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PROGENY TEST ANALYSIS AND POPULATION DIFFERENTIATION OF MESOAMERICAN MAHOGANY *(Swietenia macrophylla)*

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Palabras clave: *Swietenia macrophylla,* heredabilidad, fitomejoramiento, evaluación de progenies, poblaciones naturales.
Keywords: *Swietenia macrophylla,* heritability, tree improvement, progeny test, natural populations.

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ABSTRACT

The performance of open-pollinated single tree families of mahogany *Swietenia macrophylla* from populations in Mesoamerica was evaluated in 3 trials established in northern Costa Rica. The trials at Upala and Lagartera (Los Chiles) contain families of Costa Rican origin, while the Laberinto (Los Chiles) trial contains material from 6 Central American countries and Mexico. Data on root-collar diameter, total height, survival, and *Hypsipyla grandella* attack were collected. The analysis indicate significant family and population differences for height and diameter, but *H. grandella* attacks were uniform over all sites. Heritabilities at 1.7 years for Upala were 0.54±0.02, and 0.55±0.02 for diameter and height, respectively; after this measurement this trial was burned completely as a result of drought in El Niño year, so further measurements could not be made. Lagartera at 0.7 years presented heritabilities for diameter and height of 0.55±0.008 and 0.57±0.008. Laberinto presented heritabilities of 0.48±0.01 for diameter (2.9 years), 0.6±0.01 for height, 0.1±0.002 for *H. grandella* attack; 0.07±0.002 for number of shoots, and 0.18±0.003 for stem form 2.7 years

RESUMEN

Análisis de experimentos de progenies (familias) de una colección Mesoamericana de caoba *(Swietenia macrophylla).* El desarrollo de progenies de árboles madre de polinización abierta de caoba, *Swietenia macrophylla,* fue evaluado en 3 ensayos establecidos en la Zona Norte de Costa Rica. Los de Upala y Lagartera (Los Chiles) incluyen familias originarias de Costa Rica, mientras que el de Laberinto (Los Chiles) presenta material de 6 países centroamericanos y México. Se recolectó información sobre diámetro a la base, altura total, sobrevivencia, y ataque de *Hypsipyla grandella.* Los análisis indican diferencias significativas a nivel de progenie y procedencias para diámetro y altura, pero el ataque de *H. grandella* fue uniforme en todos los sitios. Las heredabilidades a los 1,7 años para Upala fueron de 0,54±0,02 y 0,55±0,02 para diámetro y altura respectivamente. Después de esta medición el ensayo se quemó por completo, debido a sequías bajo el efecto de El Niño, razón por la cual no pudieron efectuarse mediciones posteriores. El ensayo en Lagartera, de 0,7 años, presentó heredabilidades para diámetro y altura de 0,55±0,008 y 0,57±0,008. En Laberinto, las heredabilidades obtenidas fueron de 0,48±0,01 para diámetro (2,9

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after planting. Flooding in 1998 damaged the Lagartera trial, which was also severely attacked by *H. grandella.* This resulted in very low heritabilities, with large standard errors; therefore its genetic values in the first measurement are considered unreliable. The plantation recovered, and after 3 years genetic values were comparable with the other 2 trials. Isolated mother trees produced slow-growing families in most cases, in comparison with the clustered ones or those in natural dense forests, suggesting inbreeding mechanisms.

años), 0,6 ± 0,01 para altura, 0,1±0,002 para el ataque de *H. grandella;* 0,07±0,002 para número de ejes, y 0,18±0,003 para la forma a los 2,7 años de plantado. Las inundaciones en 1998 dañaron el ensayo de Lagartera, que además fue severamente atacado por *H. grandella.* Esto se manifestó en heredabilidades muy bajas con errores estándar altos, por lo tanto los valores genéticos en la primera medición se consideran poco confiables. La plantación se recuperó y después de 3 años los valores genéticos fueron comparables con los otros 2 ensayos. En general, los árboles madre que estaban solitarios, produjeron progenies de crecimiento lento, en comparación con las progenies de árboles madre que estaban en grupos o en bosque natural, lo que sugiere mecanismos de endogamia.

INTRODUCTION

Swietenia macrophylla is an important tree species in the neotropics, it is found in the rainforests between latitudes of 22º North and 20º South of the Equator. Graham (1999) indicates that pollen from an ancestor of the Meliaceae family was present in the Pliocene and Miocene in Mexico, which led us to believe that the species was present there many years ago.

In Meliaceae, *Swietenia* is the most important genus for wood production followed by *Cedrela.* Beginning in the 19th century and until now, the mahoganies have been the pillar of the forest industry of Meso and South America. They cover the neotropical territory from Mexico to Brazil and Argentina, and the Caribbean Islands.

During the last decades, the *Swietenia* natural populations have been severely affected and reduced by several factors, mainly due to deforestation processes that diminish populations as well as selective logging that affects the genetic makeup of populations.

The Mexican and Central American populations have been heavily exploited (Matamoros and Seal 1996), while current logging of natural populations for the international market occurs in Brazil and Bolivia.

These tree species present a low proportion of adult trees, which joined with a low natural regeneration rate, increase their rareness.

The extensive harvest of *S. macrophylla* for its valuable wood has resulted in high concern over its conservation status and sustainable use (Proposed Amendment to CITES Appendix II 1997), and a strong focus of current research on these topics (Negreros and Mize 1994, Gullison *et al.* 1996, Snook 2003, Navarro *et al.* 2003). The FAO is establishing a network to facilitate the genetic conservation of *S. macrophylla,* and other species of the Meliaceae family (Patiño 1997). *S. mahagoni* has already been heavily exploited, and both *S. mahagoni* and *S. humilis* were listed under Appendix II of CITES in 1992 (Patiño 1997).

In 1994, CATIE and ITE (Institute of Terrestrial Ecology) together with other institutions and the European Union support, made a collection of mahogany germplasm in seven Mesoamerican countries. With this material studies of genetic variation were done, gene banks and progeny trials in Costa Rica and Mexico were established. This work have been done considering the importance of using both molecular and quantitative markers for gene conservation and breeding.

This paper investigates three major aspects: (1) The genetic variation throughout Mesoamerican populations and families of *Swietenia macrophylla;* (2) The growth variation in families and populations of mahogany; (3) The influence of collecting isolated trees in their progeny performance.

The shootborer *Hypsipyla grandella* is a Lepidopteran that co-evolved with some Meliaceae species; it attacks preferentially; *Swietenia, Cedrela* and *Carapa.* Therefore, the adaptation of different *Swietenia* populations to the shootborer attack was also studied in these experiments.

MATERIALS AND METHODS

Collection

Field collection of leaves, herbarium material and seeds from natural *Swietenia* populations were carried on. The populations sampled covered a wide range of environments, population densities and degrees of exploitation.

Prior to collection, general information was sought on: (1) climatic data - including topography, geology, soil, vegetation, land use; and (2) socio-economic data - including population, agricultural surveys, economic indicators, and information on the infrastructure, roads and other means of transportation.

This information was used to:

- Define eco-geographically distinct areas in the distribution of the species for sampling;
- Estimate the likely extent of within-species variation, based on the heterogeneity in its natural distribution area;
- Assess the threat of genetic erosion; and
- Predict the best timing for collecting.

Information concerning the human and physical environment was also useful for field orientation and for thorough documentation of the collecting mission.

Collections were made from 42 different mahogany populations, ranging from Mexico to Panama. The number of trees sampled within populations varied according to its size and accessibility. Populations in each country were located using the expertise of local collaborators and previous reconnaissance. The approximate extent of each population was gauged as objectively as possible.

Trees were sampled along a transect, the initial bearing was randomly selected. Mahogany trees were either solitary or clumped. When trees were clumped, collections were restricted to individual trees more than 100 m apart. To obtain maximum diversity and avoid seeds from related trees, only five individual trees per clump were collected. Up to a maximum of 50 trees were collected within each population along the transect. Only mature trees were selected. In some cases, populations were so sparse that only solitary trees could be collected.

Herbarium material was dried and mounted at CATIE's herbarium, and seeds were dried and stored at the CATIE seed bank.

Table 1 and figure 1 show the sites of collections in Central America and Mexico. This is the most extensive single-tree collection of mahogany that has been made in this area. The Institute of Tropical Forestry in Puerto Rico made an earlier provenance collection of *S. macrophylla* in 1964 and 1965. At that time, 14 provenances were collected in Mexico and Central America (Boone and Chudnoff 1970).

Field trials

To observe variation in the quantitative genetic parameters, 3 of the 6 measurements (before and after the strong attack of *Hypsipyla grandella*) are presented in this article. Details about experimental design and dates of measurement are shown in table 2.

In the first measurement, root collar diameter, total height, and *H. grandella* attack were analyzed, while variables of stem form and attack response were added in the last one.

Table 1. Populations of *Swietenia macrophylla* sampled in Central America and Mexico. Latitude and longitude are given in decimal degrees.

Country	Population	Latitude (N)	Longitude (W)	Altitude (masl)	No. trees sampled
Mexico	Naranjal, Quintana Roo	19.36676	88.46131	50	15
	Nuevo Becal, Campeche	18.80756	89.32721	150	46
	San Felipe, Quintana Roo	18.74599	88.35480	50	20
	Escarcega, Campeche	18.60068	90.82924	50	9
	Laguna Kana, Quintana Roo	19.44662	88.44116	50	5
	Madrazo, Quintana Roo	18.03352	89.24794	150	5
Belize	Las Cuevas, Cayo	16.75180	89.00106	600	10
	San Pastor, Cayo	16.70621	88.97249	600	26
	New María, Cayo	16.82337	89.00043	600	13
	Grano de Oro, Cayo	16.71945	89.01754	600	25
	Río Bravo, Orange Walk	17.84534	89.03319	50	35
Guatemala	Bethel, Petén	16.48350	90.50282	120	32
	Tikal, Petén	17.22520	89.61216	250	56
	La Técnica, Petén	16.91341	90.91274	125	47
	Bio-Itza, Petén	16.85234	90.93113	20	2
Honduras	Corrales, Colón	15.51259	85.94703	650	12
	Lancetilla, Atlántida	15.73991	85.45721	30	35
	Mangas, Colón	15.51259	85.94703	680	1
	Comayagua, Comayagua	14.46010	87.68314	500	5
	Otoro, Siguatepeque	14.52160	88.00089	600	3
Nicaragua	Terciopelo, Sahsa	14.00675	83.93559	60	26
	Mukuwas, Bonanza	14.04645	84.49976	200	38
Costa Rica	Marabamba, Los Chiles	10.94656	84.63752	45	67
	Caño Negro, Los Chiles	10.91774	84.42994	55	37
	Santa Cecilia, La Cruz	11.06101	85.27857	300	12
	Upala, Alajuela	10.53508	85.08336	50	13
	Pocosol, Liberia	10.53364	85.35957	270	37
	Playuelas, Los Chiles	10.92175	84.69872	35	4
	San Emilio, Los Chiles	10.97147	84.77328	30	64
	Abangares, Guanacaste	10.06600	84.49641	50	6
	Orotina, Alajuela	9.55140	84.29620	250	1
	Turrubares, Alajuela	9.51212	84.31335	350	1
	Chapernal, Puntarenas	10.07469	84.82586	50	10
Panama	Quintín, Darien	8.22469	78.08581	70	10
	Punta Alegre, Darien	8.26119	78.23616	10	5
	Tonosí, Los Santos	7.44882	80.29070	100	15
	Gatún, Gatún	9.26800	79.91958	20	4
	Paraíso, Paraíso	9.03278	79.62656	50	1
	Balboa, Ancon	8.95500	79.95430	50	1
	Summit, Ancon	9.06489	79.64622	50	3
	Calabacito, Veraguas	8.24636	81.08095	50	1
	Coiba, Veraguas	7.50102	81.69603	10	1
	Cerro Hoya	7.32321	80.59560	500	23
	Total				782

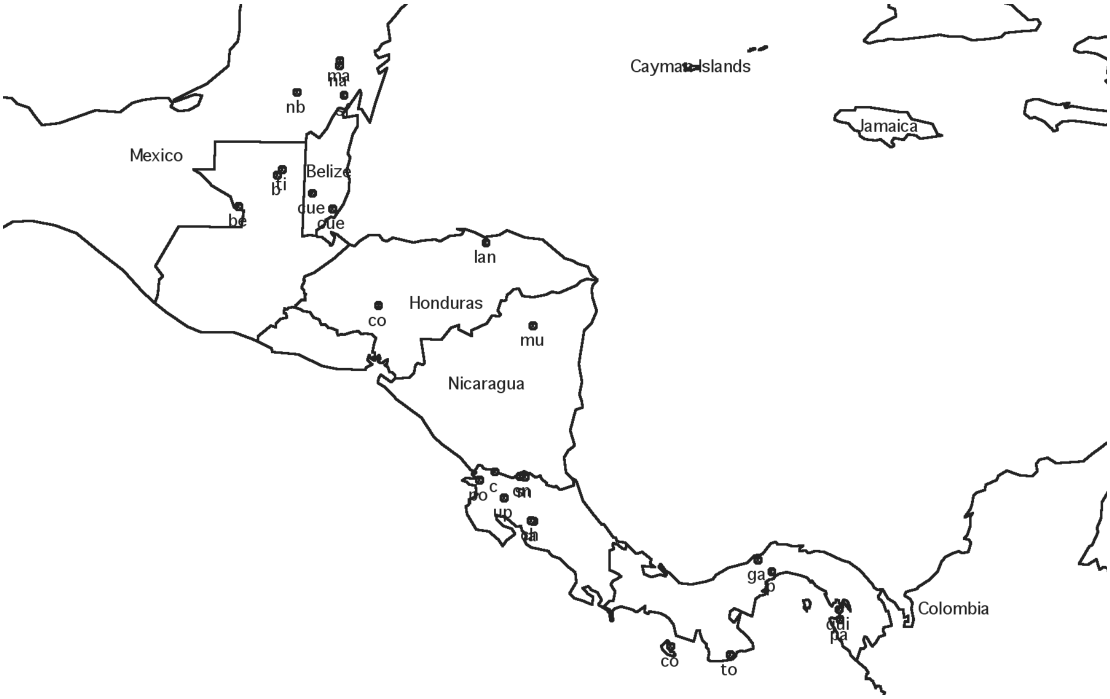

Fig. 1. Mesoamerican distribution of the populations planted in the trials of *Swietenia macrophylla.*

Table 2. Field trials data.

Trial	Location (GPS)	Experimental design	Planting date	Date of measurements in days after planting	Spacing (m)
Upala	10.53409 N, 85.02287 W	15 blocks, 31 families, 2 trees per plot, in lines with *Calophyllum brasiliense*	12th June 1996	621	3 X 3
Lagartera, Los Chiles	10.58853 N, 84.43002 W	15 blocks with 31 families and 3 trees per plot.	19th July 1996	585, 1658, 1812*	3 X 3
Laberinto, Los Chiles	10.94774 N, 84.70994 W	15 blocks with 91 families and 2 trees per plot.	14th June 1997	251, 979, 1054*, 1327	3 X 3

* only for diameter

The experiments were measured for total height (cm) from the ground to the terminal shoot, diameter was measured at the root collar and the attack of *H. grandella* was taken as a discrete variable indicating presence or absence of attack.

The trials were established at three sites in northern Costa Rica. Trials at Lagartera and Upala (Table 3) contain Costa Rican families. The trial at Laberinto, established 1 year later, contains populations from Central America and Mexico (Table 4). Laberinto has some populations in common with trials at Lagartera and Upala.

For the measurements taken during 2000 and 2001, only the trials at Laberinto and Lagartera were evaluated, and the new variables were evaluated as:

Table 3. Costa Rican families planted in trials at Lagartera (Los Chiles) and Upala.

Population	Nº mother trees (Family)	Latitude (GPS)	Longitude (GPS)
Caño Negro I	643, 644,645, 646, 647, 648, 649, 650	10.94774	84.70994
Caño Negro II	651	10.94705	84.72119
Caño Negro III	652	10.94646	84.72319
Caño Negro IV	653	10.94774	84.70994
Playuelas I	658	10.91815	84.69996
Playuelas II	660	10.92770	84.68567
Playuelas III	661	10.92635	84.68893
Marabamba I	665*	10.95426	84.65771
Marabamba II	668, 673, 674,6 76	10.95426	84.65771
Marabamba III	680, 681 682	10.95403	84.65751
Marabamba IV	683	10.97844	84.70361
San Emilio I	684, 685, 686, 687,688, 689	10.97235	84.77287
San Emilio II	690	10.95402	84.77411
San Emilio III	691	10.53615	84.47122
San Emilio IV	692	10.58191	84.46671
San Emilio V	693	10.95971	84.77346

* Family 65 was planted only at Lagartera. Roman population numbers indicate different grouping of trees within the collection transect.

- Form: 1 = straight 2 = leaning 3 = crooked
  4 = coppice 5 = stump

- Response to the attack:

1 = One shoot after the attack
2 = Two shoots (bifurcation) after the attack
3 = Three shoots after the attack
4 = Four or more shoots after the attack
5 = Bad stem form by other damages

For both measurements the variable isolation (solitary) of the mother tree was added, considering : 1. Isolated mother tree (no other trees of the same species) at a distance of less than 500 m; 2. Semi-isolated (other trees no closer than 100 m); and 3. Mother tree in clusters or associated with more than 2 trees in a radius of less than 100 m. This variable was analyzed with orthogonal contrasts, analysis of variance and Tukey means comparisons.

We examined a total of 92 families from 7 populations: Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica and Panama.

The 3 field trials are all in the life zone referred to by Holdridge (1967) as Tropical Moist Forest with climatic association. This life zone is characterized by having a biotemperature between 24 and 25°C and around 2500 mm of annual rainfall with a dry period of approximately 3 months.

The Laberinto trial was established in northern of Costa Rica in soils classified by Perez *et al.* (1978), as belonging to the Typic Tropaquept family fine silty isohyperthermic. These gley and humic gley soils are found in drained alluvial valleys, and show little evolution and presence of organic accumulations on the surface. The topography is flat in all sites.

The Lagartera trial is found on fine clay isohyperthermic soils of the Aquic Distropept family. These soils, characteristic of old terraces with little evolution, tend to be slightly acid, and the high clay content may cause drainage problems.

The Upala trial is located on fine clay isohyperthermic, reddish soils of the Oxic Dystropept family. Such soils are deep, but low in bases and associated with poor drainage.

Table 4. Families planted in trial at Laberinto, Los Chiles, Costa Rica.

Country	Population	Number of Family	Latitude GPS	Longitude GPS	Precipitation (mm)	Temperature (°C)	Dry months
MEXICO	San Felipe	11, 15, 16, 116	18.74599	88.3548	1300	25	4
MEXICO	Nuevo Becal I	121, 122, 125, 126, 129	18.80756	89.32721	1200	26	4
MEXICO	Nuevo Becal II	156, 157,159,160	18.80756	89.32721	1200	24	4
MEXICO	Naranjal	132, 133, 136, 141	19.35549	88.46355	1200	24	4
MEXICO	Madrazo	152, 153, 155	19.45218	88.44468	2000	26	4
BELICE	Las Cuevas I	22	16.7518	89.00106	2900	22	3
BELICE	Las Cuevas II	257	16.42754	88.58995	2900	22	3
GUATEMALA	Bethel	32, 326, 331, 343	16.4835	90.50282	1800	25	4
GUATEMALA	Bio-Itza	396	16.85234	90.93113	1955	28	5
GUATEMALA	Tikal I	3101	16.85009	90.9316	1955	28	5
GUATEMALA	Tikal II	3131, 3151, 3153	17.22520	89.61216	1955	28	5
HONDURAS	Lancetilla	427, 432, 434, 435, 436, 438, 440, 442, 443, 444, 445, 447	15.73991	85.45721	3278	25	3
HONDURAS	Comayagua I	453	14.45397	87.6597	1619	25	5
HONDURAS	Comayagua II	454	14.45398	87.65806	1619	25	5
NICARAGUA	Mukuwas	527, 528, 529, 531, 532, 533, 536, 541, 551, 556, 559, 560, 561, 562, 564,	14.04645	84.49976	2750	24	4
COSTA RICA	Caño Negro	644 *, 649 *	10.97774	84.70994	2885	24	3
COSTA RICA	Marabamba	682 *	10.95403	84.65751	2885	24	3
COSTA RICA	San Emilio I	687*	10.97235	84.77287	2885	24	3
COSTA RICA	San Emilio II	690*	10.95402	84.77411	2885	24	3
COSTA RICA	San Emilio III	693*	10.95971	84.77346	2885	24	3
COSTA RICA	Upala I	699	10.54085	85.09293	2558	25	4
COSTA RICA	Santa Cecilia	6109	11.06101	85.27857	2585	26	4
COSTA RICA	Abangares	6121	10.05493	84.49443	1940	27	5
COSTA RICA	Pocosol	6156	10.89688	85.60125	1510	26	6
COSTA RICA	Chapernal	6243, 6244, 6248, 6250, 6251	10.06589	84.53552	1940	27	5
COSTA RICA	Upala II	6253	10.84879	84.92218	2558	25	4
PANAMÁ	Quintin	73, 79, 710	8.25682	78.26795	2500	26	4
PANAMÁ	Punta Alegre I	711	8.04698	78.23505	2500	26	4
PANAMÁ	Punta Alegre II	713	8.26119	78.23616	2500	26	4
PANAMÁ	Tonosi	717, 719, 721, 724, 726	7.33517	80.48316	2500	25	4
PANAMÁ	Gatún	731, 732, 733	9.268	79.91958	2500	25	4
PANAMÁ	Paraíso	735	9.03278	79.62656	2500	25	4
PANAMÁ	Coiba	741	7.50102	81.69603	3500	25	4

* Also planted in trials at Upala and Lagartera.

Experimental design

A randomized block design was applied in all trials. Two tree family plots were planted at 3x3 m with 2 guard rows around the whole trial. In Upala trees were interplanted in lines with *Calophyllum brasiliense* at a 3x3 m spacing. Only Lagartera have 3 trees per family plots, details like number of families per block, families by site and blocks by site are described in table 2.

Preparation of the area involved plowing and raking the soil previous plantation. The plots were maintained with machete use and the herbicide Roundup (glyphosate).

The models used for the statistical analysis were:

- Random analysis of variance on individual trees

$Y_{ijk} = \mu + B_i + P_j + BP_{ij} + \varepsilon_{jkl}$
Y_{ijk} is the phenotypic value of the *k*th tree of the *j*th family in the *i*th block;
μ = population mean;
P_j = effect of the *j*th family;
B_i = effect of *i*th block
BP_{ij} is the interaction of *i*th block with the family *j*. Blocks and families are considered as random effects.

Thus, one may expect different family structures of the seeds from open-pollinated collections, sometimes self-pollinated due to isolation. Therefore, families of single mother-trees may be half-sibs, full-sibs or selfings.

The procedure (proc) in SAS for evaluating the last 2 measurements was:

```
proc glm;
class evaluation block population family;
model diameter height attack respatack form = eval block population
family(population) population*block eval*population*family family*eval(population);
means population;
means population/Tukey lines;
```

where eval is evaluation number and respattack is response to *H. grandella* attack.

The proc for the evaluation of the mother tree isolation for both the statement Contrast of GLM and Tukey means comparison was the following:

```
proc glm;
class block mothertree;
model diameter height attack shoots form =block mothertree;
means mothertree/Tukey lines;
contrast ‘1 vs 2y3’ mothertree 2 -1 -1;
contrast ‘2 vs 3’ mothertree 0 -1 -1;
```

The following parameters for growth in height and diameter were estimated based on individual mother trees: the additive genetic variance $\sigma^2_A = 4\ \sigma^2_{F,}$ where σ^2_F is the variance component due to open-pollinated families; the narrow-sense heritability on an individual tree basis $h^2 = \sigma^2_A / (\sigma^2_F + \sigma^2_{BXF} + \sigma^2_E)$, where σ^2_E is the residual variance. The standard errors for heritability were calculated following the formula by Dieters *et al.* (1995). The additive genetic coefficient of variation AGCV=100 (σ_A/x), where x is the population mean. Coefficient of population differentiation was calculated according to Kremer *et al.* (1997).

RESULTS AND DISCUSSION

Highly significant differences between families and populations for the variables height and diameter were found in the Laberinto trial (P<0.0001), (Tables 5 and 6). Differentiation of the populations is shown in the cluster of figure 2, a clear bifurcation between populations of

Table 5. Variance components and significancies at Laberinto trial (Los Chiles, Costa Rica).

Variables	Effect	Block	Pop	Fam (Pop)	BlockPop	Error	Among pops	Within pops	Qst
Diameter 1	VC	7.636	2.245	3.756	1.402	36.376	37.41	62.58	0.0695
	p	<.0001	<.0001	<.0001	<.0001				
Diameter 3	VC	27.134	24.623	7.446	12.1144	222.282	76.78	23.21	0.2924
	p	<.0001	<.0001	0.0062	0.0036				
Diameter 4	VC	22.985	42.898	5.523	6.177	221.83	88.59	11.40	0.4926
	p	<.0001	<.0001	0.0219	0.0329				
Height 1	VC	177.85	21.751	143.882	7.53	975.659	13.13	86.86	0.0185
	p	<.0001	<.0001	<.0001	0.0439				
Height 2	VC	581.821	741.867	208.146	358.877	4773.9	78.09	21.90	0.3082
	p	<.0001	<.0001	0.0002	<0.0001				
Height 4	VC	1231.8	3166.1	321.182	686.423	9888.4	90.78	9.21	0.5520
	p	<.0001	<.0001	0.0121	0.001				
H.g. resistance 1	VC	0.000187	0	5.48E-06	0.000371	0.0124	0	100	0
	p	<.0001	0.0711	0.6866	0.0001				
H.g. resistance 4	VC	0.000203	7.33E-05	0.000236	0.000323	0.0094	23.70	76.29	0.0373
	p	<.0001	<.0001	0.0124	0.0008				
Stem form 2	VC	0.007691	0.00314	0	0.0018	0.287	100	0	1
	p	0.0021	0.1529	0.2995	0.1033				
Stem form 4	VC	0.0279	0.04112	0.01147	0.05461	0.6193	78.18	21.81	0.3094
	p	<.0001	<.0001	0.0065	<.0001				
# shoots 2	VC	0.02278	0.01472	0.04602	0.02019	0.6895	24.23	75.76	0.0384
	p	0.0131	<.0001	<.0001	0.0683				
# shoots 4	VC	0.0686	0	0.0145	0.0026	0.642	0	100	0
	p	<.0001	0.302	0.0326	0.076				

Number after variables indicates dates of measurement: 1. 251 2. 979 3. 1054 4. 1327 days after planting

Table 6. Results of ANOVA, expected mean squares and genetic parameters for families of *S. macrophylla,* at Laberinto, Costa Rica.

	Mean (CV %)	Genetic parameters	Mean (CV %)	Genetic parameters	Mean (CV %)	Genetic parameters
	1998	1998	2000	2000	2001	2001
Diameter	19.8 (28)	h^2=0.55, AGCV=13	63 (24)	h^2=0.35± 0.01	71 (22)	h^2=0.48±0.01
Height	97.5 (30)	h^2=0.57, AGCV=14	267 (26)	h^2=0.41± 0.007	328 (31)	h^2=0.6±0.01
Attack	0.015 (720)	h^2=0.02	1 (0)	NC	0.98 (9)	h^2=0.1±0.002
# Shoots after attack of *H. grandella*			2.18 (38)	h^2=0.27± 0.004	2.5 (31)	h^2=0.07±0.002
Stem Form			1.12 (47)	h^2=0.04± 0.001	1.4 (57)	h^2=0.18±0.003

Costa Rica and Panama and the rest of Mesoamerica shows the genetic structuring of the species, these results are comparable with the ones obtained using molecular markers by Gillies *et al.* (1999). The attack by *H. grandella* showed no significant differences among families in the Laberinto trial. In table 5 variance components indicate differences among and within populations. At 251 days measurement variation within populations was greater than variation among populations, but for measurements at 979, 1054 and 1327 days, that condition changed, showing more variation among populations than within populations.

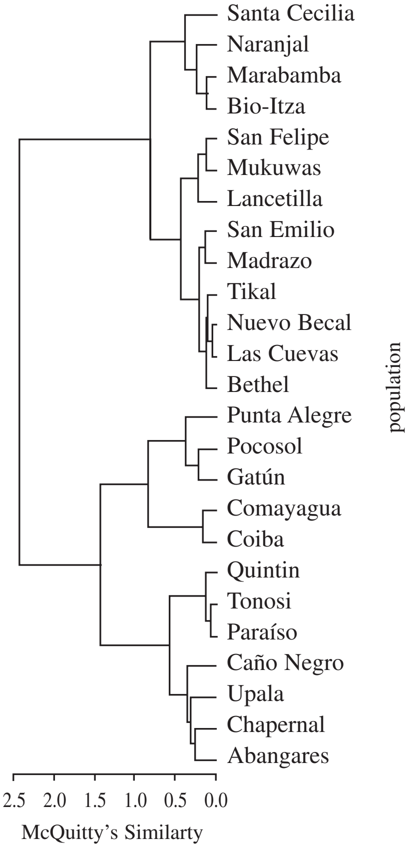

Fig. 2. Cluster for *Swietenia macrophylla* populations in Mesoamerica. Laberinto site (Los Chiles, Costa Rica) at 3.65 years.

Variation between different years of measurement was found for the coefficient of population differentiation (Qst) at 251 days and the other measurements. Also maternal effects possibly are affecting Qst values for the measurement at 251 days, where there is no differentiation for populations. From the results and comparison of means, it can be seen that populations show a variation between the best and the lowest population of approximately 30% and 21%, in diameter and height, respectively. At the family level, the variation for diameter was 125% between the highest and lowest family, while for height, the variation was 130%. The fact that there is more variation within than among populations has very important implications for gene conservation and breeding, as it suggests that local breeding activities would have high possibilities of securing substantial genetic gains.

Table 6 shows the heritabilities obtained for diameter and height at the Laberinto trial (0.55 and 0.57, respectively), and the additive genetic coefficient of variation (AGCV) with 13% for diameter and 14% for height. Pruning was applied to the experiment immediately after the measurement for the year 2000. Our heritability estimates are high in comparison with the ones shown by Cornelius (1994), who obtained mean heritabilities of 0.28 for height and 0.23 for diameter in a total of 67 studies, mainly with pines. For AGCV, Cornelius (1994) obtained a range of 5 to 15%; therefore, the present study suggests high levels of additive genetic variation for height and diameter.

The heritability in the production of shoots after attack by *H. grandella* is larger in year 2000, mainly because before that year trials were maintained without sanitary pruning. After the measurement of the year 2000, trees attacked by *H. grandella* were pruned, reducing the number of shoots.

In the measurement at 251 days at Laberinto, families 721 and 444 from Panama and Honduras, respectively, presented the best diameter increment (27 mm). Families 444 and 564 (Nicaragua) excelled in height (130 cm); these results were obtained using the measurements at 118 days as co-variables to eliminate the nursery or maternal effects in the ANOVA shown in table 7.

The best (721) and the worst (528) families differed by 127% in collar diameter. For height, the range from best (444) to worst (726) was 131%.

The Gatun (Panamá), Comayagua (Honduras) and Coiba (Panamá) populations showed the lowest performance, being inferior by 30% in diameter and 52% in height, compared to the best performers Bio-Itza and Santa Cecilia. It can be observed that variation among populations were lower than among families within locations. The trees from Bio-Itza

Table 7. Covariance analysis for families of *S. macrophylla,* at 339 days. Laberinto, Costa Rica. Co-variables diameter and height at 118 days after the sowing of the seeds were introduced in the model.

Trait/Effect	Degrees of freedom	Mean Square	F	P >F	Mean (CV %)
Diameter/Blocks (B)	14	302.29	12.35	0.0001	20.0 (21.3)
Families (P)	91	64.109	2.62	0.0001	
B * P	1229	24.469	1.35	0.0001	
D 118	1	16853.27	688.7	0.0001	
Error	1214	18.1885			
height/Blocks (B)	14	7502.00	12.70	0.0001	98.5 (21.7)
Families	91	1420.362	2.40	0.0001	
BxP	1229	590.7621	1.29	0.0001	
Alt 118	1	453304.9	767.3	0.0001	
Error (E)	1214	456.599			

(Guatemala), Tikal (Guatemala), Santa Cecilia (Costa Rica), Marabamba (Costa Rica) and Naranjal (México) came from natural stands composed by large populations; this is reflected in the superior performance of their families (381 cm of height and 77 mm of diameter in average for the five populations at 3.6 years).

Table 8 shows the analysis of variance for the family trial in Upala. As in the other trials, significant differences were found (P>0.0001) in diameter and height but not for the variable *Hypsipyla* attack. The growth of mahogany is overwhelming in this location (growth can be considered fast when root collar diameter increases by 2 cm per year and height more than 1 m per year). Mahogany registered more than 100% superiority in height increment to *Calophyllum brasiliense.* This reflects the different ecological behavior of the two species, mahogany being a light tolerant pioneer while *Calophyllum* is a shade tolerant climax species.

The individual narrow sense heritability estimates, for diameter and height, were 0.54 and 0.55, respectively in Upala trial.

The family with the best growth was No. 93 from San Emilio (see Table 3 for details), an important area of natural forest in northern Costa Rica. This family was superior by 45% to family 76 from Marabamba. Family 93 was 50% superior in diameter and height, compared to family 45 of Caño Negro (Costa Rica). These data show that

Table 8. Expected square means and genetic parameters for the trial of *Swietenia macrophylla* in Upala, Costa Rica at 621 days.

Trait	Effect	Mean square	P >F	Variance component	Mean (CV %)	Genetic parameters
Upala	Blocks (B)	1176.3	0.0001	20.85	55(14.6)	h^2=0.54 AGCV=7.4
Diameter	Families (P)	529.2	0.0001	17.45		AGCV=8
		138.34	0.0001	40.15		
		65.53		66.38		
Upala	Blocks (B)	29752.5	0.0001	567.68	246	h^2=0.55 AGCV=7.8
Height	Families(P)	12056	0.0001	373.39	(15)	AGCV=8
	BxP	2987.3	0.0001	850.82		
	Error (E)	1466		1466.88		
Upala	Blocks	0.61935	0.0001	0.008	0.8	h^2=0.065
Attack	Families	0.214551	0.0002	0.002	(36)	
	BxP	0.149037	0.0001	0.027		
	Error	0.094623		0.094		

local material of northern Costa Rica contain enough variation for an improvement program.

Table 9 shows the results of the Lagartera trial where flooding affected some blocks in the test. The effect of families was not significant for diameter but significant for the variables height and *Hypsipyla* attack (P>0.01).

Lagartera at 1812 days (4.6 years) had a diameter average of 68 mm and a coefficient of variation (CV) of 21%. Diameter differences were significant to Pr > F =0.0017.

The family 50 had the best diameter (78.8 mm), and the lowest performance was for family 68 with a diameter of 49.2 mm. The variable height registered an average of 306 cm, while the CV was 31% (Pr > F =0.0262). Again, the best family was the 50 with 306.8 cm and the lowest family the 68 with 188.8 cm, at 4.5 years**.** Pruning was applied 1 year before the 2001 measurement.

Analysis of variance is presented in tables 10 and 11. Results show that solitary (isolated) mother trees presented lower progeny performance in height and diameter (Pr > F <0.0001 and form Pr > F <0.0037).

The presence of attack was not significant in the performance of the family for the solitary analysis; nor was the response to the attack (Pr > F =0.3440). It is interesting to note that there appears to be differences due to the population structures. Thus, mother trees that grow together in clumps generally show superior families when compared to the families from mothers that grow as solitaries.

Table 10 presents the analysis of variance, table 11 the orthogonal contrast analysis, and the test of Tukey for the means. We interpret this fact as a possible indication of an increase in selfing in case of solitaries. Karkkainen *et al.* (1996) and Koski and Muona (1986) in studies with *Pinus sylvestris* have showed the same possible effect of inbreeding. Future tree improvement programs must consider the risk of inbreeding depression when collecting seed from single trees growing far apart. The mating system, including estimates of selfing, should be undertaken using relevant genes markers.

We suggest that family differences reflect 3 sources of variation: 1) among populations; 2) among families within populations due to additive genetic variability; and 3) among families due to inbreeding depression.

These differences clearly reflect adaptations to different environments such as the latitude spans from 7.5 degrees to 19.45 degrees, precipitation from 1200 to 3500 mm year^{-1} and the length of the dry season from 3-6 months per year.

The variation in the Fst values in the measurement at young stages may be caused by maternal effects; the same applies for the components of variance within and between populations. Also, for the first measurement, all trees had the same soil condition in the plastic pot, so the adaptive characters given to different microenvironments were minimized. The other measurements were done in the field where the seedlings were submitted to the edaphic and climatic conditions in the northern zone of the country.

Table 9. Results of ANOVA, expected square means and genetic parameters for the trial *Swietenia macrophylla* La Lagartera, Costa Rica at 585(1998) and 4.54 (for height) and 4.96 (for diameter) years after planting.

	Mean (CV %)	Genetic parameters	Significance	Mean (CV %)	Genetic parameters	Significance
	1998	1998		2001	2001	
Diameter	47	h^2=0.19±0.009	0.0011	68	h^2=0.46±0.03	<.0001
	(24)	AGCV=11		(21)		
Height	182	h^2=0.24± 0.01	0.0001	306	h^2=0.35±0.02	<.0001
	(27)	AGCV=14		(31)		
Attack	0.68	h^2=0.14± 0.001	0.0011	0.2	h^2=0.13±0.01	0.0111
	(65)	AGCV=26		(475)		

Table 10. Analysis of variance for the variable solitary mother tree at 3.6 years. Laberinto trial. Los Chiles. Costa Rica.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Diameter					
Block	14	76411.11960	5457.93711	19.48	<.0001
Mother tree	2	26488.79272	13244.39636	47.26	<.0001
Error	3386	948820.150	280.219		
Height					
Block	14	2772736.400	198052.600	20.11	<.0001
Mother tree	2	1312080.358	656040.179	66.60	<.0001
Error	3392	33410485.04	9849.79		
Attack					
Block	14	0.17365414	0.01240387	2.52	0.0014
Mother tree	2	0.04247855	0.02123927	4.31	0.0134
Error	3392	16.69869642	0.00492296		
Form					
Block	14	45.39012108	3.24215151	6.28	<.0001
Mother tree	2	5.78438930	2.89219465	5.61	0.0037
Error	3392	1750.014126	0.515924		
# of shoots					
Block	14	134.3258932	9.5947067	12.93	<.0001
Mother tree	2	2.2876912	1.1438456	1.54	0.2142
Error	3393	2517.478661	0.741962		

Table 11. Orthogonal contrasts for the variable solitary mother tree and Tukey grouping for the analysis of the variable solitary mother tree. Laberinto trial. Costa Rica.

Contrast Analysis	Mean Square	F Value	Pr > F	Tukey	Groups Mean (cm)	Mother tree[*]
Diameter				Diameter		
Contrast				A	70.7063	2
1 vs 2 y 3	24276.68368	86.63	<.0001	A	68.9839	3
2 vs 3	831.70919	2.97	0.0850	B	63.7809	1
Height				Height		
1 vs 2 y 3	1123677.466	114.08	<.0001	A	317.624	2
2 vs 3	9069.200	0.92	0.3373	A	312.806	3
				B	274.469	1
Attack				Ataque		
1 vs 2 y 3	0.02972101	6.04	0.0141	A	0.998144	3
2 vs 3	0.00049464	0.10	0.7513	A	0.997354	2
				A	0.990813	1
# of shoots				# of shoots		
1 vs 2 y 3	0.87230015	1.18	0.2783	A	2.37359	1
2 vs 3	0.40331726	0.54	0.4610	A	2.35450	2
				A	2.31374	3
Form				Form		
1 vs 2 y 3	3.92386213	7.61	0.0059	A	1.31802	1
2 vs 3	0.09892198	0.19	0.6615	B A	1.24339	2
				B	1.23082	3

[*] 1. Isolated mother tree (no other trees of the same species) at a distance of less than 500 m, 2. Semi-isolated (other trees no closer than 100 m) and 3. Mother tree in clusters or associated with more than 2 trees in a radius of less than 100 m.

Gillies *et al.* (1999) in a Mesoamerican study of mahogany using RAPD, found a significant portion of diversity maintained between populations within the three geographical regions in Mesoamerica (*i.e.* Yucatán Península, Central Zone and Panama); the present results also show that there is differentiation in clusters of Panama in comparison with the other populations in the northern part of Mesoamerica (Figure 2). The percentage of genetic variation among populations was 12%, Fst 0.0168, while on average for 12 values of different characters and measurements of Fst values was 0.2. These differences show the influence of the selection in *Swietenia macrophylla* because of great climatic and edaphic differences within the entire collection.

The criteria used to cut the adult trees in the natural forest are: a minimum of diameter; height; good form; and the condition of trees without a hollow trunk. In the analysis we ascertained that the trees in exploited areas have less performance in height, diameter and form, and that hollow trunks is a variable that can not be analyzed in young trees. Gillies *et al.* (1999) found that the genetic diversity in mahogany was correlated to the level of exploitation or destruction of the forest; these results can be related with those presented in this paper, given that the solitary trees presented a low performance in diameter and height. This could indicate that the dysgenic selection produced by the human exploitation of the best trees, could have reduced the variation that corresponds to that part of the populations, including the best model trees, and therefore decreasing the overall genetic diversity.

Progeny experiments made with both Costa Rican families (at Upala and Lagartera), and the Central American and Mexican trial (at Laberinto), reveal high levels of genetic variation for height and diameter growth on 2 levels, population and family. For diameter, the best populations were Bio-Itza (Guatemala) and Tikal (Guatemala) and for height, Santa Cecilia (Costa Rica) and Naranjal (México).

For the Upala trial, it was found that families 93 from San Emilio (Los Chiles, Costa Rica) and 51 from Caño Negro (Los Chiles, Costa Rica) produced the best growth in height and diameter.

As for resistance to *H. grandella,* no significant variation was found in the presence of the shootborer in any of the 3 trials. These results indicate that breeding for insect resistance in the present material is probably worthless. We believe, the best strategy to avoid insect damage is integrated pest management through the use of mixed stands, and agroforestry including important crop plants.

The heritability estimates were relatively high for diameter and height, which suggest the possibility of good genetic gains and indicate that there is additive genetic variability available for successful breeding.

The collection of seeds from individual trees to grow families has given us a reason to suggest further careful studies on population structures and especially on risks of inbreeding in sparse populations that may be the result of long-term forest exploitation. We recommend combining quantitative studies with molecular markers, including mating systems, in order to save valuable genetic resources. Only after such information it will be possible to plan optimal tree breeding programs for mahogany.

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