

Genetic variation in host susceptibility to attack by the mahogany shoot borer, *Hypsipyla grandella* (Zeller)

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- Abstract**
- 1 Attack by shoot borers (*Hypsipyla grandella* Zeller) is the main factor limiting the cultivation of *Cedrela odorata* and *Swietenia macrophylla*, two economically important members of the mahogany family. No viable methods of pest control are currently available. To assess for genetic variation in susceptibility to pest attack, a combined progeny/provenance test of *C. odorata* and a provenance test of *S. macrophylla* were established separately at CATIE, Turrialba, Costa Rica, and assessed intensively over an 84-week period.
 - 2 Variation in height growth between provenances was highly significant in both species, provenance means varying by a factor of 2.7 and 1.2 in *C. odorata* and *S. macrophylla*, respectively. *Cedrela odorata* also displayed provenance variation in foliar phenology, as 94.7% of the trees from a 'wet zone' provenance remained foliated, whereas >35% of trees from three 'dry zone' provenances abscised their leaves during the dry season.
 - 3 Both species displayed significant genetic variation in susceptibility to shoot borer attack. At the peak of attack during the second year of growth, the effect of provenance was highly significant in both species, the mean number of attacks per tree varying between 0.8–2.4 and 0.6–1.3 in different provenances of *C. odorata* and *S. macrophylla*, respectively. A provenance of *C. odorata* from San Carlos, Costa Rica, displayed consistently lower susceptibility to pest attack, being subjected to fewer attacks during the first year and demonstrating a higher mean height to first point of damage.
 - 4 The nitrogen, total tannin and proanthocyanidin concentration of foliage varied significantly between *C. odorata* provenances: nitrogen concentration was significantly lower and tannin and proanthocyanidin contents were significantly higher in trees from the San Carlos provenance, Costa Rica. This study therefore suggests that proanthocyanidins may reduce susceptibility of *C. odorata* to *H. grandella*, at least during the early period of growth.
 - 5 These results provide support for the development of plant resistance as a strategy for managing shoot borers. In particular, there may be scope for selecting for high foliar proanthocyanidin content and the ability to tolerate attack by vigorous apical growth.

Keywords *Cedrela odorata*, *Hypsipyla grandella*, mahogany shoot borer, pest dynamics, pest resistance, *Swietenia macrophylla*, tannins.

Introduction

The mahogany shoot borer (*Hypsipyla grandella* (Zeller); Lepidoptera, Pyralidae) is a serious pest of the mahogany family (Meliaceae) in the neotropics, severely restricting the cultivation of *Cedrela odorata* L. (Spanish Cedar) and *Swietenia macrophylla* King (American mahogany), both of which produce highly valuable timber. *Hypsipyla grandella* larvae destroy the terminal shoots of the host plant by boring the pith, resulting in a highly branched tree of little economic value (Newton *et al.*, 1993a). Young trees are particularly vulnerable to attack, because of their greater dependence on a single leading shoot for growth (Vega, 1987). Despite a considerable research effort (Grijpma, 1974; Whitmore, 1976a,b), no viable methods of controlling this pest are currently available (Newton *et al.*, 1993a). The development of pest-resistant planting stock would therefore be of great value for reforestation efforts with these species.

Previous research on the occurrence of pest resistance in the Meliaceae has largely centred on *Toona ciliata* (F.v. Muell.) C.DC. (Meliaceae), an Asian and African species closely related to *Cedrela* spp. which is not attacked by *H. grandella* when planted in Central America (Whitmore, 1976c). Water-soluble extracts of *Toona* foliage, which may be high in alkaloids, have been shown to be toxic to *H. grandella* larvae (Grijpma, 1976). Both *Cedrela* and *Toona* are known to contain limonoids, many of which are known to be potent insecticides or feeding deterrents (Kubo & Klocke, 1986). Such observations suggest that it may be possible to select pest-resistant individuals within species of Meliaceae for multiplication in a breeding programme (Grijpma, 1976). However, little information is currently available on intraspecific variation in these characteristics.

Pest resistance may arise as a result of three processes (Painter, 1951; Van Emden, 1987): (i) antixenosis (= non-preference), in which the plant is avoided or colonized by the pest to a lesser extent; (ii) antibiosis, in which the plant reduces the performance of the growth or survival of the pest, usually by possession of chemical defences; and (iii) tolerance, where the plant recovers from insect attack to an economically acceptable level. This investigation was designed to assess the occurrence of genetic variation in these different forms of resistance within

both *C. odorata* and *S. macrophylla*, by the use of screening trials. The trials were designed as genetic tests, incorporating a range of different provenances or half-sib families, or both, and were assessed for growth traits and the incidence of pest attack. Seasonal variation in growth, phenology and the incidence of pest attack in these trials were described by Newton *et al.* (1998). This study also involved an assessment of genetic variation in the nitrogen, total tannin and proanthocyanidin concentration of foliage from *C. odorata*. Previous research on other insect herbivores has shown that tannins, and proanthocyanidins (condensed tannins) in particular, can have detrimental effects on insects (e.g. Feeny, 1970; Rossiter *et al.*, 1988; Nicholsorians, 1991).

Materials and methods

The investigation was carried out at the Centro Agronómico de Investigación y Enseñanza (CATIE) in Turrialba, Costa Rica (9°54' N 83°40' W) at 600 m a.s.l. Mean annual precipitation and temperature of this location are ≈ 2600 mm and 22°C, respectively. Seed of *C. odorata* was collected from open-pollinated trees growing on farms, from four localities in Costa Rica, namely Carmona, Hojancha, Cañas, San Carlos, and one in Trinidad (Table 1). From each of these provenances, seed from five different mother trees was collected and kept separate, giving a total of 25 open-pollinated families. Trees from these localities were selected on the basis of stem straightness and lack of forking (clear bole > 7 m). Seed of *S. macrophylla* was obtained from bulked collections from five provenances, namely Haiti, Trinidad, Honduras and two from Puerto Rico (Table 1). Seed was germinated in seed trays, then transferred to black polyethylene bags (2.2 L capacity) containing a 1 : 1 : 1 mixture of forest soil, sand and organic compost. Seedlings were raised in full sunlight in the CATIE nursery, and received natural rainwater only.

Two separate field trials, screening *C. odorata* and *S. macrophylla*, respectively, were established on adjacent sites at Florencia Sur, CATIE, during February 1991. The soil of this area is argillaceous, with a pH of 4.4, and is considered deficient in P and Ca (Bertsch, 1986). The sites were prepared, and trials established, as described by Newton *et al.* (1998). The first

Provenance	Latitude (N)	Longitude (W)	Altitude (m)	Precipitation (mm)	Accession number
<i>Cedrela odorata</i>					
Cañas, Costa Rica	10°25'	85°6'	70–120	1829–2274	2008–2012
Carmona, Costa Rica	9°60'	85°15'	60–70	1780	2013–2017
Hojancha, Costa Rica	10°04'	85°25'	100–350	2232	2018–2022
San Carlos, Costa Rica	10°22'	84°28'	80–260	2866–3609	2003–2007
St. Andrew, Trinidad	10°28'	61°05'	10–100	2500	1998–2002
<i>Swietenia macrophylla</i>					
Dirici, Haiti	19°42'	72°24'	40	1999	2029
Guajataca, Puerto Rico	18°22'	67°00'	200	2000	2023
Juan Diaz, Puerto Rico	18°00'	66°31'	10	900	2025
La Mosquitia, Honduras	15°20'	84°24'	11–170	2859	2027
St. Andrew, Trinidad	10°28'	61°05'	10–100	2500	2028

Table 1 Origins of the seedlots used in field trials to assess variation in susceptibility to shoot borer attack. (In the case of *C. odorata*, seed was collected from five open-pollinated trees, giving five families for each provenance. Each family was accorded a separate accession number. In *S. macrophylla*, seed collected from different trees was bulked within each provenance, giving only one accession number per provenance.)

experiment included five provenances of *C. odorata*, each of which was represented by five families. Trees were arranged by family in row plots of five trees each, in nine fully randomized replicate blocks, at a spacing of 2.5 × 2.5 m. The whole experiment was surrounded by a single-row border of the same family as the adjacent plot. In the second experiment, 25 seedlings of each *S. macrophylla* provenance were arranged in square plots in a 5 × 5 array, at a spacing of 2.5 × 2.5 m. Five fully randomized replicate blocks were established. The whole experiment was again surrounded by a single-row border of the same provenance as the adjacent plot. Both of the trials were cleaned of weed growth by hand approximately every 3 months.

Each tree in both experiments was assessed for the incidence of shoot borer attack at 14-day intervals, starting on 22 April 1991 and continuing for a total of 84 weeks. Assessments of attack were made by visually inspecting each plant, and counting the number of attack loci indicated by the presence of fresh frass. The foliar phenology of the trees was also assessed, by noting the presence or absence of foliage. Tree height was measured after 26, 56 and 88 weeks. In addition, the two experiments were assessed after 141 and 177 weeks (*C. odorata* and *S. macrophylla*, respectively) for height to first branching and for the number of damage (rather than attack) loci, indicated by forking.

Data were analysed by *t*-test or ANOVA, where appropriate, using SAS (SAS, 1980). Proportions were arcsin transformed prior to analysis, following Snedecor & Cochran (1980). To assess the relative influence of different factors, the data were analysed using an individual tree model (Stonecypher, 1992) with random main effects and full interactions. Family was nested within provenance. 'F'-tests were generated using the TEST option of the GLM RANDOM statement of SAS (SAS, 1980). SAS uses Satterthwaite's (1946) approximations for appropriate degrees of freedom, when necessary. Variance components were estimated using the SAS VARCOMP procedure. Standard errors of variance components were calculated following Gordon *et al.* (1972). This approach enables the proportion of total variance attributable to each factor to be estimated readily.

During October 1994, foliage samples were taken from five trees of each of the five San Carlos families, and five trees from two of each of the remaining four provenances, giving a total of 65 trees from 13 families. Nitrogen concentration was measured by a modified micro-Kjeldhal method (Müller, 1961), total soluble tannin concentration was determined gravimetrically after precipitation with trivalent ytterbium (Reed *et al.*, 1985) and proanthocyanidin concentration was measured by the method of Rittner & Reed (1992). Data were analysed by nested (provenance and family within provenance) analysis of variance using SAS (SAS, 1980).

Results

Genetic variation in height growth was recorded in both experiments, differences between both provenances and families tending to become more pronounced with time. In the *C. odorata* trial, mean heights ranged from 101 to 165 cm in family numbers 2011 and 2006, respectively, at the first assessment (26 weeks). The relative performance of the different families remained fairly constant throughout the experiment. At the third assess-

ment (88 weeks), mean height varied by a factor of 2.4, maximum values being recorded in family 2006 (Fig. 1a). At this time, variation between families and provenances was highly significant ($P < 0.001$, d.f. = 24, $F = 23.74$; $P < 0.001$, d.f. = 4, $F = 127.8$, respectively, when tested separately by ANOVA), means ranging from 148 (Hojancha) to 313 cm (San Carlos). The variance component analysis indicated that the family effect in *C. odorata* was attributable largely to variation between provenances (Table 2). At 141 weeks in *C. odorata* mean height varied from 140 to 491 cm in families 2015 and 2006, respectively, provenance means ranging from 183 to 501 cm in Hojancha and San Carlos, respectively. Differences between families and provenances were both highly significant at this time ($P < 0.001$, d.f. = 24, $F = 30.78$; $P < 0.001$, d.f. = 4, $F = 177.28$, respectively, ANOVA).

In the *S. macrophylla* experiment, provenance means varied between 61.6 and 72.4 cm (in Juan Diaz, Puerto Rico and Honduras, respectively) at 26 weeks. At 88 weeks, the effect of provenance was highly significant ($P = 0.002$, d.f. = 4, $F = 4.40$; ANOVA), mean provenance values varying by a factor of 1.2 (Fig. 1b). At the assessment of *S. macrophylla* at week 177, provenance mean values ranged from 211 to 267 cm in Dirici and Guajataca, respectively, the effect of provenance being highly significant overall ($P < 0.001$, d.f. = 4, $F = 6.11$; ANOVA). A pronounced block effect, and an interaction between block and provenance, were also noted (Table 3).

Genetic variation in foliar phenology was observed in the *C. odorata* trial, particularly with respect to leaf abscission during the dry season. For example, at week 48 when the proportion of trees with leaves was at its lowest (Newton *et al.*, 1998), there was a pronounced difference between provenances ($P < 0.001$, d.f. = 4, $F = 60.09$; ANOVA) in the proportion of trees which remained foliated. The mean proportion of trees with leaves was 94.7 and 70.5% for San Carlos and Trinidad, respectively, with means of < 35% recorded in each of the other three provenances. Values for individual families ranged from 17–97.6% in 2018 and 2006, respectively. Pronounced variation in leaf colour was also observed in *C. odorata*. Flushing foliage in the San Carlos provenance was noticeably redder than in the other provenances. When each tree was assessed after 88 weeks for red colouration, 73% of trees in the San Carlos provenance were found to possess this characteristic, whereas values for the other four provenances were < 1%. The maximum value (80%) was recorded in family 2006. As the majority of *S. macrophylla* trees possessed foliage throughout the experiment, no analysis of variation in phenology was carried out in this species; no variation in leaf colour was noted.

In *C. odorata*, pronounced peaks in shoot borer attack were observed at weeks 12 and 68 after the initiation of assessments (Newton *et al.*, 1998). At the first peak, significant variation in the mean number of attacks per tree was observed between both families ($P = 0.017$, d.f. = 24, $F = 1.72$; ANOVA) and provenances ($P = 0.01$, d.f. = 4, $F = 3.34$; ANOVA). Values ranged from 0.02 to 0.66 in families 2005 and 2000, respectively, whereas provenance means varied between 0.09 (San Carlos) and 0.29 (Trinidad) (Fig. 2a). At the second peak after 68 weeks, the effect of both provenance and family was again highly significant (respectively $P < 0.001$, d.f. = 4; $F = 29.51$; and $P < 0.001$, d.f. = 24; $F = 5.98$, when tested separately by ANOVA; Fig. 2b).

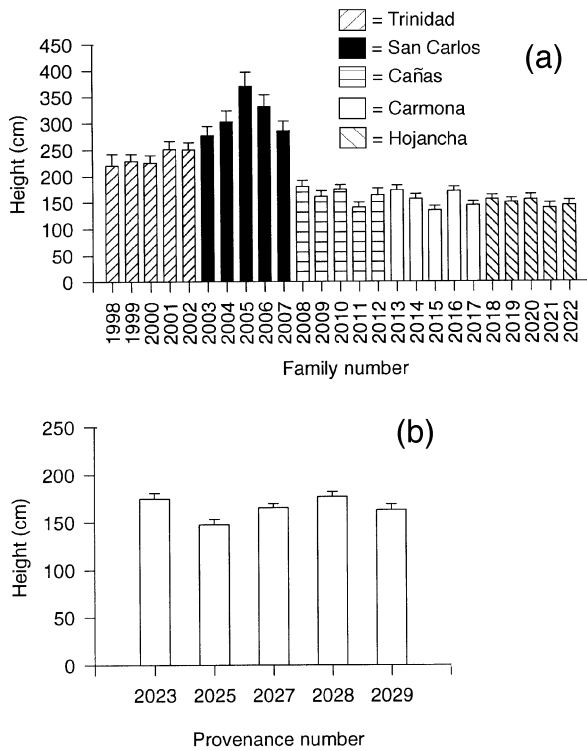


Figure 1 Variation in height growth of (a) *Cedrela odorata* and (b) *Swietenia macrophylla* in field trials at CATIE, Costa Rica, after 88 weeks. Values presented are means ($n=45$ and $n=125$ for *C. odorata* and *S. macrophylla*, respectively); vertical bars represent SEM.

Variance component analysis indicated that the family effect was entirely attributable to provenance variation (Table 2). The proportion of *C. odorata* trees attacked also varied between provenances, with 5.1–17.4% in San Carlos and Trinidad, respectively, at the first peak, and 28.0–58.9% in Cañas and Trinidad, respectively, at the second peak.

In the *S. macrophylla* trial, the number of shoot borer attacks peaked at week 60, when 559 attacks were recorded in the trial as a whole (Newton *et al.*, 1998). At this time, the number of attacks differed significantly ($P=0.014$, $d.f.=4$, $F=3.16$; ANOVA) between provenances, the mean number of attacks per tree ranging from 0.58 to 1.25 in Juan Diaz and Guajataca, respectively (Fig. 2c). A block–provenance interaction was again noted, as for height (Table 3). The proportion of *S. macrophylla* trees attacked varied between 28.5 and 52.1% in Juan Diaz and Guajataca, respectively.

The number of damage loci in *C. odorata*, assessed after 141 weeks, was also significantly affected by both family and provenance (respectively $P<0.001$, $d.f.=24$, $F=4.84$; and $P<0.001$, $d.f.=4$, $F=17.21$; ANOVA). The mean number of damage loci per tree varied between 0.7 and 3.0 in families 2015 and 1998, provenance means ranged from 1.55 to 2.64 in Hojancha and Trinidad, respectively. Similarly, the height to first damage locus was significantly affected by both family and provenance in *C. odorata* (respectively $P<0.001$, $d.f.=24$, $F=9.35$; $P<0.001$, $d.f.=4$, $F=47.41$; ANOVA; Fig. 3a). As with height and incidence of

Table 2 Analysis of variance components for growth and susceptibility to pest attack in a combined provenance/progeny test of *Cedrela odorata*.

Trait	Effect	VC (%)	SE (%)
Height growth (cm)	Block	1680 (12.6)	923 (6.9)
	Prov.	4948 (37.2)	3095 (23.3)
	Fam. (prov.)	192 (1.4)	184 (1.4)
	Block × Prov.	835 (6.3)	300 (2.2)
	Block × Fam. (prov.)	916 (35.6)	241 (1.7)
	Error	4722 (35.6)	223 (1.7)
Number of attacks Peak 1	Block	0.011 (2.4)	0.007 (1.6)
	Prov.	0.003 (0.6)	0.004 (0.9)
	Fam. (prov.)	0.000 (0.1)	0.004 (0.8)
	Block × Prov.	0.011 (2.4)	0.008 (1.8)
	Block × Fam. (prov.)	0.027 (5.7)	0.013 (2.8)
	Error	0.418 (88.8)	0.020 (4.3)
Number of attacks Peak 2	Block	0.240 (5.3)	0.147 (3.2)
	Prov.	0.524 (11.6)	0.308 (6.8)
	Fam. (prov.)	0 (0)	0.041 (0.9)
	Block × Prov.	0 (0)	0.067 (1.5)
	Block × Fam. (prov.)	0.432 (9.5)	0.129 (2.9)
	Error	3.330 (73.6)	0.162 (17.6)
Height to first damage locus (cm)	Block	8.9 (8.6)	4.92 (4.8)
	Prov.	22.3 (21.6)	15.6 (15.1)
	Fam. (prov.)	1.4 (1.4)	1.55 (1.5)
	Block × Prov.	6.5 (6.3)	2.25 (2.2)
	Block × Fam. (prov.)	0.1 (0)	2.38 (2.3)
	Error	63.9 (62.0)	3.46 (3.3)
Number of damage loci	Block	0.11 (5.1)	0.063 (2.9)
	Prov.	0.158 (7.3)	0.114 (5.2)
	Fam. (prov.)	0.054 (2.5)	0.043 (2.0)
	Block × Prov.	0.052 (2.5)	0.038 (1.7)
	Block × Fam. (prov.)	0.111 (5.1)	0.073 (3.3)
	Error	1.69 (77.7)	0.091 (4.2)

VC=variance component; SE=standard error; prov.=provenance; fam.=family.

Table 3 Analysis of variance components for growth and susceptibility to pest attack in a provenance test of *Swietenia macrophylla*.

Trait	Effect	VC (%)	SE (%)
Height growth (cm)	Block	0.088 (10.6)	0.063 (35.1)
	Prov.	0.017 (2.0)	0.026 (14.9)
	Block × Prov.	0.109 (13.1)	0.050 (27.8)
	Error	0.623 (74.3)	0.040 (22.2)
Height to first attack (cm)	Block	0.054 (9.7)	0.010 (12.1)
	Prov.	0.010 (1.89)	0.034 (39.2)
	Block × Prov.	0.029 (5.3)	0.015 (18.3)
	Error	0.460 (83.0)	0.026 (30.5)
Number of attacks	Block	0.054 (2.3)	0.012 (23.8)
	Prov.	0.026 (1.1)	0.010 (20.1)
	Block × Prov.	0.114 (4.8)	0.013 (25.6)
	Error	2.180 (91.8)	0.156 (30.4)
Number of damage loci	Block	0.137 (4.7)	0.052 (18.3)
	Prov.	0.103 (3.5)	0.040 (14.2)
	Block × Prov.	0.028 (9.7)	0.067 (23.5)
	Error	2.384 (82.0)	0.125 (43.9)

VC=variance component; SE=standard error; prov.=provenance.

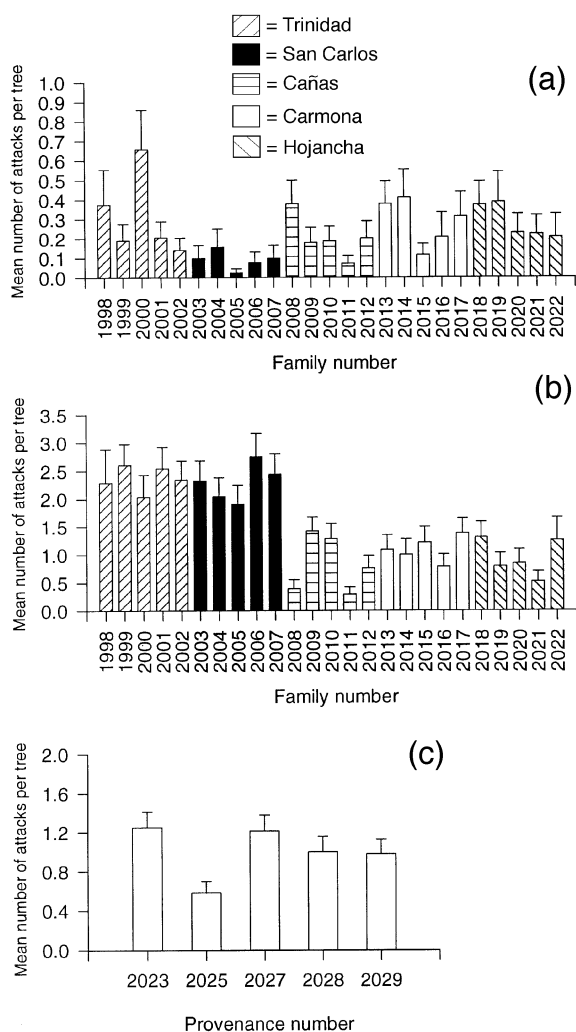


Figure 2 Variation in mean number of shoot borer attacks per tree of (a) *Cedrela odorata* after 12 weeks, (b) *C. odorata* after 68 weeks, and (c) *Swietenia macrophylla* after 60 weeks, when peaks in the number of attacks were recorded in field trials at CATIE, Costa Rica. Values presented are means ($n=45$ and $n=125$ for *C. odorata* and *S. macrophylla*, respectively); vertical bars represent SEM.

attack, the family effect was largely attributable to provenance variation (Table 2).

In *S. macrophylla*, when the trial was assessed after 177 weeks, the effect of provenance on the number of damage loci was highly significant ($P < 0.001$, d.f. = 4, $F = 6.70$; ANOVA), values ranging from 1.8 (Juan Diaz) to 2.9 (Trinidad). Provenance means of height to first damage locus ranged from 1.14 to 1.39 m in Dirici and Trinidad, respectively ($P = 0.005$, d.f. = 4; $F = 3.76$; ANOVA; Fig. 3b). A relatively large proportion of the variation was unexplained (Table 3).

Mean foliar nitrogen concentration in families of *C. odorata* varied from approximately 2–4%, with consistently lower values (on average 33% lower) recorded in the foliage of the San Carlos trees (Fig. 4a). Differences in nitrogen concentration between provenances were statistically significant ($P = 0.0001$, d.f. = 4, $F = 29.9$; ANOVA), but differences between families within

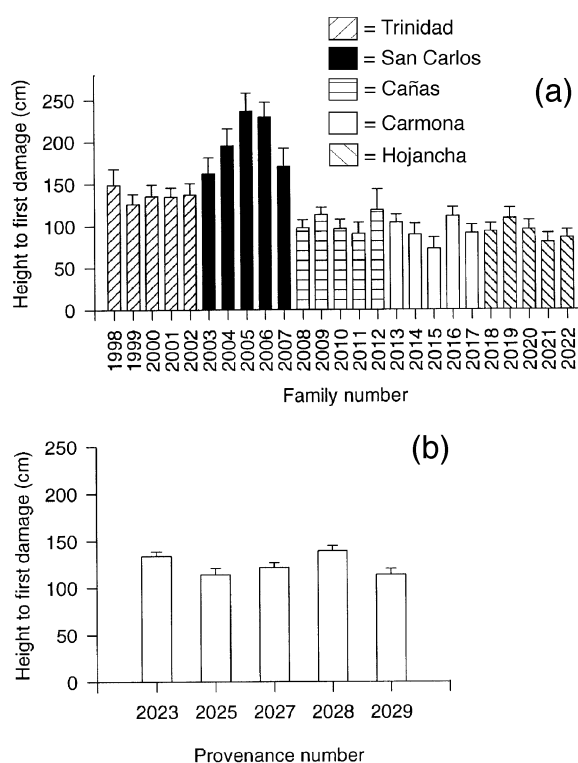


Figure 3 Variation in the height to first shoot borer damage locus in (a) *Cedrela odorata* and (b) *Swietenia macrophylla* in field trials at CATIE, Costa Rica, after 141 and 177 weeks, respectively. Values presented are means ($n=45$ and $n=125$ for *C. odorata* and *S. macrophylla*, respectively); vertical bars represent SEM.

provenances were not significant. The mean concentration of total foliage tannins varied from 27 to 39%, and was consistently higher (on average by 25%) in the San Carlos trees (Fig. 4b). Differences between provenances were significant ($P = 0.0001$, d.f. = 4, $F = 24.6$; ANOVA). On average, proanthocyanidin concentration was 19% of total tannin concentration, but showed the greatest degree of variation of the three biochemical measures, ranging from 1 to 14% in terms of total dry mass, and from 5 to 39% in terms of total tannin concentration. The highest proanthocyanidin concentrations were found in the San Carlos families, with values on average 500% higher than those recorded in the foliage of other provenances (Fig. 4c). These differences were significant at the provenance level ($P = 0.0001$, d.f. = 4, $F = 496.7$; ANOVA) but not at the family level.

Discussion

The results from the *C. odorata* trial indicate that the San Carlos provenance, derived from the Atlantic zone of Costa Rica, is highly distinctive in terms of growth characteristics and chemical content. The contrast in height growth between provenances was visually very striking, with family mean values in the San Carlos provenance being more than double the values in Carmona and Hojancha provenances. Trees in the San Carlos provenance also appeared to be morphologically distinctive, tending to have larger leaves and more leaflets per leaf than the other provenances (A. C. Newton, personal

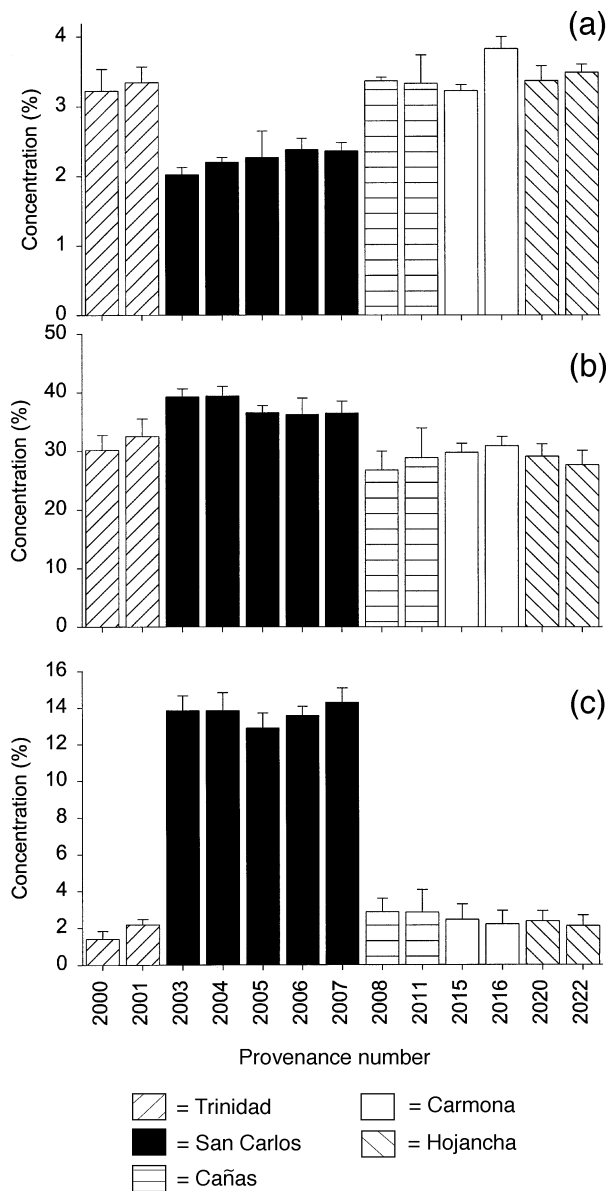


Figure 4 Concentration (percentage dry mass) of (a) nitrogen, (b) tannin and (c) proanthocyanidin in leaves of *Cedrela odorata*. Values are means ($n=5$), vertical bars represent SEM.

observation), as well as distinctive foliar colouration. Genetic differences between *C. odorata* populations from the Atlantic and Pacific zones of Costa Rica have recently been confirmed by molecular approaches (Gillies *et al.*, 1997).

The extent of genetic variation in growth rate within *C. odorata* is illustrated by results from an international series of provenance trials established in the 1960s and 1970s (Burley & Lamb, 1971; Chaplin, 1980). In all of the provenance tests established in Africa, where no problems with shoot borer attack were encountered, pronounced intraspecific variation in growth rate and form was recorded (see papers by Egenti, Kaumi and Malimbwi in Nikles *et al.*, 1978). In general, the most promising provenances in terms of growth rate were those from Costa Rica

and Belize (Chaplin, 1980). In the neotropics, few trials were successfully established, as problems with shoot borer attack and site incompatibility were encountered (Chaplin, 1980). Whitmore (1978) described results from trials established on five sites in Puerto Rico, where variation between provenances by more than a factor of three was recorded. In Trinidad, provenance means varied by a factor of six, material from San Carlos (Costa Rica) displaying a mean height of 4.34 m after 3 years (Ramnarine, 1989). The result of the current investigation, in terms of height growth and the extent of difference between provenances, were therefore consistent with previous results with this species.

Genetic variation in phenology of *C. odorata* has apparently not been recorded in any of the provenance tests established previously. The results presented here indicate a clear difference between provenances originating from low and high rainfall areas ('dry' and 'wet' zones), the former displaying a greater tendency to abscise foliage during the dry season. These results therefore suggest that leaf phenology is under a degree of genetic control. As the incidence of shoot borer attack is closely related to foliar phenology (Newton *et al.*, 1998), in that larval attack is concentrated on newly produced shoots, this is a characteristic which could potentially be exploited in a breeding programme for pest resistance.

These results clearly indicate provenance variation in the incidence of shoot borer attack in *C. odorata*. Trees of the San Carlos provenance experienced relatively few attacks during the first year and relatively high initial growth rates. Although in the second year the trees from this provenance received a relatively large number of attacks, this may be attributed to their significantly higher growth rates, providing a far larger number of suitable loci for attack than in trees from the other provenances. Despite the relatively high attack rates in the second year, trees from the San Carlos provenance displayed significantly fewer damage loci per unit stem length than the other provenances, partly reflecting the ability of individual trees of this provenance to recover from attack by vigorous growth of the leading shoot. The ability of some *Cedrela* trees to tolerate attack in this way has been observed previously (Melchior & Quijada, 1972; Sanchez *et al.*, 1976; Vega, 1976; Ramnarine, 1989). However, few data are available on variation in susceptibility to shoot borer attack within *C. odorata*. Whitmore (1978), in provenance tests established in Puerto Rico, recorded mean numbers of shoot borer attacks per tree ranging from 0.66 to 0.77 after 3 years' growth, lowest values being recorded in a Jamaican provenance which was also the slowest growing (Whitmore, 1978).

The chemical analyses presented here demonstrate that the foliage from the San Carlos provenance of *C. odorata* had a lower concentration of nitrogen, a higher concentration of total tannins, and a higher concentration of proanthocyanidins (condensed tannins) than the other provenances tested. The presence of comparatively high concentrations of tannins, and proanthocyanidins in particular, in the foliage of those trees which demonstrated the least initial susceptibility to attack, and the fact that these chemicals are thought to have detrimental effects on a number of insects (e.g. Grayer *et al.*, 1992; Gonzalez-Coloma *et al.*, 1993) and plant pathogens (e.g. Polyakova *et al.*, 1995), strongly suggest that larval growth

and survival was initially lower in the trees of the San Carlos provenance than those of the other provenances. Although it has been suggested that the biochemical basis for resistance in *Toona ciliata* may be alkaloids (Grijpma, 1976), most research on the biochemical basis for resistance to shoot borer attack in Meliaceae has concentrated on limonoids, many of which are powerful insecticides and feeding deterrents (Kubo & Klocke, 1986; Koul & Isman, 1992). No previous study, however, has linked intraspecific variation in pest-resistant characteristics in meliaceous species with intraspecific variation in plant chemistry. This raises the possibility of biochemical screening of plants for resistance to shoot borers, as has been attempted for other pests (Cai *et al.*, 1995), but it must be noted that proanthocyanidin concentrations (and the effect they may have on insect herbivores) can be affected by environmental factors such as exposure to sunlight (Dudt & Shure, 1994), defoliation and fertilizer application (Hunter & Schultz, 1995). It should also be noted that the evidence presented here for both the importance of proanthocyanidins and the occurrence of antibiosis is circumstantial, and research on tannins has not always found that they are detrimental to insect herbivores (Bernays, 1981; Bernays *et al.*, 1989; Hemming & Lindroth, 1995). Based on these results, a controlled investigation of antibiosis would be a valuable approach to adopt in future research, particularly if it could be linked with concentrations of chemicals (such as proanthocyanidins) within the foliage.

In the case of *S. macrophylla*, very little information is available concerning genetic variation in either growth or susceptibility to shoot borer attack (Newton *et al.*, 1993b). In progeny tests established in Costa Rica and Trinidad, Newton *et al.* (1996) recorded significant variation in height growth, family means varying by 132 and 192%, respectively, within the first 3 years after establishment. Genetic variation in susceptibility to shoot borer attack was also recorded, the mean number of damage loci per tree varying between 2.2–4.7 and 2.7–4.4 in Costa Rica and Trinidad, respectively. These results are consistent with those of the current investigation. However, none of the provenances of *S. macrophylla* tested was comparable to the San Carlos provenance of *C. odorata* in terms of lowered susceptibility to pest attack. Further screening, including a much larger number of provenances, would clearly be desirable to evaluate more fully the occurrence of pest resistance characteristics in this species.

These results provide evidence for at least two mechanisms of resistance (antibiosis and tolerance; Van Emden, 1987) within these tree species, suggesting that there may be scope for breeding for resistance to shoot borers by the selection of superior genotypes. Both *C. odorata* and *S. macrophylla* are amenable to vegetative propagation techniques (Newton *et al.*, 1993b, 1994), offering the possibility of clonal multiplication of genotypes displaying resistance. Genetic variation in apical dominance of *C. odorata* has been highlighted by decapitation tests of seedling material (Newton *et al.*, 1995), which may enable genotypes displaying a degree of tolerance to be identified at an early age. To realise the full genetic potential of any improved germplasm developed, particular attention should be paid to the choice of planting site (Whitmore, 1978) and silvicultural system (Mayhew & Newton, 1998). The potential exists for incorporating material with a degree of pest

resistance in silvicultural systems which encourage pest control, leading to the development of an integrated system of pest management (Newton *et al.*, 1993a; Mayhew & Newton, 1998).

Acknowledgements

The CATIE/ITE link project was financed by the U.K. Overseas Development Administration. The assistance of Marvin Hernández, José Masís, Oldemar Baeza and Carlos Castro in raising, assessing and measuring the plants is very greatly appreciated. We thank the Institute of Tropical Forestry, Puerto Rico, Mr Joel Timyan, Haiti, and the ESNACIFOR seedbank, Honduras, for provision of *S. macrophylla* seed. The advice and encouragement of Drs Roger Leakey, David Boshier, Derek Roberts and Peter Grijpma during the development of this project is gratefully acknowledged.

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Accepted 26 November 1998