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

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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):

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- 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, Hojanca, 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 Hojanca 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.

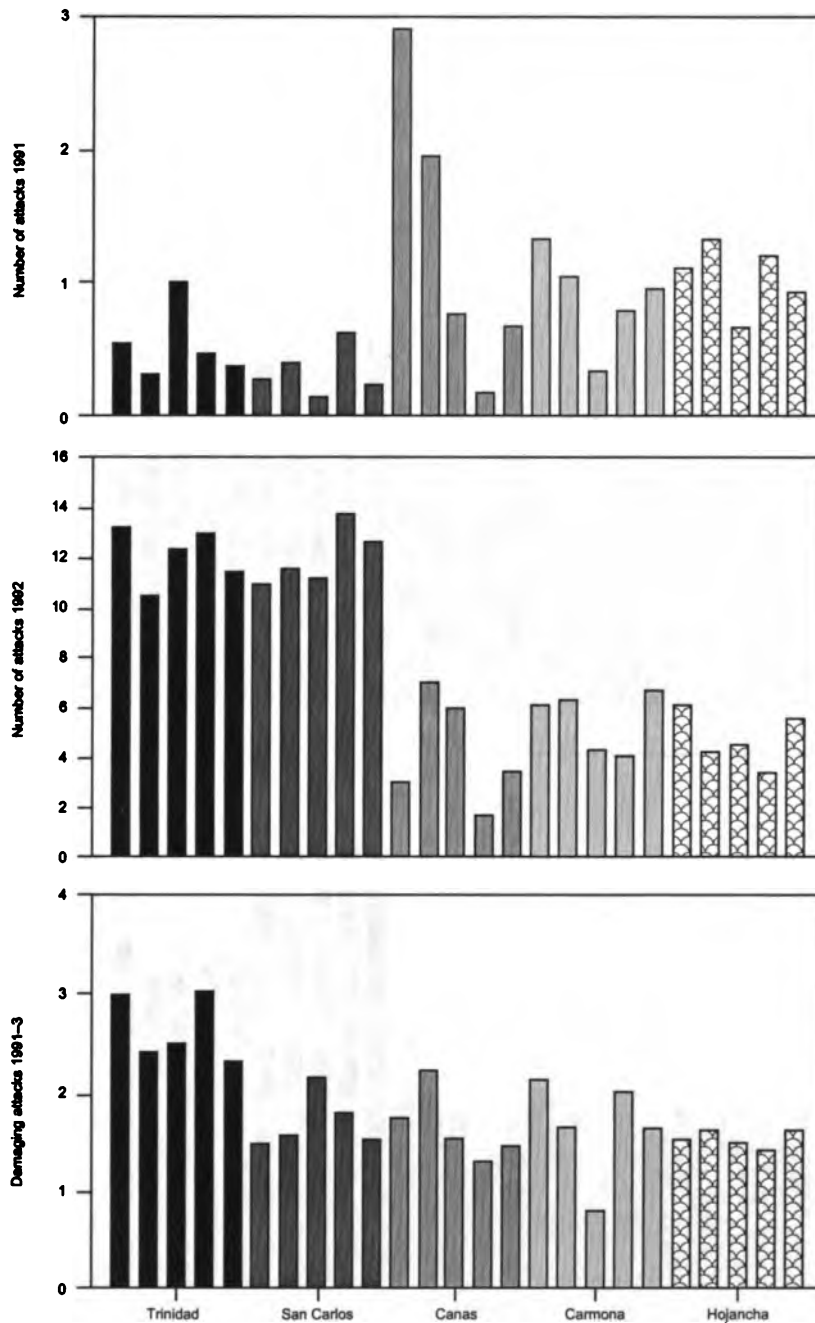


Figure 1. The numbers of shoot borer attacks to different *C. odorata* families in 1991 (top) and 1992 (middle), and the total number of damage loci resulting from attacks 1991-93, as assessed in 1993 (lower).

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).

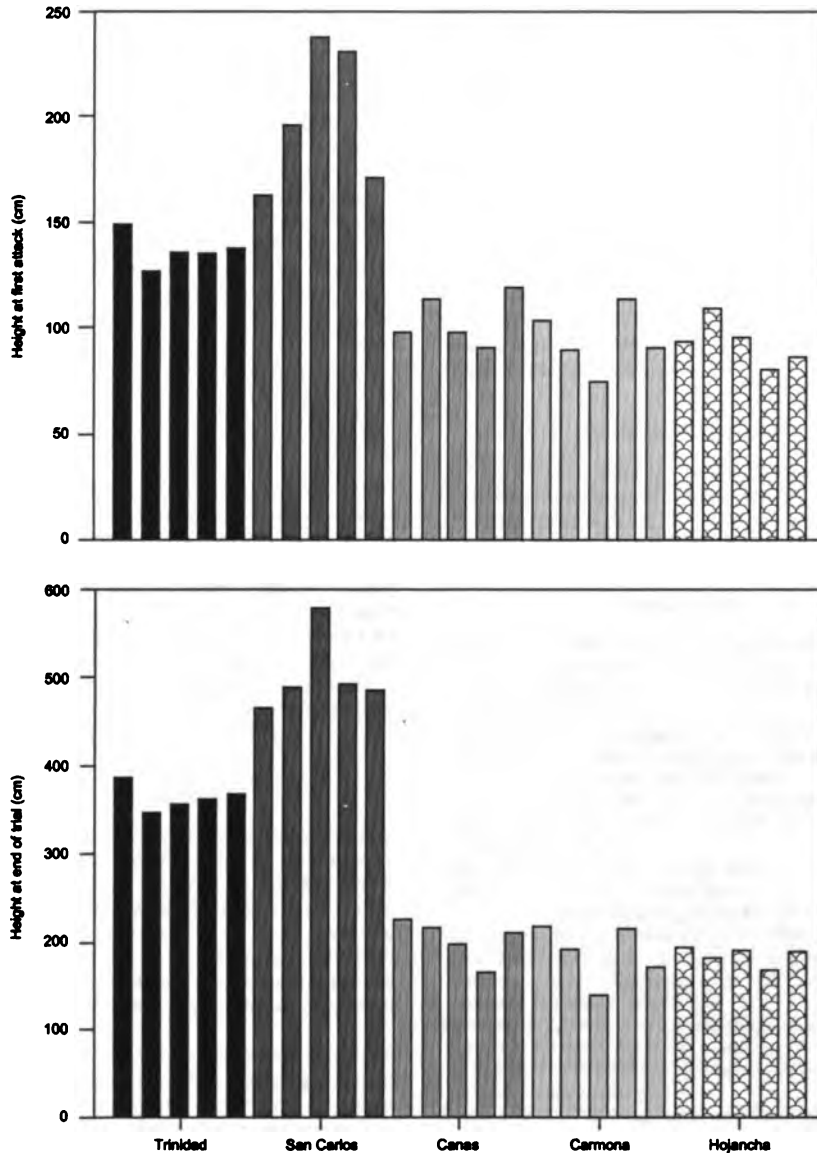


Figure 2. The height at which the first damaging shoot borer attack occurred in different *C. odorata* families (top), and the total height in 1993 (lower).

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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References

- Chaplin, G.E. 1980. Progress with provenance exploration and seed collection of *Cedrela* spp. Proc. 11th Commonwealth Forestry Conference, Commonwealth Forestry Institute, Oxford, 1-17.
- Cameron, D.M. and Jermyn, D. 1991. Review of Plantation Performance of High Value Rainforest Species. Brisbane, Queensland Forest Service/CSIRO, 60 p.
- Dudt, J.F. and Shure, D.J. 1994. The influence of light and nutrients on foliar phenolics and insect herbivory. *Ecology*, 75: 86-98.
- Van Emden, H.F. 1987. Cultural methods: the plant. In: Burn, A.J., Coaker, T.H. and Jepson, P.C., ed. *Integrated Pest Management*. London, Academic Press, 27-68.
- Van Emden, H.F. and Wearing, C.H. 1965. The role of the aphid host plant in delaying economic damage levels in crops. *Proceedings of the Association of Applied Biologists*, 56: 323-324.
- Entwistle, P.F. 1967. The current situation on shoot fruit and collar borers of the Meliaceae. In: Proc. 9th British Commonwealth Forestry Conference. Oxford, Commonwealth Forestry Institute.
- Evans, J. 1982. *Plantation Forestry in the Tropics*. Oxford, Clarendon Press.
- Gould, F. 1983. Genetics of plant-herbivore systems: interactions between applied and basic study. In: Denno, R.F. and McClure, M.S., ed. *Variable plants and herbivores in*

- natural and managed systems. New York, Academic Press, 599–653.
- Grijpma, P. 1974. Contributions to an integrated control programme of *Hypsipyla grandella* (Zeller) in Costa Rica. — PhD thesis Wageningen Netherlands.
- Grijpma, P. 1976. Resistance of Meliaceae against the shoot borer *Hypsipyla* with particular reference to *Toona ciliata* M.J. Roem. var. *australis* (F. v. Muell.) CDC. In: Burley, J. and Styles, B.T., ed. Tropical Trees: Variation, Breeding and Conservation. London, Linnaean Society, 69–78.
- Grijpma, P. and Gara, R.I. 1970. Studies on the shootborer *Hypsipyla grandella* (Zeller). II. Host preference of the larva. Turrialba, 20: 241–247.
- Grijpma, P. and Roberts, S.C. 1975. Studies on the shoot-borer *Hypsipyla grandella* (Zeller) (Lep., Pyralidae) XXVIII. Biological and chemical screening for the basis of resistance of *Toona ciliata* M.J. Roem. var. *australis* (F. v. M.) C.D.C. Turrialba, 25: 152–159.
- Haukioja, E. 1990. Induction of defences in trees. Annual Review of Entomology, 36: 25–42.
- Koul, O. and Isman, M.B. 1992. Toxicity of the limonoid allelochemical cedrelone to noctuid larvae. Entomologia Experimentalis Et Applicata, 64: 281–287.
- Kubo, I. and Klocke, J. 1986. Insect ecdysis inhibitors. In: Green, M.B. and Hedin, P.A., ed. Natural resistance of plants to insects. ACS Symposium Series 296, 206–219.
- Kyto, M., Niemela, P. and Larsson, S. 1996. Insects on trees: population and individual response to fertilisation. Oikos, 75: 148–159.
- McCarter, P.S. 1986. The evaluation of the international provenance trials of *Cordia allodora* and *Cedrela* spp. Annual Report to the UK Overseas Development Administration, Oxford Forestry Institute, Oxford, UK.
- McCarter, P.S. 1988. Report on a visit to Colombia and Ecuador. Report to the UK Overseas Development Administration, Oxford Forestry Institute, Oxford, UK.
- Newton, A.C., Baker, P., Ramnarine, S., Mesen, J.F. and Leakey, R.R.B. 1993a. The mahogany shoot borer — prospects for control. Forest Ecology and Management, 57: 301–328.
- Newton, A.C., Leakey, R.R.B. and Mesen, J.F. 1993b. Genetic variation in mahoganies — its importance, capture and utilisation. Biodiversity and Conservation, 2: 114–126.
- Newton, A.C., Cornelius, J.P., Mesen, J.F. and Leakey, R.R.B. 1995. Genetic variation in apical dominance of *Cedrela odorata* seedlings in response to decapitation. Silvae Genetica, 44: 146–150.
- Newton, A.C., Cornelius, J.P., Baker, P., Gillies, A.C.M., Hernandez, M., Ramnarine, S., Mesen, J.F. and Watt, A.D. 1996. Mahogany as a genetic resource. Biological Journal of the Linnaean Society, 122: 61–73.
- Newton, A.C., Cornelius, J.P., Mesen, J.F., Corea, E.A. and Watt, A.D. 1999. Genetic variation in host susceptibility to attack by the mahogany shoot borer, *Hypsipyla grandella* (Zeller). Agricultural and Forest Entomology, 1: 11–18.
- Newton, A.C., Cornelius, J.P., Mesen, J.F., Corea, E.A. and Watt, A.D. 1998. Variation in attack by the mahogany shoot borer, *Hypsipyla grandella* (Zeller) in relation to host growth and phenology. Bulletin of Entomological Research, 88: 319–326.
- Painter, R.H. 1951. Insect Resistance in Crop Plants. New York, McMillan.
- Roberts, H. 1966. A survey of the important shoot, stem, wood, flower and fruit boring insects of the Meliaceae in Nigeria. Nigerian Forestry Information Bulletin (New Series), 15: 38.
- Sánchez, J.C., Holsten, E.H. and Whitmore, J.L. 1976. Compartamiento de 5 especies de Meliaceae en Florencia Sur, Turrialba. In: Whitmore, J.L. ed. Studies on the Shoot Borer *Hypsipyla grandella* (Zeller) Lep. Pyralidae. CATIE, Turrialba, Costa Rica, IICA Miscellaneous Publications No. 101, 97–103.
- Tingey, W.M. 1981. The environmental control of insects using plant resistance. In: Pimentel, D. ed. Handbook of Pest Management in Agriculture. Boca Raton, Florida, CRC Press, 175–197.
- Wagner, M.R., Atuahene, S.K.N. and Cobbinah, J.R. 1991. Forest entomology in West tropical Africa: Forest Insects of Ghana. Dordrecht, Netherlands, Kluwer Academic Publishers.
- Watt, A.D. 1987. The effect of shoot growth stage of *Pinus contorta* and *Pinus sylvestris* on the growth and survival of *Panolis flammea* larvae. Oecologia, 72: 429–433.
- Watt, A.D. 1994. The relevance of the stress hypothesis to insects feeding on tree foliage. In: Leather, S.R., Watt, A.D., Mills, N.J. and Walters, K.F.A., ed. Individuals, Populations and Patterns in Ecology. Andover, Intercept, 73–85.
- Whitmore, J.L. 1976a. Myths regarding *Hypsipyla* and its host plants. In: Studies on the shoot borer *Hypsipyla grandella* (Zeller) Lep. Pyralidae. Turrialba, Costa Rica, IICA Miscellaneous Publications No. 101, 54–55.
- 1976b. Studies on the shoot borer *Hypsipyla grandella* (Zeller) Lep. Pyralidae. CATIE, Turrialba, Costa Rica, IICA Miscellaneous Publications No. 101.
- 1978. *Cedrela* provenance trial in Puerto Rico and St Croix: establishment phase. USDA Forest Service Research Note, ITF 16.
- Yamazaki, S., Taketani, A., Fujita, K., Vasques, C. and Ikeda, T. 1990. Ecology of *Hypsipyla-grandella* and its seasonal-changes in population-density in Peruvian Amazon forest. Jarq-Japan Agricultural Research Quarterly, 24: 149–155.
- Yamazaki, S., Ikeda, T., Taketani, A., Pacheco, C.V. and Sato, T. 1992. Attack by the mahogany shoot borer, *Hypsipyla-grandella* Zeller (Lepidoptera, Pyralidae), on the Meliaceae trees in the Peruvian Amazon. Applied Entomology and Zoology, 27: 31–38.