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ScienceDirect
Forest Ecology and Management 255 (2008) 346–355
Forest Ecology and Management
www.elsevier.com/locate/foreco

Performance and genetic variation of big-leaf mahogany (*Swietenia macrophylla* King) in provenance and progeny trials in the Yucatan Peninsula of Mexico

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Abstract

Stocks of the valuable big-leaf mahogany (*Swietenia macrophylla* King) are declining, and trials for growth and pest resistance are needed to select material for plantations. Seeds were collected from 67 open-pollinated trees from five provenances in the Yucatan Peninsula of Mexico and planted in three provenance/progeny trials in the state of Quintana Roo, Mexico, in order to characterize genetic variation in growth traits and for *Hypsipyla* resistance or recovery, and to assess the potential for genetic gain. Differentiation among provenances was found only for relative height growth rate (RHGR). The total years of apical attack by *Hypsipyla grandella* varied by a magnitude of 100% among families but showed little heritability. After 4 years, mean height per family ranged from 328 to 564 cm, 160 to 381 cm, and 253 to 390 cm at each site. Although heritabilities for height were too low for cross-site selection, sufficient heritability ($h_I^2 = 0.26$), additive genetic coefficients of variation (AGCV = 22%), and type B genetic correlations ($r_{b(f)} = 0.74$) for RHGR across the two sites with poorer growth indicated that this trait might be used as a surrogate. This would yield an estimated gain of about 17% for the best 15% of trees. At the site with better growth, there was sufficient heritability ($h_I^2 = 0.31$) and AGCV (20%) for height at year 5 to obtain an estimated gain of 15% for the best 15% of trees. We suggest a selection strategy using the best germplasm from the best performing trial to exploit the resources on high quality sites, and the best material from the poorer sites for lower quality areas.

Keywords: *Hypsipyla grandella*; Genetic gain; Tree domestication; Tropical hardwoods

1. Introduction

Today, the majority of big-leaf mahogany (*Swietenia macrophylla* King, family Meliaceae) wood still comes from natural stands, but these have been severely reduced. Mexico alone has lost about 76% of its natural forest area containing mahogany (Calvo et al., 2000). Whereas Mexico supplied 50% of the US market in 1950, it supplies less than 1% today due to its diminished supply (Robbins, 2000). As a result of this widespread decline, listing of the species in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Inskipp and Gillett, 2005) now restricts what can be traded legally (Winjstekers, 2005). At the same time, plantation success has been limited by the shoot borer moth, *Hypsipyla grandella* Z. (Lepidoptera, Pyralidae), whose larvae attack apical shoots of young trees, slowing growth and causing forking, thereby reducing economic return (Cornelius et al., 2004).

Selection of stock with improved growth and/or resistance to the insect would encourage cultivation of mahogany and relieve pressures on natural forests. However, and despite its high value, few genetic trials have been established for mahogany (Newton et al., 1993b; Mayhew and Newton, 1998), especially

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doi:10.1016/j.foreco.2007.09.056

compared to other widely planted tropical hardwoods, such as teak, *Gmelina* and *Eucalyptus* spp. Several small-scale genetic trials have been planted in the Yucatan, but with limited material, and *Hypsipyla* attack or tree response has not been reported in detail (Patiño, 1997).

Ejidos (communities with forest properties) and individual farmers in the Yucatan Peninsula of Mexico are attempting to regenerate mahogany stocks through plantations and agroforestry systems, but survival and performance are poor due to poor initial seedling quality, pest damage, and lack of plantation tending (Negreros, 1997; Mexal, 1996). Improved germplasm is not available for reforestation programs, and most nurseries collect seed from just a few, easily accessed trees (Wightman, pers. obs.). Although insecticides and biological control for the shoot borer have been tried with some success (Hilje and Cornelius, 2001), the limited financial resources of local farmers and local institutions constrain their use. Thus, low-cost techniques for shoot borer control and the deployment of selected genetic material may be the best prospects for minimizing insect damage and improving production of mahogany in this setting (Newton et al., 1993a).

To test and secure improved mahogany seed sources for regional reforestation programs, a collection of germplasm was made in the Yucatan and planted out in genetic trials at two communities and at a research station of the Mexican Institute for Forestry, Agricultural, and Livestock Research (INIFAP). Trials were carried out under conditions that local farmers might encounter. The research was designed to characterize genetic variation at the provenance and family levels for growth traits and for *Hypsipyla* resistance or recovery, and to assess the potential for genetic gain.

2. Materials and methods

2.1. Seed collection and nursery procedures

In February 1997, open-pollinated seed was collected from 100 trees sampled without regard to phenotype throughout the Yucatan Peninsula of Mexico. Trees were mostly located in natural forest stands and were at least 100 m apart. The five provenances were designated *post hoc* by the distance of about 100 km between collection areas, and their somewhat different climatic conditions (Fig. 1, Table 1). The Nuevo Becal material was from an unmanaged seed stand in the National Registry of Germplasm (coordinated through the Ministry of Natural Resources). These collections were part of a Mesoamerican-wide project of germplasm collection for genetic analysis coordinated by the Tropical Agricultural Research and Higher Education Center (CATIE) (Navarro and Hernández, 1998), in collaboration with local research institutions and community organizations.

Seedlings were produced at the INIFAP San Felipe Bacalar Research Station. Germination rates per family (from same mother tree) were highly variable (0–80%), mostly due to prior storage of seeds in paper bags at room temperature (species is semi-recalcitrant) but also possibly because of inherently low germination capacity, resulting in the loss of several seed lots.

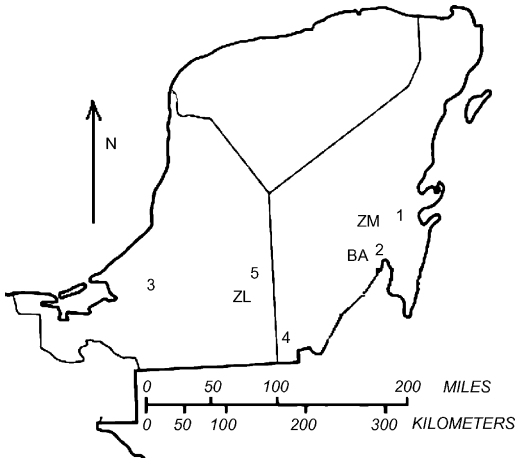

Fig. 1. Location of *Swietenia macrophylla* trials and provenances in the Yucatan Peninsula of Mexico. Trials: ZM = Zona Maya, BA = Bacalar, ZL = Zoh Laguna; provenances: 1 = Zona Maya, 2 = Bacalar, 3 = Escárcega, 4 = Carlos Madrazo, 5 = Nuevo Becal.

There was no formal experimental design used in the nursery; seedlings were grouped by family. When 6 weeks old, seedlings were transferred from germination beds to 750 cm^3 black plastic bags filled with soil found at the site. Unfortunately, this common technique caused root deformities that are known to slow tree growth and to cause tree-throw and mortality (Jaenicke and Wightman, 2000). This problem was detected by digging up dead trees, 10% of which were thus affected.

2.2. Experimental design and site management and measurements

Trials were established under conditions similar to those in which germplasm might actually be used by local communities. Sites for the community trials were limited by the tracts of land available for the study. The Zona Maya site was flat with few rocks and cambisol under blocks 1–3 of the trial (Mayan soil classification Kankab). The Bacalar station site was comprised mostly of a flat, somewhat rocky rendzina (Ka'Kab) with good drainage. The Zoh Laguna site was used because of its accessibility, but it had mostly heavy clay soils with poor drainage (Alkache). Existing vegetation at these sites is described below.

From the original 100 families of seed collected, a total of 67 families produced seedlings in sufficient quantity to distribute among the three trial sites (Table 2), with 36 families common at all three sites. At the community trials (Zona Maya and Zoh Laguna), four trees from each family were planted contiguously in rows in a randomized complete block design with five repetitions. At the Bacalar station, a compact family design was used in which families were grouped within provenances within each block with five trees from each family per block. Tree spacing at all sites was 3 m × 3 m. Different trial designs were used to meet different objectives. In the community trials, with an ultimate objective of conversion to seed stands, families and perhaps even provenances will be eliminated during thinning to select the best performing progeny for seed production. At the

Table 1
Provenance and site descriptions for seed collection and trial establishment of *Swietenia macrophylla* in the Yucatan

Provenance (location(s), state)	Corresponding trial site	Mean annual precipitation (mm)	Mean annual temperature (°C)	Latitude (°N)	Longitude (°W)	Elevation asl (m)
Zona Maya: Naranjal and Laguna Kana, Quintana Roo	Zona Maya	1200	24	19.37	88.46	50
Bacalar, Quintana Roo	Bacalar	1300	25	18.75	88.35	50
Nueva Becal, Campeche	Zoh Laguna	1000	24	18.81	89.33	150
Carlos Madrazo, Campeche	–	1600	26	18.03	89.25	150
Escárcega, Campeche	–	1200	24	18.6	90.83	50

Climatic data from SEMARNAP (2000) and Mexican National Water Commission's measurements from field stations in Quintana Roo and Campeche, 1997 and 1998.

Bacalar station, the trial was designed as a genetic conservation bank; hence, the maximum number of families and provenances were planted and will be retained.

Trees were planted during the rainy season, October to November 1997, and were ages 6 and 7 months for the Zoh Laguna and Zona Maya sites, respectively. The Bacalar site was planted 1 year later, when trees were age 21 months. Site preparation varied at each site depending on the existing vegetation. At Zona Maya 4-year-old secondary vegetation was cut and burned; at Zoh Laguna glyphosphate herbicide was initially applied at the predominately grassy site; and at Bacalar a bulldozer was used to clear the 12-year-old regrowth.

The community sites were weeded by machete three times during the first 2 years, thereafter twice annually. Vegetation, mostly woody shrubs and stump sprouts, was allowed to grow between the tree rows without dominating the planted trees, in order to provide lateral shade, foster biodiversity, and possibly act as natural barriers to *Hypsipyla*. After 2.5 years of field growth, 100 g of 18–46–0 NPK fertilizer was applied superficially at the base of each tree in a 1-m diameter circle, with an additional 100 g of 17–17–17 fertilizer applied 3.5 years after planting at the Zoh Laguna site, due to its lower fertility. At Bacalar, trees were broadcast fertilized with 50 g granular fertilizer (18–40–20) 1 year after planting, and replanting was done 3 months after establishment. No replanting was done at the community sites. The Bacalar site was weeded with similar frequency, but the vegetation (mostly grass) was kept short, and contact herbicide (Transquat®) was used to control vines during the first year. Except for one application of a systemic insecticide (Furadan®) at 9 months (at Bacalar) insecticides were not used to control *Hypsipyla* damage. At all sites, trees were pruned yearly after counting the number of multiple apical stems or branches.

Table 2
Number of *Swietenia macrophylla* families per provenance established at each trial

Provenance	Trial site		
	Zona Maya	Zoh Laguna	Bacalar
Zona Maya	19	20	19
Bacalar	10	7	7
Nuevo Becal	9	20	26
Escárcega	5	2	2
Madrazo	4	4	4
Total	47	53	58

All trees were measured after planting and yearly thereafter (for 5 years at the community trials and 3 years at the field station). Height (HT) was measured to the apical shoot tip. Relative height growth rate (RHGR) between the initial and last measurement was calculated as the annual increment per unit of height at time of planting. Diameters were initially measured at the root collar (soil line; DRC), and the last measurement was at 1.3 m (DBH). Attack, branching, and form were assessed, and then the trees were pruned. Shoot borer attack was recorded as present or absent, separately for the apex and along the stem, for each year during the first 4 years. Thereafter, the trees were too tall to accurately assess this parameter. For the first 4 years, the number of apical shoots and lateral branches from the main stem were recorded. A qualitative form grade (1 [very good] to 4 [poor] at the community trials and 1–3 at Bacalar) was assigned based on comparative size, branchiness, and vigor. Form (FORM) was recorded in year 2 only at Bacalar, but for all years at the other sites. For the analysis, the total number of years of apical attack (TyAPAT) and total number of apical shoots (TAPSH) were summed over years 1–3 for Bacalar and years 1–4 for the community trials. Tree survival between census periods was converted to longevity (AGE; number of years alive) in order to calculate heritability of survivorship. Trees accidentally cut during maintenance were eliminated from the analysis.

2.3. Statistical analysis

2.3.1. Performance and variation

The following general linear mixed model was used for across-site analysis; for within-site analysis, the site term and its interactions were removed:

$$Y_{ijklm} = u + S_i + B(S)_{ij} + P_k + F(P)_{kl} + SP_{ik} + SF(P)_{ikl} + B(S)P_{ijk} + B(S)F(P)_{ijkl} + e_{ijklm},$$

where Y_{ijklm} is the observed value for an individual, μ is the site mean, S_i is the effect of the ith site, $B(S)_{ij}$ is the effect of the jth block of the ith site, P_k is the effect of the kth provenance, $F(P)_{kl}$ is the effect of the lth family in the kth provenance, SP_{ik} is the interaction of the ith site and the kth provenance, $SF(P)_{ikl}$ is the interaction of the ith site and the lth family of the kth provenance, $B(S)P_{ijk}$ is the interaction of the jth block of the ith site and the kth provenance, $B(S)F(P)_{ijkl}$ is the interaction of the

*j*th block of the *i*th site and the *l*th family in the *k*th provenance, and e_{ijklm} is the residual or within-plot error from random error in the *m*th observation.

It should be clarified that the site term includes both differences in inherent site conditions (soil and climate) and variations in management of the site as described above.

Site and provenance effects were considered fixed (except as stated below) because they were not randomly chosen and only three were well represented. Block, family and their interactions were treated as random effects. The majority of variables were monotonic or binary. Data were not transformed, even though many variables had a non-normal distribution. Analysis of variance is relatively robust against departures from normality; of greater concern is heterogenous variance among experimental groups (Glass et al., 1972). Therefore, site and block variances were standardized to a variance of one for within or cross-site analyses as appropriate, by dividing the deviation from the site or block mean by the site or block standard deviation using SAS PROC STANDARD (SAS, 1990), in order to avoid exaggerated genetic by environment interactions (Soria et al., 1998).

PROC MIXED of SAS was used to estimate the variance components of random effects and to test the significance of fixed effects. The Satterthwaite approximation was used to obtain denominator degrees of freedom for the *f*-tests of fixed effects. Variance components were estimated using restricted maximum likelihood (REML) within PROC MIXED, which is a relatively robust method both for unbalanced designs (Huber et al., 1994) and departures from normality (Westfall, 1987). The significance of variance components was tested using the likelihood ratio statistic (Littell et al., 1996).

2.3.2. Genetic parameters: heritabilities, AGCV, correlations and gain

Individual and family level heritabilities were estimated following Wright (1976) and Hannerz et al. (1999), and within family heritabilties were estimated after Xie and Ying (1996) as:

$$h_{\mathrm{I}}^2 = \frac{\sigma_{\mathrm{A}}^2}{\sigma_{e^2} + \sigma_{BF(P)}^2 + \sigma_{SF(P)}^2 + \sigma_F^2}$$

$$h_{\mathrm{F}}^2 = \frac{\sigma_{F(P)}^2}{(\sigma_e^2/x_{\mathrm{f}} + \sigma_{BF(P)}^2/n_{\mathrm{b}} + \sigma_{SF}^2/n_{\mathrm{s}} + \sigma_{F(P)}^2)};$$

$$h_{\mathrm{w}}^2 = \frac{3\sigma_{F(P)}^2}{\sigma_{BF}^2(P) + \sigma_e^2}$$

where h_{I}^2 is the individual heritability; h_{F}^2 is the family within provenance heritability; h_{w}^2 is the individual within family heritability; σ_{A}^2 is the additive genetic variance, which is $4\sigma_{F(P)}^2$; $\sigma_{F(P)}^2$ is the variance component due to among family variation; $\sigma_{BF(P)}^2$ is the variance component due to the block-by-family interaction; $\sigma_{SF(P)}^2$ is the variance component due to the site-by-family interaction; σ_e^2 is the variance component due to within plot variation; n_{b} is the number of blocks; n_{s} is the number of sites; and x_{f} is the harmonic mean of number of trees per family.

The coefficient of relationship of 0.25 was used for individual heritabilities, after Navarro and Hernández (2004), because most of the mother trees were in natural forest. Mahogany in native forests is known to be predominantly outcrossed (Loveless and Gullison, 2003; Lemes et al., 2003). Since some selfing may occur (Lemes et al., 2003), the heritabilities calculated here can be considered upper limits. Harmonic means were used as a more conservative estimate of mean number of trees per family, due to unbalanced data resulting from tree mortality. For within-site heritability calculations, the site-by-family interaction was removed. As tree selection will be done with measurements adjusted for block means, this variance component was excluded from the denominator for heritabilities (Cotterill, 1987). The standard errors for individual heritabilities were determined after Swiger et al. (1964) and for family level heritabilities after Wright (1976). In order to determine the capacity to reject the hypothesis $h_{\mathrm{I}}^2 = 0$ when false, power analysis was carried out, after Lynch and Walsh (1998).

To obtain an index of the absolute amount of genetic variation available for selection for a given trait, the additive genetic coefficient of variation (AGCV) for each trait was assessed using the formula $\mathrm{AGCV} = 100(\sigma_{\mathrm{A}}/x) \times \mathrm{S.D.}_{(\mathrm{blocks})}$, where σ_{A} is the additive genetic standard deviation, x is the provenance mean, and $\mathrm{S.D.}_{(\mathrm{blocks})}$ is the mean standard deviation for block for a given trait. Since the intrablock variance had been standardized by dividing deviations from the mean by the block standard deviation, the additive genetic variation was multiplied by the mean standard deviation for blocks. The estimated genetic gain was calculated using combined within-family and among-family selection, after Shelbourne (1969) and Becker (1992), for the best 15% of the trees (100–200 trees) at each site. Similar selection intensity was used for each site in order to compare responses.

Provenances were treated as fixed in most analyses, except for type B genetic correlations and for comparison of family and provenance level variation, where they were treated as random. Type B genetic correlations across sites for families and provenances were determined as $r_{\mathrm{b(f)}} = \sigma_{F(P)}^2/(\sigma_{F(P)}^2 + \sigma_{SF(P)^2})$ and as $r_{\mathrm{b(p)}} = \sigma_P^2/(\sigma_{P^2} + \sigma_{SP}^2)$, after Yamada (1962) and (Sierra-Lucero et al., 2002). The Bacalar–Zoh Laguna cross-site analysis is reported here, since the type B cross-site genetic correlation for RHGR for that site combination was greater than 0.7, and higher than across all three sites or for the Zoh Laguna–Zona Maya or Bacalar–Zona Maya combinations (type B correlations greater than 0.7 indicate sufficient phenotypic stability for cross-site selection (Xie, 2003); see Sections 3 and 4). Family and provenance level variation were compared using the formula $\theta = \sigma_P^2/(\sigma_{F(P)}^2 + \sigma_P^2)$ (Sierra-Lucero et al., 2002). Genetic correlations were calculated after Stonecypher (1992).

3. Results

3.1. Growth and Hypsipyla attack

We compared all three sites in the same year of measurement. As mentioned above, seedlings for all trials

Table 3
Summary of family-mean performance and coefficient of variation (cv) by trial location for *Swietenia macrophylla*

Traits	Year(s) after planting	Zona Maya			Zoh Laguna			Bacalar		
		Mean	Range	cv (%)	Mean	Range	cv (%)	Mean	Range	cv (%)
HT (cm)	5	453	328–564	13	262	160–381	16	na	na	na
	4	363	264–478	14	238	147–324	16	na	na	na
RHGH (cm cm^{-1} year^{-1})	0–5 (0–4 Bacalar)	2.1	1.4–2.9	18	1.2	0.6–2.0	25	1.5	0.9–2.3	23
DBH (cm)	5 (4 Bacalar)	4.1	3.1–5.5	15	2.6	1.8–3.9	15	3.1	2.5–4.1	11
HYPSATAP (%)	4	66	33–100	24	79	43–100	16	6	0–40	116
	3	34	8–63	39	49	18–72	27	97	78–100	5
	2	7	0–20	94	67	28–88	19	10	0–40	77
	1	1	0–9	195	20	5–42	45	na	na	na
TyAPAT	1–4 (1–3 Bacalar)	1.1	0.8–1.6	20	2.2	1.4–2.7	13	1.1	0.8–1.6	12
TAPSH	1–4 (1–3 Bacalar)	2.3	1.1–5.6	35	3.1	1.3–4.6	20	3.6	1.9–5.6	21
FORM	5 (2 Bacalar)	1.9	1.3–3.1	20	2.4	1.4–3.2	17	2.1	1–2.4	4.1
SURVIVAL (%)	1–5 (1–4 Bacalar)	71	45–90	15	74	40–95	17	94	76–100	7

"na" indicates not available. HYPSATAP is the percentage of each family attacked at the apex by *Hypsipyla* in the indicated year. SURVIVAL is the percentage of each family alive at the indicated year. For labels for other traits and the scale for Form, see Section 2.

were started at the same time in the nursery, but the Bacalar trial was planted out 14 months later than the community trials. Mean family performance, their ranges and coefficients of variation are listed by site in Table 3. Total height in 2001 (4 years after outplanting), the last year when all sites were measured, was greatest in Zona Maya at 363 cm, and lowest in Zoh Laguna at 232 cm; RHGR followed a similar trend. Mean family survival was 74% at Zoh Laguna 71% at Zona Maya, and 94% at Bacalar (site where replanting occurred).

The family mean number of trees affected by *Hypsipyla* varied greatly by site and year. During the second trial year, there was little *Hypsipyla* attack in Bacalar and Zona Maya ($\leq$10% per family), but much in Zoh Laguna (67%; Table 3). In year 4, attack was high in Zona Maya and Zoh Laguna, 66 and 79%, respectively, but only 6% in Bacalar (but note, 116% CV at Bacalar). The family mean sum of apical shoots over the evaluation period ranged about four-fold over all three sites.

3.2. Provenance and family variation

Results from mixed model analysis across Bacalar–Zoh Laguna using the 36 families common to all three sites, and for each trial separately, are given in Table 4. Provenance effects were significant only for RHGR across all three sites (not shown), across Bacalar–Zoh Laguna, and at Zoh Laguna and Bacalar individually. For this trait, provenance variation ranged between 21 and 68% of the total variation among provenance and families across and at each site (Table 4). The Bacalar provenance performed best at Zoh Laguna and Bacalar, but not at Zona Maya (Table 5).

Family level effects were significant for RHGR across all three sites (not shown), and across Bacalar–Zoh Laguna (Table 4). Family level effects were significant for growth traits at Zona Maya and Zoh Laguna individually, for total years of apical attack and longevity only at Zoh Laguna, and for total apical shoots at Zona Maya (Table 4). At Bacalar, the only significant family effects were for RHGR and total apical shoots. From year to year, there was no indication of a consistent family effect on attack or number of shoots (not shown). Family variation in tree form was significant only at Zona Maya, where at year 5 the majority of trees (78%) were in the excellent or good class, compared to Zoh Laguna where only 40% of the trees were rated in a good or better class (results not shown).

Across Bacalar–Zoh Laguna, the provenance-by-site and family-by-site interactions were not significant (Table 4). Across sites, and at Zona Maya and Zoh Laguna, the family-by-block interactions were usually much larger and more often significant than the family-by-site and the provenance-by-block interactions. Provenance-by-block interactions were significant only at Bacalar.

3.3. Genetic parameters

Individual level heritabilities across all sites (not shown), and across Bacalar–Zoh Laguna, were small (less than 0.1), except for RHGR ($h_I^2 = 0.26$; Table 6) and the sum of apical shoots ($h_I^2 = 0.11$; Table 6). Across all 3 sites, type B genetic correlations for families within provenances for RHGR were 0.57, but 0.74 across Bacalar–Zoh Laguna. The type B genetic correlation for total apical shoots was 1.00 across Bacalar–Zoh Laguna. The power to reject the hypothesis of no heritability when false dropped off for heritabilities less than 0.1 across sites and less than 0.2 at each site (Table 6).

For each site individually, the highest heritabilities were for height and RHGR (Table 6). Moderate heritability for DBH (0.33) and form (0.20) occurred at Zona Maya. Heritabilities over time at Zoh Laguna and Zona Maya appeared to be stabilizing for height, and were smaller for diameter at root collar and form (not shown). At these two sites, heritabilities for attack and branching were erratic through time (not shown) and often equal to zero.

AGCVs for growth traits were between 12 and 35% at the two community sites, but very low at Bacalar except for RHGR (Table 6). AGCVs were also relatively high for form at Zona Maya ($\sim$26%) and for total apical shoots at Bacalar ($\sim$24%). At

Table 4
Significance for fixed effects and variance components associated with the analysis of variance of *Swietenia macrophylla* provenance/progeny trials in the Yucatan peninsula of Mexico

Bacalar and Zoh Laguna	Ht year 4	RHGR years 0–4	FORM year 2	TyAPAT	TAPSH	AGE
(A) Fixed effects ($p < \alpha$)						
Site	**	ns	ns	****	*	****
Provenance	ns	**	ns	ns	ns	ns
Site × provenance	ns	ns	ns	ns	ns	ns
(B) Random effects (variance component as percent of total variation and $p > X^2$)						
Block (site)	99.84****	1.14ns	0.27ns	3.01**	12.94****	4.57***
Family (provenance)	0.00ns	6.24*	0.00ns	0.01ns	2.34ns	1.14ns
Site × family (provenance)	0.01ns	2.19ns	0.00ns	3.01ns	0.00ns	0.60ns
Block (site) × provenance	0.01***	4.33*	0.00ns	0.00ns	2.07ns	0.40ns
Block (site) × family (provenance)	0.04****	16.77****	9.03***	0.00ns	4.41*	3.47ns
Residual	0.10	69.33	90.70	93.97	78.24	89.81

Zona Maya	HT year 4	HT year 5	RHGR years 0–5	DBH year 5	FORM year 5	TyAPAT	TAPSH	AGE
(A) Fixed effects ($p < \alpha$)								
Provenance	ns	ns	ns	ns	ns	ns	ns	ns
(B) Random effects (variance component as percent of total variation and $p > X^2$)								
Block	99.97****	99.98****	8.42****	98.11****	2.74ns	8.42**	35.71****	23.23*
Family (provenance)	0.00*	0.00**	10.30ns	0.16*	4.91ns	10.30***	0.76*	0.00*
Provenance × block	0.54ns	0.00ns	0.10ns	0.02ns	0.00ns	0.10ns	0.02ns	0.27ns
Block × family (provenance)	0.01****	0.01****	24.26****	0.38****	0.00ns	24.26****	10.27****	8.57ns
Residual	0.02	0.02	56.92	1.33	99.63	56.92	52.26	67.94

Zoh Laguna	HT year 4	HT year 5	RHGR years 0–5	DBH year 5	FORM year 5	TyAPAT	TAPSH	AGE
(A) Fixed effects ($p < \alpha$)								
Provenance	ns	ns	*	ns	ns	ns	ns	ns
(B) Random effects (variance component as percent of total variation and $p > X^2$)								
Block	99.91****	99.95****	4.34****	94.31****	7.65**	3.85**	2.89ns	5.76**
Family (provenance)	0.01**	0.00**	12.13**	0.16ns	2.80ns	2.15ns	1.13ns	3.13*
Provenance × block	0.00ns	0.00ns	0.46ns	0.00ns	0.00ns	0.00ns	0.85ns	1.66ns
Block × family (provenance)	0.02****	0.01****	14.82****	1.37****	27.06****	10.43**	6.61ns	1.80ns
Residual	0.06	0.04	68.25	4.16	62.49	83.57	88.52	87.64

Bacalar	HT year 4	RHGR years 0–4	DBH year 4	FORM year 2	TyAPAT	TAPSH	AGE
(A) Fixed effects ($p < \alpha$)							
Provenance	ns	**	ns	ns	ns	ns	ns
(B) Random effects (variance component as percent of total variation and $p > X^2$)							
Block	99.75****	0.00ns	80.80****	0.04ns	0.00ns	12.96***	0.00ns
Family (provenance)	0.00ns	13.03****	0.28ns	1.09ns	1.32ns	2.42*	1.26ns
Provenance × block	0.03****	5.77****	2.43****	0.15ns	1.17ns	3.26***	0.00ns
Block × family (provenance)	0.05****	14.22****	3.25****	4.83*	0ns	3.61ns	2.32ns
Residual	0.17	66.98	13.24	93.89	97.52	77.75	96.41

See Section 2 for trait labels. For fixed effects the significance of F tests ($p > F$) and for random variables the significance of the likelihood ratio statistic ($p > X^2$) are given as: ns not significant.
* $p < 0.05$.
** $0.01 < p < 0.05$.
*** $0.001 < p < 0.0001$.
**** $p < 0.0001$.

each site the AGCV for total years of apical attack was between 0 and 12%. AGCVs across Bacalar–Zoh Laguna were less than 10%, except for RHGR and total apical shoots.

Combined selection was used for estimating the gain from selecting the best families and best trees within families. Across Bacalar–Zoh Laguna, the gain in RHGR would be approximately 17%, and for total apical shoots about 12%, for the best 15% of trees (Table 6). At Zoh Laguna and Zona Maya individually, the gains for height would be near 15%, for the best 15% of trees. Gains for RHGR at each of the three sites would range from 23 to 34%. Gain would be about 17% for form at Zona Maya. Gains for resistance to *Hypsipyla* attack for the best 15% of trees would be less than 6% at each or across sites.

The genetic correlations between RHGR and initial height were −0.73 at Zoh Laguna, −0.72 at Zona Maya, −0.95 at Bacalar, and −0.96 across Bacalar–Zoh Laguna. Heritabilities for final height at Bacalar were too low to use in genetic

Table 5
Provenance performance across and within sites for relative height growth rate (cm cm^{-1} year^{-1}), as determined with least square means (LSM)

Provenance	Bacalar–Zoh Laguna RHGR years 0–4 1.47[a]	Zoh Laguna RHGR years 0–5 1.23[a]	Zona Maya RHGR years 0–5 2.07[a]	Bacalar HGR years 0–4 1.52[a]
Bacalar	1.94	1.51	2.14	1.99
Calakmul	1.46	1.10	2.15	1.38
Escarcega	1.26	1.11	1.91	1.53
Madrazo	1.29	1.19	1.89	1.30
Zona Maya	1.39	1.26	2.25	1.40

The overall LSM and LSMs by provenance are indicated.
[a] Overall LSM.

correlation calculations. Genetic correlations between RHGR and final height were 0.55 at Zoh Laguna and 0.77 at Zona Maya, and those between initial and final height were 0.19 at Zoh Laguna and −0.13 at Zona Maya. The genetic correlation between RHGR and total apical shoots was −0.31 across Bacalar–Zoh Laguna. The heritabilities for total apical shoots at each site were too low to calculate genetic correlations.

4. Discussion

This research yielded some firm conclusions applicable to the conditions under which the tested germplasm is likely to be used by Yucatan farmers and communities, despite some limitations to the study. A more consistent response to selection was found for growth traits than for form or susceptibility to shoot borer attack. Cross-site heritabilities, AGCVs, and type B

Table 6
Individual (h_I^2), family (h_F^2), and within family (h_w^2) level heritabilities, standard errors (S.E.), additive genetic coefficient of variation (AGCV), estimated gain of the best 15% trees, provenance % of total family and provenance variation (θ), type B genetic correlations for families within provenances ($r_{b(f)}$) and provenances ($r_{b(p)}$)

	h_I^2	S.E.	Power (%)	h_F^2	S.E.	h_w^2	AGCV (%)	Gain (%)	θ (%)	$r_{b(f)}$	$r_{b(p)}$
Bacalar and Zoh Laguna											
HT year 4	0.00	0.03	5	0.00	0.01	0.00	0.00	0.00	100	0.00	1.00
RHGR years 0–4	0.26	0.09	100	0.68	0.02	0.21	21.87	16.55	68	0.74	0.99
FORM year 2	0.00	0.02	5	0.00	0.01	0.00	0.00	0.00	nd	nd	nd
TyAPAT	0.00	0.03	5	0.01	0.01	0.00	0.00	0.04	nd	0.00	nd
TAPSH	0.11	0.05	90	0.82	0.01	0.08	21.88	12.26	0	1.00	nd
AGE	0.05	0.03	58	0.63	0.01	0.04	6.06	2.45	0	0.65	nd
Zona Maya											
HT year 4	0.31	0.12	97	0.44	0.12	0.25	17.03	12.92	16		
HT year 5	0.36	0.14	99	0.48	0.14	0.30	16.70	13.69	21		
RHGR years 0–5	0.45	0.15	100	0.53	0.13	0.36	25.46	23.02	9		
DBH year 5	0.33	0.13	98	0.47	0.11	0.27	18.44	14.58	0		
FORM year 5	0.20	0.10	82	0.40	0.09	0.16	25.58	16.58	0		
TyAPAT	0.00	0.06	5	0.00	0.06	0.00	0.00	0.00	100		
TAPSH	0.05	0.07	18	0.11	0.06	18.80	18.80	6.05	0		
AGE	0.00	0.04	5	0.00	0.05	0.00	0.00	0.00	100		
Zoh Laguna											
HT year 4	0.29	0.11	98	0.44	0.10	0.24	19.04	14.23	12		
HT year 5	0.31	0.11	98	0.45	0.10	0.25	20.12	15.40	10		
RHGR years 0–5	0.51	0.15	100	0.61	0.13	0.44	34.79	33.71	28		
DBH year 5	0.11	0.08	45	0.20	0.07	0.09	11.80	5.56	0		
FORM year 5	0.12	0.10	42	0.20	0.08	0.09	13.58	6.53	0		
TyAPAT	0.09	0.07	44	0.22	0.07	0.07	12.28	5.46	20		
TAPSH	0.05	0.06	21	0.13	0.06	0.04	14.59	4.82	0		
AGE	0.14	0.07	84	0.40	0.07	0.10	12.33	7.04	0		
Bacalar											
HT year 4	0.05	0.04	31	0.12	0.05	0.03	5.12	1.65	0		
RHGR years 0–4	0.55	0.11	100	0.68	0.14	0.48	30.48	31.03	54		
DBH year 4	0.07	0.05	48	0.18	0.05	0.05	0.05	2.93	0		
FORM year 2	0.04	0.04	0	0.05	0.03	3.16	3.16	1.08	1		
TyAPAT	0.05	0.04	38	0.22	0.05	0.04	0.04	3.15	0		
TAPSH	0.1	0.1	81	0.4	0.1	0.09	0.09	12.66	0		
AGE	0.05	0.04	38	0.21	0.05	0.05	0.04	1.11	0		

See Section 2 for trait labels. ND indicates cannot be determined.

genetic correlations showed promise for selection for RHGR and sum of apical branching. Differentiation was found among the provenances sampled only for RHGR.

Several limitations on our results were placed by variability in tree performance on sites with different characteristics, experimental design, and relatively low replication of trees within families. Sites with sufficient space for these trials were few. Block variance components were usually greater than 98% of the total variance for height diameter, indicating that the experimental design had removed most of the inter-tree variation. However, a more efficient trial design using single-, two-tree, or non-contiguous plots (Loo-Dinkins and Tauer, 1987) might have produced greater within- and cross-site heritabilities by reducing the family-by-block and within-plot (error) variance components. Use of more trees per family would have improved the power to reject the hypothesis of no heritability when false. Despite these limitations, we were able to draw firm conclusions about across- and within-site selection because of confluence of support from estimates of heritabilities, AGVCs, and type B genetic correlations. Type B genetic correlations (r_b) affect the utility of selecting across sites.

4.1. Provenance differentiation

Provenance variance components across and at each site were insignificant for all traits except RHGR. The provenance differentiation for RHGR showed a significant interaction across all three sites (not shown): the Bacalar material performed best at Bacalar and at Zoh Laguna, but not at Zona Maya (Table 5).

As experienced by big-leaf mahogany, the environmental gradients in temperature and soil in the Yucatan Peninsula may not be steep enough to promote strong population differentiation: the climate may be too homogenous or the scale of soil variation too small. Population differentiation might also be inhibited by large-scale historical disturbances from hurricanes, or from deforestation associated with past high population densities of the Maya. Other authors have reported provenance differences in big-leaf mahogany, but in samples spanning the Mesoamerican region, not solely from Mexico (Geary et al., 1973; Newton et al., 1999; Ward and Lugo, 2003; Navarro and Hernández, 2004). More differentiation was found among provenances of *C. odorata* from the Yucatan; these provenances may have arrived earlier in the peninsula and had more time to differentiate than those of big-leaf mahogany (Ward et al., 2008).

4.2. Genetic parameters

4.2.1. Growth

Height growth was comparable to reported values in the Yucatan Peninsula (Haggar, 2000) where rainfall average is lower than in many other parts of big-leaf mahogany's natural distribution. Overall, tree form and growth were best at the Zona Maya site, possibly due to better soils and the release of nutrients from the controlled burn. In the community trials, trees grew most in the blocks located in deeper soils and least in stony areas. At Zoh Laguna, overall performance was poorest, especially on the areas with heavy clay soils and poor drainage. In this analysis we used overall tree growth as an indication of the quality of site and management used.

By site, heritabilities and AGCVs for height and RHGR were sufficient to warrant selection. These heritabilities set an upper limit because a coefficient of relationship for complete outcrossing was used (0.25). Although mahogany is predominantly outcrossed (Loveless and Gullison, 2003; Lemes et al., 2003), inbreeding may occur in some trees (Lemes et al., 2003). Height heritabilities at year 5 for Zona Maya and Zoh Laguna (0.36 and 0.31; Table 6) compared favorably with those reported for a range of species (Cornelius, 1994: mean = 0.28). A trial in Costa Rica which included material from this study as well as from Central American sources produced heritabilities ranging from 0.35 to 0.60 for height and diameter (Navarro and Hernández, 2004). In our study, the AGCVs for height at Zona Maya and Zoh Laguna (16–20%) were larger than the mean of 11.1% reported for other species (Cornelius, 1994). The prospective gains at these sites for the 15% best trees were over 13% for height and over 20% for RHGR.

The low heritabilities, AGCVs, and potential gains for height and diameter at Bacalar supported the use of this site strictly for genetic conservation of planted families. The heritability for height growth at Bacalar may have been reduced by inhibition of root growth caused by the delay before planting out from the nursery to the field. However, the low genetic correlations between initial and final height at Zoh Laguna and Zona Maya (not calculable for Bacalar), and the significant heritability for RHGR at Bacalar, suggested that, in time, height may be sufficiently differentiated among families to yield useful heritability and AGCVs.

All indicators were against cross-site selection for height. Heritability and the associated power were very low across all three sites (not shown) and across Bacalar–Zoh Laguna for height (Table 6). The AGCV for height for this analysis was also very low, and the genetic gain with 15%, or 100–200 trees per site, would be only 3.6% (Table 6). Stronger potential selection was not considered, in order to maintain genetic diversity for reforestation programs.

Genetic correlations indicated that RHGR may be a good surrogate for height growth potential. At Zona Maya and Zoh Laguna, RHGR had negative genetic correlations with initial height, but positive genetic correlations with final height. Initial height also had negative genetic correlations with RHGR across all combinations of sites (not shown) and at Bacalar. The heritabilities across sites and at Bacalar for final height were too low to obtain the genetic correlation with RHGR. RHGR had a relatively high heritability across all sites at 0.21 (not shown), although the family level type B genetic correlation was below the 0.7 cut-off, indicating insufficient trait stability for region-wide selection (Xie, 2003). Across Bacalar–Zoh Laguna, this heritability was 0.26 and the type B genetic correlation was 0.74, pointing to successful selection across these two sites for this trait. Power across Bacalar–Zoh Laguna for RHGR was almost at 1.0, the maximum.

A two-fold approach for selection could be considered using Zona Maya for seed for high quality sites or more intensive

management. The top 10 families in height at Zoh Laguna and Bacalar, sites with poorer growth, had less variable growth across sites than the top 10 families at Zona Maya, a better site (*t*-tests: $p = 0.002$ for both comparisons), with no significant difference between Zoh Laguna and Bacalar ($p = 0.32$). This is consistent with the general finding that genotypes better adapted to poor conditions show more stable growth than those adapted to better conditions (Simmonds, 1991). Selection combined across the Bacalar–Zoh Laguna sites may yield germplasm with more predictable growth on poor sites. Gain for RHGR from the best 15% of trees across these two sites would be 16.6% (Table 6). The top-performing families at Zona Maya might be used to exploit more fully the resources available at more favorable sites.

4.2.2. Shoot borer attack and branching

The yearly variation we observed in *Hypsipyla* attack is typical for reforestation in open areas. *Hypsipyla* populations vary with temperature (Taveras et al., 2004a), and multiple attacks are possible within 1 year (Taveras et al., 2004b). More frequent observations to measure intensity might have provided insight into attack rates. Other studies that measured attack more frequently or used clonal material probably assessed *Hypsipyla* attack more accurately (Newton et al., 1999; Cornelius and Watt, 2003). For this study, however, yearly observation demonstrated that *Hypsipyla* is a constant threat to trees during the first few years after planting.

Since the main impediment to cultivation of mahogany in plantations remains the shootborer, we were interested in heritability for attack or branching response to attack. Low heritabilities, AGCV, and gains of less than 6% (for selection of 15% of trees) for attack across and within sites indicated that other traits should be the focus. Attack has been considered the main cause of branching (Cornelius et al., 2005). Higher across-site heritability for total apical shoots indicated potential for gain in this trait instead of attack. Across Zoh Laguna–Bacalar, the AGCV for total apical shoots (19.4%, Table 6) approached the mean reported for other species (Cornelius, 1994: mean branching traits AGVC = 16.30). Selection could be made across these two sites to reduce the number of apical shoots, since there was sufficient heritability and AGCV to result in 12% gain with the best 15% trees selected, and the type B genetic correlation was 1.0. The genetic trial in Costa Rica which included families from this study resulted in heritabilities ranging from 0.07 to 0.24 for number of shoots, from 0.4 to 0.18 for form, and 0.1 and below for attack (Navarro and Hernández, 2004). In our study, the negative genetic correlation ($r = -0.31$) between RHGR and total apical shoots across Zoh Laguna–Bacalar indicated that selection could be carried out simultaneously to increase growth and reduce shoot number across these sites.

5. Conclusions

5.1. Strategies for tree improvement

Selection for height at Zona Maya might yield germplasm that would perform well on good quality sites or under intensive management. Selection on height or RHGR at Zoh Laguna, or on RHGR across Bacalar–Zoh Laguna, may produce useful material for poor sites. Although individual heritabilities for height seem to be stabilizing at Zoh Laguna and Zona Maya through time, there may not yet be high correlation with adult height. But if early accrual of clear bole for merchantable timber is the main goal, these early heritabilities have direct application, since the tallest families were reaching 4 m and beyond by year 5. Pruning may be necessary to achieve sufficient clear bole.

Because trees were pruned, it is uncertain if apical dominance would have been established by one of the apical shoots. However, form values stayed constant over time in Zoh Laguna, even improving in Zona Maya from an average of 70% of the trees with good or excellent form to 82% by year 4. Pruning probably cannot improve tree growth rate, especially on poor sites, but it can help form the minimum clear bole length of 4 m needed for merchantable timber.

Sufficient heritability and AGCV across Zoh Laguna–Bacalar for total apical shoots, and the negative genetic correlation with RHGR, indicated that selection could be carried out simultaneously for these traits across these sites. This would also help to minimize pruning costs (Cornelius and Watt, 2003). Heritabilities and AGCVs for total years of apical attack were too low for sufficient gain. Since attack was greater at the site with less growth (Zoh Laguna), site quality may be important for gaining sufficient early growth to out-distance the effects of attack.

Selection for improved germplasm should be coupled with appropriate nursery care, appropriate match of germplasm to site, and pruning. Future collaborative efforts should focus on testing new material using more sensitive experimental designs as well as cloning of selected material from these trials.

Acknowledgements

The Research and Scientific Exchange Division of the Foreign Agriculture Service of the US Department of Agriculture funded this work through grant no. FG-CR-112. We thank the local community organizations that helped identify seed areas and obtained permission to collect seed and establish the trials: the Xpujil Regional Agrosilvopastoril Council (CRASX) and the Organization of Ejido Forest Producers of the Zona Maya (OEPFZM). We thank Lionel Cotto and Carlos Navarro of CATIE for their help in seed collection. We thank David Boshier, Nicholas Brokaw, and anonymous reviewers for comments which greatly improved the manuscript.

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