

# The Biology and Ecology of *Hypsipyla* Shoot Borers

M.W. Griffiths<sup>1</sup>

## Abstract

The *Hypsipyla* shoot borers are apparently restricted in their feeding to plants belonging to the family Meliaceae, subfamily Swietenioideae, including the high value timber species of *Swietenia*, *Khaya*, *Toona* and *Cedrela*. The two most important *Hypsipyla* species with respect to shoot borer activity are *H. grandella* (Zeller) occurring in the Americas, and *H. robusta* Moore occurring through areas of Africa and the Asia/Pacific region. Larvae of these species tunnel in the developing shoots of young trees, and in some regions also feed upon the flowers, fruit and occasionally bark of their hosts. Feeding on these non-shoot plant parts may have a significant impact on the population dynamics of the species. A generation usually takes 1 to 2 months, extending to 5 months if larvae enter diapause. Females mate only once and lay between 200 and 450 eggs over 5 to 8 nights. Adults are strong fliers, able to locate host trees over considerable distances. Egg and early instar mortality are high, however even low levels of feeding can significantly impact on tree form. Shoot-feeding larvae pupate within the stem tunnel or amongst soil and plant material at the tree base. The behaviour of larvae and the sites of oviposition and pupation while feeding on fruit, flowers and bark are less well known, and vary according to the host species and the plant part being eaten. Damage to fruit results in their premature shedding, which is circumvented in some areas by webbing produced by the feeding larva. Larval diapause has been reported from areas of low temperature or low rainfall, and occurs immediately following cessation of fruit-feeding despite apparently suitable climatic conditions.

DAMAGE from shoot borers of the genus *Hypsipyla* Ragonot (Lepidoptera: Pyralidae) presents the greatest deterrent to the establishment and cultivation of the high value timber species belonging to the family Meliaceae, including species of *Swietenia*, *Khaya*, *Toona* and *Cedrela*. The most serious damage to the tree results from the tunnelling of the larva in the developing shoots. This boring leads to the death of the terminal shoot and subsequent production of laterals, eventually resulting in a stunted, continuously branched and crooked tree of greatly diminished value for timber production. Growth rate is reduced and death can result from heavy and repeated attacks. Damage has been recorded on trees from age three months old and 50 cm height (Beeson 1919, 1941; Kalshoven 1926), up to age 14 years and 15 m height (Froggatt 1923; FAO 1958; Streets

1962; Morgan and Suratmo 1976; Suratmo 1977). The borer is thus a problem to both nursery and planted stock.

The *Hypsipyla* species have attracted considerable attention, with mention in over 300 publications. The great majority of these works focus on the shoot-feeding habit of the insect and are directed towards management and control. Although causing greatest economic damage during shoot boring, *Hypsipyla* larvae also feed upon the flowers, fruit and occasionally bark of their hosts. Few studies have been directed at or even mention the biology and population dynamics of the insect when feeding on these alternative plant parts. This review describes the biology and ecology of the main *Hypsipyla* species and highlights areas warranting further research.

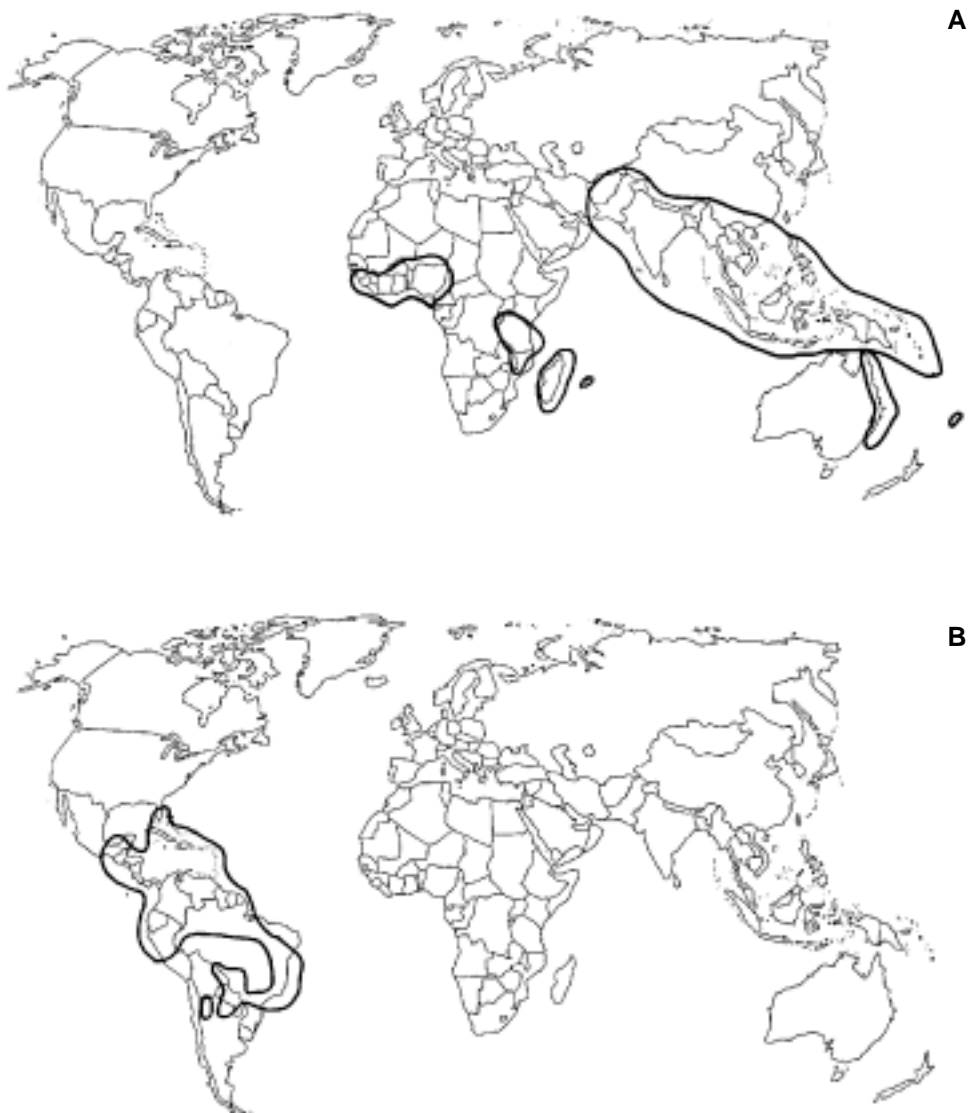
## Distribution

Eleven species of *Hypsipyla* are currently recognised (Horak these Proceedings) of which four occur in the Americas and seven in the Africa/Asia region (Heinrich 1956; Bradley 1968). *Hypsipyla robusta*

<sup>1</sup>CSIRO Entomology, Private Bag No. 3, Indooroopilly, Queensland 4068 Australia. Current address: Queensland Forestry Research Institute, PO Box 631, Indooroopilly Queensland, 4068, Australia.

(Moore) is the most widely distributed, occurring through West and East Africa, Asia and the Pacific (Fig. 1). *Hypsipyla grandella* (Zeller) is found throughout Central and tropical South America, in the Caribbean and on the southern tip of Florida (Entwistle 1967) (Figure 1).

The remaining species are less well known and are more restricted in distribution. Those occurring in the Americas are *H. dorsimaculata* (Schaus), *H. fluviatella* Schaus, and *H. ferrealis* (Hampson), and those present in the African region are *H. albipartalis* (Hampson), *H. ereboneura* Meyr., *H. debilis*



**Figure 1.** Geographic distribution of *Hypsipyla robusta* (A) and *H. grandella* (B).

Caradja, *H. elachistalis* Hampson, *H. rotundiplex* Hampson, and *H. swezeyi* Tams.

### Host plants

*Hypsipyla* spp. are generally restricted in their feeding to plants belonging to the family Meliaceae, subfamily Swietenioideae. The Swietenioideae comprises 13 genera, most of which have been recorded as hosts of *Hypsipyla* spp. The lack of records of *Hypsipyla* feeding on some genera may be a result of limited work on these groups rather than a true reflection of their host status. Despite the strong association between *Hypsipyla* and the subfamily Swietenioideae, there are a number of reports of feeding damage on plants in other groups (Olliff 1890; Beeson 1919; Queensland Forest Service 1921; FAO 1958; Streets 1962; Entwistle 1967; Browne 1968; Rao and Bennett 1969). These reports are generally single records and probably constitute misidentification of the insect and/or misinterpretation of the damage (see Kalshoven 1926; Diakonoff and Bradley 1976; Luego 1989). Some records may represent chance feeding events.

The Swietenioideae is one of two major subfamilies within the Meliaceae. It is biochemically distinct from the other major subfamily, the Melioideae, specifically in the structural form of its limonoid compounds (Das et al. 1984; Agostinho et al. 1994). Limonoids are a group of tetranortriterpenoids with antifeedant or toxic properties against a wide range of invertebrate species (Taylor 1981; Arnason et al. 1987; Jacobson 1989). The apparent restriction of *Hypsipyla* spp. to hosts of a single subfamily containing limonoids of a particular structural type suggest possible coevolution between *Hypsipyla* and the Swietenioideae.

*Hypsipyla grandella* and *H. robusta* generally feed on growing shoots however feeding on flowers, fruit and bark has been reported for some host species and/or geographical regions. Larvae normally feed on shoots, and on other plant parts only when new shoots are not available (Beeson 1919, 1941). However, feeding on reproductive parts occurs concurrently with feeding on shoots in the high wet forest areas of Nigeria, in Java and in Australia (Kalshoven 1926; Roberts 1966; Campbell 1966; Griffiths 1997). Feeding by larvae of *H. robusta* on *Xylocarpus* mangroves is apparently restricted to the fruits and flowers (Das and Dev Roy 1982; Hutacharern and Tubtim 1995; Horak (these Proceedings)). *Hypsipyla ferrealis* feeds on the fruit only of *Carapa guianensis* Aubl. (Becker 1973; Heinrich 1956; McHargue and Hartshorn 1983). The absence of feeding records for alternative plant parts of many species may reflect the extent of observations undertaken, rather than the

extent of feeding damage inflicted. Non-shoot feeding may have a significant influence on the population dynamics of the species, with fruit feeding larvae often occurring at very high densities (Department of Public Lands, Queensland 1917; Beeson 1941; Entwistle 1967; Mathur 1967; Bennett and Yaseen 1972; Brunck and Mallett 1993; Wali-Ur-Rehman 1993).

### Reproduction and host plant choice

The reproduction of *H. grandella* has been studied by Grijpma (1971), Samaniego and Sterringa (1973), Sliwa and Becker (1973), Sterringa (1973) and Holsten and Gara (1977b), and of *H. robusta* by Beeson (1919), Atuahene and Souto (1983), Mo and Tanton (1996), Mo (1996) and Griffiths (1997). The two species are similar in many respects. Pheromones are produced by the female moth (Assiri Bosson and Gallois 1982; Borek et al. 1991). Mating occurs within six days of emergence, and females commence egg laying on the following night. Females mate once and proceed to oviposit throughout their life (approximately 5–8 days), laying between 200 and 450 eggs. Sex ratios of adults are variable with reports of even (Atuahene and Souto 1983; Griffiths 1997), male dominated (Beeson 1919; Intari 1978) and female dominated sex ratios (Achan 1968). Adults are generally nocturnal (Grijpma and Gara 1970a; Holsten and Gara 1974; Griffiths 1997).

*Hypsipyla* adults have a strong flight capacity as evidenced by laboratory flight studies (Fasoranti et al. 1982) and their ability to locate isolated hosts. The period of maximum flight activity differs between the sexes. Females are most active for the first two nights after emergence, during which time they probably disperse and locate hosts (Fasoranti et al. 1982). After this time females become less active and more attractive to males (Holsten and Gara 1977a; Mo 1996). Males have capacity for sustained flight over a longer period (Fasoranti et al. 1982), and will mate on several consecutive nights (Holsten and Gara 1977b) which allows them to locate distant females. Although *Hypsipyla* moths have a great capacity to disperse, they are unlikely to leave an area of active infestation while new shoots are available, thus causing severe local damage.

Successful mating and oviposition of adult *Hypsipyla* spp. in captivity have been difficult to achieve (Beeson 1919; Queensland Forest Service 1921; Roberts 1968; Grijpma 1971; Fasoranti 1985). Mating is generally more successful in outdoor cages than in laboratory conditions, possibly due to greater illumination (Campbell 1966; Griffiths 1997),

exposure to wind (Mo and Tanton 1996), or a greater propensity for flight (Fasoranti 1985).

Eggs of both *H. grandella* and *H. robusta* are oval and dorso-ventrally flattened, measuring 0.7–1.0 mm × 0.5–0.7 mm (Ramirez Sanchez 1964; Atuahene and Souto 1983; Griffiths 1997). Eggs are white when first laid and develop distinct red and white banding within 24 hours if fertilised. The head capsule of the developing larva is visible through the chorion during the final 24 to 48 hours of development. Eggs hatch after three to five days, although egg mortality is high for both species (Allan et al. 1970; Griffiths 1997).

Eggs laid on young trees are deposited singly, or occasionally in clusters of three to four, on the shoots, stems and leaves, particularly the upper leaf surface (Beeson 1919, 1941; Kalshoven 1926; Ramirez Sanchez 1964; Roberts 1968; Rao and Bennett 1969; Owadally 1980; Yamazaki et al. 1990; Griffiths 1997). Eggs are concentrated around the growing shoots (Beeson 1919, 1941; Kalshoven 1926; Roberts 1966; Yaseen 1984; Yamazaki et al. 1992) but may occur at all heights, including low on the stem (Ramirez Sanchez 1964; Griffiths 1997). Eggs are often placed in concealed locations such as leaf axils, leaf scars, veins, lenticels and fissures in the bark (Ramirez Sanchez 1964; Lamb 1966; Grijpma 1971; Brunck and Fabre 1974). Adults are apparently attracted to young trees bearing new foliage (Grijpma and Gara 1970a; Gara et al. 1973; Yamazaki et al. 1990, 1992; Howard 1991), and to trees with existing damage and frass (Grijpma and Gara 1970a; Holsten and Gara 1977c; Yamazaki et al. 1990; Griffiths 1997). Eggs laid on fruit are initially deposited singly on the fruit surface (Beeson 1919; Roberts 1966; Rao and Bennett 1969) but are later laid in clumps of up to 12 among the frass and webbing associated with existing damage on fruit of *T. ciliata* in Australia (Griffiths 1997). Sites of oviposition prior to flower and bark feeding are unknown but are probably close to the feeding sites (Beeson 1941; Roberts 1966, 1968).

#### Immature development and diapause

Larvae of *Hypsipyla* spp. exhibit developmental polymorphism, with the reported number of instars ranging from 4 to 6 for *H. robusta* (Beeson 1919; Achan 1968; Roberts 1968; Atuahene and Souto 1983; Mo and Tanton 1995; Griffiths 1997), 5 to 7 for *H. grandella* (Hidalgo-Salvatierra and Berrios 1973; Ramirez Sanchez 1964; Yamazaki et al. 1990), and 3 to 4 for *H. ferrealis* (Becker 1973). The total development time takes 1 to 2 months, including a 10 day pre-pupal and pupal period. The life cycle can extend to 5 months if larvae enter diapause (Beeson

1941). Feeding behaviour, sites of pupation, and damage inflicted vary greatly according to the part of the tree being eaten.

#### Shoot feeding

Newly hatched larvae wander over the plant surface before commencing to feed, generally directly into the growing tip or into a nearby leaf or leaflet axil (Kalshoven 1926; Froggatt 1923; Ramirez Sanchez 1964; Roberts 1966; Grijpma and Gara 1970b). Feeding larvae spin a network of webbing across their feeding site onto which plant fragments and frass pellets are attached, eventually producing a dense mat. The webbing and associated material potentially provide protection for the burrowing larva from natural enemies, desiccation and rain water. Older larvae behave similarly when commencing feeding at new sites (Gu and Liu 1984). Shoot boring larvae will also feed on leaves, particularly during early instars (Kalshoven 1926; Ramirez Sanchez 1964; Roovers 1971; Suharti and Santosa 1990).

Larvae usually move and initiate feeding at several locations on a plant, particularly during the early instars (Anon. 1882; Kalshoven 1926; Gu and Liu 1984; Yamazaki et al. 1992; Mo 1996; Griffiths 1997). The reasons for these movements is not known but it is possible that larvae may move to avoid plant defences, predators and/or competitors, or to locate more nutritious feeding sites. Frequent wandering by first instar larvae probably contributes to the high rates of mortality by increasing exposure to natural enemies, weather and accidental loss (Kalshoven 1926; Griffiths 1997). Despite poor survival amongst early instars, the damage they inflict can have a significant impact on tree form since even very low levels of feeding on the growing tip can destroy apical dominance and lead to heavy branching.

Pupation occurs within cocoons spun in the stem tunnels, or amongst the leaf litter and soil around the tree base. Cocoons in a stem are usually located beneath a silken mat within the tunnel, while at the base of a tree they incorporate soil and plant material.

#### Fruit feeding

The behaviour of larvae feeding on fruit varies considerably according to the host species. *H. robusta* feeding on *T. ciliata* fruit initially feed externally on the epidermis and then feed inside seeds and fruit (Beeson 1919; Griffiths 1997). Neighbouring fruits are often joined by a tunnel of silk and frass through which larvae move, and surrounding fruit are incorporated into a large, loose conglomeration. On fruit of *K. senegalensis* (Desr.), larvae feed singly or in small, mixed age groups, ejecting frass and only moving between fruit as older instars (Roberts 1966).

In fruit of *Carapa procera* DC, larvae have been observed to feed in groups of up to 26, retaining frass around the point of feeding and not moving between fruit (Roberts, 1966). These differences in behaviour may be related to the size of the fruit and the amount of food required to complete larval development. The fruits of *T. ciliata* are relatively small (1.2 cm diameter × 2.5 cm length). Fruits of *K. senegalensis* are larger (4–6 cm diameter, spherical), and those of *C. procera* larger still (9 cm diameter × 15 cm length).

Larvae feeding on host species which have large fruits generally pupate inside the fruit, either within the canopy, or on the forest floor following fruit fall (Prosser et al. 1965; Robert, 1966). Larvae feeding on the smaller fruit of *T. ciliata* generally emerge from the fruit to pupate beneath the bark towards the base of the tree, or amongst surrounding soil and leaf litter (Beeson 1919, 1941; Griffiths 1997).

*Hypsipyla* spp. feeding on the fruit of some species such as *Khaya* species in Nigeria (Roberts 1966, 1968) and *T. ciliata* in Australia (Griffiths 1997) results in premature fruit fall. In Australia, the larvae circumvent fruit fall by spinning a mat of webbing across the point of abscission so that larvae complete feeding in the tree canopy.

#### Flower feeding

Larvae hatching from eggs deposited on flowers feed gregariously within the inflorescence of *T. ciliata* (Beeson 1919, 1941) but individually on flowers of *Khaya* spp. (Roberts 1966, 1968). During feeding, larvae spin a network of silken threads, within which there are denser cells or tunnels considered to be either moult cells (Beeson 1919) or a daytime retreat (Roberts, 1966). Larvae lower themselves on silken threads (Beeson 1919) or crawl down the trunk (Roberts 1966) to pupate in crevices or recesses under the bark on the trunk or larger branches.

#### Bark feeding

Later instar shoot-feeding larvae often resort to feeding on lignified tissue when younger material is no longer available (Kalshoven 1926; Ramirez Sanchez 1964; Gu and Liu 1984; Yamazaki et al. 1992; Griffiths 1997). In addition, some populations of *Hypsipyla* seem to feed exclusively beneath bark. In Nigeria, there have been instances of larvae of *H. robusta* feeding entirely beneath the bark of *K. grandifoliola* C.DC (Roberts 1966), causing damage similar to that described for *H. albipartalis* on mahogany in Malawi (Ballard 1914). Larvae of *H. grandella* have been observed to strip away bands of bark from around the base of *Cedrela odorata* L. in Cuba (Menendez and Berrios 1992), and may even extend their feeding to the roots of some hosts (Yamazaki et al. 1990).

#### Diapause

The incidence of diapause varies between regions. In some regions, attack is continuous with larvae going through 10–12 generations per year (Kalshoven 1926; Gu and Liu 1984). However, under conditions of low temperature or low rainfall, as experienced in regions such as Northern India, Myanmar, the Nigerian savannah and sub-tropical Australia, larvae may undergo a period of arrested development during the last instar, with the total number of generations reducing to four or five (Beeson 1919; Brunck and Fabre 1974). Also, in southern Queensland, larvae completing development in the fruits of *T. ciliata* enter diapause at a time when larval activity in shoots continues for at least a further five months (Griffiths 1997). The triggers inducing or breaking diapause in different localities have not been identified.

#### Conclusion

The biologies of *H. robusta* and *H. grandella* are similar in many ways, allowing some research results to be applied across regions. A number of differences and discrepancies exist, both between and within the currently recognised species. Some of these apparent differences may reflect a lack of knowledge rather than true biological differences. Further work is required to clarify many aspects of the biology and ecology of *H. robusta* and *H. grandella* so that integrated pest management strategies can be devised with confidence.

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# Biology and Impact of *Hypsipyla robusta* (Moore) on *Toona ciliata* M. Roem. in Himachal Pradesh

T.D. Verma and N. Kaul<sup>1</sup>

## Abstract

*Toona ciliata* M. Roem. is a versatile timber tree that grows in forest and agroforestry situations under sub-tropical and tropical conditions of India, Southeast Asia and the Pacific. It is attacked by an insect, *Hypsipyla robusta* (Moore) which voraciously feeds on its fruits and shoots. The infested trees become stag-headed with crooked boles. Studies on the biology of *H. robusta* revealed that oval, white eggs with an average size of  $0.9 \times 0.5$  mm were laid on young fruits and shoots. Incubation period was 3–4 days. There were five brownish instars. Full-fed larvae were violet blue and pupated in a cocoon. Pupae were obrect,  $14.2 \times 4.07$  mm in size and lasted for 10–11 days. Male moths were smaller (26 mm in wing expanse) than females (28 mm). Insects completed four generations in a year and over-wintered as prepupae from October to mid-March. Larvae fed voraciously, particularly after the third instar. A single larva was found to feed on 6–10 fruits, or to form a tunnel with an average length of 65 cm in shoots. Trees between 2 and 3 m in height had the highest incidence of damage (93.3%) and the maximum shoot infestation per tree (66.5%). In addition to the effects on form and growth of the affected saplings, insect infestation also adversely affected seed germination. There was 20% seed germination in heavily infested fruits compared with 98% in seeds obtained from healthy fruits. The impact of insect damage on natural regeneration of *T. ciliata* saplings growing in pure stands and in solitary situations was studied.

THE SHOOT BORER, *Hypsipyla robusta* (Moore) (Lepidoptera: Pyralidae) is an important pest of trees belonging to family Meliaceae in the tropical and sub-tropical parts of the world. A related species, *H. grandella* (Zeller), causes similar damage to species of Meliaceae in the Americas. These pests are the major constraints to successful planting of multipurpose trees like *Toona ciliata* M. Roem., mahogany and other trees of this family. In India, Beeson (1919) reported that the life history and sequence of generations of *H. robusta* vary with the food plant and climate. During 1994–1995, the biology and impact of this pest on *T. ciliata* was studied at Nauni campus of the Y.S. Parmar University of Horticulture and Forestry, Himachal Pradesh (31°N, 77°E) situated at 1200 m above sea level.

## Materials and Methods

An insect culture was raised from fruits and shoots of *T. ciliata* collected in the field. Insects were reared on their natural food by placing plant parts in rearing cages ( $60 \times 58 \times 70$  cm) with their cut ends placed in water, or by using potted plants maintained in an outdoor cage. Observations on life stages of the insect were made by splitting open the infested parts. Insect incidence and seasonal history were studied under field conditions by examining relevant plant material at suitable time intervals.

The nature and extent of insect damage were studied on both the fruits and shoots of *T. ciliata*. Ten fruit-bearing trees were selected and 100 fruits from five branches in each crown were collected. Fruit were categorised into heavily infested (>60% damage), moderately infested (30–60% damage), slightly infested (1–30% damage) and uninfested fruits with no damage to seeds. Germination tests were conducted using 100 seeds from each damage category and percent germination was calculated. In addition, the effect of insect infestation levels on

<sup>1</sup>Department of Entomology, Y.S. Parmar University of Horticulture and Forestry, Nauni – Solan (H.P.) – 173 230 India

natural regeneration of *T. ciliata* was recorded by counting newly germinated seedlings within a 5 m radius of mature trees of known levels of fruit infestation. The nature of damage on fruit was studied and the number of damaged fruits was recorded.

*T. ciliata* saplings were grouped into 0–1, 1–2, 2–3, 3–4 and 4–5 m height classes. The proportion of trees damaged, length of tunnels made by the larva, and number of lateral shoots infested were determined for trees in each height class. Ten observations were taken in each case.

## Results and Discussion

### Biology

#### Egg

White, oval eggs were laid on young green fruits in the first generation and on new unexpanded leaves and growing shoots in the subsequent generations. The average size of the egg was  $0.87 \times 0.45$  mm and hatchability was 82.3%. This stage lasted for 3–4 days. Beeson (1941) reported the egg size as  $0.9 \times 0.75$  mm and duration of egg stage as 4–5 days.

#### Larva

A larva was observed to shed its skin four times before pupating thus having five instars. Linear measurements of larval stages are given in Table 1. All the instars had numerous black spots on their body and each black spot had two light brown setae. The appearance of each instar varied. In some cases even within an instar there were colour differences including pale straw-brown, pink, green or blue. Beeson (1941) reported four larval stages at Dehra Dun.

**Table 1.** Linear measurements of larval stages of *H. robusta*.

Instar	Length (mm)		Width (mm)	
	Range	Mean $\pm$ S.E. (n=10)	Range	Mean $\pm$ S.E. (n=10)
I	3.3–3.5	3.4 $\pm$ 0.1	0.5–0.6	0.6 $\pm$ 0.05
II	7.0–7.2	7.1 $\pm$ 0.1	0.9–1.0	1.0 $\pm$ 0.04
III	11.0–11.5	11.2 $\pm$ 0.2	2.0–2.1	2.0 $\pm$ 0.05
IV	15.4–15.8	15.7 $\pm$ 0.2	2.7–3.0	2.9 $\pm$ 0.12
V	26.7–27.5	27.1 $\pm$ 0.3	3.5–4.0	3.9 $\pm$ 0.20

#### Prepupa and pupa

Fully fed fifth instar turned violet-blue before prepupal formation. Under laboratory conditions, larvae of the first generation came out of the fruit and, after a brief prepupal period, pupated under the flakes of

damaged fruits in a silken cocoon. In the field, larvae descended the tree trunk with the help of a silken thread and pupated in crevices of the bark in loosely woven white silken cocoons. Pupae were reddish brown and of obtect type. These observations are in conformity with those of Beeson (1919). The prepupae measured  $22.63 \times 3.97$  mm and the pupa  $12.40 \times 4.07$  mm. The duration of the prepupal stage ranged from 3–4 days and that of pupae from 10–11 days. Beeson (1919) reported prepupal and pupal periods as 4–5 and 8–12 days respectively.

#### Adult

The adult was grey, fore wings darker with black crossed zigzag lines and patches on hind-wings that were whitish, semi-hyaline with darker margins and costal zones. Adults usually emerged during the evening. Male moths were smaller than females, measuring 13.8 mm in mean body length and 26.0 mm in wing expanse, whereas females measured 14.7 mm and 28.1 mm in mean body length and wing expanse, respectively. Adults survived for 10–12 days without food under laboratory conditions.

#### Seasonal history

The insect had four generations under sub-tropical/sub-temperate conditions. Field and laboratory observations revealed that adults from the over-wintering generation emerged during the first week of March and laid eggs during the second week. Eggs of the second, third and fourth generations were noticed during the second week of May, the first week of July, and the last week of August respectively. The fourth generation prepupae started over-wintering from mid October and pupated toward the beginning of March. Beeson (1941) reported five generations in Dehra Dun which may be attributed to climatic variations.

### Nature and extent of damage

#### Fruit generation

Eggs of the first generation were laid on inflorescences and soft developing fruits. The first instar mainly fed on the epidermis. Older larvae bored into the fruits and fed voraciously leaving only the hard epidermal tissues. During feeding, larvae would bind 5–7 fruits together with silken threads and entangled pieces of fruit and excrement in the web. After consuming edible parts of the fruit, another fruit was fastened by silken threads to the partially eaten fruit and feeding would continue. Thus, a larva could damage 6–10 fruits during its lifetime. Infestation of fruit varied from 12–44%. Trees with lowest fruit infestation (12%) had 12 seedlings under them com-

pared with only 4 seedlings under trees with the highest infestation rate (44%). The degree of insect infestation also affected seed germination. Seeds obtained from healthy fruits had 98% germination compared with 20% for seeds from heavily infested fruit.

#### Shoot generations

Eggs of subsequent generations were laid on unexpanded leaves and growing shoots. The larvae initially fed on epidermis and produced irregular patches during the process of finding a suitable spot to enter into a shoot. A gummy mass of frass bound with silken threads marked the entrance hole of the larvae. The larva fed inside the shoot and excavated a tunnel downward. The shoot above the entrance hole eventually died and fell off. Even below the site of entry, the buds and lateral shoots dried up. Usually one larva infested a shoot but sometimes it abandoned the infested shoot and entered into an adjacent shoot. The observations on the nature of damage are in conformity with earlier work (Beeson 1919).

The length of tunnel in shoots of saplings of different height classes ranged from 9.3–26.6 cm (Table 2). Most of the tunnelling was formed by larvae in the third to fifth instar (Table 3) with later instars feeding the most. Saplings less than 1 m high were not attacked while saplings between 2 and 4 m height had in excess of 50% of shoots infested (Table 4). Furthermore, more than 90% of saplings in the 2 to 3 m height class were infested while saplings of less than 1 m height or over 4 m height were less frequently infested (Table 5).

**Table 2.** Length of tunnel formed by *H. robusta* larvae in shoots of saplings of *T. ciliata* of different height.

Height class (m)	Mean tunnel length (cm) (n=10)
0–1	9.3
1–2	35.5
2–3	54.3
3–4	62.4
4–5	68.3

**Table 3.** Length of tunnel formed by different instars of *H. robusta* in *T. ciliata* shoots.

Instar	Length of tunnel (cm)	
	Range	Mean $\pm$ S.E. (n=10)
I	0–1	0.8 $\pm$ 0.1
II	3–5	4.4 $\pm$ 0.3
III	8–13	10.6 $\pm$ 0.8
IV	16–24	19.9 $\pm$ 1.8
V	26–32	29.9 $\pm$ 0.8

**Table 4.** Percent infestation of lateral shoots in saplings of different height classes.

Height class (m)	Number of shoots/ sapling	Percent shoot infestation
0–1	1	0.0
1–2	4	50.0
2–3	8	62.5
3–4	13	53.8
4–5	16	37.6

**Table 5.** Percent of saplings of *T. ciliata* in different height classes that were infested by *H. robusta*.

Height class (m)	Percent of saplings infested
0–1	10.0
1–2	66.6
2–3	93.3
3–4	63.3
4–5	26.6

In Indonesia, Suratmo (1977) also reported that the degree of infestation decreased with greater age and height. Trees growing in solitary situations were less infested than in pure stands. However, saplings growing under mature *T. ciliata* suffered more shoot borer attack than otherwise. Saplings growing under dense canopy had 15.5% infestation as compared with 63.6% in open situations. Various workers have reported that saplings growing under a dense canopy suffer less attack from *Hypsipyla* species than trees in open situations. This may be due to the release of attractants from the host tissues (Beeson 1941; Dourojeanni 1963; Yamazaki et al. 1990). As a result of insect attack on shoots, apical growth was stopped and lateral shoots developed, resulting in the production of bushy and stag-headed trees with forked and crooked boles that rendered them unsuitable for timber production.

## Conclusion

This study on the biology and impact of *H. robusta* on *T. ciliata* described the behaviour of this pest in northern India and indicated that damage from the insect had an adverse effect on growth and germination of the host tree species. It revealed that 2–3 m high saplings were most attacked by insects. Results relating to the location of damaged saplings can be useful in planning plantings of this tree species.

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## **Discussion Summary**

### **Taxonomy, Biology and Ecology of *Hypsipyla* spp.**

**M.W. Griffiths**

DESPITE the critical role of *Hypsipyla* spp. in limiting the commercial production of species of Meliaceae, many aspects of the taxonomy, biology and ecology remain unknown. A proper understanding of these issues was recognised by the Workshop as fundamental to the development and implementation of many proposed management options.

Foremost, a thorough taxonomic investigation of the group is required in the light of recorded variation in the morphology, biology, behaviour, and pheromone composition within the species currently recognised as *H. robusta*. This review will require collection of specimens throughout the geographical range of the species and from a range of host species and plant parts. In addition to morphological examination, molecular and bio-chemical techniques may be necessary to determine the taxonomy. Protocols for collecting, storing and sending material and for accessing the information obtained should be established. The relationship of the plants on which *Hypsipyla* spp. occur must also be clarified, since there are concerns over the taxonomy of some of the host species within the Swietenioideae.

Most studies on *Hypsipyla* spp. have been directed towards pest management rather than towards biology or ecology. In particular, the biology and population dynamics of *Hypsipyla* in natural stands and when feeding on non-shoot plant parts have been little studied. The behaviour of both adults and larvae is central to life history studies. However, adult movement and flight capacity, which influence mating, dispersal and host location, and larval movement, which has a significant impact on survival and the distribution and impact of damage, are not sufficiently understood. Several sites of pupation have been identified but their relative importance and the mortality rates in each are not known. The incidence of dormancy, its nature and triggers are not known, despite its importance in influencing seasonal fluctuations and population dynamics.

The study of the biology and ecology of *Hypsipyla* spp. is difficult, since the adults are nocturnal, larvae feed in concealed locations, and population densities are generally low. Many researchers have experienced difficulties in rearing shoot borers in captivity. The development of an artificial diet and techniques to maximise mating and oviposition success in captivity are required for successful rearing.

The research priorities identified by the meeting were:

- Taxonomic revision of the genus *Hypsipyla* and closely allied species, particularly from the Old World.
- Investigation of adult mating behaviour, dispersal, host location and oviposition, larval movement, pupation and dormancy.
- Understanding of population regulation and shoot borer behaviour in natural forests, particularly in relation to host tree phenology.
- Establishment of practical and effective rearing techniques, including improved mating in captivity and successful artificial diets.

# Resistance in Mahoganies to *Hypsipyla* Species — A Basis for Integrated Pest Management

A.D. Watt<sup>1</sup>, A.C. Newton<sup>2\*</sup> and J.P. Cornelius<sup>3\*\*</sup>

## Abstract

Considerable research effort into *Hypsipyla* shoot borers has failed to produce effective methods of control. However, the deployment of pest-resistant planting stock as a basis for managing these pests has not been considered until recently. This paper reviews evidence for the existence of different forms of resistance in Meliaceae to shoot borers, with particular emphasis on research carried out in Costa Rica on resistance to *Hypsipyla grandella* Zeller in *Cedrela odorata* L. and *Swietenia macrophylla* Jacq. This research has shown that appreciable genetic variation in resistance to attack by shoot borers occurs in these tree species. The basis for resistance appears mainly to be tolerance, but variation in non-preference and antibiosis may also occur within *C. odorata*. Strategies for future research are discussed and it is concluded that the best option for successful shoot borer management lies in the deployment of resistant planting stock in silvicultural or agroforestry systems that encourage natural biological control or otherwise minimise the abundance and impact of shoot borers.

WITHIN the context of these Proceedings, the *Hypsipyla* problem needs little introduction. Mahogany shoot borer species, *Hypsipyla grandella* Zeller in the neotropics and *Hypsipyla robusta* Moore elsewhere, have severely restricted reforestation programs with *Cedrela odorata* L., *Swietenia macrophylla* Jacq., *Toona ciliata* M. Roem., *Khaya ivorensis* A. Chev. and other Meliaceae species (Entwistle 1967; Newton et al. 1993a; Wagner et al. 1991; papers in these Proceedings). The larvae of these pyralid moths destroy the terminal shoots of the host plant by boring the pith, which results in a highly branched tree of little economic value (Newton et al. 1993a).

Considerable research effort into these pests (Grijpma 1974; Whitmore 1976a, b) has failed to

produce effective methods of control (Newton et al. 1993a). However, recent research on resistance to *H. grandella* in *C. odorata* (Spanish cedar) and *S. macrophylla* (American mahogany) has indicated that the deployment of pest resistant planting stock could form an effective basis for managing this shoot borer (Newton et al. 1993b, 1996, 1998, 1999).

The aims of this paper are:

- 1) to discuss the ways in which plants may show resistance to insect pests and the value of resistance in pest management;
- 2) to describe research on resistance to shoot borers in Meliaceae species, with particular reference to recent work on resistance to *H. grandella* in *C. odorata* and *S. macrophylla*; and
- 3) to discuss research priorities in the development and deployment of resistance to mahogany shoot borers.

## Resistance to Insect Pests

Much has been written about resistance in plants to insects and pathogens. Generally, three different forms of resistance in plants to insect attack are recognised (Painter 1951; Tingey 1981; Van Emden 1987):

<sup>1</sup>Centre for Ecology and Hydrology Banchory, Hill of Brathens, Glassel, Banchory AB31 4BY, Scotland, UK

<sup>2</sup>Centre for Ecology and Hydrology Edinburgh, Bush Estate, Penicuik, Midlothian, EH26 0QB, Scotland, UK

<sup>3</sup>Tropical Agronomic Centre for Research and Higher Education (CATIE), Turrialba 7170, Costa Rica

\*\* Overseas Development Administration, UK

\* Current address: The Institute of Ecology and Resource Management, University of Edinburgh, Darwin Building, Mayfield Road, Edinburgh, EH9 3JU, UK

- 1) non-preference (or antixenosis), where a plant is not preferred for colonisation, oviposition or feeding by insect pests;
- 2) antibiosis, where insects on a plant take longer to develop, suffer greater rates of mortality, grow more slowly or produce less offspring;
- 3) tolerance, where a plant shows a tendency to recover from insect attack.

Several aspects of resistance should be noted:

- All categories of resistance define phenomena that are relative. A tree may be attacked by pests; these pests may survive on that tree and that tree may show signs of damage, but it may be resistant in comparison to other individuals or provenances of that tree species (or in comparison to other tree species). Thus, resistance in a clone, family or provenance may or may not be economically acceptable to a farmer or forester.
- The above definitions are based on the insect-plant relationship, the first two being defined by the response of the insect and the third being defined as the response of the plant. However, all forms of resistance are caused by some plant property — chemical, morphological or physiological. Thus, a plant may demonstrate non-preference because of leaf hairiness or the composition of the volatile chemicals emitted by the plant; a plant may demonstrate antibiosis because of leaf toughness or the chemical composition of the plant; and a plant may be tolerant because it grows vigorously or because of its particular response to damage, e.g. apical dominance.
- A plant may show different forms of resistance. For example, plant factors that cause antibiosis may also cause non-preference (Tingey 1981).
- Apparently, insignificant resistance may bring about acceptable damage suppression in conjunction with other control methods such as biological control (Van Emden and Wearing 1965).
- Insect pests and pathogens can evolve to overcome plant resistance (Gould 1983). The identification of resistance in plants must, therefore, be followed by the formulation of a strategy, or strategies, to fully exploit and conserve that resistance.

This paper concentrates on genetically-based resistance in plants. However, as discussed elsewhere (these Proceedings), plants may show resistance in its widest sense in other ways too, including:

- phenological variation in non-preference, antibiosis and tolerance (Watt 1987);
- shade-induced antibiosis (Dudt and Shure 1994);
- fertiliser-induced antibiosis and tolerance (Kyto et al. 1996);
- stress-induced antibiosis (Watt 1994);
- insect damage-induced antibiosis (Haukioja 1990).

These forms of resistance in plants mean that the environment of a plant may be manipulated to the detriment of insect pests (Hauxwell, Mayhew and Newton, these Proceedings). However, the fact that resistance to insect pests in its widest sense depends upon so many factors means that genetically-based resistance may be masked. Thus, studies on genetically-based resistance must include field trials established with statistically sound designs across as wide a range of growing conditions as possible.

To summarise, resistance in plants is a potentially valuable means of managing insect pests. Several forms of resistance occur and resistance has a variety of underlying causes. Resistance may usefully be combined with other approaches to pest management and, indeed, given the possibility that resistance may be overcome by pests, the deployment of resistance with one or more other methods of pest control in a pest management program is likely to be a much more successful strategy than the use of resistant plants alone. The next sections consider the extent to which resistance may be used to manage shoot borers.

### Resistance to *Hypsipyla* Spp.

Newton et al. (1993a) reviewed published research on resistance between and within Meliaceae species. This is summarised below.

Although *Hypsipyla* spp. only attack Meliaceae spp., most susceptible species are in the sub-family Swietenioideae. Most Melioideae, including *Guarea* spp., *Melia* spp. and other desirable timber tree species, are not attacked by these shoot borers. It has frequently been suggested that these, apparently resistant, species are suitable plantation trees (e.g. Grijpma 1976).

Within the Swietenioideae, exotic (non-native) species have often been reported to be resistant to the native species of *Hypsipyla*. There are reports that the neotropical *S. macrophylla* has been successfully established in plantations in Southeast Asia and the south Pacific (Evans 1982) suggesting that *S. macrophylla* is susceptible to *H. grandella* but is resistant to *H. robusta*. However, most reports from countries in Asia, the Pacific and Africa in these Proceedings show that *S. macrophylla* is susceptible to *H. robusta*. Similarly, there are conflicting reports of the susceptibility of the neotropical *C. odorata* to *H. robusta*. This tree species is susceptible to *H. grandella* and although plantations of this species have been successfully grown in West Africa (Atuahene, these Proceedings), there are reports of damage caused by *H. robusta* to *C. odorata* in, for example, Australia (Cameron and Jermyn 1991) and Indonesia (Entwistle 1967). Reports on resistance to

*H. grandella* in *Khaya* spp. and *Toona ciliata* may be more reliable. *Khaya* spp., which are attacked by *H. robusta* in West Africa, have been successfully grown in Latin America and the Caribbean (Motta Maues, these Proceedings; Duarte et al. these Proceedings). Similarly, *Toona ciliata*, native to Asia and the Pacific and susceptible to *H. robusta*, is apparently resistant to *H. grandella* (Whitmore 1976).

It is still unclear which type, or types, of resistance are operating in the cases where resistance does occur but there is evidence to suggest that both non-preference and antibiosis confer resistance to *H. grandella* in *T. ciliata* (Roberts 1966; Grijpma and Gara 1970; Grijpma and Roberts 1975). Although it has been suggested that the biochemical basis for resistance in *T. 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 and Klocke 1986). One limonoid in particular, cedrelone, which is found in *Toona* and *Cedrela*, is a powerful insect growth inhibitor (Kubo and Klocke 1986; Koul and Isman 1992).

Although the evidence for resistance to shoot borers in species planted out with their natural ranges is more convincing for *T. ciliata* than other species, it is notable that attempts to establish plantations of this species have ended in failure (Sanchez et al. 1976), probably as a result of incompatibility of the tree species with local growing conditions (Newton et al. 1993a). Clearly, the use of exotic Meliaceae, in plantation monocultures at least, is not the answer to the shoot borer problem.

Despite the repeated suggestion that variation in resistance to shoot borers may occur within Meliaceae species (Roberts 1966; Grijpma 1976), there have been few attempts to screen for genetic variation in resistance. Some information on resistance within *C. odorata* has, however, been obtained from international provenance trials (Whitmore 1978; Chaplin 1980; McCarter 1986, 1988). Although survival in these trials has usually been poor and they have been heavily attacked by *Hypsipyla*, a few provenances in these trials have shown apparent resistance to shoot borer attack, in each case tolerance through pronounced vigour and the production of a new single strong leading shoot after attack.

Thus, there is sufficient published information to warrant a closer examination of the presence of resistance to shoot borers within Meliaceae species. It was considered that these earlier experiences justified a closer examination of the presence of resistance to shoot borers within Meliaceae species. Such

a study was launched in 1990 as a joint initiative of ITE (Institute of Terrestrial Ecology, Edinburgh) and CATIE (Tropical Agronomic Centre for Research and Higher Education, Costa Rica).

#### **Case study: resistance to *H. grandella* in *C. odorata* and *S. macrophylla***

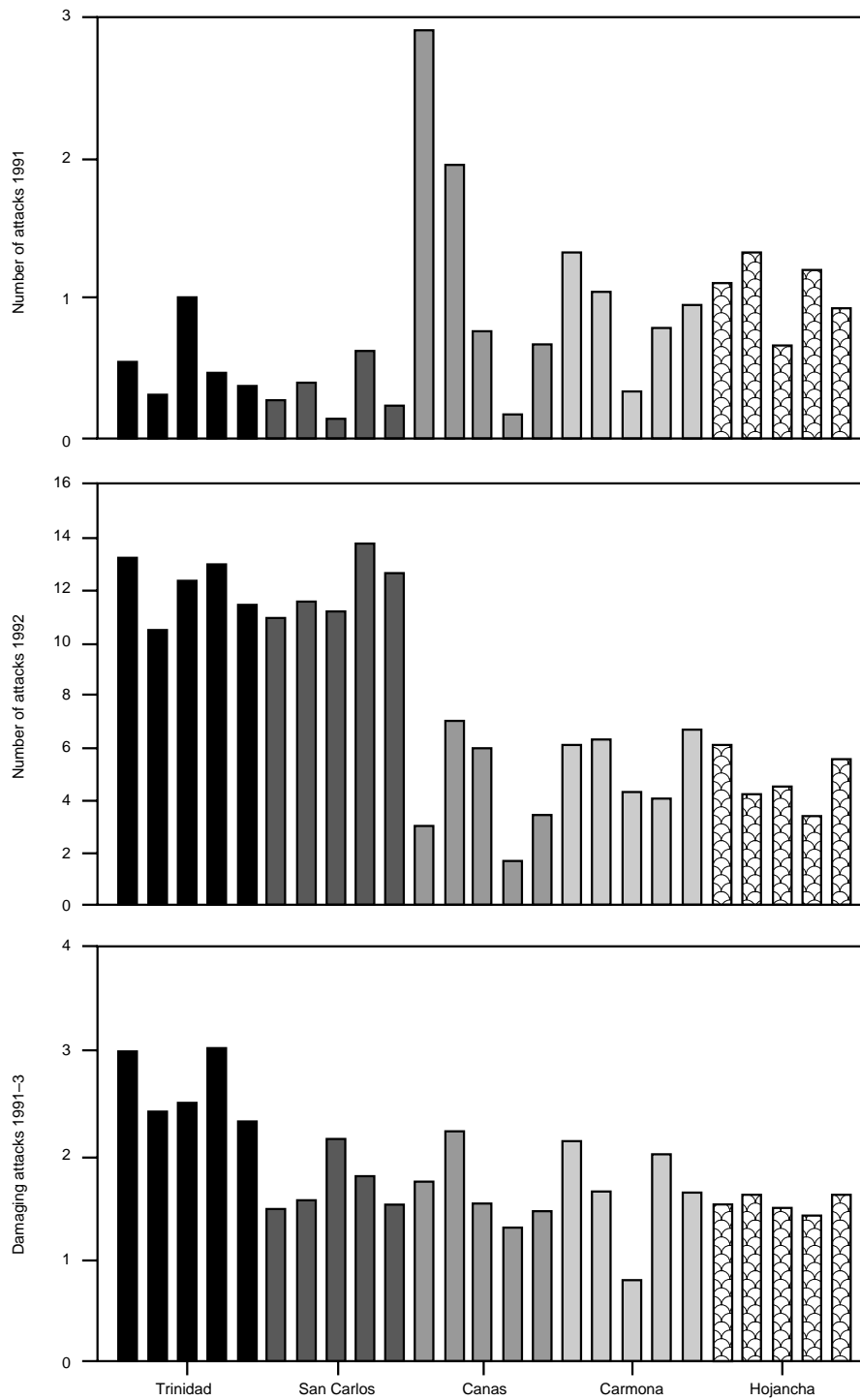
An investigation designed to assess the occurrence of genetic variation in characteristics conferring pest resistance in *C. odorata* and *S. macrophylla* by the use of seedling screening trials was started in 1990 at CATIE (Newton et al. 1995, 1996, 1998, 1999).

Seed of *C. odorata* was collected from trees in four localities (provenances) in Costa Rica, namely Carmona, Hojancha, Cañas, San Carlos and from one locality in Trinidad. These trees were selected on the basis of stem straightness and lack of forking. Seed of *S. macrophylla* was obtained from bulked collections from five provenances, namely Haiti, Trinidad, Honduras and two from Puerto Rico. Details of seed origins and seedling establishment are given in Newton et al. 1995.

Two field trials, screening *C. odorata* (25 families divided equally between the five provenances) and *S. macrophylla* respectively, were established at CATIE, during February 1991 (Newton et al. 1995). *C. odorata* trees were arranged by family in fully randomised 5-tree row plots, in nine replicate blocks. In the second trial, seedlings of *S. macrophylla* were arranged in fully randomised square plots of 25 trees in five replicate blocks.

Each tree in both experiments was assessed for the incidence of shoot borer attack at 14-day intervals, for 84 weeks from April 1991. 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 loci, indicated by forking.

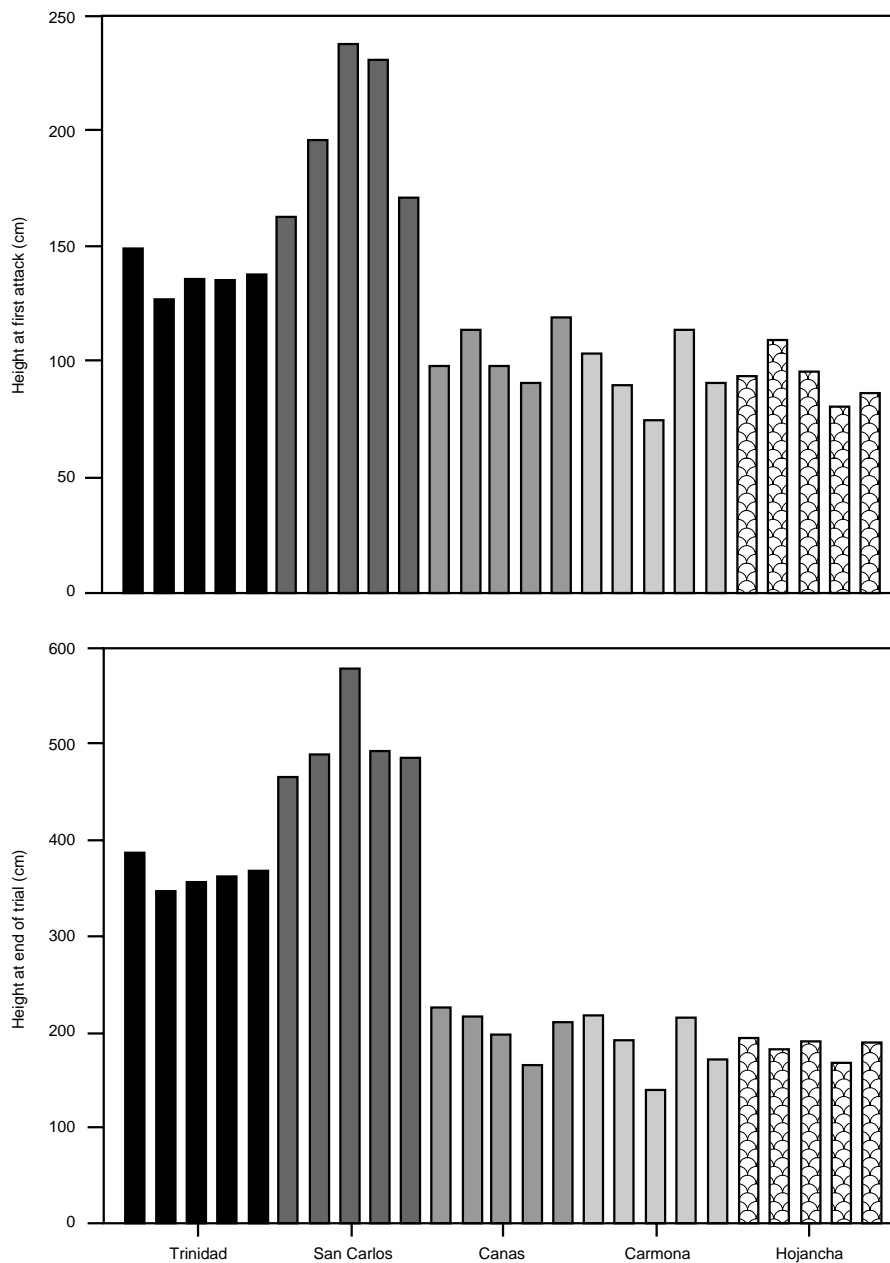
The results of these trials are fully described by Newton et al. (1996, 1999). In summary, genetic variation in height growth was recorded for both tree species, differences between both provenances and families tending to become more pronounced with time. At the final assessments, *C. odorata* mean height ranged from 183–501 cm in Hojancha and San Carlos respectively (Figure 1) and *S. macrophylla* provenance mean values ranged from 211–267 cm in Dirici and Guajataca respectively. Genetic variation in *C. odorata* phenology was also observed, particularly with respect to leaf abscission during the dry season, trees from San Carlos and Trinidad being more heavily foliated than the other three provenances. The majority of *S. macrophylla* trees possessed foliage throughout the experiment.



**Figure 1.** The numbers of shoot borer attacks to different *C. odorata* families in 1991 (top) and 1992 (middle), and the total number of damage loci resulting from attacks 1991–93, as assessed in 1993 (lower).

In *C. odorata*, two pronounced peaks in attack were observed, one each year (Newton et al. 1998) (Figure 2). At the first peak, the San Carlos provenance was least attacked, but these trees and those from the Trinidad provenance experienced the greatest number of attacks during the second peak. A single peak of

attack was observed in *S. macrophylla*, in the second year of the trial. The number of damage loci in *C. odorata*, assessed after 141–177 weeks, was significantly affected by provenance. The mean number of damage loci per tree varied between 1.55–2.64 in Hojancha and Trinidad respectively (Figure 2).



**Figure 2.** The height at which the first damaging shoot borer attack occurred in different *C. odorata* families (top), and the total height in 1993 (lower).

Thus, the results from the *C. odorata* trial were particularly promising, indicating that the San Carlos provenance, derived from the Atlantic zone of Costa Rica, is highly distinctive in terms of leaf morphology, growth and resistance to *H. grandella*. In terms of resistance, San Carlos provenance trees showed evidence of non-preference through a lower incidence of shoot borer attack in the first year of growth than trees from other provenances.

In addition, although San Carlos trees were heavily attacked after their first year of growth, they showed a greater degree of tolerance than other provenances, having a lower number of damaging attacks than expected for their height, and reaching a greater height than other provenances before experiencing their first damaging attack. Trees from the Trinidad provenance also demonstrated tolerance to *H. grandella* attack but they did so by producing several vigorously growing stems, whereas the San Carlos trees tended to respond to attack by producing a single main stem. The latter provenance therefore demonstrated better apical dominance, an important characteristic in the response of trees to pests such as the mahogany shoot borers and a characteristic which can be selected for in seedling decapitation tests (Newton et al. 1995).

Antibiosis is difficult to demonstrate in field trials such as this one. However, the fact that large numbers of shoot borer attacks led to small numbers of damaging attacks may have been due to antibiosis as well as tolerance. That is, some of the attacks may have been reduced in severity because of greater larval mortality in the San Carlos trees. Support for this possibility comes from the greater concentrations of proanthocyanidins (condensed tannins) in the foliage of San Carlos trees relative to trees from other provenances (Newton et al. 1999).

### Discussion

Recent research in Costa Rica (summarised above) has shown that genetic variation in resistance to attack by *H. grandella* occurs in *C. odorata* and *S. macrophylla*, the results on the former tree species being particularly promising. As with previous provenance trials, the basis for resistance appears to be tolerance but this study has also demonstrated that variation in non-preference and antibiosis may occur within *C. odorata*.

These results should serve to encourage studies on resistance to shoot borers in other Meliaceae, such as *Khaya* spp. in West Africa. However, two points should be emphasised. First, the recent research in Costa Rica has been unique in combining regular assessments of attack (similar to that carried out by Yamazaki et al. 1990, 1992) with assessments of

growth, form and damage. Future research should also include assessments of both shoot borer attack and the impact of that attack.

Second, as discussed above, resistance to insect pests is a characteristic to be cherished and used to the maximum effect. Thus, research on resistance should go hand in hand with research on other potential control methods so that resistant mahoganies once identified can be deployed in an integrated management strategy. We therefore agree with the conclusion of Newton et al. (1993a) that the greatest potential for successful management of shoot borers lies in incorporating resistant planting stock in appropriate silvicultural or agroforestry systems. These systems include those that encourage natural biological control by predators and parasitoids or otherwise reduce the abundance and impact of shoot borers (Speight, these Proceedings). We do not believe that effective control will be achieved by a single method of controlling shoot borers, be it silvicultural control, resistance or any other method. An integrated approach is strongly recommended.

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