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Growing Australian Red Cedar

and other Meliaceae species in plantation

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"All living things are interrelated. Whatever happens to the earth will happen to all children of the earth".

Jefe Seattle 1785-1866

"It merely requires interest and effort, so that one day there will be avenues, small forests and garden cedars across the length and breadth of the country; and if they do take one hundred years to mature, we can be sure that future generations will be very pleased with us, for 'Toona australis' is the most beautiful of all cedars."

John Vader (1987) in: Red Cedar, The Tree of Australia's History

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Foreword

Red cedar is famed for its beautiful deep red, easy-to-work timber, and a history of logging associated with early Australian settlement. The timber is now so rare that it can fetch a high price, particularly once made into fine furniture. Many have tried to grow this tree in woodlots, often unsuccessfully, and it has been concluded, somewhat wistfully, that the species cannot be grown into a straight timber tree. This book, an initiative of the authors, explains the relationship that a number of cedar species worldwide have with the *Hypsipyla* shootborer, and outlines the current state of knowledge on the insect-cedar interaction and their chemistry. The authors demonstrate that they have successfully reared their red cedar woodlots to several metres in height, and show that with vigilance, this species can be grown.

Publication of this book was funded by the Joint Venture Agroforestry Program (JVAP), which is supported by the Rural Industries Research and Development Corporation (RIRDC), Land & Water Australia, and Forest and Wood Products Research and Development Corporation (FWPRDC), together with the Murray-Darling Basin Commission (MDBC). The R&D Corporations are funded principally by the Australian Government. Both State and Australian Governments contribute funds to the MDBC.

This book is an addition to RIRDC's diverse range of over 1,200 research publications and forms part of our Agroforestry and Farm Forestry R&D Sub-program which aims to integrate sustainable and productive agroforestry within Australian farming systems.

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Peter O'Brien
Managing Director
Rural Industries Research and Development Corporation

Preface

The rich resources of Australian red cedar (*Toona ciliata* var. *australis*), which European immigrants found as they displaced Aboriginal Australians along the northern two-thirds of Australia's east coast, catalysed the colonial exploration and exploitation of forests in this region. By the early 20th Century, red cedar had been exploited to economic extinction in much of its range, and the embryonic forest services in Queensland and New South Wales devoted effort in seeking to re-establish the species on a commercial scale. Their considerable efforts, then and subsequently, were defeated, almost without exception, by the cedar tip moth (*Hypsipyla robusta*).

Australian red cedar is one of many species world-wide within the commercially valuable tree family Meliaceae. During the 1980s and 1990s, increased interest in restoration of the resources of other Meliaceae, similarly depleted by forest conversion and unsustainable harvesting, prompted a higher level of activity in research on the Meliaceae and their pests.

Fyfe and Tricia Bygrave, who enjoy the joint delights of being both academics and farm foresters experimenting with red cedar, have contributed to this renewed research effort in the terms they describe in this book. Their efforts, reported here, should give us some hope that the cause of re-establishing Australian red cedar – with consequent benefits for both ecological restoration and commercial forestry – is an exciting challenge rather than a lost cause. We hope it will catalyse further work with this signature Australian tree.

Peter Kanowski
Professor of Forestry
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About the authors

In 1980 Fyfe and Patricia Bygrave bought a run-down property on the mid-north coast of New South Wales located near the Nambucca River. In an attempt to reafforest the property they began to plant eucalypt trees. Learning that Australian red cedar once had grown in the area, they then planted a stand of these beautiful trees. Soon after planting however they observed that the young trees had been attacked by the tip moth. This led to the commencement of a research program with members of the Forestry Department at the Australian National University. Their interest and challenge in successfully growing red cedar led to the writing of this book.

Fyfe and Patricia are academics now retired from their university careers. Fyfe, a biochemist, was a Professor at the Australian National University and Patricia, who has a PhD in Education/Psychology involving music, worked at the University of Canberra. Their reafforestation and research programs have been fully self-funded.

Acknowledgments

This book was made possible by the research performed over many decades by a very large number of dedicated scientists. We especially acknowledge the following for discussions and for access to research documentation on various topics discussed in this book –

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Dr Manon Griffiths (Queensland Department of Primary Industries - Forestry Research) kindly provided a copy of her PhD thesis and Ms Tess Heighes (Kangaroo Valley, New South Wales) provided copies of her field-work. Many of the healthy *Toona* seedlings we have grown over the years were obtained from Anika Farber (Possumwood Plants**,** Repton, New South Wales).

Sections of the book were written in Siena, Italy and we thank Professor Angelo Benedetti (Dipartimento di Fisiopatologia e Medicina Sperimentale, Universita degli Studi di Siena) for kind hospitality during this period.

We particularly acknowledge with gratitude, Professor Peter Kanowski for introductions to key scientists, Dr Allan Watt and Professor Roger Leakey for kind hospitality at Banchory and Bush respectively, and Jonathan Cornelius also for kind hospitality and arrangements during our visit to CATIE, Turrialba, Costa Rica. These visits were made possible by approval from The Australian National University for FLB to undertake leave whilst this book was in preparation. The bulk of the writing was done during his tenure as a Visiting Fellow in the School of Biochemistry, Faculty of Science at the Australian National University in Canberra.

Professor Eric Bachelard (former Head of Forestry at the Australian National University) was kind enough to read an early draft and offered many helpful suggestions both to the format and some of the issues discussed. Dr Rosemary Lott (Rural Industries Research Development Corporation) provided numerous editorial suggestions that improved the flow and context of the various issues discussed. Others who provided useful comments were Professor Jack Elix (Chemistry Department, Australian National University), Dr Ross Wylie and Dr Manon Griffiths (Queensland Department of Primary Industries - Forestry Research) and David Carr (Greening Australia, Canberra). Our children, Drs Louise, Stephen and Lee Bygrave, also contributed with support over the years and with useful suggestions to the manuscript.

Contents

Foreword iii
Preface iv
About the authors v
Acknowledgments vi

Chapter 1: General Introduction 1

Chapter 2: Features of tropical forests 3

Current state of the world's tropical forests 3
Consequences of forest destruction 4
Exploitation of Australian red cedar *(Toona ciliata)* 4

Chapter 3: The timber trees of the Meliaceae family 6

Taxonomy 6
Geographic distribution of the species 7
Phenology 7
Wood and other uses 8

Chapter 4: The biology of the Meliaceae shootborer *Hypsipyla* 10

Taxonomy of *Hypsipyla* 10
Geographic co-location of Meliaceae and *Hypsipyla* 10
Life cycle of *Hypsipyla* 11

Chapter 5: Sex pheromones of *Hypsipyla* 15

General points 15
Pheromone chemistry 15
Chemical analysis of pheromones 15
Pheromone perception by the male 16

Chapter 6: The role of tree chemistry and physiology in insect/plant interactions 18

General points about insect/plant interactions 18
Secondary plant compounds as feeding stimuli 19
Chemical factors considered to induce *Hypsipyla* host preference 20

Chapter 7: Genetic studies on Meliaceae populations 22

Background 22
Technical approaches to identifying genetic variation in tree populations 22
DNA polymorphisms can establish genealogies 24
Evidence for genetic variation in Meliaceae populations 24
Evidence for genetic variation of *Toona ciliata* in Australia 25

Chapter 8: From natural forest to forest plantation 26

Establishing plantations of Meliaceae 26
Role of shade in relation to the incidence of attack 27
Chemical and biological control 28
Silviculture of Meliaceae 28

Chapter 9: Planting Australian red cedar *(Toona ciliata)* 30

Efforts to plant *Toona ciliata* and exotic species of Meliaceae in Australia 30
Current information and research in Australia on *Hypsipyla robusta* and *Toona ciliata* 31

Chapter 10: A successful plantation of *Toona ciliata* and *Cedrela* species in Australia 37

Planting sites 37
Species planted 37
Planting details 37
Growth of trees 38
Incidence of *Hypsipyla* attack 38
Research on our trees 38
Observations from the graft research 40

Chapter 11: Summary and conclusions 41

References 43

Glossary 53

Appendices

Appendix 1. Rearing *Hypsipyla* in the laboratory 56
Appendix 2. Behavioural analysis of female sex pheromones 58
Appendix 3. Laboratory testing of plant secondary compounds on insects 59

Figures

Figure 1. Outline of the interrelating events involved in shootborer infestation of Meliaceae species 2
Figure 2. A chronology of the logging of *Toona ciliata* (Australian red cedar) on the east coast of Australia 5
Figure 3. Phenology of *Toona ciliata* located on the south coast of New South Wales, Australia 8
Figure 4. World distribution of Meliaceae and *Hypsipyla robusta* and *Hypsipyla grandella* 11
Figure 5. Outline of stages in the life-cycle of *Hypsipyla robusta* 12
Figure 6. Chemical structures of the pheromonal secretions of Ivory Coast virgin females of *Hypsipyla* 16
Figure 7. Diagrammatic representation of a sensillum 17
Figure 8. Manufacture of secondary compounds in plants 19
Figure 9. General chemical structures of secondary compounds isolated from Meliaceae sensitive to *Hypsipyla* 20
Figure 10. Application of molecular marker technology to the study of genetic variation in plants 23
Figure 11. Hypothetical dendogram illustrating genetic variation between populations of a given species 24
Figure 12. Design of grafting experiment using Meliaceae species 39

Tables

Table 1. Rates of deforestation (1981-1990) of tropical forests in selected countries 3
Table 2. Principal timber trees of the Meliaceae family (subfamily – Swietenioideae) 6
Table 3. Abbreviated botanical descriptions of some of the Swietenioideae genera discussed in the text 9
Table 4. Outline of behavioural patterns of adult *Hypsipyla grandella* and *Hypsipyla robusta* 12

Chapter 1
General Introduction

Carefully examine a piece of antique furniture made from Australian red cedar or mahogany and what do you see? Generally we see only the beautiful grain and deep red colour of the timber. Little do we ponder the age of that timber and where it came from. Rarely do we ask why it is that the timber is now scarce or why it is not grown successfully in plantation both here in Australia or elsewhere in the world. Many in Australia appear unaware that red cedar trees, synonymous with the early history of Australia, now are difficult to find (see e.g. Jervis 1940; Vader 1987; McPhee *et al*. 2004), or that mahogany and related species of valuable timber may soon become extinct (Newton *et al*. 1993).

Species of mahogany and true cedar such as Australian red cedar and the cedrelas of Central and South America are among the most valuable timber trees found world-wide in tropical forests. They are members of the sub-family Swietenioideae within the family Meliaceae. The timber of all of these trees is much sought after because of its fine grain, colour and durability.

We know that in the appropriate climate they are fast growing. Mahogany and cedar trees can grow in height almost several metres a year and so by 25-30 years will have reached considerable height and diameter. Moreover, cedar seedlings, saplings and mature trees maintain the ability to survive damage from drought, fire and frost; they readily sprout from any affected parts. Only 200 years ago red cedar grew in great abundance along the entire east coast of Australia, from the Clyde River in southern New South Wales to far north Queensland, before being virtually wiped out through human intervention by early last century. So what is the impediment to regenerating these trees?

The underlying factor affecting regeneration is that the Meliaceae are attacked by an insect, a tipmoth or shootborer, that eats out the (apical) growing tip of the young tree. The female insect lays its eggs on the tree and the larvae that emerge burrow into the succulent sapwood, especially that of the dominant growing tip, thus rapidly destroying many centimetres of new growth. The tree compensates by pushing out shoots below this point of attack, resulting in a tree that is multi-branched and of little commercial value. Such attack has long been the major source of frustration to those who have endeavoured to grow and establish cedar and mahogany plantations world-wide.

Figure 1 outlines the close interrelationship between the insect shootborer[1] known as *Hypsipyla* and the Meliaceae host. The tree possesses specific chemicals, one (or more) of which are thought to serve as an attractant to the adult female insect, and one (or more) other chemicals that serve as a feeding attractant to the newly-emerged larvae. Thus underlying this interrelationship is a complex set of ecological interactions involving the biochemistry and physiology of *Hypsipyla* and their Meliaceae host (Grijpma 1974a, 1974b; Floyd and Hauxwell 2001; Newton *et al*. 1993; Whitmore 1976).

Over the past half-century or so, much research involving a number of scientific disciplines has been conducted in efforts to determine how the deleterious effects of the insect on the young tree might be understood and controlled. In this book we describe and collate these wide-ranging results to provide the interested reader and the professional scientist with a unique overview of the major points. It should serve also as a good general guide for the student of biology and ecology.

[1] *The literature refers to the insect Hypsipyla either as 'tipmoth' or 'shootborer'. For consistency the latter term will be used hereafter in this book.*

There are three broad practical aspects to the story:

The first (Chapters 1-3) is an overview of the state of tropical forests; their vital role in the ecology of this planet and the extent to which they are being destroyed by human activity. As well, a description is given of the important and endangered mahogany and cedar timber species that remain in these forests.

The second (Chapters 4-8) is a description of the biology of the shootborer and aspects of the chemistry and physiology of the Meliaceae trees. This information is central to understanding the insect/host interrelationship. The genetic aspects and the silviculture of the tree species are also discussed. This forms a basis to determining the best trees to plant and how to manage them.

The third (Chapters 9 and 10) is an account of the efforts being undertaken to plant areas of Australia with red cedar. In particular, the book concludes on a positive note - how, from the authors' own experience, it is possible to establish a plantation of Australian red cedar.

Relevant literature for each chapter is cited at the end of the book. To assist the reader, some of the scientific terms used are defined in an extensive glossary, also at the end of the book.

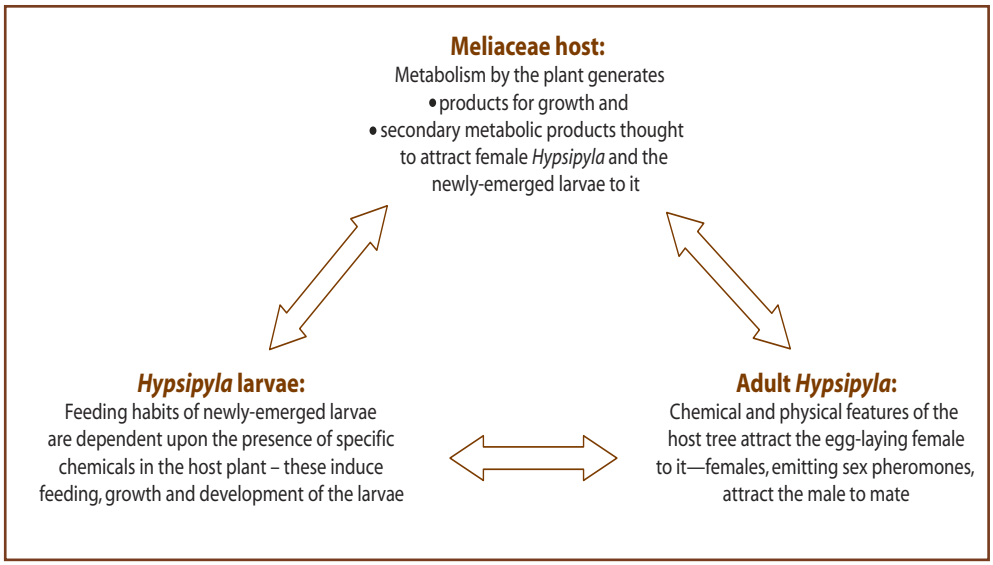


Figure 1. Outline of the interrelating events involved in shootborer infestation of Meliaceae species

Chapter 2
Features of tropical forests

Over the millennia tropical forests have provided humans with numerous natural resources such as the raw material for valuable timber and paper, and continue to be a rich source of medicines found nowhere else on earth. Although they cover less than 2 % of the Earth's surface, tropical forests contain the bulk of the world's species of flora and fauna (see e.g. Westoby 1989; Wilson 1992). Indeed, tropical forests are not simply a single ecosystem but rather a multitude of unique ecosystems that also provide a home to tens of millions of people.

Healthy, sustainable forests are extremely dynamic systems characterised by variability and continual change. They play a dominant role in the patterns of large-scale energy flow and nutrient cycling around the planet. By absorbing carbon dioxide and releasing oxygen, they clean the air and moderate global climate. Forests protect critical watersheds and stabilise river flows.

Much evidence indicates that tropical forests are among the most fragile of all habitats. After forest clearing, many of the nutrients are leached from the soil surface following rains and do not penetrate deeply into the soil (Snook 1996). Once cut and burnt, tropical forests have insufficient remnant humus and litter to support further plant growth.

Current state of the world's tropical forests

It would seem that the world's tropical forests have been in a state of crisis for some time. They are diminishing on a scale and rate not seen previously in human history. Information in Table 1 illustrates the rate of forest destruction in some selected regions.

	Forest Area[1]	Area Deforested Annually[1]
Latin America:		
Brazil	347 000	3 200
Colombia	41 400	350
Peru	73 000	300
Venezuela	42 000	150
Bolivia	55 500	60
Africa:		
Zaire	103 800	200
Cameroon	17 100	80
Asia:		
Indonesia	108 600	1 315
Malaysia	18 400	255
Phillippines	6 500	110

[1] *Figures shown are thousands of hectares*

Table 1. Rates of deforestation (1981-1990) of tropical forests in selected countries *(data sourced from Burgess 1993)*

The rate of destruction is such that some countries have lost over 90% of their forest cover, most of them located in the tropics. In the two largest tropical forests - the Amazon Basin and Indonesia - where over half of the remaining tropical rainforest lies, the rate of forest destruction is high and continues unabated. Figures released in mid-2003 by the Brazilian government indicate that the deforestation rate in the Brazilian Amazon increased by 40% in the previous year. Almost 24 000 sq km of virgin forest were lost, mainly to soya farming and logging (www.guardian.co.uk/conservation).

Consequences of forest destruction

The cutting of ancient forests also is an overriding threat to biological diversity everywhere. Of the world's existing tropical forests, it is estimated that well over half are fragmented (Thompson 2000; Young and Clarke 2000). This leads to a discontinuity in ecological landscapes and reduction of niches for species diversity. Wilson (1992) points out that a 10-fold decrease in (forest) area diminishes the number of species by one-half. In Southeast Asia and Oceania, only about 12 % of the remaining tropical rainforests are found in large wilderness blocks. A further consequence of forest destruction is the loss of gene pools from which all the plant and animal species derive their very existence (Spears 1979; Wilson 1992). Also, the erosion resulting from clearing, in many countries, causes significant silting of major river systems.

Thus once a natural forest is damaged or perturbed in any way, changes occur in the ecological balance that has developed over time. Insect populations can increase; this results in damage to susceptible species. Pest outbreaks and consequent damage to the host-tree often occurs. As a result a particular tree species may tolerate an insect population that exists in relatively low numbers but will show stress when the insect population increases dramatically. Clearing of a natural forest will also often lead to a decline in habitats of natural insect predators such as birds. The extent to which these issues influence Meliaceae – *Hypsipyla* interactions is unclear at this stage.

Exploitation of Australian red cedar (*Toona ciliata*)

Many of the rainforests in Australia that once contained red cedar *(Toona ciliata)*, have suffered the same fate as those forests mentioned above. The vast expanse of forests along the entire east coast of Australia was noted by Joseph Banks during the 1770's while accompanying Captain James Cook on his exploration of Australia and New Zealand. Following the landing of the First Fleet in Botany Bay on 20 January 1778, some of the first tasks undertaken by Captain Arthur Phillip and members of his ship were to fell trees for a variety of needs. Good quality timber was needed and this was largely filled by the discovery around 1790 of a large number of giant trees along the Nepean and Hawkesbury rivers. These trees were later identified as red cedar.

Specimens of red cedar timber were sent to London where the Admiralty, recognising its potential for ship building, ordered returning convict transport ships to bring back as much cedar as possible. As the population around Sydney grew so did the demand for housing, building and furniture; with this the demand for timber increased. Red cedar was quickly recognised by carpenters and boat builders as the best available timber, because of its excellent quality and resistance to timber pests.

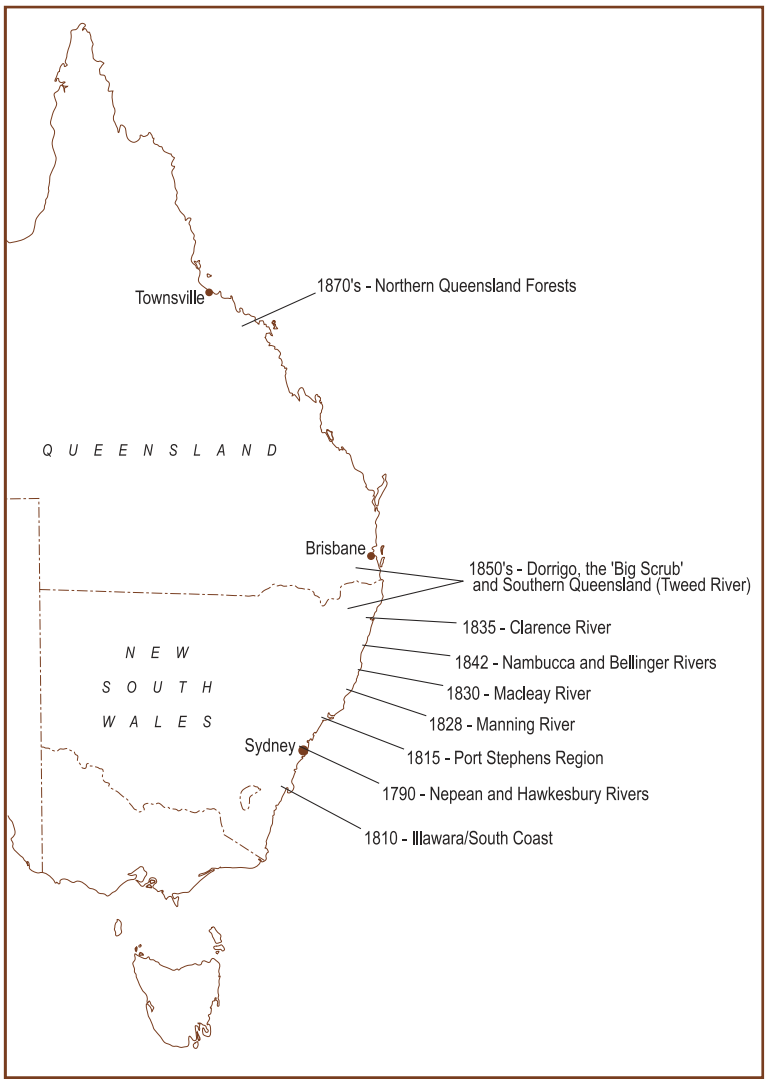
Red cedar trees were felled at such a rate that by 1795, regulations were issued to control their felling in New South Wales. Soon red cedar became referred to as 'red gold'. Not long after, cedar in the forests north, south and west of Sydney were being logged, especially along and inland from the banks of creeks and rivers.

Felling of red cedar first commenced in the areas around the Hawkesbury River soon after European settlement. By 1801, cedar getters had reached what is known as Cedar Arm on the Patterson River and the Shoalhaven River by 1805.

The felling of cedar gradually moved northwards (see Figure 2). The Big Scrub of Northern New South Wales was Australia's largest rainforest and one of the largest cedar-bearing areas in the world (Stubbs 1999). By 1900, the best of the cedar in Australia had been felled and the Big Scrub had been reduced from 75 000 ha to practically nothing (Vader 1987). Much of the rainforest including cedar also was cut and burned by people wanting to grow crops on productive farmland. Thus while at the end of the 19th century some 3000 m^3 was harvested from forests of north Queensland alone, in 1995 approximately 200 m^3 was harvested from that entire State (see Griffiths *et al.* 2001).

Moist, humid conditions favoured development of red cedar so that it grew well along fertile margins of coastal streams and between the sea and the ranges of Australia's East Coast. Few areas of rainforest remain today as the land is largely used for grazing or farming. Many of the trees were massive, as can be gauged from early photographs and from reports of measurements made by foresters. These show individual trees of 2 to 3 metres in diameter and containing well over 100 m^3 of timber; many would have been several hundred years old. The banks of the rivers were a source of the valuable timber, and the rivers also provided a convenient means of floating the logs downstream to local ports for shipment around the country and overseas.

Figure 2. A chronology of the logging of *Toona ciliata* (Australian red cedar) on the east coast of Australia
(information sourced from Gaddes 1990; Grant 1989; McPhee et al. 2004; Vader 1987).



Chapter 3
The timber trees of the Meliaceae family

As mentioned earlier, the Meliaceae family are considered amongst the most valuable timber trees (Mayhew and Newton 1998). The major members of this family are found in the sub-family Swietenioideae and are listed in Table 2. Many species of this family have been destroyed to the extent that few individuals remain (see for example, Rachowiecki and Thompson 2000; Snook 1996; Valera 1997; Weaver and Sabido 1997; Wilson 1992). In this chapter we examine the general features of the Swietenioideae, especially the closely-related genera *Toona* and *Cedrela*.

Genera	Species	Common Name	Natural range
Swietenia	*S. macrophylla* (King)	Big leaf mahogany[1]	Mexico through Central America and North-East region of South America to Brazil
	S. mahagoni L. (Jacquin)	West Indian mahogany	Southern Florida, Bahamas, Cuba, Jamaica, Dominican Republic
	S. humilis (Zuccarini)	Pacific mahogany	Pacific Coast from Mexico to Costa Rica
Khaya	*K. senegalensis* (Desr.) A.Juss	African mahogany	Central African Republic, Gambia, Ghana, Senegal, Nigeria, Uganda
	K. ivorensis A. Chev	Nigerian mahogany	Cameroon, Nigeria, Ghana
Cedrela	*C. odorata* L.	Spanish cedar	Mexico through Central America and Caribbean to Brazil
	C. fissilis (Vellozo)	Rose cedar (South American cedar)	Costa Rica to north of Argentina
Toona	*T. ciliata*	Australian red cedar	Australia, South-East Asia
	T. sinensis (A. Juss.) M. Roem.	Chinese cedar	Nepal to Java
	T. sureni (Bl.) Merr		India to New Guinea
	T. fargesii A. Chev.		South China to India
Chukrasia	*C. tabularis* (A. Juss)	Burma almondwood	India, through Asia to Taiwan and south to Malaysia, Borneo
	C. velutina (M. Roemer)		India, through Asia to Taiwan and south to Malaysia, Borneo
Xylocarpus	*X. granatum* (Koenig)	Mangrove	India, Indochina, Thailand, Papua New Guinea, Australia
	X. moluccensis (Lam. ex Roem)		India, Indochina, Thailand, Papua New Guinea, Australia

Table 2. Principal timber trees of the Meliaceae family (subfamily – Swietenioideae) *(data sourced from Edmonds 1995; Kalinganire and Pinyopusarek 2000; Mabberley 1997; Pennington and Styles 1975, 1981)*

[1]*The name mahogany is used widely to describe many valuable timber trees. Strictly speaking, however, only the genus* Swietenia *are the original mahogany species.*

Taxonomy

Trees of the Meliaceae family are medium to large. They grow up to 30-40 m in height and can reach over 1 m in diameter at breast height; large specimens, however, are now rare. Many attain a straight bole with a well-developed open crown containing large spreading limbs. Older trees in some of the genera tend to be buttressed at the base. The bark on young trees is smooth but becomes rough and scaly or fissured as the trees age. Table 3 describes some species.

In the classification of Mabberley (1997), characteristic features of the sub-family Swietenioideae (Table 2) include: buds usually with scaled leaves, five-valved fruit having a woody capsule with central columella and winged seeds, or a rudimentary columella and

seeds with woody or corky sarcotesta. The tribe *Cedreleae* comprises the genera *Cedrela* and *Toona* and the tribe *Swietenieae* comprises nine genera that include *Khaya*, *Swietenia* and *Chukrasia*. Another genus of the Swietenioideae is *Xylocarpus* which belongs to the tribe *Xylocarpeae*. *Xylocarpus* are commonly called mangrove (e.g. cannonball mangrove, apple mangrove) and species include *X. granatum* (Koenig) and *X. moluccensis* (Lam. ex Roem). They have a wide coastal distribution.

For some time *Toona* and *Cedrela* were placed in the same genus. Today, however, they are placed in separate genera despite being closely related. Features that distinguish *Toona* from *Cedrela* are the columnar androgynophore (being longer than the ovary) and the seedlings, which have entire leaflets. A further difference recently revealed (see Chapter 6), is the chemical composition of the leaves and stems of the two genera. It has been suggested by Edmonds (1995) that *Toona* consists of several species that are wide-ranging and highly variable. These are *T. sinensis* M. Roem., *T. fargesii* A. Chev., *T. sureni* Merrill, *T. calantas* Merr. & Rolfe, and *T. ciliata* M. Roem.

The two high-value species of *Swietenia, S. humilis* and *S. macrophylla,* differ from each other in that, among several features, the bark of the former is rough and scaly similar to that of *Toona*, while the bark of the latter (*S. macrophylla*), is striated.

Geographic distribution of the species

The geographic distribution of the various Meliaceae species is outlined in Table 2. Of the *Toona* species, *T. ciliata* is the most wide-ranging occurring naturally over a large area encompassing India and Pakistan in the west, to south China in the north-east, and to Australia in the south-east (see Edmonds 1993). Soil preference for most genera is rich volcanic or alluvial with sites, well-drained and confined largely to moist gullies or closed rainforest habitats.

Rainfall preference has a major influence on the geographic distribution of many of the species. Thus, for instance, *S. humilis* can tolerate an annual rainfall of ca. 600 mm while *S. macrophylla* requires a minimum annual rainfall of ca. 1200 mm. Consequently, *S. humilis* is found mainly in the dry forests and *S. macrophylla* in the wet and humid forests as in Costa Rica (Carlos Navarro, personal communication, and Table 2). *S. mahogani* grows best in regions with an annual rainfall of 1000-1500 mm, near the sea and at altitudes of 100-500 m. It thrives best on deep, rich, well-drained sandy soils. Thus the original habitat of *S. mahogani* appears to have been in many islands of the Caribbean.

Similary *C. odorata* (preferring an annual rainfall of 1000-3500 mm and altitude up to 2000 m) and *C. fissilis*, have different geographic distributions with a small degree of overlap (Table 2). Yet another example is *Khaya*; *K. ivorensis* prefers an annual rainfall of ca. 2000 mm and grows at low altitudes, while *K. senegalensis* prefers an annual rainfall of 400-1700 mm and grows at altitudes to 1800 m.

Phenology

Phenology is the timing of flowering, fruiting and leaf production. The Swietenioideae vary in their phenology and seed maturation. Both of these can be influenced by factors such as altitude, seasonal temperature and rainfall variations. For instance, *C. odorata* flowers at the commencement of the rainy season, produces seeds every 1 to 2 years and the fruit develop over some 9 to 10 months. *K. ivorensis* develops new leaves in the period September-November, flowers in the period July-January peaking from September-December, and fruit ripen in the period February-May. *S. mahogani* flower and fruit according to climate, but shortly before the rainy season. Development from flower to mature fruit takes 8 to 10 months. Many *S. mahogani* trees do not produce fertile seeds until some 20 years of age and often at later years.

The information in Figure 3 illustrates, as an example, the seasonal phenology of *T. ciliata* on the south coast of New South Wales. In this location, *T. ciliata* usually lose their leaves towards the end of May and new foliage commences around the end of July. Thus the seasonal cycle of events depicted in the figure, takes place over a period of some 9 months.

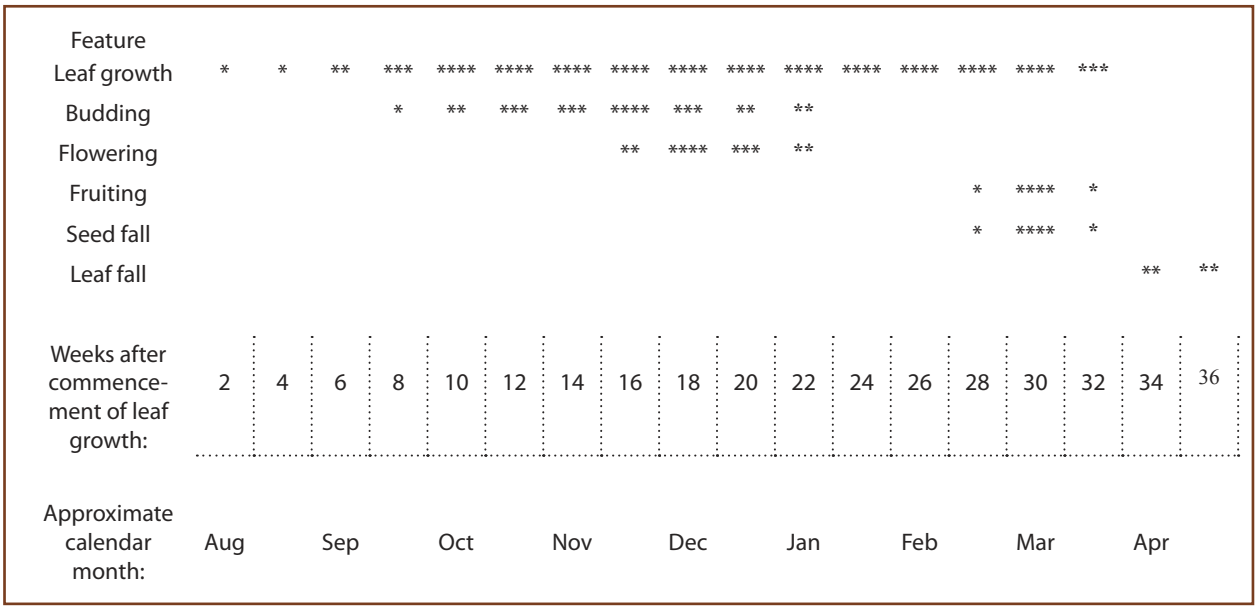


Figure 3. Phenology of *Toona ciliata* located on the south coast of New South Wales, Australia *(data, averaged from 20 individual trees, are modified from unpublished observations of D.J. Boland and T. Heighes in the Kangaroo Valley of New South Wales during 1998-1999)*

Notes:

- *The number of asterisks at each time interval in the figure, reflects abundance; * is the commencement or decline and **** is the peak*
- *On the south coast of New South Wales, leaf growth commences towards the end of July and leaf fall by about the end of May - early colour is red turning to russet then to green. Duration of developmental stages is qualitative; timing and length of stages will vary according to the seasonal climatic conditions as well as geographic location.*

Wood and other uses

The wood of all timbers of the Swietenioideae has a strong aromatic odour and is resistant to termite attack due to the presence of volatile oils. The grain is straight or slightly interlocked and the wood texture coarse and sometimes uneven. The timber is easy to dry but requires careful stacking. Shrinkage is approximately 2 % radial and approximately 4% tangential. It is light (density of timber of mature *T. ciliata* for example is ca. 450 kg/m^3 when dry) and easily sawn and worked. Although the heartwood of *T. ciliata* is yellow-pinkish when first cut, it darkens to a rich reddish-brown (Bootle 1983). It is estimated that trees need to be 30-40 years old before they are able to develop these latter colour characteristics. The fast grown timber appears to have mechanical properties similar to those of large logs.

Timbers of the Swietenioideae are used for high quality furniture, carvings, decorative panels, veneers, flooring, special boxes, musical instruments, housing, bannisters, and boat construction. *Toona* species also provide a number of additional uses (Edmonds 1993): they provide shade, wind-breaks, and tree avenues, for landscaping and in agroforestry. Additionally, other parts of the tree can be used: the leaves as a vegetable in Malaysia/ China and animal fodder in India; the flowers contain nyctanthin, quercetin and a flavone used in red and yellow dye production in India; and the bark is used in tannin and leather work with some barks also having medicinal properties.

	Tree	Foliage	Inflorescence	Fruit	Seeds
Swietenia macrophylla	Tall to 40m; bole to 1m at DBH; short trunk with spreading crown; bark becomes dark grey, rough and scaly	Evergreen; parapinnate; 6-12 ovate leaflet pairs 10-15cm; leathery, dark green above, pale green below	Small pale green-white flowers; in terminal panicles; buds large and broad	Oblong capsule ca. 5-10cm; 5-valved and splitting from the capsule base; light brown; commences when trees are ca. 15 years	Small, long winged; wind dispersed
Cedrela odorata	Tall to 40m; bole 1m at DBH; few buttresses; bark rough and fissured	Deciduous; alternate paripinnate; 5-12 ovate leaflet pairs 7-16cm; glabrous	Small green-white flowers in terminal panicles; glabrous filaments	Oblong to ovoid red-brown capsules ca. 2-4cm; woody, 5-valved; commences when trees are 10-15 years	Sharply angled winged columella; 2-3cm long; ca. 40 seeds per capsule; wind dispersed
Toona ciliata	Tall to 40m; bole 3m at DBH; buttressed; open crown; bark dark brown	Deciduous; alternate imparipinnate; 4-8 ovate leaflet pairs 7-12cm; dark green above, pale green below; new growth bright red	White to creamy-white flowers; terminal pendulous panicles to 40cm; pyramidal, many flowered, fragrant	Oblong capsules ca. 2x1cm; 5-valved; commences when trees are 6-8 years	Membraneous wings at each end; ca. 1.5x0.5cm; light brown; ca. 5/loculus
Chukrasia tabularis	Tall to 40m; branch-less to 25m; bole >1m at DBH; but-tressed; bark dark brown, fissured-dependent on age and location	Deciduous; alternate pinnate with terminal spike; 6-20 ovate leaflets10-17cm	Creamy-green or yellowish flowers; fragrant; at the end of branchlets	Ovoid or ellipsoidal capsules; ca. 3x2cm; 3-5 valved; commences when trees are 5-6 years	Membraneous and flat-winged; ca. 1x0.5cm; brown; ca. 60-100/locule
Khaya ivorensis	Large to 50m; bole to 2m at DBH; well buttressed; bark thick and coarse, red-brown; widely spreading crown	Evenly pinnate; 4-7 leaflet pairs, oblong, ca. 10x3 cm	White, small flowers, numerous in panicles at the end of branchlets	Round woody capsules ca. 8x3cm; 5-valved	Narrow, flat winged; ca. 2.5cm in diameter; ca. 15 per capsule

Table 3.Abbreviated botanical descriptions of some of the Swietenioideae genera discussed in the text *(data sourced from Boland 1998; Mabberley 1997; Pennington and Styles 1975, 1981)*

Chapter 4
The biology of the Meliaceae shootborer *Hypsipyla*

As stated earlier, efforts to establish stands of Meliaceae species have been thwarted by a shootborer of the *Hypsipyla* species (Lepidoptera: Pyralideae). Over time much information has been accumulated about the biology and behaviour of the insect. However, it needs to be stressed that much of this has been derived from laboratory studies and that relatively little information is available concerning its behaviour in the natural forest (see e.g. Speight and Wylie 2001). We present this information on *Hypsipyla* to assist the reader to better appreciate the biological features of the shootborer. Additionally, knowledge about *Hypsipyla* allows for better planning of plantation management strategies.

Hypsipyla has a pantropical distribution and is the only genus of insect that is a serious pest of Meliaceae on all three continents viz. America, Africa and Australia (Schabel *et al*. 1999). As a pest, it has a low action threshold in that only a small population is sufficient to cause destruction - one female lays many eggs and only one larva is sufficient to render malformation on an individual tree.

Taxonomy of *Hypsipyla*

The taxonomy of *Hypsipyla* is still far from resolved even though descriptions of the insect were first made over 100 years ago. Currently, four *Hypsipyla* species are recognised from the New World (the Americas) and seven from the Old World (Africa, Asia, Australia). In the context of shootborer activity, *H. grandella* is the species that has been studied most. This species is especially prominent in the Americas. It is distributed widely in South and Central America, across the Carribean and to the southern tip of Florida; its host preference is *Cedrela* and *Swietenia* species (Grijpma 1973, 1976; Mayhew and Newton 1998; Newton *et al*. 1993). *Hypsipyla robusta* on the other hand, is the species that attacks members of the Meliaceae family in East and West Africa, Madagascar, South East Asia, India, and some areas in the Pacific and Australia. Its host preference is *Toona*, *Khaya* and *Chukrasia*. Some Pacific Island nations, e.g. Fiji and Hawaii, remain free of the insect (see e.g. Mayhew and Newton 1998).

Small morphological and possibly pheromonal differences exist between the African and Asian/Australian populations of *H. robusta*. For example, while the larvae of Asian/Australian populations of *H. robusta* feed mainly on shoots and seeds, those of the African populations feed more commonly on bark (Horak 2000, 2001).

Geographic co-location of Meliaceae and *Hypsipyla*

The world-wide distribution of *H. grandella* and *H. robusta,* together with the distribution of the Meliaceae species for which they have a particular preference, is shown in Figure 4. Note that the combined distribution of the two *Hypsipyla* species overlaps with those of *Toona, Cedrela, Swietenia, Khaya* and *Chukrasia*.

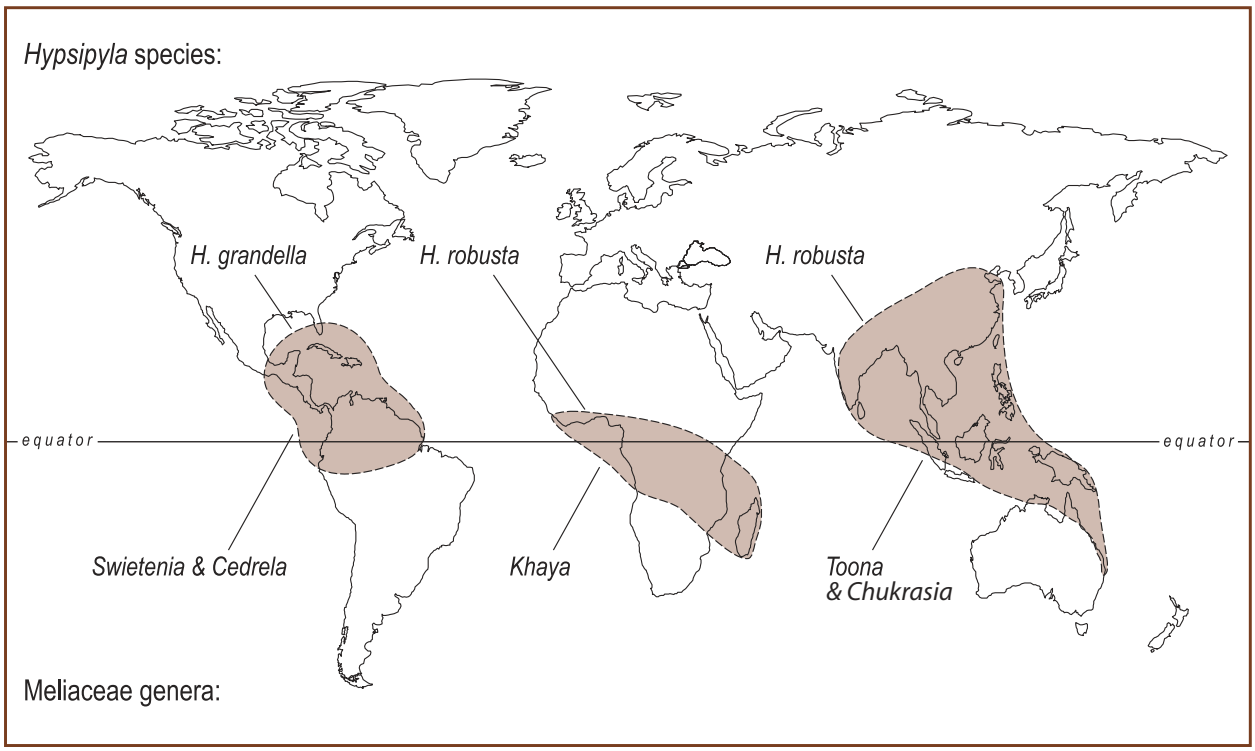


Figure 4. World distribution of Meliaceae and *Hypsipyla robusta* and *Hypsipyla grandella* *(Map compiled from data presented in Chapters 3 and 4. Refer to Table 2 for description of natural range of Meliaceae species.)*

Life cycle of *Hypsipyla*

General features

Research has provided much information about *Hypsipyla* and especially details of the life-cycle of the insect. While most of the published information relates to *H. grandella*, more recent studies in Australia have added important details concerning *H. robusta* (see below). These reveal that the life-cycles of *H. grandella* and *H. robusta* have a number of common features (Table 4). It should be noted however that details in the research reports of the life-cycles of each species can be influenced by factors such as whether the study involved field or laboratory observations, differences in climate, food source and shade, and the nature of the host trees in the region. The information presented in Table 4 and Figure 5 is therefore an overview of these life-cycles.

The major difference known to date between the two insect species is, as mentioned, their host preference (Table 4). While *H. grandella* prefers *Cedrela* and *Swietenia*, *H. robusta* is found on *Toona, Khaya, Chukrasia* and *Xylocarpus* spp. While several other tree species have been reported as hosts for *H. robusta* (see Griffiths 2000), these (reports) remain largely unsubstantiated.

There is some evidence of host specificity from plantings of non-endemic Meliaceae. Grijpma (1973, 1976) found that the degree of attack by *H. grandella* on *T. ciliata* grown in Central or South America is not as great as that on *Swietenia* and *Cedrela* species. Similarly, the degree of attack by *H. robusta*, on *Cedrela* species grown in Australia, appears to be less than that on *T. ciliata*. This issue is expanded upon later in the book.

Event	
Preferred hosts:*#	*H. grandella: Cedrela* and *Swietenia* *H. robusta: Toona, Khaya, Chukrasia*, also *Xylocarpus* spp.
Activity:	nocturnal (in daylight at rest in surrounding foliage)
Mating: – Females:	once only, peaks by 1am - 3am, ceases by approx. 5am
– Males:	once per night up to three nights
Host selection:	by females from late evening to midnight
Cues: – Females:	olfactory commences start of wet season when new foliage produced (new foliage thought to produce volatile chemical attractants)
– Males:	attracted to females by female sex attractants (pheromones; see Chapter 5) - production of pheromones peak 2 to 3 days after emerging from the pupal stage
Egg deposition:	early morning on leaves and stems, singly or in small clusters - in the dry season when trees are leafless, females oviposit on stems
Number eggs laid:	several hundred per female
Adult longevity:	ca. 6 days on average (range 4-14 days)

Table 4: Outline of behavioural patterns of adult *Hypsipyla grandella* and *Hypsipyla robusta* (see text and references therein for details)

**Host selected by virgin female; #* H. grandella *prefer* C. odorata *to* S. macrophylla *in Central America (Carlos Navarro, personal communication) and prefer* C. odorata *to* C. fissilis *in the Peruvian Amazon forests (Yamazaki et al. 1990,*

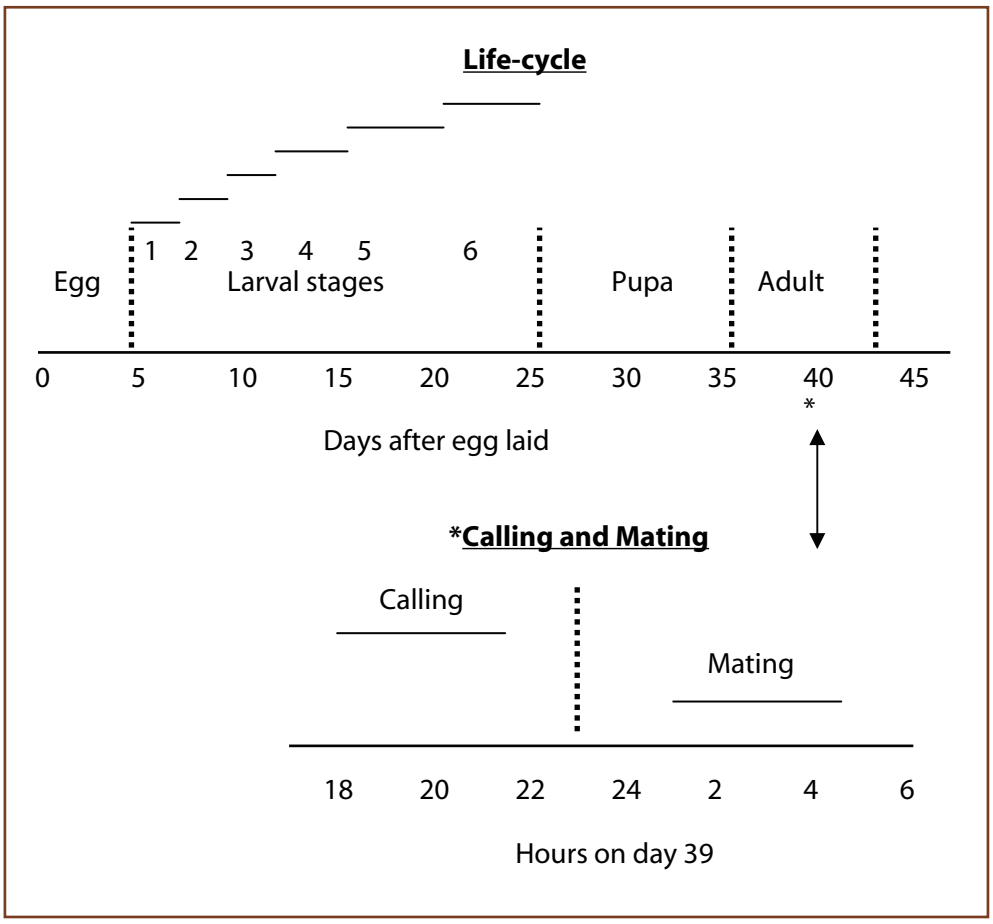


Figure 5. Outline of stages in the life-cycle of *Hypsipyla robusta* *(data sourced from Griffiths 1997 and Mo 1996)*

A generalised insect life-cycle

(information sourced from American Peoples Encyclopedia)

All insects develop from eggs which are laid by the female singly or in masses near the particular food the young will eventually eat. Those that deposit their eggs in exposed places such as on leaves or twigs, may lay several hundred. In the process of growth from egg to adult, most insects pass through a series of changes called metamorphosis. In the case of many insects there are four stages in this development: (1) the egg stage, ending when the young insect (larva) emerges from the egg; (2) the larval or instar stage during which the insect feeds vigorously and sheds its exoskeleton several times; (3) the pupal stage (a period of relative inactivity) in which the body changes markedly and (4) the adult stage.

For many insect species the larval stage, involving a number of instars, is the longest period of the insect's life. Those that have been dwelling within a plant will stay there. The pupal stage may be completed in a few days or may take all winter. At the end, the adult insect breaks out of its pupal skin and dries its wings. Adult insects then have the important task of reproducing; they mate, deposit eggs and many die soon after.

Specific features of *Hypsipyla* life cycle

The articles by Beeson (1918, 1919) contain considerable detail of all stages of the life cycle of *H. robusta*. Other authors who provide relevant details are Entwistle 1967, Fasoranti *et al*. 1982, Gara *et al*. 1973; Griffiths 1997, 2001; Grijpma and Gara 1970a, 1970b; Holsten 1976; Holsten and Gara 1974; Holsten and Gara 1975; Holsten and Gara 1977a, 1977b; Mo 1996; Mo and Tanton 1995, 1996; Morgan and Suratmo 1976; and Roberts 1968. Specific details are now outlined below. Most of the features apply to both *H. grandella* and *H. robusta*.

Size and activity: The adult male of both species has a wing-span of ca. 3 cm and the female ca. 4 cm. The adult male and female moths are largely nocturnal. During the day they are relatively sedentary, resting on surrounding foliage away from host trees. Adult moths appear able to fly considerable distances in search of host trees to which they have been attracted. Activity increases at dusk, especially that of the virgin females who are attracted to the host tree, most likely by olfactory cues given off by the host. The precise chemistry of these cues remains to be determined. There is evidence that compounds like sesquiterpenes and limonoids are involved (see Chapter 6 for further details on this).

Calling: This takes place by the virgin females in late evening. Mating follows during the early morning and ceases by around 5am (Figure 5 at bottom). Males are attracted to the virgin females by sex pheromones that begin to be produced by the females 2 to 3 days after they emerge. *H. robusta* females appear to mate only once and lay up to 500 eggs usually in small clusters on or near leaf axils or veins. *H. grandella* may oviposit over several days. Males on the other hand probably mate several times (Griffiths 1997; Holsten and Gara 1977a). Moth longevity, as judged from laboratory studies, is about 4-14 days with averages around 6 days; females tend to live slightly longer than males.

Eggs and larvae: Eggs of both species are oval-shaped and white when first laid and soon after develop distinct white and red bands. Larvae hatch after ca. 4 days. Newly-hatched larvae actively seek out new foliage (shoots) on the host tree following a short period of wandering. They burrow into stems or leaf mid-ribs usually at the leaf axil. This burrowing activity provides both food and protection from any predators. The succulent terminal shoot is often preferred but larvae can also feed on the flowers and fruit (Griffiths 1997, 2000). The larvae cover the entrance after several days with a sticky web composed of plant pieces and frass. As they develop through the instar phases (Figure 5), they feed on the inner soft tissue of the shoot. In so doing they bore deep into the stem rendering it useless for growth (Plate 1). Larval development occurs over some 23 days for *H. robusta* during which there are five to six instars, each of slightly longer duration as development progresses (Mo and Tanton 1995). While early instars have a brown colour, during the fifth to sixth instar a characteristic blue colour develops with black spots (see Plate 1).

Pupation: This occurs in remnants of the bored stem or around trees that have been attacked, and occasionally in the soil. The late-instar larvae spin a cocoon near the entrance to the tunnel. During this phase, which lasts approximately 9 days, the blue colour changes to black and the coat hardens. Moths emerge at around sunset with a sex ratio of 1:1 common for both *Hypsipyla* species (Griffiths 1997).

Generations of insect population per season: Several generations of *Hypispyla* can be produced during a single season. The actual number of generations that results depends on temperature and general climate, particularly rainfall (see below). Under optimal conditions, such as relatively constant temperature and rainfall throughout the year, generations are continuously produced. In climates having a degree of cold and dryness (as for example on the south-east coast of Australia), there can be up to three to four generations per season. This climatic condition provides an opportunity for trees to recover from attack. Thus "attack" occurs in the Australian south-east coast geographic region from September/October through to March/April and largely in synchrony with the annual phenological changes of the host tree (cf. Figure 3). In north Queensland *Hypsipyla* undergo more generations (Griffiths 2000). Each of these seasonal situations reflects the continual production or otherwise of new shoots. Indeed, there is a close correlation reported in the literature between rainfall, shoot production and shootborer attack (see e.g. Taveras 1999). We have observed on our property (Chapter 10) that this attack can be exacerbated when the host trees are concentrated together as occurs in plantations, and is less in trees dispersed in natural and regenerating forests.

Importance of ambient temperature on *Hypsipyla* development: Like many other organisms that are ectothermal, *Hypsipyla* relies on external sources of heat to maintain body temperature and thus its growth and development. The development time of the insect through the life-cycle (shown in Figure 5) will therefore vary according to the local environmental temperature. Clearly, the lower the ambient temperature, the longer the development from egg to adult will take. For these reasons, the population of *Hypsipyla* and the consequent interactions with the Meliaceae host is enhanced during spring/summer ie. the period when the ambient temperatures are higher than in the autumn/winter period. This phenomenon is known as the "day-degree" or more generally, the "time-temperature" concept. Once this information is known for a particular insect species, its practical importance lies in the ability to be able to predict the time at which the population peaks in numbers. In the case of *H. grandella*, Taveras (1999) provided evidence from both laboratory and field studies, that a population will reach its maximum in close to 1880 day-degrees.

A series of close-up photographs detailing the different stages in the life cycle of *H. grandella*, is contained in the article of Holsten (1976). As well, a series of colour photographs of different developmental stages of *H. robusta* can be seen in the following web site – http://www.usyd.edu.au/su/macleay/larvae/pyra/robust.html.

Type of damage to trees by *Hypsipyla*: As mentioned in Chapter 1, damage to trees arises where shootborer larvae tunnel in the interior of stems and eat out the central pith (Plate 1). This is especially significant when the stem is the apical (terminal) one. Tree growth is retarded and the response of the host tree is to compensate by producing branches below the site(s) of attack. Consequently the tree that grows is multi-branched with little straight bole, is often stunted, and thus of little commercial value.

Damage is especially prevalent in young trees up to approximately 3 metres in height. If infestation is relatively slight, the trees will outgrow the damage. In many locations the tree does not die following shootborer attack. As trees mature with concomitant development of bole thickness, they appear to develop a degree of resistance to attack. Adult trees are also attacked. In many countries throughout the tropics, damage from shootborer attack has been so severe on young newly-established trees of all Meliaceae species, that efforts to grow the tree in plantation have been abandoned (Newton *et al*. 1993).

Chapter 5
Sex pheromones of *Hypsipyla*

The mating behaviour of the adult male and female, described in the previous chapter, is a crucial feature in the life-cycle of *Hypsipyla* and is clearly a determining factor in the rise or fall of a population of this insect. Knowledge about such behaviour is also important if insect control is ever to be achieved. Much research has been conducted on how the male is attracted to the female and especially on the principal factor involved in male/female attraction - the sex pheromones of the female *Hypsipyla*. In this chapter we provide some insights into the nature of the sex pheromones and consider the potential of this knowledge as a means to control an insect population.

General points

Insect pheromones are volatile chemicals used for communication within species. In the case of butterflies and moths (Lepidoptera), over 500 species are known to have pheromones. Sex pheromones are those produced and liberated by the female for the specific purpose of attracting the male and inciting copulation (see e.g. Holsten and Gara 1977). They are secreted in special glands located towards the end of the female abdomen and transmitted in vapour form to the male members of the species. They also have great signalling (attracting) power with only a few molecules needed to produce a response - the same molecules can be effective over a great distance. An "active" air space of several kilometres in length and 10 metres width can be produced by the female and any male of the species down-wind in this space will be drawn towards the female (see e.g. Birch 1974; Birch and Haynes 1982).

Pheromone chemistry

From a chemical viewpoint, female sex pheromones are quite simple molecules. However, sex pheromones usually are present in the female as a complex mixture. Permutations arise in their geometry, functionality and chain length with most being highly volatile hydrocarbon derivatives (see Figure 6). In any one insect species, the chemical structure of the sex pheromones is very specific. Any minor change in molecular structure will destroy or diminish their activity. Generally, a given species will have its own special blend of pheromone.

Chemical analysis of pheromones

The complexity of the mixture, together with its presence in the virgin female in extremely minute amounts, makes the laboratory analysis of these molecules difficult. Such analyses require the ability to separate compounds differing in geometry and the position of the double bond. This has to be done with the very small (nanogram, ie. 10^{-9} g) amounts produced by one female (Schoonhoven 1976).

In the laboratory, the last few segments of the female abdomen are clipped off and extracted with organic solvents to obtain the pheromone mixture (Schoonhoven 1976). It is vital that in the process the sex pheromones are not contaminated with other similar "non-sex" molecules. The sex pheromone mixture is analysed with a very sensitive technique employing capillary gas chromatography with high resolution glass or fused-silica columns coupled to a mass spectrometer.

In the case of *H. robusta*, there is evidence for the blend shown in Figure 6 (as reported by Bosson and Gallois 1982; see also Borek *et al.* 1991). Analyses by Bellas (2001) however, reveal that more than three components might be present in the sex pheromones of *H. robusta* isolated from the individuals sourced by the author from the New South Wales mid-north coast of Australia. The ratio of individual components, one to the other, is as crucial for optimum activity as is the chemistry of the individual components. What this also reflects is the remarkably sensitive nature of the receptors on the male antennae that sense the volatile vapour of the emitted pheromone.

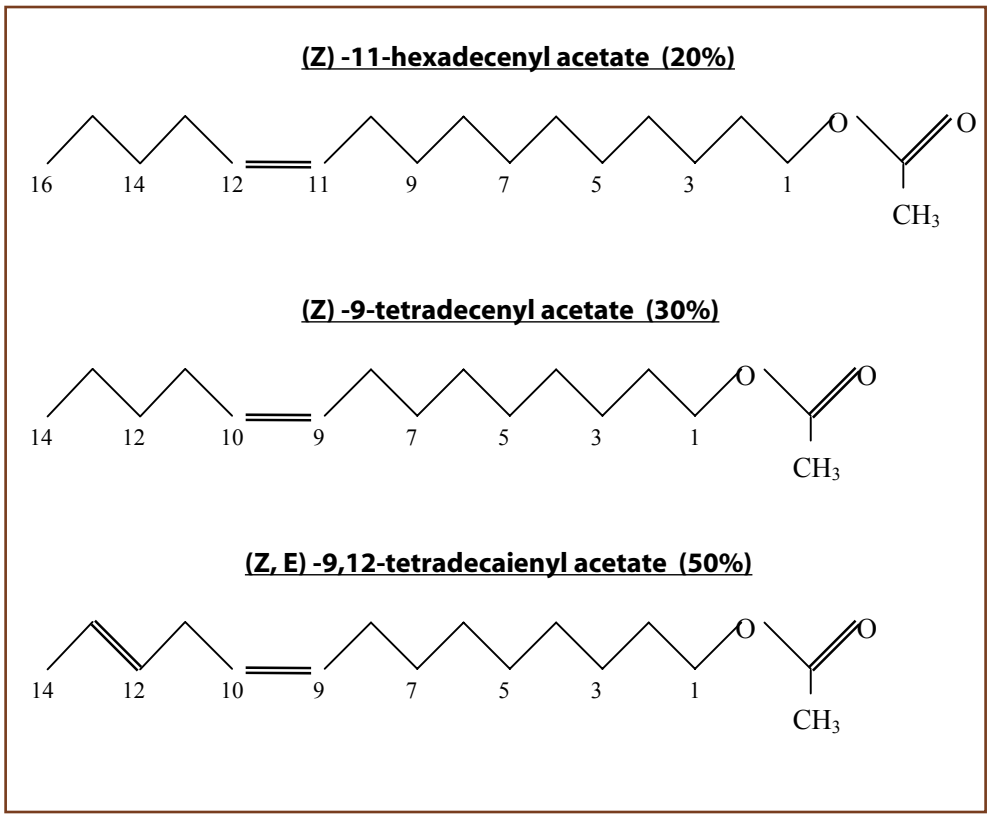


Figure 6. Chemical structures of the pheromonal secretions of virgin females of *Hypsipyla* obtained from the Ivory Coast*
(data sourced from Bosson and Gallois 1982)

**Note: Each of the lines shown represents a carbon-carbon bond with hydrogen atoms (two for a single bond and one for a double bond) attached to the carbon atoms. The numbers 1-14 and 1-16 represent the number of carbon atoms distant from the C-CH_3 group located at right of each formula.*

Pheromone perception by the male

The male of the species have odour filters known as sensilla on their antennae that are specialised to sense the sex pheromones released by the female (Figure 7). These collect the air-borne pheromone molecules that stream across the antennae. The molecules enter the fine pores (diameter 100-200 angstroms) to reach the interior of the sensilla. Here they interact with specialised nerve-endings that in turn transform the molecular message into a bioelectric response. This is transmitted to the central nervous system of the insect. Clearly, the greater the number of molecules entering the sensilla, the greater the bioelectric response recorded in the brain, a feature that is important in the analysis of behavioural responses. Like most "messenger" molecules in nature, the sex pheromones are degraded to inactive compounds immediately following their molecular interaction with the nerve-endings.

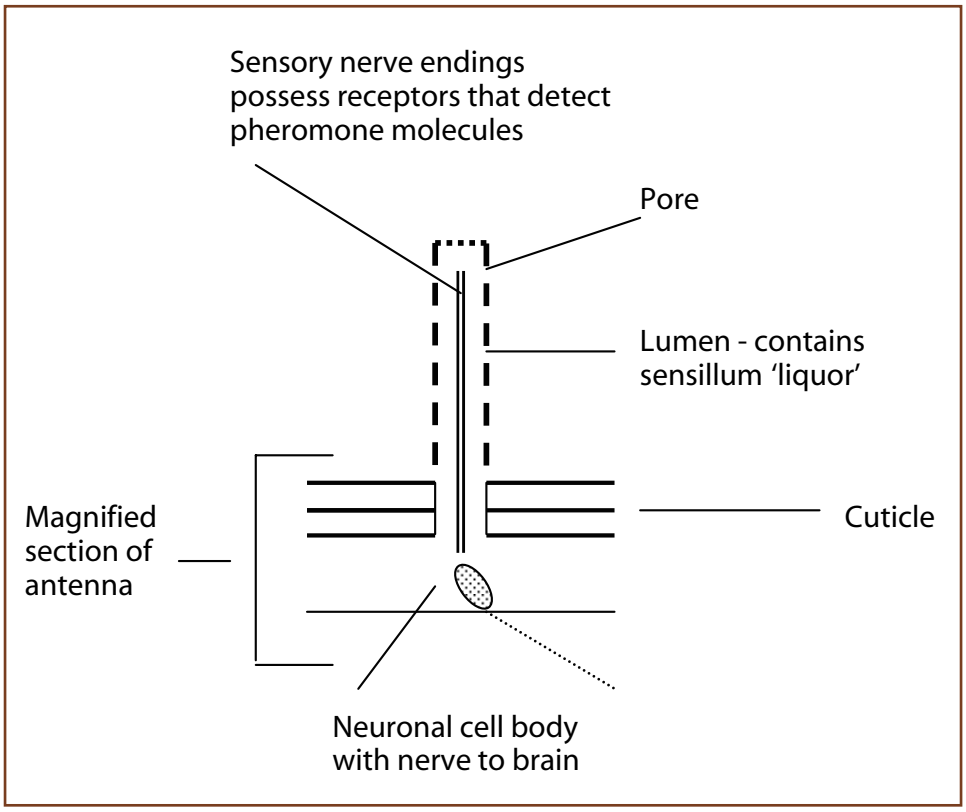


Figure 7. Diagrammatic representation of a sensillum
(diagram modified from Birch and Haynes 1982)

An important practical outcome of pheromone knowledge relates, as alluded to above, to the issue of insect pest control. Traps containing blends of pheromone can be established in the field. Many such blends now can be obtained from commercial sources and the technique has been applied to controlling a range of insects. The male of the species in question is attracted to these traps and not to the female. This reduces the chances of mating. This technique has been used successfully to control for example, the attack on apples by the coddling moth. Additionally, it is possible to establish traps with non-specific volatiles - these would confuse the male and also lessen the chances of mating. Lack of specific information about the sex pheromones of *Hypsipyla* (text above and Figure 6) however, has to this point, hindered its use in controlling attack on Meliaceae.

Chapter 6
The role of tree chemistry and physiology in insect/plant interactions

To this point, we have considered information about the Meliaceae tree species and aspects of the biology of the shootborer *Hypsipyla*. It will be seen from this that there must be features of the host tree that specifically attract this particular insect to it. With this as background, we can now consider those features of the host Meliaceae that result in the attraction of both the adult female and the larvae of *Hypsipyla* (cf. Figure 1). At present we can only speculate in general terms as, despite much research pointing to a chemical basis for such interactions, knowledge still is lacking about those specific chemicals that might be involved in the attraction of *Hypsipyla* to Meliaceae. We will see that while the chemical components of the host are probably crucial in such attraction, others such as smell and vision might also play a role either as external excitatory or inhibitory inputs. These inputs would then determine acceptance or rejection by the insect of the host.

General points about insect/plant interactions

Phytophagous insects, including *Hypsipyla* species, are able to select the foods they eat ie. they are able to discriminate between different plants through their chemical senses. Even larvae have the capacity to distinguish host from non-host and can determine the quality of the host for feeding, survival and development.

Chemicals produced in the plant are important for host-plant selection. They can be classified according to the response of the insect to the plant. Thus:

- **attractants** are chemicals that cause an insect to orientate towards the source of the stimulus
- **repellents** are chemicals that cause an insect to orientate away from the source of the stimulus
- **feeding** or **oviposition stimulants** are chemicals that elicit feeding or oviposition, and
- **deterrents** are chemicals that inhibit feeding or oviposition.

The first two of these have an orientation component and are effective at some distance from the source. The second two require the insect to be in physical contact with the plant. Since chemicals are present in the plant as a complex mixture, the combination of volatiles rather than any individual volatile, is usually important in generating the odour that stimulates arousal and eventual orientation (see Bernays and Chapman 1994). Such involvement of several volatiles in the arousal response is not unlike that found in the composition of sex pheromones we saw in Chapter 5.

Other stimuli involved in host-plant interactions are visual, such as target shape, size and colour. The physical properties of the plant are also important, in particular the plant surface which is covered by a layer of wax. This can influence whether insects will come to rest on a plant, as well as influence feeding and oviposition (ie. egg deposition) behaviour. Stimulants that appear to be especially important are plant nutrients, particularly sucrose and fructose.

It is not known whether *Hypsipyla* larvae feed on a single plant species or on several closely related species in the same genus. It is of interest to note in this context that *Hypsipyla* larvae feed on species of the mangrove *Xylocarpus* (Griffiths 1997) which generally is not a timber tree. Since many plants have similar nutritional values in terms of content of sugars, lipids, polysaccharides, amino acids and proteins, it is possible that the chemical nature of so-called 'secondary compounds' (see following section) is more important to the insect in selecting the appropriate nutritional source (see Harborne 1988).

Secondary plant compounds as feeding stimuli

Secondary compounds are those manufactured by the plant that generally are non-essential for plant growth and development. Often such compounds are unique to a particular species. They are all produced from a relatively small number of key molecules. As illustrated in Figure 8, chemical energy generated from light and photosynthesis is used to make sugars for plant growth. This same chemical energy is also used to manufacture, from simple precursor molecules, many different types of secondary compounds that can be found in an individual plant. These in turn can influence insect behaviour (Bernays and Chapman 1994). Almost every class of secondary compound has been implicated as stimuli of some sort; those that are toxic or repellent generally are prominent. In most cases more than one compound is implicated as a feeding attractant. Olfactory attractants stimulate the insect larvae to feed through their sense of smell, with many larvae able to detect these in leaves even when they are some 3 cm distant (see Bernays 1997).

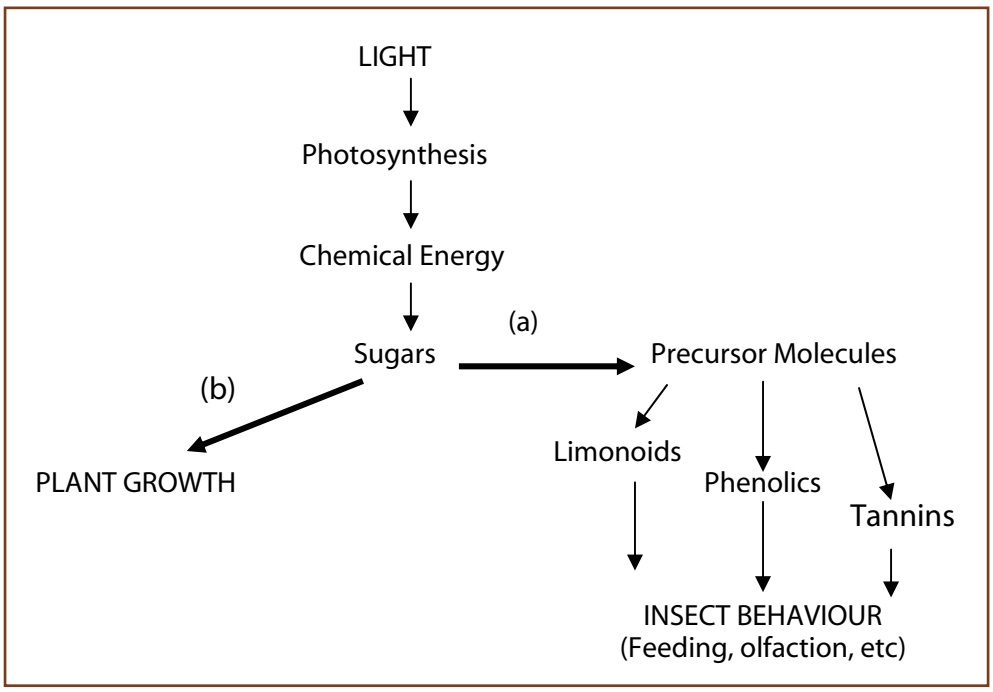


Figure 8. Manufacture of secondary compounds in plants (pathway 'a') uses the same chemical energy as that used for growth (pathway 'b')

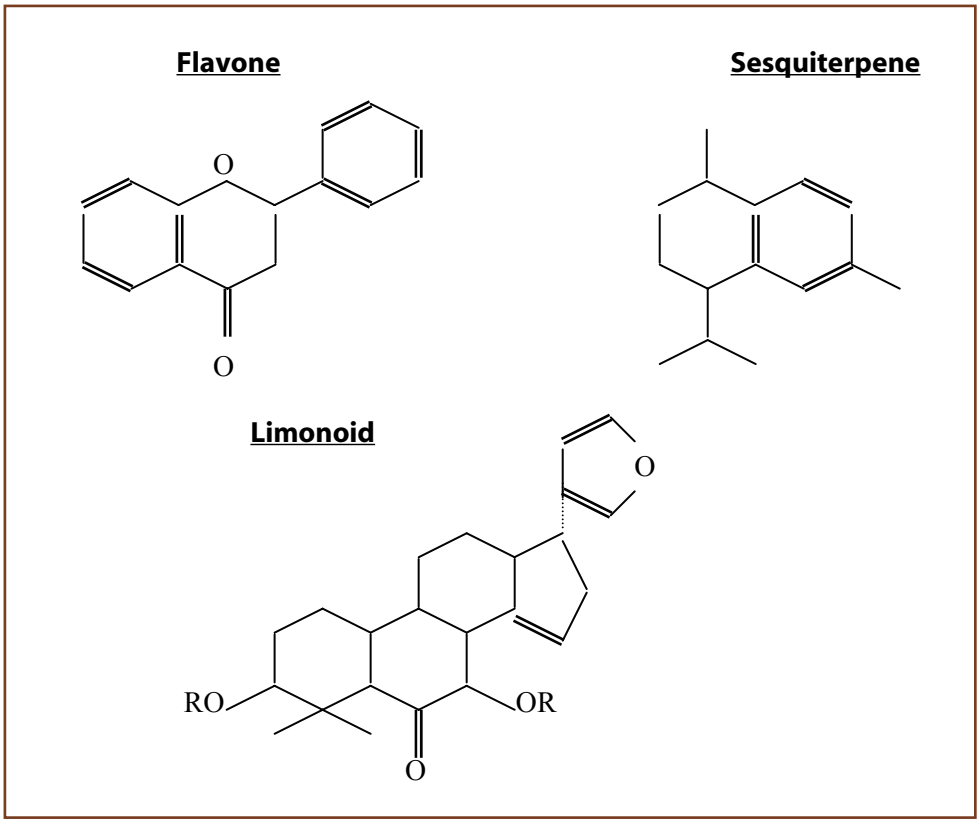
As mentioned earlier, plants can attract, repell, stimulate or deter insects through chemical stimuli. Likely chemical attractants are mixtures of monoterpenes, some of which may also be an oviposition stimulant. Factors that induce larvae to bite are acting as general feeding stimulants; examples being flavonoids, terpenoids and sugars. Swallowing factors are chemicals that provide the larvae with the stimulus to swallow. Examples are inorganic elements like silicates and phosphate as well as cellulose, the cell wall component. Other feeding attractants are alkaloids and phenylpropanoids.

Feeding deterrents generally are monoterpenes, alkaloids, terpenoids, flavonoids, sesquiterpenes and tannins. Sometimes though, these same compounds can act as attractants and oviposition stimulants. This most likely arises because of varying concentrations of the chemicals in different plants as well as the differing physiology of

the consumer. As we will now see there is much research being conducted to test these various possibilities. The general chemical structures of some of these groups of secondary plant compounds are shown in Figure 9.

Figure 9. General chemical structures of secondary compounds isolated from Meliaceae considered to be sensitive to *Hypsipyla** *(for further details see Agostino et al. 1994; De Paula et al. 1997, 1998)*

**Note: Each of the lines shown represents a carbon-carbon bond with hydrogen atoms attached to the carbon atoms as described in Figure 6.*



Chemical factors considered to induce *Hypsipyla* host preference

It was noted earlier that *H. grandella* and *H. robusta* each have a different host preference (Figure 4, Table 4). However, *Toona* species grown in the Americas are not so readily attacked by *H. grandella* and *Cedrela* species grown in Australia are not so readily attacked by *H. robusta*. Grijpma (1973, 1976) undertook experiments in Costa Rica and observed that all the Latin American Meliaceae species tested (*C. odorata*, *S. macrophylla* and *S. humilis*) were attacked by *H. grandella* with *C. odorata* the most susceptible. However, the exotic species *T. ciliata* and *K. ivorensis* were not attacked. Grijpma (1974) speculated that specific volatile essential oils in the shoots and leaves attracted the adult moth to the native host trees (ie. *C. odorata*, *S. macrophylla* and *S. humilis*). These particular oils presumably are either absent or masked in the exotic Meliaceae species. Thus he envisaged olfactory orientation to be a key feature in the interaction of the adult female *H. grandella* with the host.

In further experiments in the laboratory, Grijpma (1974) observed with 4 month old grafts, that such resistance of *T. ciliata* to *H. grandella* was lost when the *T. ciliata* (as scion) were grafted onto *C. odorata* (as root stock). Like Grijpma (1973, 1976), we have raised the question as to whether some specific chemical is carried across the graft from the rootstock to the scion that then induces the attraction of the female insect to the previously resistant tree. We have shown in field studies on the east coast of Australia, that *C. odorata* grafted on to *T. ciliata* lose their resistance to *H. robusta* (Bygrave and Bygrave 1998, 2001, 2003; see Chapter 10 for further details).

A number of laboratories have undertaken research on the identity of chemical agents that might attract *Hypsipyla* to Meliaceae tree species (Brunke *et al.* 1986; Chan *et al*. 1968; Chatterjee *et al*. 1971; Connolly 1983; Kraus and Grimminger 1980, 1981; Mulholland and

Taylor 1992; Nagasampagi *et al*. 1968; Veitch *et al*. 1999). In particular, the group of Das da Silva in Brazil (see Agostinho *et al*. 1994; Das da Silva *et al*. 1984, 1999; De Paula *et al*. 1997, 1998), has been carrying out extensive studies on the chemistry of extracts from roots, stems and leaves of *T. ciliata* grafted on *C. odorata* in attempts to unravel the factor(s) that might be responsible for host preference. Particular interest is focussed on the secondary compounds of the type shown in Figure 9. Specifically they are attempting to determine the phytochemical basis of *T. ciliata* resistance against *H. grandella* and through this to also gain a better understanding of the taxonomic position of *Toona* in the Meliaceae. There is also the incentive that understanding the phytochemical basis of *T. ciliata* resistance will allow tree breeding to achieve more successful planting of Meliaceae in the New and Old Worlds.

This type of research can be difficult to execute with few definitive results having been produced to date. Work involving bioassays could be the most instructive at present as illustrated by that of Soares *et al.* (2003). This involves extracting chemicals (essential oils) from different parts of the plant (as above) and determining the electrophysiological responses of the adult insect to these in what are known as electroantennogram experiments (see Appendix for details). Another approach also involving bioassays, is to feed larvae with different fractions of these extracts and measure their feeding responses (see Appendix for details).

As intimated, despite much effort the chemical identity of one or more individual secondary compounds specifically involved in the interactions between Meliaceae and *Hypsipyla* remains to be determined. For instance, in a recent paper, Das da Silva *et al*. (1999) showed that the particular limonoids they had found to date were of little value in clarifying the basis of the induced resistance of *T. ciliata* to *H. grandella*.

On the other hand, their work is providing important insights into subtle chemical differences between Meliaceae species that could have implications for the taxonomic grouping of *Cedrela* and *Toona*. Das da Silva *et al*. (1999) provide evidence that *Toona* differs from the other genera of the Swietenioideae in that *Toona* lack the limonoids of the mexicanolide group. Such fine chemical differences between *Cedrela* and *Toona*, they suggest, could form the basis of a reassessment of the taxonomic placement of *Toona*. Clearly, however, definitive information concerning chemical factors in the *Hypsipyla*/ Meliaceae interactions has yet to be obtained.

Chapter 7
Genetic studies on Meliaceae populations

Background

An understanding of a species' genetic variation aids assessment of population life history, resilience and conservation "health", and can also be used to select provenances or individuals with better growth or greater resistance to environmental variables, such as insect attack. For tree breeding, it is important to select source plants from a broad base of original natural genetic material, to ensure that representative genetic variation has been sampled.

Sustainable management of Meliaceae species relies on understanding the effects of forest disturbance, in particular logging and deforestation, on regeneration and growth. Uncontrolled logging for economic gain involves the removal of the "best" trees ie. those with good height and form. As a result of uncontrolled logging, those trees which remain become few in number and generally are highly branched and thus lack a commercially useful form. As the population diminishes, the extent of inbreeding is likely to increase, thus further reducing the amount of genetic variation in a population. A potential consequence of a small genetic base is a reduced ability of the population to adapt to environmental change. This could lead to a further decline in population size and vulnerability to extinction. In light of this scenario, it is necessary to consider the genetic variation in Meliaceae populations that might be utilised in any conservation and breeding program.

Technical approaches to identifying genetic variation in tree populations

As a first step, we need to review how genetic variation is assessed. Until recently the principal method to assess genetic variation has been to compare the growth of trees from different geographical origins, using provenance (regions) and progeny (offspring) trials. In this respect genetic variation generally has been characterised on the basis of morphological and growth features. While these approaches have generated much data, they are limited by the subjectivity in assessment of tree characters, influence of the nature of environmental or management practices, and on occasions, the expression of a character only at one particular stage of development.

In recent years modern biochemical research on gene structure and function in all living things has brought an intellectual revolution to biology. Research into every aspect of the biological and medical sciences is greatly influenced by this new knowledge. It is common now to read or hear about the application of DNA technology to many aspects of everyday living. As we will now see, the same intellectual logic is being applied to tree breeding. While some methods can be influenced by environmental conditions or management practices (Morrell *et al*. 1995), a range of DNA-based procedures (ie. involving molecular biology) are now commonly applied to detect genetic variation.

As just indicated, knowledge about the genome at the molecular level has led to the development of a number of DNA-based techniques for studying plant variation. Many make use of the polymerase chain reaction (PCR). Discovery and use of this reaction (see box below) has been central in revolutionising many aspects of the biological sciences. In short, the reaction is able to specifically amplify a single region of DNA in a genome or

it can be used to scan a genome for polymorphisms ie. variations in the DNA sequence. The result is an exponential amplification of a single copy of a DNA molecule that yields sufficient DNA for electrophoretic analysis (see box below and Figure 10).

PCR and genetic analysis of DNA

DNA is contained in three organelles of the plant cell; the nucleus, the chloroplast and mitochondria. Chloroplasts are also the site of photosynthesis. Mitochondria are the major cellular site for generating energy used in most cellular functions. In plants it is the nuclear DNA, the largest proportion of the total, that is most important for studies on genetic variation.

DNA molecules are very long and consist of hundreds of genes each of which occupies a specific site on the single DNA molecule. Nucleotides, made of phosphate, sugar and a nitrogenous base, are the type of compounds that constitute DNA. The DNA molecule is usually double-stranded consisting of two chains of these nucleotides spiralling around an imaginary axis to form a double helix. Special enzymes in the cell are able to separate these chains and in the laboratory they can be separated from each other by gentle heating.

The importance of DNA-based analyses of genetic variation in plants lies in the uniqueness of genetic 'markers' ie. parts of the DNA sequence that are unique to a given species and individuals within the species. Clearly, the DNA sequence of an organism is independent of environmental conditions or management practices. Also, the plant can be tested/analysed at any stage of growth assuming the supply of sufficiently pure material. Finally, the ability to amplify DNA with the PCR (polymerase chain reaction) technique, enables rapid and simple profiling and requires only small quantities of material. Most studies make use of the following laboratory techniques: the ability of gentle heating to separate the two long strands of DNA; the ability of specific enzymes to cut the DNA strand into shorter lengths; and the ability to attach 'probes' to specific loci on these strands so that they can be subsequently detected.

Details of DNA-based techniques in this type of work can be found in references such as Harris (1999), Loveless and Hamrick (1984), O'Hanlon *et al*. (2000) and Peakall *et al*. (1998).

A simplified illustration of the application of gene marker technology to the analysis of genetic variation in plants is shown below (Figure 10). The procedure essentially involves extracting the DNA from the plant material, generating larger quantities of the DNA, separating the DNA pieces on a gel and analysing the bands that form on the gel. Polymorphisms are readily identified as the absence, presence or alteration in the banding pattern on a gel stained with ethidium bromide to visualise the DNA. Only small samples are required (often only a single leaf is needed) for the analyses as the DNA is amplified by the polymerase chain reaction (see box above). In the present context, the importance of the techniques is that they enable an assessment of the extent of genetic variation within and between Meliaceae populations.

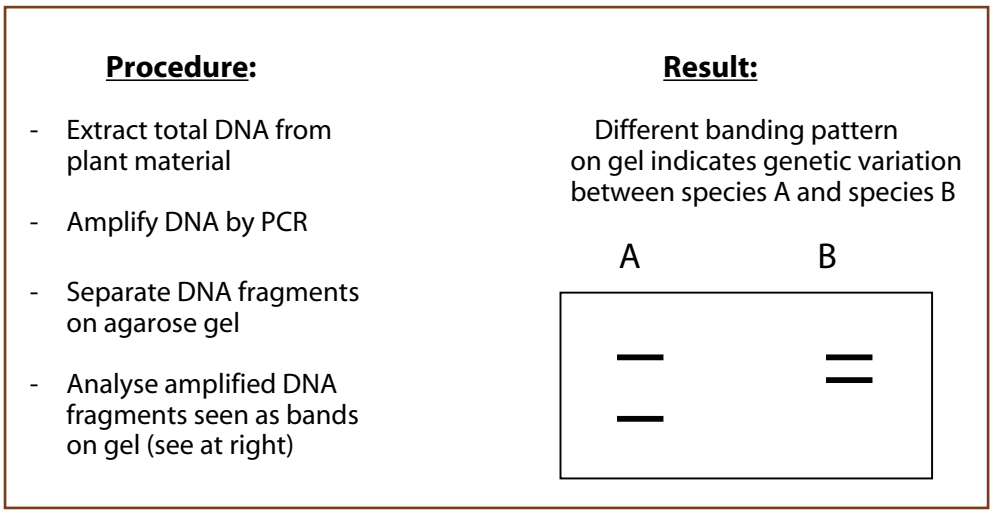


Figure 10. Application of molecular marker technology to the study of genetic variation in plants

DNA polymorphisms can establish genealogies

The genetic or evolutionary relationship among populations within a species can be further established by determining how a series of polymorphic DNA sequences are distributed among the populations. This information, often derived from data like those shown in Figure 10, is often represented in the form of a matrix of pairwise differences from which the genetic relationships can be most easily visualised in a "family tree" or dendogram.

To illustrate: The hypothetical example in Figure 11 shows a dendogram in several populations (P1-P5) of a given species. The length of the horizontal axis is indicative of the difference in DNA sequence (ie. genetic variation) between them. Thus in this case, there is no variation between populations P1 and P2. On the other hand, the illustration indicates significant variation between these two and the other three, especially P5.

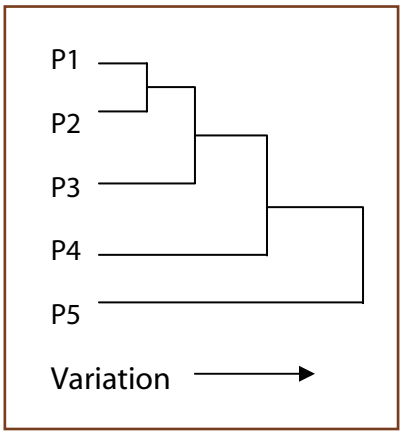


Figure 11. Hypothetical dendogram illustrating genetic variation between populations of a given species

Evidence for genetic variation in Meliaceae populations

Numerous studies have analysed genetic variation among populations of Meliaceae (for reviews see Chalmers *et al*. 1994; Newton *et al*. 1993, 1996). The following gives several examples of this research.

A series of provenance trials were carried out in the 1960s and 1970s to examine genetic variation in *C. odorata*. Seedlots from 14 provenances were distributed to 21 collaborating countries located throughout the tropics. A major finding was a difference in mean height growth of up to a factor of six between some provenances; those from Costa Rica and Belize appeared especially promising (Burley 1973; Burley and Lamb 1971).

Using the DNA-based RAPD approach, Gillies *et al.* (1997, 1999) analysed 420 mature mahogany (*S. macrophylla*) trees from 20 populations located in seven Mesoamerican countries and three other geographical regions. This wide-ranging survey provided indications of limited seed and pollen flow following widespread deforestation and logging. Gillies *et al.* (1999) were thus able to provide quantitative indications that logging reduced out-breeding and was thus having a detrimental effect on genetic diversity of this species. They noted that one consequence of inbreeding is the fixation of deleterious genetic information leading to a population that becomes weaker and less able to adapt to environmental change.

Further to these studies, in a combined progeny and provenance study carried out in Costa Rica, it was shown that *C. odorata* displayed significant variation in susceptibility to attack by *H. grandella* (Newton *et al*. 1999). The study combined regular assessments of attack with assessments of growth, form and damage. Variation in height growth, foliar phenology and shootborer attack, including the mean number of attacks per tree, were all evident. Moreover, chemical analyses of nitrogen, tannin and proanthocyanidin concentrations of foliage, varied significantly between *C. odorata* provenances. The marked variation in concentration of the secondary compound (see Chapter 6) proanthocyanidin in particular (highest where attack was least) led the authors to suggest a relationship between such concentrations and the propensity for shootborer attack, especially at the early stages of growth.

An earlier study was carried out by Newton *et al*. (1995) with *C. odorata* using a decapitation test on young pot-grown seedlings belonging to 30 progenies from five provenances in Costa Rica. This indicated significant differences between provenance and progenies in apical dominance. The authors suggested that significant potential exists for selection of *C. odorata* genotypes with relatively high apical dominance. This would aim to select trees which, following damage, replace the leading shoot with a single new leader. Ideally these might also exhibit superior form (light branching) and tolerance to

pests. They noted, however, that apical dominance and apical control are known to be influenced also by a range of environmental factors and that such tests must be done under controlled conditions (Ladipo *et al*. 1992).

Evidence for genetic variation of *Toona ciliata* in Australia

A recent sudy (Australian Tree Resources News, Number 7, June 2002) investigated the extent of genetic variation in *T. ciliata*. An allozyme study of red cedar was undertaken by CSIRO Forestry and Forest Products to characterise genetic diversity in a number of natural populations from Australia, Papua New Guinea and Bangladesh. The study revealed very low levels of genetic diversity for this widely distributed species; that is the nine populations had similar low levels of variation. Further work is required to explore reasons for this low diversity (http:www.ffp.csiro.au/tigr/atrnews/atrn07/atrnews7_05.htm).

Nevertheless, individual plant variation in physical characters and resistance to attack may be important. Griffiths (1997) examined intra-specific variation in *T. ciliata* trees germinated from seeds collected over a broad geographical range extending from the southern to the northern parts of the east coast of Australia. The deciduous nature of *T. ciliata* (Figure 3) enabled an examination of several features including shoot growth and deciduousness. A number of variations seem dependent on seed source, including differences in the colour of flushing-foliage, degree of leaf pubescence and of red colour in new foliage, height growth, extent of oviposition and dormancy. While a number of these differences might be attributable to seasonal/climatic variations, it was suggested by Griffiths (1997) that some of the observed variability could have a genetic basis, particularly where the seed source was from a relatively isolated geographic location. Provenance seed collections covering a wide range of the east coast of Australia, are being carried out by Larmour (1999) in order to test variation between provenances in growth and performance. Another project is currently measuring damage by shootborers to young trees from a range of provenances of *T. ciliata* planted in provenance trials (Chapter 9).

A vital question that now arises is how any genetic information concerning resistance to attack, superior form, apical dominance, and tree vigour for example, might be "captured" and used in any form of research into *in situ* or *ex situ* conservation and/or management (Newton *et al.* 1994). The best way to capture such variation in individual trees, according to Professor Roger Leakey (personal communication), is through vegetative propagation. Several members of the Meliaceae have been found to be easily rooted as single-node leafy stem cuttings (e.g. *Khaya ivorensis*, Tchoundjeu and Leakey 1996, 2000; *T. ciliata*, Haley 1957, Collins and Walker 1998; *C. odorata,* Nikles and Robson in press). Tissue culture techniques have also been developed (Mathias 1988; Newton *et al.* 1995). Clonal approaches to forestry and agroforestry allow considerable improvements in yield and quality (Leakey 1987) provided that a carefully managed strategy is employed (Leakey 1991). Species such as mahogany, which have severe pest problems but resistant individuals, are an excellent 'customer' for this approach (Leakey and Simons 2001).

If resistant individuals can be identified or successful methods of silviculture developed to overcome shootborer damage, larger numbers of red cedar or other Meliaceae could be grown. The following chapter overviews the extent of knowledge about silviculture (management) of *Hypsipyla*.

Chapter 8

From natural forest to forest plantation: Silvicultural management of *Hypsipyla*

Thirty years ago in Costa Rica, 60 000 ha of forest were being cut each year with no efforts to reafforest. Authorities began to recognise the overall impact of such destruction and today only 4000 ha per year are being cut legally under managed supervision. More importantly some 12 000-15 000 ha are being reafforested per year (Dr Francisco Mesen, personal communication). As a result, 25% of the area of Costa Rica is now forested and protected (see National Strategy for the Conservation and Sustainable Use of Biodiversity, May 2000, Ministry of the Environment and Energy (MINAE) publication). Moreover, the number of people travelling to Costa Rica to visit these forests is increasing year by year.

When considering the establishment of a plantation, whether it be a monoculture or a mixed species, it is important to appreciate its difference from a natural forest. In contrast to a natural forest, a monoculture consists exclusively of trees of a similar age and single plant species. The genetic variation (see Chapter 7) within the plantation in growth-rate, branching, straightness, flowering, and wood quality between individuals, depends on the level of plant breeding prior to selection of planting material (e.g. provenance or clones).

A natural forest in the tropics might have, for instance, five to six Meliaceae trees per hectare. On the other hand, a monoculture plantation could have the same number in an area of only 15-20 square metres! The high density of trees in the latter situation will most likely lead to increases in the risk of insect invasion, insect spread and provide an unimpeded food source for the insect (Chey *et al.* 1997; Speight 1997; Speight *et al*. 1999). As alluded to in Chapter 1, attack by *Hypsipyla* has led to the abandonment of Meliaceae plantation establishment in many tropical regions. However, some regions are now reafforesting. The prime objective then in establishing a plantation of Meliaceae is how best to manage such insect invasion.

In this chapter we focus on those environmental features that can impact on the establishment of plantations of Meliaceae species. The following features of *Hypsipyla* biology (Chapter 4) contribute to the difficulty of controlling the insect when attempting to establish plantations of Meliaceae (Griffiths 2000):

- the nature of the damage due to feeding
- the boring habit of the larvae leading to their being concealed
- the many years for which tree protection is required, and
- the apparent ease with which the adults locate hosts.

Establishing plantations of Meliaceae

There are reports of successful establishment with minimal attack (Newton *et al*. 1998). In Puerto Rico, over 1000 ha of *Swietenia* were planted in a range of spacings under a canopy of secondary forest that was later removed. The low incidence of attack was attributed by them to low initial planting density (< 100 trees per ha), the presence of lateral shade and the maintenance of some ecological conditions of the original forest. In Belize, 700 ha of

S. macrophylla were established. Success was attributed to good species-site matching and early maintenance including weed control. In Costa Rica and in Nigeria, shade trees appear to have been useful in keeping attack at a minimum. In Surinam, *Cedrela* species were planted in large numbers in natural vegetation, using line enrichment and in open plantation. Intensive site management involving canopy opening, weed clearing, use of lateral shade and the pruning of lateral branches, all appear to have been positive factors in establishing plantations. These trials in Surinam are yielding 150-270 trees per ha with an estimated rotation of 35 years based on early tree growth. In Brazil, *S. macrophylla* plantings were found to be less damaged on ridge tops possibly due to the effect of wind on moth dispersal.

These more successful plantings appear to involve growing the trees in a mixed population with other species, and good management practices. The mixed population together with low planting density, possibly serves several functions including the provision of lateral and overhead shade, which could aid in confusing the female moth in her attempts to locate the preferential host species. Much of the information in the literature regarding shade is, however, anecdotal and sometimes contradictory (see below).

Role of shade in relation to the incidence of attack

In Chapter 6 (see Figure 8), we discussed the role of light in the photosynthetic process and manufacture of not only sugars essential for plant growth, but also a range of secondary compounds. Any shading over or around a particular plant thus has the potential to influence the efficiency of photosynthesis and the generation of these compounds.

Shade has the potential to affect the host-insect relationship and growth by:

- altering shoot morphology - an open plantation may produce shoots that are morphologically different to those grown under shade
- affecting the nutritional value of shoots; differences can arise in the content of secondary plant compounds, nitrogen, sugar and water giving rise to alterations in ovipositing
- changing plant defence systems (physical and chemical), sap flow, tannin content, etc
- reducing vertical growth
- affecting the local microclimate that can in turn influence populations of natural enemies and of the insect.

Reports vary on the effects of shade and its role in reducing shootborer attack in Meliaceae (see e.g. Annandale 2000; Griffiths 1997). There is anecdotal evidence that the frequency of *H. robusta* attack on *T. ciliata* is reduced when trees are shaded (e.g. Cameron and Jermyn 1991; Keenan *et al*. 1995). Similarly, recent additional evidence suggests that the degree of shade can influence oviposition preference: In Sri Lanka, Mahroof (1999) and Mahroof *et al*. (2002) undertook research designed to investigate the influence of light availability on *H. robusta* attack on *S. macrophylla*. Seedlings were established under three different artificial shade regimes. The seedlings were then examined for oviposition preference of adults, neonatal larval survival and growth and development of shootborer larvae. The researchers found that (a) adult female moths prefer low shade to medium and high shade for oviposition, (b) larval growth rates were faster and tunnel lengths longer under high shade, but pupal mass was lower, suggesting high shade plants were nutritionally inferior (cf. Figure 8). They concluded that shading of mahogany seedlings may reduce the incidence of shootborer attack and thus be useful in silvicultural approaches to controlling such attack.

In similar work, Cunningham *et al*. (2004) observed that *H. robusta* preferred to oviposit on leaflets of *T. ciliata* from low shade than high shade plants. The authors suggested that

their findings were in keeping with the view that the insect preferentially attacks trees of high vigour rather than those that might be stressed.

Such work calls into question the benefits, or otherwise, of interplanting with other species which are able to provide partial shading effects. What is clear is that since Meliaceae are light-demanding, shade comes at a cost to growth rate. The need to distinguish between the relative benefits of lateral and overhead shade therefore becomes important.

The spacing between trees in a stand and extent of mixing species can also influence the insect/host-tree relationship. This is clearly a complex issue and requires further research as well as a good knowledge of the local environment. Some of these issues of spacing and mixing species are currently under investigation in several Central American countries where Meliaceae species are being grown at 5 to 10 metre intervals within crops such as cocoa and coffee (Carlos Navarro, personal communication).

Chemical and biological control

For many decades, attempts have been made to find a chemical insecticide suitable for controlling *Hypsipyla* attack (Allan *et al*. 1976; Wilkins *et al*. 1976). Success to date has been limited for a number of reasons. The climatic conditions in which the *Hypsipyla* populations thrive (viz. high rainfall and relatively high temperatures) are those that can diminish the effectiveness of any contact insecticides and some of the more effective systemic insecticides are quickly biodegraded. Moreover, once *Hypsipyla* larvae gain access via tunnelling into the host shoot, they gain physical protection from any contact insecticides subsequently applied to the tree. For any of the current insecticides to be effective in protection against *Hypsipyla* attack, would require multiple applications. This would involve the use of excessive amounts to compensate for leaching and evaporation loss, which is likely to be environmentally and economically unacceptable.

It would seem that if chemical control is to be effective, it is best confined to the nursery where limited applications and amounts can be used. An up-to-date review of the range of insecticides that have been trialled both in laboratories and in the field throughout the tropics on *Hypsipyla,* is found in the article by Wylie (2001).

At this stage, as with chemical control, the prospects for biological control of *Hypsipyla* species appear limited (see e.g. Sands and Murphy 2001). Although a number of natural parasitoids of the species is known, there are risks associated with their use such as the impact on other species. Similarly the use of entomopathogens (Blanco-Metzler *et al*. 2001; Hauxwell *et al*. 2001) is limited by the fact that the larvae are cryptic (ie. live in the shelter of the infected stem) and thus may not become readily infected once housed within the shoot. Moreover, microbial insecticides, like chemical insecticides, would need to be applied at frequent intervals, a potentially costly exercise.

Silviculture of Meliaceae

The information presented above and in much of the relevant literature (see e.g. Annandale 2000; Floyd *et al*. 1997; Hauxwell *et al*. 2001; Keenan *et al*. 1998; Mayhew and Newton 1998; Watt *et al*. 2001) suggest the following silviculture of Meliaceae:

- **Site and local topography:** Ensure adequate drainage such as by planting on a slope and avoiding frost-prone sites. In Queensland, for example, a number of trees in many trials have been lost to frost (Dr Ross Wylie, personal communication). As Meliaceae can be prone to wind damage, some form of protection with wind breaks also might be considered. The best soils for the Meliaceae family appear to be those rich in nutrients and organic matter; some species prefer volcanic soils with a moderate pH and high calcium content which seems to confer some resistance to *Hypsipyla grandella*. Depending on the location, the plantation may need to be fenced for protection from animals.

- **Planting:** Planting out of younger seedling stock having high vigour is preferred as it gives the young plant time to establish a high root:shoot ratio. This does not occur when trees are around 1 to 2 metres tall prior to planting. Consideration needs to be given to the best time of year to plant. For instance the success rate would be increased by planting in the wet season, if this is predictable.

- **Density**: High density planting (ca. 2x3 m or 3x3 m spacing) promotes form development by encouraging apical growth. It is also possible to plant at 1x2 m spacing and to thin later.

- **Weeding**: This assists in reducing the competition for water and nutrients especially at early stages of growth. Later, when trees are established, this is not so crucial. Indeed, there is evidence that the absence of weeding at later stages can contribute to conservation by providing an understory environment for various faunal groups (e.g. Chey *et al.* 1997) and bring benefits for pest management of the crop tree.

- **Pruning**: This is a most important aspect of silviculture especially following shootborer attack in open plantations. The aim is to selectively prune the lower branches leaving about 60% crown and establishing a central trunk. This can be continued until a bole height of some 3 to 4 metres is attained. Support for adopting a pruning regime is shown by the work of Cornelius (2000). He carried out an experimental study in Costa Rica involving the effectiveness of pruning in mitigating *H. grandella* attack on young *Swietenia macrophylla* trees. Thirteen pairs of trees were subjected to contrasting pruned/unpruned treatments. He observed that 29 months after planting, pruned trees had significantly better form with no apparent difference in growth traits and concluded that pruning can mitigate the attack by *Hypsipyla*. Work by ourselves (see Chapter 10), supports this conclusion.

- **Mixtures in plantations**: It is important to try to simulate the natural forest situation. However, for many of the reasons discussed above and elsewhere in this book, this can be difficult. One tree species referred to in many reports as suitable for mixed planting with Meliaceae is *Grevillea robusta*. Particular advantages of this species are that it has rapid apical growth and does not develop a broad crown. Interplanting of Meliaceae species with agricultural crops is also becoming very common in Latin America where often *Cedrela* species, for example, are being grown at ca. 10 metre spacings amongst coffee, maize, cocoa and citrus.

Considering all of the above, it is clear that each plantation situation has to be considered in its specific context.

Future research could test whether the following practices reduce both the incidence and severity of attack in plantations:

- *Reducing host suitability*: From what has been described in earlier chapters, genetic modifications to alter the host tree's chemistry has the potential to (i) alter the signals that attract the insect to it and (ii) render the tree biochemically unsuitable for insect development. This could involve increasing the resin flow to minimise tunnelling and/or enhancing complex secondary plant compounds such as limonoids which may be insecticidal or antifeedants. Enhancement of height development by encasing young seedling trees with growtubes also can be carried out, especially since in the authors' experience, attack seems to be more severe with smaller/younger trees.

- *Encouraging natural enemies*: This can be assisted by establishing plantations with mixed tree populations.

- *Recovering form and height increment*: It would seem that factors that promote vigorous apical growth also increase the incidence of attack. It is also clear that vigorously growing trees are subsequently better able to recover from attack.

Chapter 9
Planting Australian red cedar *(Toona ciliata)*

Efforts to plant *Toona ciliata* and exotic species of Meliaceae in Australia

A broad overview of the past and current state of Meliaceae plantings in Australia is provided in the article by Griffiths *et al.* (2001). Some exotic species have developed well although there is occasional poor form. This has been attributed in part to insect attack but also to wind damage, frost, poor soil and damage from browsing animals. Species grown with some success include *C. odorata* and *Khaya*, which in northern Australia (north Queensland and Darwin, NT) received only minor attack from *H. robusta*. What is continually evident from the literature is that *Hypsipyla*-induced damage to trees is the predominant reason why so few people have attempted to establish commercial plantations of *T. ciliata*.

A recent trial for instance, examined the growth of 28 individuals of each of 16 high-value rainforest species including three species from *Toona*, *Cedrela and Khaya* in the Meliaceae family (Lamb and Borschmann 1998). These were grown in a mixed species plantation established at 3 metre spacings. The site, 70 km north of Brisbane, was formerly rainforest but later cleared for agriculture. Measurements of growth rate and tree form were made over a six-year period. This trial found that all 28 *T. ciliata* trees suffered shootborer damage. Whereas tree height growth for *Toona* over the trial period was ca. 3 metres, that for *C. odorata* was some 8 metres. Damage to *Cedrela* by shootborer appears to have been minimal in this trial.

During the last century a number of enrichment plantings of *T. ciliata* in canopy openings of suitable forests were undertaken in New South Wales (e.g. Cumberland State Forest and Whian Whian State Forest) and in Queensland (Grant 1989; Jervis 1940; Mitchell 1971; Vader 1987). In some of these situations, light intensity was about 40-50% of that in the open and some degree of protection against *Hypsipyla* attack appears to have been effected (Cameron and Jermyn 1991; Keenan *et al.* 1995). There has been little follow up on the development of many of these plantings (Campbell 1998). Such enrichment plantings, however, can be costly to achieve and maintain. This has limited their wider adoption as a means of reducing *Hypsipyla* attack (see Griffiths *et al*. 2001).

A number of trials have been carried out to determine the most appropriate companion species that might be planted with *T. ciliata* to find a successful technique for plantation culture. Cameron and Jermyn (1991) reviewed a number of trials in Queensland in which *T. ciliata* was underplanted to various species including *Grevillea robusta* (southern silky oak), *Araucaria cunninghamii* (hoop pine), *Agathis robusta* (Queensland kauri pine) and *Flindersia brayleyana* (Queensland maple). They concluded that underplanting of *T. ciliata* to three-year old *F. brayleyana* allowed the best height increment and that underplanting to *G. robusta* also produced reasonable results. Note that not all plots in these trials gave the same performance.

Results of a mixed species rainforest plantation trial at Wongabel State Forest in Queensland involving *T. ciliata* were reported by Keenan *et al*. (1995). The performance of *T. ciliata* planted in the open was compared with *T. ciliata* planted at varying lengths of time after the planting of *G. robusta* as a cover species. Survival of *T. ciliata* was higher for those planted under the older *G. robusta* and the incidence of shootborer attack was also less. Thus these trees also had better form. Keenan *et al*. (1995) suggested that the

optimum regime for *T. ciliata*, at least on this site, would be to underplant in two year old *G. robusta*, remove the *G. robusta* at age ten, thin the *T. ciliata* to about 150 stems per ha and clearfell at age 50.

Griffiths *et al*. (2001) conclude that the most promising results for underplanting are attained with *G. robusta* (see also information in the following chapter). In addition, early growth rates can be accelerated significantly by using growtubes –placed around young trees, these translucent plastic tubes have also been shown to offer early shelter and protection against damage to wind and animals (Applegate and Bragg 1989).

A recent example of successful plantings of *T. ciliata* can be found in Kempsey on the mid-north coast of New South Wales. In 1986 Kempsey Shire Council planted an avenue of *T. ciliata* on the Pacific Highway immediately north of the town. These healthy specimens are now quite large approaching 10 to 15 metres in height and diameters of ca. 30 cm.

Current information and research in Australia on *Hypsipyla robusta* and *Toona ciliata*

The following research is being undertaken by groups in Australia and involves investigations into *H. robusta* and its attack on *T. ciliata*.

1. CSIRO Division of Forestry and Forest Products, Canberra has collected *T. ciliata* seed from many trees located along the east coast of Australia, to enable assessment of genetic variation in growth characteristics and resistance to shootborer. Seed was collected as part of the South Pacific Regional Initiative on Forest Genetic Resources (SPRIG), funded by AusAID. This seed was used in project 2 below, to establish field trials in Australia and southeast Asia (see http://www.csiro.au/news/mediarel/mr1999/mr9924.html).

2. A detailed international study with the purpose of (1) identifying resistant genotypes of *T. ciliata* and *C. tabularis*, (2) examining mechanisms of resistance and (3) establishing protocols for mixed plantings is being carried out by scientists at CSIRO (Canberra) and Queensland Department of Primary Industries and Fisheries- Horticulture and Forestry Science (previously QFRI, Brisbane). The work also involved collaborators in Thailand, Vietnam, Lao PDR, Philippines and Malaysia. The project is funded primarily by ACIAR, with additional support from some Australian trials from JVAP and NHT. Field trials have been established at selected sites in Queensland.

   The program commenced in early 1999 and phase 2 of the project is to commence in January 2005. Already several observations have been made that are noteworthy (see Annandale 2000; Cunningham and Floyd 2004; Cunningham *et al*. 2004; Griffiths 2000, Cunningham and Floyd 2002, Cunningham *et al*. 2001 and reports in http://www.ento.csiro.au/history/natres/hypsipyla). This research has found that:

   - Common in all trials was a positive relationship between tree height and *Hypsipyla* damage to trees during the first few years of growth (measured up to age 4).

   - In genetic resource trials, *K. senegalensis*, *C. odorata* and *C. tabularis* performed better than *T. ciliata* in that they suffered less *Hypsipyla* damage and grew longer boles. The trials across all countries indicate that *H. robusta* prefers endemic hosts to those introduced from other regions.

   - Tree form was not improved by pruning open-grown trees after two years.

   - Trees grew better in understorey and gap plantings than open plantings. Laboratory experiments confirmed that *Hypsipyla* preferred to lay eggs on the leaves of trees grown in high light (low shade).

- A study involving plant chemistry, suggested that variation in *Hypsipyla* damage to *T. ciliata* is linked to the terpenoid compound bicyclo elemene. Relatively low amounts were detected in leaves of trees that suffered more damage and high amounts on those that suffered less damage.

3. A study by CSIRO Division of Entomology, Canberra in conjunction with the Australian Centre for International Agricultural Research (ACIAR) includes:

   - Establishing the identity of the putative *Hypsipyla robusta* throughout its range (including Australia, southeast Asia and Africa).

   - Confirming that the populations of *Hypsipyla* on *T. ciliata* and *Xylocarpus* mangroves in Australia are the same species.

   - Establishing the identity of all Indo-Australian species presently referred to as *Hypsipyla* (see: – http://www.aciar.gov.au/web.nsf/doc/JFRN-5J472Q
     – http://www.ento.csiro.au/history/natres/hypsipyla/pdfs/Hypsipyla_ taxonomy.pdf
     – http://www.ento.csiro.au/anic/lepidoptera.html

4. A number of other studies include *Toona ciliata*. The CRC for Greenhouse Accounting is investigating the dendroclimatology of red cedar to explore effects of climate and atmospheric CO_2 levels on tree growth (http:/www.greenhouse.crc.org.au/crc/education/students/program_c.htm).

5. More generally, the Cooperative Research Centre (CRC) for Tropical Rainforest Ecology and Management, North Queensland is conducting research which involves:

   - an assessment of which tropical tree species to plant

   - the best sites on which to plant, and

   - the effect of both plantation design and management practices on plantation performance (see: http://rainforest-australia.com/plantation.htm).

For the interested grower, Queensland Department of Natural Resources, Brisbane has produced a range of relevant documents for tree planting. See for example, "Tree Facts" (T38), a document entitled 'Growing rainforest timbers in Queensland', December 1996.

In addition, a range of individuals and community groups throughout the eastern seaboard of Australia have planted red cedar in mixed species rainforest plantings and are monitoring and measuring their growth e.g. Subtropical Farm Forestry Association (Novak pers. comm.); Kooyman (1996), Noosa and Barung Landcare (G. Clarke pers. comm.), Central Queensland Forestry Association (R. Allen and G. McKenzie pers. comm.) and Community Rainforest Reforestation Program and its successors (see Erskine et al., in press). Chapter 10 gives a description of Meliaceae stands planted by the authors (see also Bygrave and Bygrave 1994).

Colour Plates

Colour Plates

Colour Plates

Chapter 10
A successful plantation of *Toona ciliata* and *Cedrela* species in Australia

At this point, based on the information already discussed, it could be assumed that any attempt to establish stands of Meliaceae species in Australia would be unsuccessful. This would be particularly so in areas where *Hypsipyla* is known to exist. The following account of our own experience in undertaking the planting of Meliaceae species, however, would indicate that this is not necessarily so and provides a description of what can be achieved over time.

Planting sites

The sites on which we have established stands of *T. ciliata* are located on a property on the mid-north coast of New South Wales. In former years this was a dairy farm. When purchased, the farm had degenerated to the extent that there was much secondary forest growth. The area is undulating with the highest point being approximately 25 m above sea level and is situated within 10 kilometres of the coast. Being close to the Nambucca River, and adjacent to wetlands, it seems probable that in some earlier time, *T. ciliata* trees grew there prior to being cleared for grazing purposes. The lower gully sections are surrounded by substantial stands of various species of *Eucalyptus* trees such as *E. grandis* and *E. saligna*. These act as protection from winds, have provided the opportunity to interplant, and promote biodiversity in the area.

Species planted

The first plantings of *T. ciliata* were made approximately 16 years ago. A monoculture of 220 seedlings was established in a 3x3 m grid on a section of the property sloping gently to the east (Plate 2). A year later, and adjacent to this, a number of other species (predominantly *Grevillea robusta* but including also *Flindersia australis* and *Gmelina leichardtii*) were planted in a 6x6 m grid; a year later *T. ciliata* were interplanted among these also at 6 m intervals. Not long after, and adjacent to the latter mixed plantings, a further monoculture of *T. ciliata* was established to bring the total number of *Toona* seedlings planted at this site to approximately 500. Some 400 *T. ciliata* seedlings were also planted on other sites on the property. These included about 150 in clearings under open canopy among the established eucalypt trees mentioned above. In addition to the *T. ciliata*, approximately 150 of each of *C. odorata* and *C. fissilis* were planted at various times during this period on various sites.

Planting details

The vast majority of plantings have been carried out with seedlings 10-20 cm tall obtained from local nurseries. This height gave the young trees the opportunity to establish an adequate root system prior to later growth. Plantings were carried out in the wet season whenever possible, to assist with root establishment. None of the trees was irrigated. Natural rainfall in the district is generally about 1200 mm per year. Small amounts of fertiliser were applied to the open holes before planting. The herbicide 'glyphosate' is routinely sprayed around the trees (1-2 m diameter) to minimise competition with weeds. Where access permits, the areas are also slashed to keep undergrowth to a minimum.

Growth of trees

On these sites seedlings were able to grow over 1 metre in height each year if not attacked. This compares favourably with trials carried out elsewhere in Australia (see Chapter 9). Despite attack, however (see below), many of the *T. ciliata* trees now are up to 8-10 m in height and have attained a diameter at breast height of 15-20 cm (Plates 2 and 3). As predicted from observations of others (see Chapter 7), *T. ciliata* growing in the open, quickly attain both height and bole girth. In contrast trees planted among the *Eucalyptus* species have attained greater height but less girth than those in the open. Survival rates have been very high for both trees grown in the open and those grown among the *Eucalyptus* species. Of all the several hundred *T. ciliata* seedlings planted, approximately ten have been lost - probably due to water deprivation in the early stages of growth. Growth during the initial 18 months for many of the *Cedrela* plantings was slow but after this period, growth was almost as rapid as that of *T. ciliata*. Many of the *Cedrela* species planted have now attained a height in excess of 10 m with the majority branchless to ca. 3 to 4 metres.

Incidence of *Hypsipyla* attack

None of the *Cedrela* species planted out in this site has suffered from *Hypsipyla* attack. This is consistent with reports (see Chapter 4) that the species appears not to be a preferential host for *H. robusta*. By contrast, all of the *T. ciliata* trees have been attacked; this commenced during the first summer period about 6 months after planting out. Consistent with other observations (see Chapter 8), attack has been most aggressive while trees were 1 to 2 metres tall. However, the attack has not been uniform across all planting sites. The most severe damage occurred to a small group located near a wetlands section of the property, and the least damage was in the sheltered environment among the *Eucalyptus* trees. Indeed, in these latter locations *T. ciliata* were free from attack for several years. In recent years there has been some attack. There appears to have been little permanent damage to the trees with many now having a straight bole for up to 3 to 4 metres.

Aside from maintaining the trees in the open stands through herbicide application and slashing, pruning has been carried out on a regular basis to assist in the establishment of a straight bole. The aim has been to prune the lower branches before they develop too large a diameter and to retain some 50-60% of crown mass. As mentioned, this has proved successful with many of the trees now having good form up to 3 to 4 metres (Plates 2 and 3).

Research on our trees

The establishment of the species described provided considerable opportunity for research on several aspects of *Hypsipyla*/Meliaceae interactions. Early research was carried out in a joint study with Dr Mick Tanton and a PhD student Mr (now Dr) Jianhua Mo. This involved investigations into several aspects of the biology of *H. robusta* at the sites described. As well, considerable laboratory work was carried out at the Forestry Department, the Australian National University on the growth of the trees as well as the development and mating behaviour of insects taken there from the property (Bygrave and Bygrave 1994, 1998, 2001, 2003; Mo 1996; Mo *et al.* 1997a, 1997b, 1998, 2001).

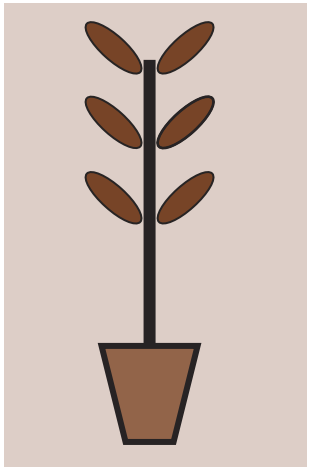
The large number of established trees now allows scope to select individual trees that exhibit resistance, good form and vigour (cf. Chapter 8). From such trees it should be possible to collect seeds for germination and/or propagation.

Earlier we mentioned that *H. grandella* has a particular preference for *Cedrela* and *Swietenia,* while *H. robusta* prefers *Toona* species such as *T. ciliata*. These observations have been the impetus to produce 40 grafts with both *C. odorata* and *C. fissilis* as scion, and *T. ciliata* as rootstock. These have been assessed in the field for degree of attack and rate of growth. The three treatments used were ungrafted *T. ciliata, C. fissilis* grafted on *T. ciliata*

and *C. odorata* grafted on *T. ciliata*. (Ungrafted *C. fissilis* and *C. odorata* were not tested in this experiment.) This graft work commenced in 1995 and measurements have now extended over a period of approximately seven years (for details on this work see Bygrave and Bygrave 1998, 2001). At the time of planting out in the field all three types were initially ca. 0.5 m in height. Many of these grafts are now well over 10 metres tall (Plate 4).

At 14 months, ie. following exposure of the trees to two summer periods and thus to a high probability of shootborer attack in this location, most of the *T. ciliata* and the *C. odorata* grafts had been attacked (Figure 12 and Plate 4). However, although of a similar average height, none of the *C. fissilis* grafted on *T. ciliata* has been attacked. This preference by *H. robusta* for *T. ciliata* and grafted *C. odorata* continues to date.

The attack by *H. robusta* on *T. ciliata* at all sites on the property, is similar to that described by others (see Chapter 4) in that it is characterised by dead/dying shoots, tunnelling by larvae, accumulation of frass at tunnel openings and the presence of smaller brown or larger blue larvae at the base of the tunnels. These features are seen also in the infected shoots of grafted *C. odorata*, but it would appear that damage is even greater in comparison to that seen in *T. ciliata*. This is reflected in the extent of tunnelling by the larvae which is generally deeper in these grafts, sometimes up to twice the depth found in *T. ciliata*. As a consequence, branching occurs to a greater degree. This contrasts sharply with the *C. fissilis* grafted on *T. ciliata* where most have retained a single straight bole (Plate 4).



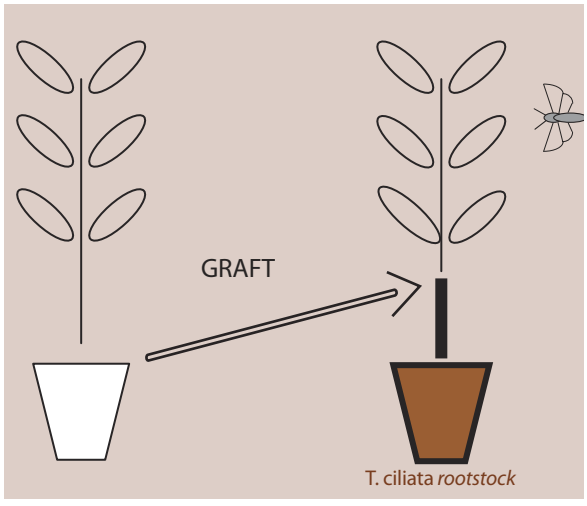
1. Ungrafted *T. ciliata* (control treatment)

T. ciliata (**attacked** by *H. robusta)*

Figure 12. Experimental design used in the grafting of Meliaceae species and summary of resulting attack by *Hypsipyla robusta*
(Source of material for three treatments is illustrated here.)

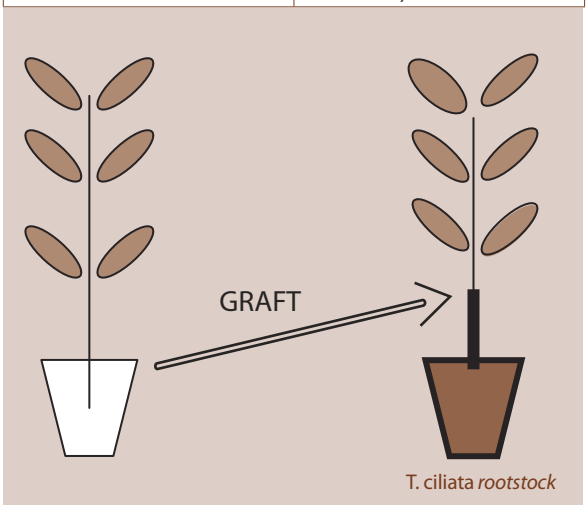
2. *C. odorata* grafted on *T. ciliata*

*C. odorata**	2. *C. odorata* scion on *T. ciliata* root stock
(source of scion material)	(**attacked** by *H. robusta*)



3. *C. fissilis* grafted on *T. ciliata*

*C. fissilis**	2. *C. fissilis* scion on *T. ciliata* root stock
(source of scion material)	(**not attacked** by *H. robusta*)



**Note none of the Cedrela planted on this site were attacked by* Hypsipyla

Observations from the graft research

The following gives some new information about both the biology of *Hypsipyla* and the growth and development of the Meliaceae species being investigated.

- **Growth response of *Cedrela* species to grafting** - Early growth of *Cedrela* species at this location is slower until some 18 months after planting out. Most of the grafted trees, by contrast, grew as rapidly as *T. ciliata* from the time they were planted out and 5 years later, some scions have attained a height of 10 metres and have a diameter at breast height approaching 15 cm (see Plate 4).

- **Host preference of *Hypsipyla*** - *H. robusta* appears to have an almost absolute preference for grafted *C. odorata* over grafted *C. fissilis* in that to date the latter have not been attacked. This could relate to possible differences in the (secondary) chemistry of the species involved in attracting *H. robusta* and/or the clear differences in leaf and petiole structure that might influence oviposition. This remains to be tested. We are yet to determine, for instance, whether eggs are laid on either the leaves or stems of the *C. fissilis* grafts.

- **Damage to shoots of *C. odorata* grafts is greater than to shoots of *T. ciliata*** - Observations indicate *C. odorata* grafts are multi-branched and the larvae penetrate deeper in each individual branch. The larvae also eat out more of the shoots leaving only a bare thin-walled tube. By contrast, the *T. ciliata* shoots retain quite a thick-walled tube. The differing extents to which the larvae eat out the pith could reflect the presence of more tender material in the early stages of shoot development of *C odorata* grafts, or that the (secondary) chemistry of the pith has changed as a result of the graft such that it is now more succulent to the larvae.

- We assume chemical substances that are attractive to the adult and larvae of *H. robusta* are being translocated from *T. ciliata* to *C. odorata* across the graft. Failure of the *C. fissilis* grafts to attract *H. robusta* might suggest the presence of secondary plant metabolites in *C. fissilis* that mask or antagonise that/those in *T. ciliata* which induce attraction. The grafts potentially provide material for chemical analysis that could assist in locating possible (chemical) factors that might be responsible for *Hypispyla*/ Meliaceae preference and non-preference (Bygrave and Bygrave 2003).

- **Grafts have produced flowers** - Grafts of both *C. odorata* and *C. fissilis* produced flowers and seeds only 5 years after planting out. This early flowering opens up possibilities for establishing progeny lines and assessing, for example, degrees of resistance to *Hypsipyla* attack in such progeny.

- **Continuing work** - Approximately 60 grafted trees from a variety of Meliaceae species have now been planted out in an area adjacent to the main *T. ciliata* stand. As well, 50 *Swietenia macrophylla* seedlings have been planted not far from this stand. Over time further information should therefore be attained on host preference of *Hypsipyla* at this site.

Contrary to widely-held perceptions then, the growing of *Toona ciliata* and *Cedrela* species in plantation in Australia can be successful. This has been achieved despite attack by the shootborer. The growth and bole size of these trees, resulting from careful management over 16 years, provides significant evidence to indicate such success.

Chapter 11
Summary and conclusions

Summary of Chapters 1-10:

- Tropical forests that include the valuable Meliaceae timber trees of the genera *Swietenia*, *Khaya*, *Cedrela*, *Toona* and *Chukrasia*, continue to be destroyed at alarming rates.
- There is a need to establish plantations of Meliaceae species throughout tropical and sub-tropical areas to replenish Meliaceae trees and stands that are rapidly disappearing as a result of current and past logging practices.
- All members of the subfamily Swietenioideae of Meliaceae described here are hosts, albeit to varying degrees, to species of shootborers from the genus *Hypsipyla*.
- While details of the taxa of *Hypsipyla* have yet to be clarified, *H. grandella,* found in the New World (the Americas), appears to have a host preference for *Cedrela* and *Swietenia*, while *H. robusta*, found in Africa, Asia and Australia, prefers *Toona*, *Khaya*, *Chukrasia* and *Xylocarpus.*
- Only a single *Hypsipyla* larvae, tunnelling into the apical stem of a young tree, is needed to induce deformity in that tree. Such deformity leads to a multi-branched tree whose commercial value is greatly reduced.
- Numerous investigations both in the field and in the laboratory, have provided a considerable knowledge base about the biology of *Hypsipyla*.
- Control of *Hypsipyla*, either by biological or chemical means, remains difficult.
- Chemical analyses of the host trees is being conducted and is yet to test for potential attractants.
- Molecular studies on Meliaceae populations suggest that genetic variation exists which might be useful in breeding trees resistant to *Hypsipyla* attack.

Most authors consider the only way forward at this time, is to adopt an Integrated Pest Management approach to minimising attack by *Hypsipyla*. This involves:

- planting tree individuals that show resistance to *Hypispyla* attack and which exhibit good form and vigour
    - researchers with permits can select these trees from existing forests or plantations for trial
    - new material can be propagated from these selected trees
- careful selection in the choice of planting site and establishment measures to protect newly-established stands from high winds
- establishing mixed stands that contain other species that offer a degree of shade as well as shelter
    - appropriate spacing between trees needs to be considered, e.g. 3x3 m spacing with the intention to thin at later years

- encouraging trees to establish a bole of ca. 4-5 m height; this process can be assisted by:
  - careful pruning (including multi-branched trees formed in response to shootborer damage) to retain 50-60% of the crown mass
  - possible early use of grow-tubes
  - eliminating competition from any undergrowth
- in respective countries, by planting *Cedrela* and *Swietenia* species in areas free of *H. grandella* and by planting *Toona* species in areas free of *H. robusta*.

As described in Chapter 10, a number of the above-mentioned practices have proved effective in the successful establishment of *T. ciliata* stands on a property on the mid-north coast of New South Wales.

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Glossary

[the term 'pest' is used generically here to indicate the shootborer or tipmoth]

Agroforestry	the planting of trees in widely spaced rows to allow the management of crops or pastures between the rows
Allele	an alternative form of a given gene
Androgynophore	male component of the flower
Angstrom	a unit of length; one hundred-millionth of one centimetre
Antibiosis	a property of the tree that affects the performance of the insect pest in terms of its growth, survival, etc.
Antixenosis	(non-preference) - situation in which a tree is avoided or less colonised by pests
Apical dominance	concentration of growth at the tip of a plant shoot where a terminal bud partially inhibits axillary bud growth
Artifical selection	the selective breeding of domesticated plants to encourage the occurrence of desirable traits
Axillary bud	an embryonic shoot present in the angle formed by a leaf and stem
Cedrela	a member of the Meliaceae family considered to comprise several species - two considered in this book are *C. odorata* and *C. fissilis*
Chloroplast	an organelle found only in plants and photosynthetic organisms that absorbs sunlight and uses it to drive the synthesis of organic compounds from carbon dioxide and water
Chukrasia	a member of the Meliaceae family considered to comprise several species
Cloning	production of genetically identical cells from a single starting cell
Cryptic	hidden from predators
Cytogenetic	relating to the combined study of heredity and the structure and function of cells
Day-degree concept (time-temperature)	reflects the fact that ectotherms require a combination of both time and temperature for development; also referred to as *physiological time*
Dendogram	a computer-generated figure that shows the genetic relationships among the members of a population
DNA	deoxyribonucleic acid, the molecule that stores genetic information; it consists of ribbons of sugars and phosphates held together in two opposite strands by four different bases or nucleotides. These are Adenine (A), Guanine (G), Cytosine (C) and Thymine (T).
Ecology	the study of how organisms interact with their environments
Ecosystem	any unit of nature that includes all of the organisms in a given area interacting with the physical environment so that a flow of energy leads to a clearly defined trophic structure, biodiversity and biogeochemical cycles
Ectotherm	organisms that rely on external sources of heat to maintain body temperature
Electroantennogram	the recording of the summated responses of the insect antennae receptors to a stimulus
Electrophoresis	separation of compounds based on their different charge
Endotherm	organisms that regulate their body temperature by the production of heat from within their own bodies
Enzymes	a class of proteins serving as catalysts that change the rate of the reaction without themselves being consumed by the reaction
Fauna	the animals of a region
Frass	the excrement of larvae; the refuse left behind by boring insects
Gel electrophoresis	the separation of nucleic acids or proteins on the basis of size and electrical charge by measuring their migration through an electrical field on a gel

Gene	a discrete unit of hereditary information located on the chromosomes and consisting of DNA
Genetic marker	any genetic character that can be identified, measured and quantified
Gene pool	the total aggregate of genes in a population at any one time
Genetic variation	this arises from the presence of one or more alternative forms at a given locus; such variation reflects variation in the sequence of nucleotides arising either from an altered sequence of the 4 bases, or variation in length due to insertion or deletion of bases
Genome	the complete complement of an organism's genes; an organism's genetic material
Genus	a taxonomic category above the species level, designated by the first word of a species binomial Latin name
Greenhouse effect	the warming of planet Earth due to the atmospheric accumulation of carbon dioxide which absorbs infrared radiation and slows its escape from the irradiated Earth
Grow-tube	a commercially-available plastic 'tube' that is placed around a young plant in the early growth stages. It gives both physical protection and a humid environment each of which lead to enhanced growth and development
Homology	similarity in characteristics resulting from a shared ancestry
Host	an organism that harbours and provides nourishment for another organism
Hypsipyla	a genus of insect of which two members *H. grandella* and *H. robusta* have a particular preference for feeding on genera of the Meliaceae family and particularly the subfamily Swietenioideae
Instar	an immature stage of an insect between molts
Isozyme	enzymes that catalyse the same chemical reaction but have different physical properties
Khaya	a genus of the Meliaceae family, comprising several species - two considered here are *K. senegalensis* and *K. ivorensis*
Kingdom	a taxonomic category, the second broadest after 'domain'
Larva	a free-living, sexually immature form in some insect and animal life cycles that may differ from the adult in morphology, nutrition and habitat
Limonoids	family of chemicals found in higher plants considered to influence insect behaviour
Locus	a particular place along the length of a certain chromosome where a given gene is located
Mass spectrometer	a sophisticated laboratory instrument used to determine the chemical structure of molecules
Meliaceae	trees in this family include a range of economically important genera
Meristem	plant tissue that remains embryonic as long as the plant lives, allowing for indeterminate growth
Metabolism	the totality of an organism's chemical processes, consisting of catabolic and anabolic pathways
Microsatellite (marker)	a type of genetic marker that consists of numerous repeats of short DNA sequences. They are currently the marker of choice for population studies as they are found throughout the individual's DNA and are likely to be polymorphic
Mitochondria	organelles in eukaryotic cells that serve as sites of cellular respiration
Monoculture	cultivation of land areas with a single plant variety
Monophagous	herbivorous insects that feed on a single plant species
Monoterpenes	a group of chemicals consisting solely of carbon and hydrogen many of which occur in the volatile oils of plants
Morphological	the form or external physical appearance of animals and plants
Mutation	a change in the DNA of genes that ultimately creates genetic diversity
Nanogram	a measure of weight equivalent to one millionth of a gram
Nucleotide	building block of a nucleic acid consisting of a five-carbon sugar bonded to a nitrogenous base and a phosphate group
Nucleus	the chromosome-containing organelle of a eukaryotic cell

Oligophagous	herbivorous insect that feeds on a relatively few species belonging to only a few plant general and families
Pantropical	refers to all of the tropical regions
Phenology	the study of the timing of recurring natural phenomena
Phenotype	the physical and physiological traits of an organism
Pheromones	volatile chemicals used for communication within insect species
Photosynthesis	the conversion of light energy into chemical energy that is stored in glucose and other organic compounds
Phytochemical	relating to the chemistry of plants
Phytophagous	the ability of an insect to discriminate between plants through its chemical senses
Plantation	forest stands established by planting and/or seeding in the process of afforestation or reforestation. They are either of introduced species or indigenous species which meet all of the following criteria: one or two species at planting; similar age class; regular spacing; often underplanted.
Polymerase Chain Reaction (PCR)	a technique for amplifying DNA in vitro by incubating with special primers, DNA polymerase molecules and nucleotides
Polymorphism	variations in the DNA sequence within a species or population detected by the presence of one or more alternative forms at a given genetic locus
Polyphagous	ability to feed on any plant
Primer	an already existing DNA sequence bound to the template DNA to which nucleotides must be added during DNA synthesis
Progeny	the offspring of a particular tree or mating
Provenance	the geographic location of a group of trees from which the seed came
Pupation	the encased developmental stage that intervenes between the larva and the adult insect
Resistance	the ability of a tree to grow and develop normally despite any attack by insects
Restriction enzymes	degradative enzymes that recognize and cut up DNA at specific base sequences
Restriction Fragment Length Polymorphisms (RFLPs)	differences in DNA sequence on homologous chromosomes that result in different patterns of restriction fragment lengths; useful as genetic markers for making linkage maps
Secondary compounds	chemical compounds synthesised through the diversion of products of major metabolic pathways for use in defence by prey species
Sensilla	odour filters on male insect antennae that sense the sex pheromones released by the female
Silviculture	the art and science of controlling the establishment, growth, composition, health and quality of forests and woodlands to meet the needs and values of landowners and society on a sustainable basis
Somatic cell	any cell of a multicellular organism except a sperm or egg cell
Species diversity	the number and relative abundance of species in a biological community
Striated	highly ordered arrangement of cells
Susceptibility	a measure of how much a tree is attacked by an insect
Swietenia	a genus of the Meliaceae family considered to comprise at least three species - *S. macrophylla* King, *S. humilis* Zucc. and *S. mahagoni*
Taxonomy	the study of the classification of flora or fauna into like groups
Tolerance	the ability of a tree to overcome pest attack; often reflected in exceptional vigour and the ability to produce a single strong leader shoot following attack
Toona	a member of the Meliaceae family considered to comprise a number of species - one of the most common in the Australasian region is *T. ciliata* (Australian red cedar)
Tropical rainforest	the most complex of all communities, located near the equator where rainfall is abundant; harbours more species of plants and animals than all other terrestrial communities combined

Appendices

Appendix 1. Rearing *Hypsipyla* in the laboratory

The need to artificially rear *Hypsipyla* in the laboratory (ex situ) arises because much about the behavioural, developmental and feeding patterns of the insect alluded to in this article, can only be studied in the laboratory. To this end several authors have reported on techniques of artificial rearing.

Two papers describe the experimental details of the rearing of *H. grandella* (Grijpma 1971; Sterringa 1976). Recently however, two separate studies on insect rearing (Griffiths 1997; Mo and Tanton 1996; Mo *et al.* 1998) were conducted in Australia that, along with earlier findings, provide quite detailed information about the development of the larvae, together with the emergence and mating behaviour of *H. robusta* (Table 4, Figure 4). This information in turn has assisted in the development of improved rearing programs.

One way to commence a program of study in the laboratory, is to initially collect larvae from the field and raise them on an artificial diet (Couilloud and Guiol 1980) contained in flat plastic dishes and maintained in a temperature-controlled atmosphere and with controlled light/dark periods. Mo *et al.* (1998) used cylindrical cores containing the diet to simulate a growing tip. Further to the study of Atuahene and Souto (1983) and in addition to the basic diet of Couilloud and Guiol (1980), Mo *et al.* (1998) also added dry leaf powder of *T. ciliata*. Final instar larvae were placed in glass jars containing a small amount of cotton wool to facilitate pupation and the caps loosely fitted. Following emergence, moths were then placed in large cages for mating and egg laying. The cage contained corrugated paper towelling on the floor, cotton wool soaked with 5% sugar solution in Petri dishes, and a current of air was passed from one end to the other to facilitate mating. Eggs that had been laid were placed in plastic vials containing damp paper towelling to encourage hatching and the process above repeated. In this way, Mo *et al.* (1998) were able to rear *H. robusta* for 23 generations.

Significant among the difficulties of rearing insects in the laboratory, is the problem of having the larvae feed on the synthetic diet and that of inducing male and female adults to mate in indoor cages. It needs to be appreciated also that in any artificial rearing program involving *Hypsipyla*, the larvae are cryptic in nature, feeding mainly in situ by tunnelling inside the growing shoots of host plants.

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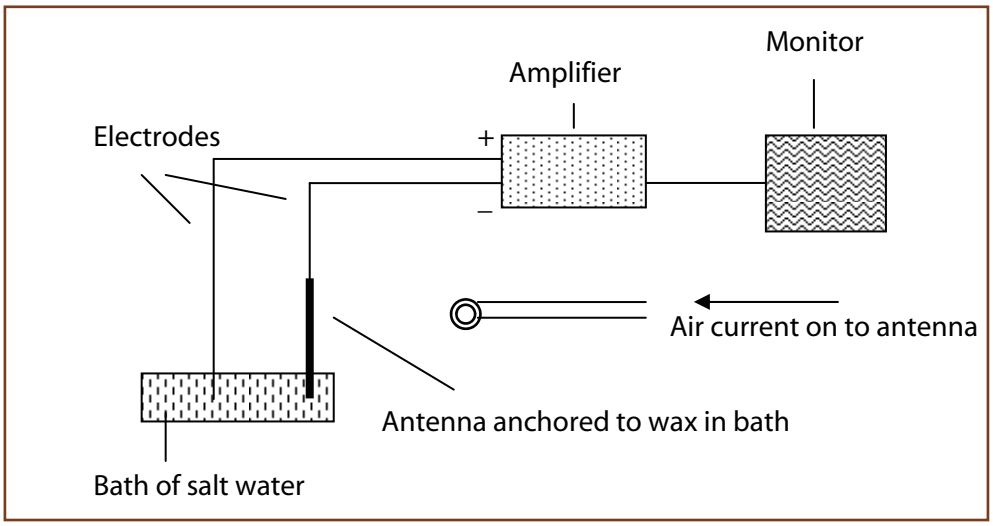
Appendix 2. Behavioural analysis of female sex pheromones

Another important aspect of this work is the analysis of the behaviour of the male to the emitted female sex pheromones. This involves 'activity' or 'attraction' bioassays which can be studied with the aid of a wind tunnel and/or cage, as well as by electrophysiological means. In the first of these, pre-courtship behaviour, such as male orientation and activation, can be examined in a wind tunnel through which air is pulled at a constant rate. The female is placed in the upward end and the male lowered into the downward end of the airstream and its responses observed. Close-range courtship interactions can be observed in a small plexiglass cage when a calling female is placed therein with a male. Equally, synthetic blends of the sex pheromones can be placed in the cage or wind tunnel and the behaviour of the male noted.

Pheromones can also be studied in the laboratory by examining electrophysiological events using the electroantennogram (EAG) technique (see Figure below). The EAG is a recording of the summated responses of the antennae receptors to a stimulus ie. the interaction of the sex pheromones with the sensilla (Figure 7). In this technique, clean air is passed over the antenna at a constant rate and samples of pheromone introduced into it and the electrical (EAG) response analysed. The technique can be used to analyse and screen a range of compounds having the potential to attract and does not require the presence of the female.

An important practical outcome of pheromone knowledge relates, as alluded to above, to the issue of insect pest control. Traps containing blends of pheromone, can be set up in the field. Many such blends now can be obtained from commercial sources. The male of the species in question will be attracted to these and not to the female and so reduce the chances of mating. Additionally, it is possible to establish traps with non-specific volatiles - these would 'confuse' the male and so lessen the chances of mating.

Electroantennogram technique used to measure the response of the antenna to specific pheromones
(diagram modified from Schoonhoven 1976)



Reference

Schoonhoven, L. M. (1976). Electroantennograms (EAG) as a tool in the analysis of insect attractants. In: Studies of the shoot borer *Hypsipyla grandella* (Zeller) Lep. Pyralidae. Ed. J. L. Whitmore. Miscellaneous Publication No. 101 of the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Turrialba, Costa Rica, Vol. 2. pp. 59-63.

Appendix 3. Laboratory testing of plant secondary compounds on insects

A number of procedures in the laboratory, listed below can be used to assess the attractiveness of specific secondary metabolic products or plant extracts isolated from plants to insect larvae.

- Larvae feeding - this involves making up agar plates containing the compound(s) in question. Several samples can be placed in a Petri dish and the larvae provided with limited quantities of choices.
- Further to the above, unlimited quantities can be provided in an artificial diet and the growth and development of the larvae examined.
- The instincts of the adult female can be tested by placing samples on leaves and examining the degree of oviposition.
- Wind tunnel and electrophysiology experiments also can be carried out as with pheromones (Figure 6) with a range of samples to attract/deter the adult female.

It needs to be stressed again that these experiments are generally carried out in the laboratory. They thus rely on the ability to rear the insect in the laboratory (see Appendix 1 above). Many such studies have been reported in the literature with some selected examples noted in the reference section. However definitive information specifically concerning chemical factors in the *Hypsipyla*/Meliaceae interactions has yet to be obtained.

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