Early results from genetic trials on the growth of Spanish cedar and its susceptibility to the shoot borer moth in the Yucatan Peninsula, Mexico

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Abstract

Cedrela odorata (Spanish cedar) is a neotropical broadleaf tree species that is in high demand for furniture and interior fittings. In 1998, seed collections were made from Spanish cedar in the Yucatan Peninsula, Mexico, for genetic conservation and tree improvement projects. Progeny from these collections were established in genetic trials at Bacalar, Noh Bec, and Zoh Laguna in the Yucatan. Survival at 2 years was 73.5% at Bacalar, 72% at Noh Bec, but only 20% after 6 months for several replicates at Zoh Laguna. Mean 2-year height, number of years of Hypsypyla attack on apical shoots (over 2 or 3 years) and total branching over 2 years, were 1.3 m, 0.04 years, and 2.5 branches at Bacalar, and 1.9 m, 0.35 years, and 1.6 branches at Noh Bec. Selection of the three best provenances (Escárcega, Bacalar, and Calakmul) would result in an estimated cross-site gain of 8.6% in 2-year height. Within-provenance, cross-site heritabilities for 2-year height, shoot borer attack, and branching were 0.1/C6 0.02, 0.0/C6 0.02, and 0.0/C6 0.02, respectively. Single-site heritabilities for height at 2 years, shoot borer attack, and branching were 0.09/C6 0.05, 0.02/C6 0.04, and 0.09 ± 0.05 at Bacalar and 0.16 ± 0.07, 0.0 ± 0.06, and 0.0 ± 0.07 at Noh Bec. Given the known advantage of rapid growth to avoid Hypsypyla damage over the long term and the stable performance of provenances across sites for growth traits, we recommend provenance selection over multiple trials to reduce the risk of serious damage by the insect. Good provenances and other suitable seed sources, as well as proper site selection and silvicultural practices, are important tools for increasing yields from plantations of C. odorata.

Keywords: Cedrela odorata; Hypsypyla grandella; Tree improvement; Heritability; Genetic gain; Tropical hardwoods

1. Introduction

Cedrela odorata (Spanish cedar) has desirable wood characteristics, similar to mahogany (Swietenia spp.) in strength, low and even shrinkage, and easy workability (Longwood, 1962). Internationally and in Mexico, it is one of the most highly valued cabinet woods (Cintron, 1990; FAO, 2000; ITTO, 2006). In 2004, Mexico imported more Spanish cedar than it exported (ITTO, 2005). The future availability of the wood is a concern because of the continued high demand yet low yield from natural forests. Due to this dwindling supply of wood and its fragile conservation status in natural stands, Spanish cedar has recently been proposed for inclusion in Appendix II of the Convention on International Trade in Endangered Species (CITES, 2007), which would restrict its trade to documented sources only.

Establishment of C. odorata in plantations would benefit both local and international markets, and help conserve the remaining stock in natural forests. However, the susceptibility of C. odorata to the shoot borer, Hypsypyla grandella, limits its successful establishment in plantations within its natural distribution (Navarro, 2002; Cintron, 1990) and in forest enrichment plantings. Identification of germplasm resistant to or tolerant of shoot borer attack (Newton et al., 1993a) would increase the likelihood of plantation success.

The objectives of our research were to determine patterns of genetic variation among families and provenances in Spanish cedar for height, diameter, stem form, amount of branching, and amount of attack by the shoot borer. Field trials of C. odorata were established at the Bacalar Experimental Station, Yucatan Peninsula, Mexico, and at nearby ejidos (Yucatan communities...
with forest properties) to quantify variation in these important economic traits. It was appropriate to carry out this test on ejido properties, as these local communities are likely to establish plantations or attempt enrichment planting within their own natural forest. We report on early results from these trials because of the importance of these results for understanding how to reduce the impact of shoot borer attack.

As revised by Pennington and Styles (1981), *C. odorata* is a canopy emergent (to >30 m height), deciduous tree, with a natural distribution from northern Mexico (ca. 26°N) and the Caribbean islands to northern Argentina (ca. 28°S) (Patino Valera et al., 1997). The altitudinal distribution of the species ranges from sea level to 1200 m asl (Pennington and Styles, 1981). It tolerates a range of climatic conditions but is most common in regions with a well-defined dry season (Lamb, 1968). However, trees are stunted when the mean annual rainfall is less than 1250 mm (Lamb, 1968), as well as on compacted and waterlogged soils (Cater, 1945). The species may also be sensitive to other features of soil structure and fertility (Cater, 1945; Vega, 1974). Superior growth occurs on well-drained soils, and it is commonly found growing on Maya ruins (Belize) and limestone ridges (Trinidad) (Lamb, 1968). Spanish cedar usually occurs as scattered, individual trees in semi-deciduous forests (Holdridge, 1943; Combe and Gewald, 1979). It is a long-lived pioneer tree, with a high light requirement, but it persists in mature forests. The thin canopy provides a light shade useful for coffee (Fuentes Flores, 1979; Navarro et al., 2004). Under favorable conditions it attains up to 2.3 m year⁻¹ in height (Lamb, 1968); new shoot growth is initiated after the rainy season begins (Borchert, 1983). Trees can start flowering at the 10th year (Lamb, 1968). The seed is light and winged for wind dispersal.

2. Methods

2.1. Seed collection and nursery procedures

From February to April 1999, open-pollinated seed was collected from 152 trees located in five provenances throughout the Yucatan Peninsula of Mexico. Trees were located mostly in villages and along roads and in home gardens, and were at least 100 m apart. Although every effort was made to look for trees in the native forests, few were found, due to high local demand and illegal cutting. This effort was part of a Mesoamerican-wide germplasm collection to determine provenance and family variation in the species, and was coordinated by the Tropical Agricultural Research and Higher Education Center (CATIE), in cooperation with local research institutions and community organizations (Navarro, 2002). Provenance designation was somewhat ambiguous, but collection locations were characterized by different annual rainfall and soil types and separated by 75–150 km distance (Fig. 1) (Wightman et al., 2008).

Seedlings were produced at three locations in the Yucatan: San Felipe Bacalar Research Station of the Mexican Institute for Forestry, Agricultural and Livestock Research (INIFAP), the Zoh Laguna community nursery, and a private nursery in Bacalar. Seeds were directly sown in bags, to avoid root deformities, in a 50% soil–50% organic compost blend. Germination rates were high, about 85% for most of the seed lots. In the community and private nurseries seedlings were grouped in blocks in order to minimize environmental effects.

2.2. Site management, experimental design, and data collection

Trials were established at Noh Bec and Zoh Laguna community sites and at the Bacalar research station (Table 1). Both community trials were established in two sections because of the limited size of available parcels of land. At Noh Bec three blocks were planted at Las Casetas (site slashed and burned of secondary growth), and two at Naranjal (unburned, abandoned citrus grove) about 2 km distant. Three blocks were planted at Zoh Laguna on an unburned grassy site, and the other two blocks at a location about 10 km away called “20 noviembre” in slashed and burned secondary growth. At Bacalar a bulldozer was used to clear away the 8–10 years old regrowth. At all sites trees were planted during the rainy season, from October to November 1999, when the seedlings were about 6 months old. At the community sites, trees were weeded by machete three times per year during the first year, and thereafter twice annually. Vegetation (mostly woody shrubs and stump sprouts) was allowed to grow between the tree rows but not to dominate the planted trees, in order to provide lateral shade, foster biodiversity, and possibly act as natural barriers to *H. grandella*. Trees were fertilized at age 6 and 12 months with 100 g of 17–17–17 NPK fertilizer at both community sites. The Bacalar site was weeded with similar frequency, but the vegetation (mostly grass) was kept short, and there was no fertilizer treatment.

Trial spacing at all sites was 3 m × 3 m. At the community trials, families were planted in four-tree row plots with five replications in a randomized complete block design. At the
Bacalar station, a compact family design was used in which families were planted in five-tree row plots and grouped within provenances within each of 5 blocks. Of the 152 open-polliﬁnated families that were collected in the Yucatan, 144 were planted and 59 were represented at all three trial sites.

Trees were measured at 5 months after planting, and at 1, 2, and 3 years post-planting in the Noh Bec and Zoh Laguna trials; and at planting, and at 1 and 2 years post-planting in the Bacalar trial. Branches were pruned after measurement (see below). The three blocks at Zoh Laguna were not measured again after planting, due to the 80% mortality which occurred within 6 months. This was attributable to sun scald, which cracked the bark and permitted attack by Chysobothris yucatanesis, a beetle with stem boring larvae that penetrate at the soil line, as well as to a secondary fungal infection. Since the 20 novembre blocks had much higher survival than the other blocks at Zoh Laguna, measurement there was continued.

Tree height (HT) was measured to the apex of the leading meristem. Diameter was first measured at the soil line (diameter at root collar or DRC) and then at year 3 as diameter at breast height (DBH at ca. 130 cm above ground). Trees were assigned a qualitative form grade (FORM) based on amount of branching and straightness of the stem (1 [very good] to 4 [poor] at the community trials and 1–3 at Bacalar). Shoot borer attack at the apex was recorded as present or absent, the number of apical shoots and lateral branches from the main stem were recorded, and then trees were pruned to one apical shoot. The mean number of years of apical attack (MYAPAT) was determined over 2 years across trials and for Bacalar, and over 3 years for the community trials. The total number of apical shoots was summed over years 1 and 2 across trials (TAPSH). The total number of apical shoots and branches (TBR) were summed over years 1 and 2 for Bacalar and over years 2 and 3 for the community trials. Tree survival between census periods was converted to longevity for determining heritability (AGE; number of years alive—up to 3 years at the community trials, and 2 years at Bacalar and across trials).

2.3. Data analysis

Additional Central American families from Panama and Costa Rica had been planted only at Bacalar, and were excluded from most analyses since their survival was consistently poor.

2.3.1. Performance and variation

The following general linear mixed model was used for across-site analysis:

\[ Y_{ijklm} = \mu + S_i + B(S)_{ij} + P_k + F(P)_{kl} + S(P)_{ik} + S/F(P)_{ikl} + B(S)P_{ijk} + B(S)F(P)_{ijkl} + e_{ijklm}, \]

where \( Y_{ijklm} \) is the observed value for an individual, \( \mu \) is the overall mean, \( S_i \) is the effect of the \( i \)th site, \( B(S)_{ij} \) is the effect of the \( j \)th block of the \( i \)th site, \( P_k \) is the effect of the \( k \)th provenance, \( F(P)_{kl} \) is the effect of the \( l \)th family in the \( k \)th provenance, \( S(P)_{ik} \) is the interaction of the \( i \)th site and the \( k \)th provenance, \( S/F(P)_{ikl} \) is the interaction of the \( j \)th block of the \( i \)th site and the \( k \)th provenance, \( B(S)P_{ijk} \) 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. The site term includes both differences in inherent site conditions (soil and climate) and variations in management of the site as described above. For within-site analysis, the site term and its interactions were removed. The two remaining blocks at 20 noviembre were included in the across-site comparison because of the added replication at another location.

Site and provenance effects were considered ﬁxed (except as stated below). Block, family and their interactions were treated as random effects. Site and block variances were standardized to a variance of one for within or across-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 (SAS, 1990) 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.

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 heritabilities were estimated after Xie and Ying (1996) as:

\[ h_I^2 = \frac{\sigma^2_A}{\sigma^2_e + \sigma^2_{BF(P)} + \sigma^2_{SF(P)} + \sigma^2_F}, \]

\[ h_F^2 = \frac{(\sigma^2_A/x_I)^2 + (\sigma^2_{BF(P)}/n_b)^2 + (\sigma^2_{SF(P)}/n_s)^2 + \sigma^2_F}{\sigma^2_{BF(P)} + \sigma^2_F}, \]

\[ h_w^2 = \frac{3\sigma^2_{F(P)}}{\sigma^2_{BF(P)} + \sigma^2_F}, \]

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; \( \sigma^2_A \) is the additive genetic variance, which is \( 3\sigma^2_{F(P)} \) (see below); \( \sigma^2_{BF(P)} \) is the variance component due to among family variation; \( \sigma^2_{SF(P)} \) is the variance component due to the block-by-family interaction; \( \sigma^2_F \) is the variance component due to the site-by-family interaction; \( \sigma^2_e \) is the variance component due to within plot variation; \( n_b \) is the number of blocks; \( n_s \) is the number of sites; and \( x_I \) is the harmonic mean of number of trees per family.

Most of the \( C. odorata \) families used were from source trees within ejido settlements and might represent related individuals. Therefore the value of 0.33 (\( \sigma^2_{F(P)} = 0.33 \sigma^2_A \)) for the coefficient of relationship, rather than the usual 0.25 for true half-sib families (\( \sigma^2_{F(P)} = 0.25 \sigma^2_A \)), was used to estimate individual tree heritabilities (after Navarro et al., 2004 who first determined narrow sense heritabilities for this species). Heritabilities were considered to be significant if the 95% confidence interval (\( h_I^2 \pm 1.96 \text{S.E.}; \) Lynch and Walsh, 1998) did not include zero. For within-site heritability calculations, the site-by-family interaction was removed. The standard errors for individual heritabilities were determined after Swiger et al. (1964) and for family level heritabilities after Wright (1976).

The power of the experimental design, or capacity to reject the null hypothesis of \( h_I^2 = 0 \) when this was false, was determined for each trait 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 AGCV = 100(\( \sigma^2_A/x \times \text{S.D. (blocks)} \)) where \( \sigma^2_A \) is the additive genetic standard deviation, \( x \) is the provenance mean, and \( \text{S.D. (blocks)} \) 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.

When the impact of provenance was significant, provenance performance was compared using the least significant difference tests on least square means (LSM), with a Tukey adjustment for pair-wise comparisons (SAS, 1990). Provenances were treated as fixed in most analyses, except for type B genetic correlations, comparison of family and provenance level variation, and determination of best linear unbiased predictors (BLUPS), where provenances were treated as random. Type B genetic correlations across sites for provenances were determined as \( r_{(p)} = \frac{\sigma^2_F}{\sigma^2_P + \sigma^2_{SP}} \) after Yamada (1962) and Sierra-Lucero et al. (2002). Type B correlations greater than 0.7 indicate sufficient phenotypic stability for across-site selection (Xie, 2003; see Sections 3 and 4). Family and provenance level variations were compared using the formula \( \theta = \frac{\sigma^2_P}{\sigma^2_{F(P)} + \sigma^2_F} \) (Sierra-Lucero et al., 2002).

The BLUPS for provenance performance were determined by treating provenances as random and separating out interactions and family effects, after Hodge and Dvorak (2004) and Ræbild et al. (2002), and reported as the % difference from the overall LSM. Gain was then estimated for selection of specific provenances by weighting BLUPS by the proportional representation of each provenance per trial, with the Yucatán and Zona Maya provenances eliminated. Estimated genetic gain within provenances was calculated using combined within-family and among-family selection, after Shelbourne (1969) and Becker (1992), for the best 70% of families within provenance and the best 30% of trees within family, or about 20% of the trees at each site. Phenotypic correlations were carried out between traits across and at each site, but genetic correlations were not calculated, since individual heritabilities were too low (Lynch and Walsh, 1998).

3. Results

3.1. Performance and provenance differences

Least square means for height, diameter, survival, attack, and branching for the 59 families in common to all sites, and all trees at Bacalar, Noh Bec, and the remaining blocks at 20 noviembre, are given in Table 3. Survival at Bacalar, Noh Bec, and 20 noviembre at 2 years was 73.5%, 72%, and 57%, respectively (not shown). HT2 and mean number of years of apical attack (MYAPAT) were greatest at Noh Bec. Total number of apical shoots and branches (TBR) was greatest at Bacalar. The worst FORM (Table 3) occurred in the 20 noviembre replicates.

Across all sites and at each site, there were significant differences among provenances for height, and no differences in MYAPAT. Across sites and at each site individually, the Escárcega, Bacalar, and Calakmul provenances were usually taller and sometimes larger in diameter, and with more TAPSH or TBR than the Yucatán and Zona Maya provenances. Central American families from Panama and Costa Rica had been planted at Bacalar, but since their survival was less than 50%, they were not considered further.

3.2. Genetic parameters

For the traits examined, more than 80% of genetic variation across sites, and usually more than 50% at each site, occurred among provenances rather than among families (Table 4). Significant individual heritabilities occurred for HT2 at Noh Bec, and DRC2 at Bacalar. Power, or capacity to reject the null hypothesis of \( h_I^2 = 0 \) when false, was \( \geq 70\% \) for these heritabilities. Heritabilities for attack were near zero. Within
sites, the AGCVs for diameter and height were > 10%. AGCVs were >25% for MYAPAT and TBR at Bacalar. The type B genetic correlations across sites were > 0.85 at the provenance level for HT and FORM.

Estimated gains in HT at the provenance level (with the Yucatán and Zona Maya provenances removed) across sites (8.6%) and within sites (6.1–12.1%) were accompanied by an increase in number of branches (Table 3). Additional estimated gain among families within provenances of at least 7% was found at Noh Bec for HT and DBH, and at Bacalar for DRC, for the best 20% of trees at each site.

Phenotypic correlations at each site between final tree height and TBR, between MYAPAT and TBR (Table 5), and amount of branching between years (not shown) were generally positive and significant (α ≤ 0.05). There was no consistent correlation between MYAPAT and final tree height (Table 5), between apical attack and height growth rate either in the same or the next year, or for attack between years (not shown). Attacked trees tended to be taller than unattacked trees, but there was much overlap in height between the two groups (not shown).

4. Discussion

4.1. Performance and provenance differences

Although these were the first extensive trials of C. odorata established in the Yucatan Peninsula, other trials have been conducted elsewhere using material from the region. In the 1970s the Oxford Forestry Institute (OFI) conducted the International Cedrela Provenance Trials, which consisted of 14 provenances and other seed sources of Cedrela spp. planted in 18 countries, including one from Matamoros (near Escárcega), Campeche. The reported height of this provenance in trials ranged from 1.5 to 3.5 m at 3 years in Puerto Rico and St. Croix, US Virgin Islands, to 6.6 m at 2 years in Tanzania (Karani, 1973; Omoyiola, 1973; Raunio, 1973a,b; Whitmore, 1978). The better height growth rates in Africa may have been influenced by the lower incidence of attacks by the local shoot borer (H. robusta). At our trial sites, mean height (about 2.6 m at 3 years; Table 2) was low compared to that in the African OFI trials, although it was better than the performances in Puerto Rico and St. Croix. Mean height growth in our study also compared favorably to that in other reports from Mexico (0.5–1.25 m year⁻¹; Wadsworth, 1960). Navarro et al. (2004) reported greater mean heights per provenance (1.75–2.5 m at 2 years) for a subset of the families used in our trials but planted at Turrialba, Costa Rica. Our trials had less shoot borer attack and branching than the Mexican germplasm in the Costa Rica trials, and less attack than the Mexican source in the St. Croix trials, but more branching than this source in the Puerto Rico and St. Croix trials (Whitmore, 1978; Navarro et al., 2004).

In our study, significant differences occurred among provenances across and at each site in most size traits (Table 3), with the provenances from Yucatán and Zona Maya growing more poorly than those from Escárcega, Bacalar, and Calakmul (Table 4). Differences in height growth among provenances by a factor of five or more have been found in trials established by the OFI and others in Africa and Colombia (Newton et al., 1993b; Guevara Marroquí, 1988).

There was greater differentiation in height among Yucatan provenances of C. odorata than in Swietenia macrophylla trials carried out simultaneously in the region (Wightman et al., 2008). This result held for height at year 2, even when the Yucatán provenance from the lowest annual rainfall area was excluded (not shown). (This exclusion made the geographic areas covered by the C. odorata and S. macrophylla collections more comparable.) Dry zone populations of C. odorata are hypothesized to have arrived in Mesoamerica and the Yucatan from South America before the formation of the Isthmus of Panama (Cavers et al., 2003) about 3 million years ago (Coates, 1997), providing time for genetic divergence in quantitative traits among populations. Swietenia macrophylla is possibly a more recent arrival to the Yucatan, with less time for differentiation. The greater rarity of C. odorata than S. macrophylla (Navarro, 2002; Patiño Valera et al., 1997), and presumed greater site selectivity, may reduce gene flow, which would also increase population differentiation.

We found a great deal of phenotypic variation in TBR and MYAPAT (Table 3) and significant differences among provenances for TBR, but not for MYAPAT. However, our annual assessments demonstrated that, as in a mahogany (Swietenia macrophylla) study (Wightman et al., 2008), Hypsipyla can be a threat during the first few years of growth. Other studies have found genetic variation in C. odorata for attack, branching, or apical dominance (Newton et al., 1995; Cornelius and Watt, 2003; Navarro et al., 2004).

4.2. Genetic parameters

More replicates would have allowed for greater precision in estimates of genetic parameters, but our trial sizes were limited by the dimensions of available land and the local conditions. Despite these limitations, blocking was effective in removing at least 99% of variation for height measurements (not shown).

At Noh Bec and Bacalar, the within-provenance AGVC for metric traits compared favorably to those reported for other tree species (mean of 11.1 for height, 9.1 for diameter; Cornelius, 1994), although the within-provenance heritabilities in the trials (Table 5) were lower than usual (mean of 0.28 for height and 0.23 for diameter; Cornelius, 1994). In a provenance/progeny trial established in Costa Rica in a coffee plantation with provenances from Mexico to Panama (Navarro et al., 2004),
there was significant variation among provenances and families for height and diameter. A similar within-provenance individual heritability for height (0.12) but greater heritability for diameter (0.20) was found compared to our study (Table 5). A clonal trial in Cuba yielded broad-sense heritability estimates of 0.85 for height and 0.62 for diameter at 14 years (Lahera et al., 1994). Sufficient genetic variation existed among provenances across sites to allow for an estimated gain of 8.6% in height by using the correct provenances. The across-site provenance-level type B genetic correlation for height at year 2 was 0.87 (Table 5), indicating that this trait was sufficiently stable (<0.7) to select certain provenances across the range of sites tested.

### Table 3
Provenance performance by trait indicating probability of a greater $F$ value for the provenance effect, the overall LSM, provenance level BLUPS as % difference from overall LSM, and estimated gain with the Yucatán and Zona Maya provenances eliminated

<table>
<thead>
<tr>
<th>HT2</th>
<th>DRC2</th>
<th>MYATAP</th>
<th>TAPSH12</th>
<th>FORM2</th>
<th>AGE2</th>
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<tr>
<td>All trials</td>
<td></td>
<td></td>
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<tr>
<td>Provenance ($p &gt; F$)</td>
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<td>0.006</td>
<td>0.48</td>
<td>0.0001</td>
<td>0.0001</td>
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<tr>
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<td>ab</td>
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<tr>
<td>Provenance ($p &gt; F$)</td>
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<td>0.64</td>
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<td>% BLUPS</td>
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<td>Bacalar</td>
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<td>Yucatán</td>
<td>−9.9</td>
<td>abc</td>
<td>−10.2</td>
<td>ab</td>
<td>−5.3</td>
<td>0.0</td>
</tr>
<tr>
<td>Zona Maya</td>
<td>−6.5</td>
<td>d</td>
<td>−5.7</td>
<td>c</td>
<td>−3.5</td>
<td>0.0</td>
</tr>
<tr>
<td>Estimated gain (%)</td>
<td>6.1</td>
<td>5.7</td>
<td>3.1</td>
<td>0.0</td>
<td>9.8</td>
<td>0.0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>HT2</th>
<th>HT3</th>
<th>DBH3</th>
<th>MYATAP</th>
<th>TBR23</th>
<th>FORM3</th>
<th>AGE3</th>
</tr>
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<tbody>
<tr>
<td>Bacalar</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Provenance ($p &gt; F$)</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.05</td>
<td>0.64</td>
<td>0.21</td>
<td>0.63</td>
</tr>
<tr>
<td>Overall Ismean</td>
<td>133.2</td>
<td>34.2</td>
<td>0.04</td>
<td>2.5</td>
<td>1.2</td>
<td>1.7</td>
</tr>
<tr>
<td>% BLUPS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bacalar</td>
<td>11.7</td>
<td>a</td>
<td>9.1</td>
<td>a</td>
<td>0.0</td>
<td>23.4</td>
</tr>
<tr>
<td>Calakmul</td>
<td>26.5</td>
<td>bcd</td>
<td>20.5</td>
<td>bcd</td>
<td>0.0</td>
<td>40.2</td>
</tr>
<tr>
<td>Escárcega</td>
<td>−4.4</td>
<td>b e</td>
<td>−5.8</td>
<td>b</td>
<td>0.0</td>
<td>−5.2</td>
</tr>
<tr>
<td>Yucatán</td>
<td>−28.1</td>
<td>ace</td>
<td>−21.6</td>
<td>ace</td>
<td>0.0</td>
<td>−44.4</td>
</tr>
<tr>
<td>Zona Maya</td>
<td>−5.7</td>
<td>d</td>
<td>−2.2</td>
<td>d e</td>
<td>0.0</td>
<td>−14.1</td>
</tr>
<tr>
<td>Estimated gain (%)</td>
<td>12.1</td>
<td>8.6</td>
<td>0.0</td>
<td>21.0</td>
<td>−4.9</td>
<td>2.1</td>
</tr>
</tbody>
</table>

See text for details. Letters indicate significantly different pairs of provenances ($p < 0.05$) based on least significant differences of LSMs with a Tukey–Kramer modification for pairwise comparisons. HT = tree height, DRC = diameter at root collar, DBH = diameter at breast height, MYATAP = mean number of years attacked at the apex, TAPSH = total number of apical branches, TBR = total number of apical and stem branches, FORM = stem form, AGE = the number of years alive. Numbers indicate the years of measurement.
At Noh Bec and Bacalar there were sufficient within-provenance heritability and AGCV to project an additional estimated gain of 5.4–9.2% in height for the best 20% of trees at each site. Stronger selection was not considered, in order to maintain genetic diversity for reforestation and forest enrichment programs. Performance remains to be investigated in the driest part of the range of *C. odorata* in the Yucatan, since none of these trials were established there.

### 4.3. Strategy for tree improvement

We suggest selection across sites for the fastest growing provenances to maximize early tree height growth in order to reduce the impact of attack. We found no correlation between attack and tree height or attack and height growth rate (Table 5).

In *Toona australis*, a closely related species, attack intensity (percent of shoots attacked) decreased with tree height as the number of shoots increased (Mo et al., 1997). Since the number of branches also increased with tree height in *C. odorata* (Table 5), attack intensity on taller trees should also be less. In addition, many tree development studies indicate that there is high genetic correlation between juvenile and adult height growth, and clone means for very early and third year growth in *C. odorata* can be highly correlated (Cornelius and Watt, 2003), supporting the value of tree selection at an early age. Since we found variation among provenances for height at a young age, we recommend early selection for metric traits to maximize improvement in the amount of merchantable timber.

**Table 4**

<table>
<thead>
<tr>
<th>Across sites</th>
<th>$h_I^2$</th>
<th>S.E.</th>
<th>Power (%)</th>
<th>$h_F^2$</th>
<th>S.E.</th>
<th>$h_W^2$</th>
<th>AGCV (%)</th>
<th>Gain (Family) (%)</th>
<th>$\theta$ (%)</th>
<th>$rb_{up}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>HT2</td>
<td>0.01</td>
<td>0.02</td>
<td>11</td>
<td>0.05</td>
<td>0.00</td>
<td>0.01</td>
<td>3.6</td>
<td>0.6</td>
<td>97</td>
<td>0.87</td>
</tr>
<tr>
<td>DRC2</td>
<td>0.00</td>
<td>0.02</td>
<td>5</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.0</td>
<td>0.0</td>
<td>100</td>
<td>0.53</td>
</tr>
<tr>
<td>MYATAP</td>
<td>0.00</td>
<td>0.02</td>
<td>5</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.0</td>
<td>0.0</td>
<td>nc</td>
<td>nc</td>
</tr>
<tr>
<td>TAPSH12</td>
<td>0.00</td>
<td>0.02</td>
<td>5</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.0</td>
<td>0.0</td>
<td>100</td>
<td>0.45</td>
</tr>
<tr>
<td>FORM2</td>
<td>0.01</td>
<td>0.03</td>
<td>15</td>
<td>0.10</td>
<td>0.00</td>
<td>0.01</td>
<td>3.9</td>
<td>0.9</td>
<td>92</td>
<td>0.93</td>
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<tr>
<td>AGE2</td>
<td>0.01</td>
<td>0.02</td>
<td>14</td>
<td>0.09</td>
<td>0.00</td>
<td>0.01</td>
<td>4.0</td>
<td>0.8</td>
<td>0</td>
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</tr>
</tbody>
</table>

**Table 5**

<table>
<thead>
<tr>
<th>Traits</th>
<th>Noh Bec</th>
<th>20 noviembre</th>
<th>Bacalar</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$r$</td>
<td>$\alpha &lt; p$</td>
<td>$r$</td>
</tr>
<tr>
<td>HT3</td>
<td>MYATAP</td>
<td>0.02 0.57</td>
<td>−0.08 0.08</td>
</tr>
<tr>
<td>HT3</td>
<td>TOTBR123</td>
<td>0.42 0.0001</td>
<td>0.10 0.04</td>
</tr>
<tr>
<td>MYATAP</td>
<td>TOTBR123</td>
<td>0.30 0.0001</td>
<td>0.20 0.0001</td>
</tr>
</tbody>
</table>

HT = tree height, DRC = diameter at root collar, DBH = diameter at breast height, MYATAP = mean number of years attacked at the apex, TAPSH = total number of apical branches, TBR = total number of apical and stem branches, FORM = stem form, AGE = the number of years alive, nc = not calculable. Numbers indicate the years of measurement.

(Sierra-Lucero et al., 2002). At Noh Bec and Bacalar there were sufficient within-provenance heritability and AGCV to project an additional estimated gain of 5.4–9.2% in height for the best 20% of trees at each site. Stronger selection was not considered, in order to maintain genetic diversity for reforestation and forest enrichment programs. Performance remains to be investigated in the driest part of the range of *C. odorata* in the Yucatan, since none of these trials were established there.

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Genetic improvement of *C. odorata* needs to be viewed within the ecology and appropriate silviculture of the species.
Improved germplasm should be used in conjunction with selection of appropriate sites, lateral shade, and pruning in order to obtain sufficient clear bole (Guevara Marroquín, 1988; Navarro et al., 2004; Vega, 1974; Cornelius and Watt, 2003; Snook and Negreiros, 2004; Goulet et al., 2005). Identification of the appropriate growing conditions is essential (Whitmore, 1978) in order to achieve maximum possible growth rate and thereby reduce the impact of shoot borer attack (Vega, 1974; Newton et al., 1993a). The limited financial resources of local land owners in the Yucatan need to be considered in recommendations of specific silviculture practices, since expenses such as fertilizer and insecticides may be prohibitive.

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 Agrosilvopastoral Council (CRASX) and the Organization of Ejido Forest Producers of the Zona Maya (OEFPZM). We thank Lionel Cotto and Carlos Navarro of CATIE, and the Calakmul Biosphere reserve for their help in seed collection. We thank Ismael Paté from the Instituto Tecnologico Agropecuaria No. 16 for arranging student help in data collection and entry. We are grateful to David Boshier, Nicholas Brokaw, and anonymous reviewers for helpful suggestions.

References


