, and for the taper index, it was moderate (Table 1). For number of attacks and response to damage by *H. grandella*, genetic control was relatively reduced (H^2_C = 0.33 and 0.28).

Genetic and phenotypic correlations: Genetic correlations (r_g) were higher than phenotypic correlations (r_p) (Table 2). The r_g for growth characteristics at two years were high and positive ($r_g \geq 0.95$); these variables are closely related and correlated positively with taper index, and particularly with volume (r_g = 0.88). This indicates that when clones with more voluminous trunks are propagated, the propagules will be more cylindrical in the first part of the trunk.

Response of the clones to *H. grandella* attack positively correlates, phenotypically and genetically, with taper index, diameter, height and volume. This means that the clones that repair the damaged area by quickly reestablishing apical dominance, or by evading attack, will grow more. Genetic correlation between response to and incidence of attacks was negative and high; that is, when selecting materials with better response, the propagules should have fewer attacks, and *viceversa*.

Clones 58, 91, 2, and 13 had the largest volume (Table 3). Clones 91, 52, 58, and 59 had the fewest attacks, partly explaining the larger volume of clones 91 and 59 (the only two with more than 3 dm^3), and it is a possible sample of evasion as a mechanism of resistance to attack by *H. grandella*. Clones 2, 46, 13, and 76 had the best response to attack by this

TABLE 1
Mean, standard error (s.e.), variance of clones (σ^2_C), error variance (σ^2_e), heritability of ramets (H^2_i) clone mean heritability (H^2_C) and phenotypic variance of the clone means (σ^2_P) for growth and resistance to *Hypsipyla grandella* characteristics in a clonal trial of *Cedrela odorata*

Characteristic	Mean ± SE	σ^2_C	σ^2_e	H^2_i	H^2c	σ^2_P
DBH (cm)	2.322 ± 0.049	0.2916	0.7958	0.27	0.81	0.3716
Total High (m)	2.841 ± 0.045	0.2438	0.6887	0.26	0.80	0.3209
Volume (dm^3)	1.390 ± 0.066	0.5263	1.4512	0.27	0.81	0.6436
Stem taper index	0.869 ± 0.004	0.00062	0.00469	0.12	0.61	0.0015
Number of attacks	1.117 ± 0.028	0.0145	0.3438	0.04	0.33	0.0440
Response to damage	2.326 ± 0.040	0.0246	0.7185	0.03	0.28	0.0858

TABLE 2
Genetic (below the diagonal) and phenotypic correlations (above the diagonal) of the traits evaluated in a clonal trial of *Cedrela odorata*

Characteristic	DBH	Total High	Volume	Stem taper index	Number of attacks	Response
DBH	-	0.93	0.91	0.35	-0.07	0.24
Total High	0.96	-	0.89	0.57	-0.11	0.34
Volume	0.97	0.95	-	0.37	-0.11	0.30
Stem taper index	0.39	0.48	0.88	-	-0.08	0.36
Number of attacks	-0.29	-0.24	-0.31	-0.36	-	-0.47
Response to damage	0.51	0.56	0.62	0.74	-0.83	-

TABLE 3
Average values of the best four clones of *Cedrela odorata* for each variable

Clone	DBH (cm)	Clone	High (m)	Clone	Volume (dm^3)	Clone	STI[1]	Clone	No. of attacks	Clone	Response
58	3.570	58	4.037	58	3.378	85	0.970	91	0.750	2	2.917
91	3.504	46	3.868	91	3.035	91	0.918	52	0.833	46	2.750
13	3.474	19	3.650	13	2.949	43	0.913	58	0.833	13	2.667
2	3.158	2	3.616	2	2.779	19	0.911	59	0.833	76	2.667
Mean	3.427		3.793		3.035		0.928		0.813		2.750

[1] = stem taper index.

TABLE 4
Expected genetic gain for direct selection, for the volume by selecting another variable and for the other variables when using volume as a criterion of selection

Selection variable	Expected genetic gain							
	by direct selection for each variable		for the volume by indirect selection using the other variables			for the other variables by indirect selection using volume		
		%	dm^3	%	efficiency[1]		%	efficiency[1]
DBH	0.8691 cm	37.43	1.1138	80.13	0.9757	0.8463 cm	36.44	0.9736
High	0.8023 m	28.24	1.0780	77.55	0.9444	0.7697 m	27.09	0.9593
Volume	1.1415 dm^3	82.13	–	–	–	–	–	–
Taper index	0.0410	4.72	0.8730	62.81	0.7648	0.0418	4.82	1.0212
Number of attacks[2]	-0.122	-10.88	0.2319	16.68	0.2032	-0.061	-5.43	0.4991
Response to the attack	0.147	6.31	0.3962	28.50	0.3471	0.145	6.22	0.9857

[1] = genetic gain by indirect selection / genetic gain by direct selection, [2] = when selecting clones with fewer attacks, the volume increases.

insect. Most of the ramets of clone 13 formed only one dominant shoot, evidencing tolerance to damage caused by the insect. Clone 2 had several ramets that escaped attack and others with adequate growth after damage, apparently combining the two strategies of resistance to damage by this insect.

Genetic gain: Expected genetic gain in volume was two times more than in diameter at breast height and almost three times that of height, and 13 times greater than that expected for response to attack (Table 4). By using the four best clones in volume, a genetic gain of 82 % will be obtained in this variable, while if large-scale planting of the four with best recovery from *H. grandella* attack, gain would be only 6.3 % in reaction to damage.

Indirect selection: With the selection of another variable different from that of volume, less genetic gain is obtained for this trait when clones are propagated massively. However, selection by diameter is quite efficient since if diameter is used, a genetic gain of 80.12% in volume is obtained (Table 4); an efficiency of 97.5 % would be obtained comparing to select directly by volume. The selection of clones with the best response to attack by *H. grandella* would result in a genetic gain of 62.8 % in volume.

DISCUSSION

The 40 tested clones had a growth rate in height superior to that of a provenance trial in Central Mexico, conducted in the same area and evaluated after five years (Sánchez-Monsalvo et al., 2003). In fertile well-drained soils of Central America, annual growth rates of up to 3 m in height and 4 cm in diameter have been reported (Cintron, 1990). The taper index of the trunk was 0.8695, nearly cylindrical. A cylindrical trunk is associated to certain resistance to *H. grandella* attack (Briceño-Vergara, 1997).

Hypsipyla grandella larva attacks on *C. odorata* shoots is greatest at two years of age, when the tree is most vulnerable because its growth depends on a single main shoot (Newton et al., 1995). The female insect looks for individuals with vigorous foliage for optimal development of the larvae (Macías-Sámano, 2001; Gara, Allan, Wilkins, & Whitmore, 2009). In our study, the vigorous trees grew more; if they were attacked, they were better at tolerating the damage. In addition, if foliage quality (vigor) varies among ramets of the same clone because of differences in the root stock, estimation of heritability by resistance cannot be high.

The results of high heritability of growth variables agree with the findings of Sánchez-Monsalvo et al. (2003). In a clone assay in Cuba, H^2_C values of 0.85 and 0.62 were found for height and diameter (Lahera, Alvarez, & Gamez, 1994). The magnitude of heritability of growth variables in this population revealed a favorable situation for selection of *C. odorata* clones that could have important genetic gains if these clones were used in commercial plantations (White et al*.,* 2007). The results obtained are notable since the 40 clones included in the test were selected for their resistance to *H. grandella* damage and little progress would be expected. With the four best clones in volume, a genetic gain of 82 % is obtained and resistance to the insect is moderately improved due to the negative genetic correlation. Negative values indicate that clones of more rapid growth and better taper shape (more cylindrical shape) will produce propagules with lower number of attacks, either because of evasion mechanisms or antixenosis, that is, it is not preferred by the insect (Sánchez-Monsalvo et al., 2003). Moreover, the clones that recover better forming a single growth sprout will grow more. However, selecting clones directly for fewer attacks will generate a small gain in volume (Table 4) because of low heritability of the former variable and its low genetic correlation with volume (Table 2). Wind can modify the insects' flight direction causing fortuitous attacks, and closeness to trees that have already been attacked modifies exposure to others. Thus, evaluation of insect attack is not precise (López-Upton, Blakeslee, White, & Huber, 2000).

Volume was the variable with the largest gains. However, genetic gain by indirect selection may make it sufficient to measure only diameter at breast height (DBH) for improving this species. Operatively, it is much faster and economical to measure only diameter at breast height. Moreover, the efficiency of measuring only DBH to predict tree height was 0.96 % (28.24 % of genetic gain by direct selection vs. 27.23 % by indirect selection with DBH, data not shown) and 0.81 % of gain between DBH and response to attack.

The main benefit to early selection is that, in the critical stage of borer attack, genotypes that are tolerant with good response to damage and adequate growth or that escape insect attack can be obtained. For example, it has been determined that attraction or repellence of the pest is related to phenol and limonoid type secondary metabolites (Mariscal-Lucero, Rosales-Castro, Sánchez-Monsalvo, & Honorato-Salazar, 2015), which make these materials an option for use in the central region of Veracruz. The main limitation for commercial plantations of *C. odorata* is attack by *H. grandella*, which causes costs to go up and even total abandonment of plantations (Cornelius & Watt, 2003). For this reason, selecting less attacked clones (mechanisms of evasion) or with better response after attack (tolerance) will produce tangible benefits. The use of resistant *C. odorata* genotypes is a promising strategy for control of the shoot and bud borer, complemented with integrated pest management and implementation of silvicultural techniques to promote vigorous development of the plantation, including its establishment in fertile sites that favor its growth (Hilje & Cornelius, 2001). Besides corroborating the results with older plants, it is necessary to establish genetic assays in other regions to determine whether the best clones for one site are the best in others and recommend their widespread use.

Mean heritabilities of dasometric characteristics of clones were high, while heritability of the response to attack by *H. grandella* was low. Genetic correlations for growth characteristics after two years were very high and positive and with the characteristics of resistance to attack they were positive, but low, indicating that selection of rapid growth clones will not increase damage by *Hypsipyla grandella*. Using the four best clones in terms of volume, 10 % selection intensity, a genetic gain of 82 % is obtained for volume and 6.22 % for response to *H. grandella* attack. Evaluating only diameter at breast height for selection can adequately improve both growth in volume and trunk quality as well as resistance to the borer.

Ethical statement: authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgements section. A signed document has been filed in the journal archives.

RESUMEN

Parámetros genéticos de crecimiento, y resistencia al barrenador de brotes, en clones jóvenes del árbol ***Cedrela odorata*** **(Meliaceae).** El daño por *Hypsipyla grandella* limita el éxito de las plantaciones de *Cedrela odorata*. El periodo más crítico y vulnerable es durante los primeros tres años. El objetivo del estudio fue estimar la ganancia genética esperada en la selección de clones de mayor crecimiento y resistentes al ataque del insecto. Un ensayo de 40 clones producidos por injertos fue plantado en Veracruz, México. Con datos a la edad de dos años se estimaron: la heredabilidad, correlaciones genéticas y ganancia genética de los clones. El ensayo presentó una supervivencia del 97 % (466 rametos vivos en total), con 2.84 m de altura y 2.32 cm de diámetro normal promedio. El 9.9 % de los rametos no presentaron ataques, indicando evasión, y se estimó un 0.6 % sin respuesta al ataque. Con respuesta al ataque 89.5 % de los rametos (diferentes niveles de tolerancia): 29 % con un solo brote, 14.2 % con varios brotes, y 46.3 % con un brote dominante de varios brotes formados. La heredabilidad clonal del diámetro normal, altura, volumen, índice de conicidad, número de ataques y respuesta al ataque fue de H^2_c = 0.81, 0.80, 0.81, 0.61, 0.34 y 0.26, respectivamente. Las correlaciones genéticas entre la altura, diámetro y volumen fueron ≥ 0.95, y del volumen con la incidencia y la respuesta al ataque de r_g = -0.31 y r_g = 0.62, es decir se presentó una disminución en el número de ataques y el aumento moderado en la tolerancia. Con una intensidad de selección del 10 %, seleccionando los cuatro clones de mayor volumen se obtuvo una ganancia genética de 82 % para el volumen, una disminución de 10.9 % de ataques y 6.3 % mejor recuperación del daño, esto es más tolerancia al ataque del insecto. La ganancia genética justifica la utilización de los mejores clones en plantaciones comerciales para Veracruz.

Palabras clave: barrenador de brotes; correlaciones genéticas; ganancia genética; heredabilidad; resistencia a insectos.

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