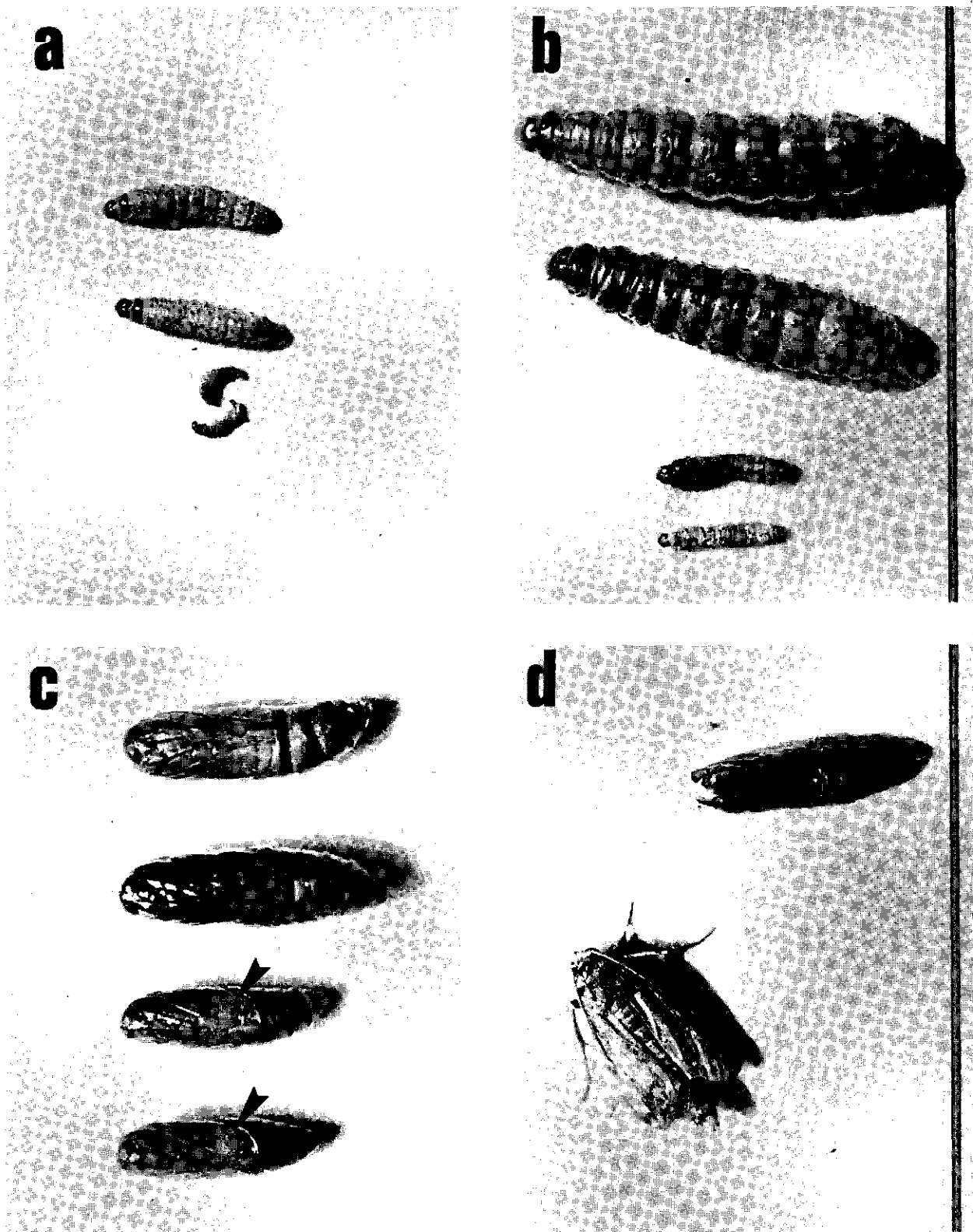


CONTRIBUTIONS TO AN INTEGRATED CONTROL PROGRAMME OF
HYPSPYLA GRANDELLA (ZELLER) IN COSTA RICA



Comparison of the effect of aqueous leaf extract of the Australian cedar (bottom specimens in a, b and c) with that of Spanish cedar (top specimens in a, b and c) incorporated in diet, on the mahogany shootborer. a. After 14 days of feeding. b. After 24 days of feeding. c. Pupae obtained after 28 days and 40 days from diet mixtures containing Spanish cedar and Australian cedar respectively. d. Adult with shortened wings reared on diet containing Australian cedar. For accompanying text refer to chapters 2.1.3. and 3.

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P. GRIJPMAN

CONTRIBUTIONS TO AN INTEGRATED CONTROL PROGRAMME OF
HYPPIPILA GRANDILLA (ZELLER) IN COSTA RICA

(MET EEN SAMENVATTING IN HET NEDERLANDS)

BIBLIOTHEEK
DER
LANDBOUWHOGESCHOOL
WAGENINGEN

PROEFSCHRIFT
TER VERKRIJGING VAN DE GRAAD
VAN DOCTOR IN DE LANDBOUWWETENSCHAPPEN,
OP GEZAG VAN DE RECTOR MAGNIFICUS, DR. IR. H. A. LENIGER,
HOGLERAAR IN DE TECHNOLOGIE,
IN HET OPENBAAR TE VERDEDIGEN
OP VRIJDAG 20 DECEMBER 1974 DES NAMIDDAGS TE VIER UUR
IN DE AULA VAN DE LANDBOUWHOGESCHOOL TE WAGENINGEN

157-104107

Dit proefschrift met stellingen van

PIETER GRIJPMA

landbouwkundig ingenieur, geboren te Bandoeng, Indonesië, op 7 april 1932, is goedgekeurd door de promotoren Dr. J. de Wilde, hoogleraar in het dierkundige deel van de plantenziektenkunde en door Dr. L. M. Schoonhoven, hoogleraar in de algemene en vergelijkende dierfysiologie.

De Rector Magnificus van de Landbouwhogeschool,
H. A. Leniger

Wageningen, 16 september 1974.

Stellingen

I

In een geïntegreerd bestrijdingsprogramma van Hypsipyla verdient het aanbeveling plantmateriaal van Meliaceeën te gebruiken, waarvan de nieuwe loten synchroon en weinig frequent uitlopen. In een dergelijk programma zouden eiparasieten van het geslacht Trichogramma van groot nut kunnen blijken te zijn.

II

Het is niet aannemelijk dat de waardkeuze van Hypsipyla spp. bepaald wordt door de oorspronkelijk toxische secundaire plantenstoffen, waaraan het insect zich gedurende de evolutie heeft aangepast.

GARA, R.I. et al. Zeitschrift für angewandte Entomologie 72(3): 259-266. 1973

III

Ten onrechte wordt Cedrela salvadorensis Standley als synoniem van C. tonduzii C.DC. gehandhaafd.

SMITH, E.A. Rhodora 74: 124-126. 1972

IV

Wijzigingen in het voorkomen en in de onderlinge verhouding van voedselcomponenten in de waardplant tijdens het larvale stadium van insecten zijn mogelijk van groot belang voor de waardkeuze van de daaruit voortkomende adulten.

V

De vermelding van het genus Erythrina (Leguminosae) als waardplant van Hypsipyla grandella (Zeller) wordt onvoldoende door veldwaarnemingen gesteund.

TILLMANN, H.J. Boletín del Instituto Forestal Latinoamericano de Investigación y Capacitación 14: 82-92. 1964

ENTWISTLE, P.F. The current situation on shoot, fruit and collar borers of the Meliaceae.

Oxford, Commonwealth Forestry Institute, 1968. 15 p. Paper of the 9th Commonwealth Forestry Conference, New Delhi, 1968.

VI

Bij het gebruik van individuele boompercelen in aanpassingsproeven met houtsoorten voor monocultures in de tropen van Latijns Amerika wordt te weinig rekening gehouden met het effect van de individuen op elkaar.

BRISCOE, C.B. Statistically valid planting trials. Proceedings of the 2nd World Eucalyptus Conference. Sao Paulo, 1961. pp. 525-531.

VII

In aansluiting op het psychotechnisch onderzoek dat bij langdurige uitzending van technici plaatsvindt, verdient het aanbeveling dat niet alleen de betrokken werknemer, doch ook diens echtgenote op geschiktheid daarvoor wordt gekeurd.

VIII

Het resultaat van het in de Derde Wereld uitgevoerd onderzoek dient, na gebleken geschiktheid, bij voorkeur in de in die regio verschijnende vakbladen te worden gepubliceerd. Internationale organisaties, zoals de Voedsel- en Landbouworganisatie van de Verenigde Naties en het Ministerie van Ontwikkelingssamenwerking zouden deze publicaties niet alleen behoren te stimuleren, doch zelfs van hun werknemers dienen te verlangen.

P. Grijpma

"Contributions to an integrated control programma of Hypsipyla grandella (Zeller) in Costa Rica.

20 december 1974.

PREFACE

On relatively few occasions plantbreeders, foresters or entomologists have had the privilege to come across a plant species which at once combined a natural immunity to a notorious insect pest with all desired qualities of the plant. My interest in Hypsipyla grandella, the shootborer of Meliaceae, was aroused when I introduced the Australian red cedar (Toona ciliata var australis) into Costa Rica in adaptability trials of forest tree species, during which it proved to be resistant against the attacks of this borer.

It was a fortunate circumstance that this applied silvicultural-entomological research was carried out in the framework of a Technical Assistance Project of the Netherlands Government, which allowed for the proper development of the project, assistance and channels of dissemination.

Although several aspects of this research remain to be solved, it is encouraging to know that the Australian cedar is at present being planted in the majority of the Latin American countries and that these trials have confirmed the tree's resistance against this serious forest insect.

I am greatly indebted to Prof. Dr. J. de Wilde and Prof. Dr. L.M. Schoonhoven, who, with great interest, followed the development of this research and who introduced me into new fields of plant-insect investigations, thereby widening my entomological horizon and reinforcing my interest in this relationship. Their guidance and assistance, as well as the critical appraisal of the manuscript, is gratefully acknowledged.

My gratitude is also extended to the Netherlands Bureau of International Development Cooperation and the International Agricultural Centre, in particular to Mr. H. J. van Rongen and Ir. A. Glas for their early recognition of the potentials of this research project and for allowing an additional year to round off and write up these studies.

In particular I want to thank Dr. J. E. Araujo, Director General of the Inter-American Institute of Agricultural Sciences of the Organization of American States, Ing. M. Elgueta, Director of the Tropical Research and Training Centre, and Dr. W. Albertin, Head of the Department of Tropical Forest Sciences as well as Miss M. D. Malugani, Director, and Ing. A. Gorbitz, Technical Editor of the Documentation and Information Centre for their unwavering support during this research project.

My sincere gratitude is also extended to Prof. Dr. R. I. Gara of the University of Washington, who very much stimulated my first steps in Hypsipyla research at the Tropical Research and Training Centre in Turrialba and provided me with fresh insights in insect ecology.

The joint investigation with Dr. S. C. Roberts on the toxic compounds of Toona was a gratifying and fruitful experience which convinced me of the important role which organic chemists should play in investigations on plant-insect relationships.

With pleasure I recall the long discussions with members of the Inter-American Working Group on Hypsipyla; more specifically I would like to express my appreciation to Ing. V. O. Becker, Dr. O. Hidalgo-Salvatierra, Dr. K. Katiyar, Prof. Dr. G. G. Allan, Dr. F. D. Bennett, Dr. R. M. Wilkins and Dr. D. D. Sliwa thereby thanking them for contributing to my scientific and personal formation.

The help received from colleagues, staff and personnel of the Laboratories of Animal Physiology and Entomology has been of great value. In particular, I would like to thank Ir. E. A. Goewie, Ir. J. Wiersma, Drs. W. F. Tjallingii, Ir. F. Dieleman, Drs. J. H. Visser, and Mr. C. van der Burg for their assistance and advice. The kind cooperation of Miss E. van der Meijden, Mr. C. van Eden and Mr. A. G. M. Roos during my stay in Wageningen is deeply appreciated.

Last, but not least, I am most grateful for the assistance received on numerous occasions from Ir. J. T. Sterringa and the team of Costa Rican workers under guidance of Mr. Oscar Ovaras. Their diligent collaboration will long be remembered.

Wageningen, September 24th, 1974.

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1. INTRODUCTION

- 1.1. General aspects of the Hypsipyla problem
- 1.2. Organization and framework of the investigations
- 1.3. Location and climatic conditions
- 1.4. The economic importance of Hypsipyla grandella (Zeller)
 - 1.4.1. General information on the insect
 - 1.4.2. General information on the host plants
 - 1.4.3. Economic importance
 - 1.4.4. Possibilities of control
 - 1.4.4.1. Silvicultural control
 - 1.4.4.2. Chemical control
 - 1.4.4.3. Biological control
 - 1.4.4.4. Integrated control
 - 1.4.5. Literature cited

1.1 General aspects of the Hypsipyla problem.

The oligophagous shootborer Hypsipyla (Lep.:Pyralidae) is a pantropical genus of insects which attacks commercially important tree species of the family of Meliaceae.

Although this serious forest insect pest was already described in 1848, methods to control its detrimental effects on artificial plantations were inadequate or only partially successful.

The main damage caused by Hypsipyla spp. in the tropics of Africa, Asia, Australia and Latin America is inflicted by the larvae which destroy the principal terminal shoot by boring into the tips and tunneling in the stems of young saplings.

Resprouting of the plants, followed by repeated attacks of the insects results in the development of numerous side branches and consequently in badly formed trees, unsuitable for timber production.

Economically valuable tree species of the genera Khaya and Entandrophragma in Africa, Cedrela and Swietenia in Latin America and Toona in Asia and Australia are, among other genera, highly susceptible to infestation by the native Hypsipyla. Trials to establish large scale pure plantations of native Meliaceae in countries of these continents invariably failed, which in turn unfavourably influenced the interest in research on these species by forest services and private forest companies.

In the natural hardwood forests of the tropics commercially sized Meliaceae occur in limited numbers, often only at a rate of 1-5 per hectare, and mixed with numerous other tree species of the abundant vegetation.

The relatively low number of tree species presently considered of economic value makes exploitation of the heterogeneous hardwood forests an unattractive enterprise, often employing the lowest-of-income and working on a non-sustained production basis.

In developing countries of the tropics, agrarian reform programmes, colonization schemes and population pressure on the land, tend to regard the existing large areas of these forests as unproductive lands. As a consequence, extensive forest areas containing Meliaceae are felled and burned after superficial exploitation, to satisfy the need for higher immediate benefits, thereby disregarding the long term capacity of the soil for these alternative agricultural uses. The rate of forest destruction in Latin

America was estimated at 10 million hectares per year in 1962 (18). Construction of new transportation routes, such as the recent Trans-Amazonian Highway, has opened up large tracks of virgin forest which will face a similar fate, thereby increasing this figure considerably.

The rapid pace of destruction and depletion of the existing natural resources of Meliaceae, together with the obstacles encountered in successfully establishing and maintaining plantations of the native meliaceous species, stressed the need to promote a programme of increased research on this insect pest.

1.2 Organization and framework of the investigations.

The concern of international organizations such as the Food and Agricultural organization of the United Nations and the Commonwealth Forestry Institute with regard to the problem of Hypsipyla has been expressed repeatedly.

In a paper presented in 1968 at the 9th Commonwealth Forestry Conference, on Entwistle, summarizing the situation on the shootborers, concluded that the status of investigations on the control and plans for future research on Hypsipyla were weak and alarming (17). Since forest services and forest research organizations in tropical countries are particularly restricted in developing research projects on insect pests due to their extremely lean budgets, the need to centralize available resources, efforts and manpower in a Hypsipyla research project was indicative.

Supported by the Inter-American Institute of Agricultural Sciences of the Organization of American States, the Netherlands Bureau of International Development Cooperation, FAO, the University of Washington and the University of Purdue, the Inter-American Working Group on Hypsipyla was established in September 1970 at the Tropical Training and Research Centre in Turrialba, Costa Rica.

This working group adopted as its main objective to execute research projects for the development of a programme of integrated control of Hypsipyla.

Hereto several fields of investigation were embarked upon, which incorporated the following projects:

a. Manipulation of the micro-environment as a partial control of Hypsipyla.

- b. Biological control.
- c. Chemical control by means of controlled release insecticides.
- d. Development of an artificial rearing system.
- e. Hostplant selection and flight behavior.
- f. Natural resistance of Meliaceae against the shootborer.

The investigations carried out by the author fitted in this overall scheme and referred to the projects on natural resistance of Meliaceae, hostplant selection and flight behavior, development of an artificial rearing system and biological control. Except for the publication "Hexameris albicans (Siebold) (Nematoda:Mermithidae) a parasite of the larva", the investigations comprised in this dissertation were executed with the author as main investigator. The chemical aspects of the research on the toxic fraction of the Australian red cedar were taken care of by Mr. S. C. Roberts, Department of Chemistry, University of Washington.

1.3 Location and climatic conditions.

The investigations were executed in the laboratories, in the Florencia Sur tree species trials and in the Puente Cajón experimental plantations of the Department of Tropical Forest Sciences at the Tropical Training and Research Centre of the Inter-American Institute of Agricultural Sciences in Turrialba, Costa Rica.

The vegetation in this area is classified as Premontane Tropical Wet Forest according to Holdridge's Life Zone System (27). Several Meliaceae of the genera Cedrela, Guarea and Trichilia occur naturally in this area, Cedrela being represented by C. odorata L. and C. tonduzii C. de Candolle. In addition, plantations of Swietenia macrophylla King, which has its natural distribution in the North Western part of Costa Rica, Toona ciliata M. Roem. var australis and Khaya ivorensis A. Chev. respectively from Australia and Africa, have been established in the experimental area.

According to observations over a 26-year period of the meteorological station of the Centre, located at 83°38' W. L. and 9°53' N. L. at an altitude of 602 m. a.s.l., the climatic conditions are characterized by the following means: annual temperature 22.3°C, daily amplitude 9.2°C, relative humidity 87.7 percent and an annual precipitation of 2,682.5 mm (Table 1). Sugar cane and coffee are the main crops under culture in the area.

Table 1. Summary of meteorological data at the Tropical Training and Research Centre, Turrialba, Costa Rica.
(Period 1944-1970).

Month	Temperature (°C)			Precipitation (mm)			Relative humidity (%)		
	Average maximum	Average minimum	Mean	Absolute maximum	Absolute minimum	Average monthly		Maximum in 24 hours	Average no. days with > 0.1 mm
January	25.87	16.07	21.00	31.0	10.0	176.4	164.9	18.5	86.6
February	26.26	16.06	21.08	30.0	10.4	147.8	247.5	15.1	85.7
March	27.08	16.60	21.85	31.5	10.5	79.0	81.5	13.5	84.5
April	27.35	17.37	22.34	31.7	11.8	135.1	287.9	15.3	85.2
May	28.00	18.18	23.07	32.0	13.5	225.3	65.0	23.0	87.0
June	28.04	18.53	23.22	31.5	15.2	284.9	85.5	24.7	88.5
July	27.32	18.30	22.76	30.6	14.1	270.4	102.4	25.0	90.3
August	27.60	18.17	22.81	30.0	14.9	234.0	99.1	24.3	88.9
September	28.01	18.02	23.04	30.8	14.8	249.8	99.1	22.3	88.2
October	27.79	18.00	22.85	30.8	14.5	249.1	109.2	24.0	88.8
November	26.56	17.66	22.10	30.1	13.7	283.1	115.3	23.0	89.4
December	25.84	16.92	21.38	29.9	10.9	347.6	288.3	22.3	89.2

1.4 The economic importance of Hypsipyla grandella (Zeller).

1.4.1 General information on the insect.

The genus Hypsipyla is represented in Latin America by H. grandella (Zeller), H. ferrealis (Hampson), H. fluviatella Schaus and H. dorsimacula (Schaus) (22). Of the four species which all occur in Costa Rica, H. grandella is the most harmful species, attacking the terminal shoots of all members of the genera Cedrela and Swietenia in Latin America, whereas H. ferrealis has been reported to attack exclusively the fruits of Carapa guianensis Aublet. A morphological description of all the Latin American species is given by Heinrich; lately Becker (7) provided a redescription of H. grandella and H. ferrealis. The hostplants of H. fluviatella and H. dorsimacula are unknown yet.

With the exception of Chile, Hypsipyla grandella has its natural distribution throughout Latin America and the Caribbean islands to the Southern tip of the United States, where it has been recorded in Miami, Florida. It is a native American species closely resembling H. robusta (Moore) which causes considerable damage to Meliaceae in Africa, Asia and Australia.

The biology of H. grandella has been studied primarily by Ramírez (37) and Roovers (43) in Barinitas, Venezuela. A review of the existing literature on the insect was published in 1964 by Tillmanns (54), However, since then several other authors have published complementary information (7,23, 24,44,45,46,47,). A summary of the most important biological data is presented below.

The eggs of H. grandella are oval and flattened, measuring approximately 0.98 mm in length and 0.50 mm in width. Immediately after oviposition they are whitish coloured turning into red within 24 hours. Generally the eggs are laid separately but at times in small clusters of 3 to 4 in or near the leaf-axils. Oviposition occurs on the leaves (44 percent) as well as the stem of the hostplant (54 percent). Preferred oviposition sites are located in and near the leaf-axils, on leaf scars, and adjacent to the mid- or side veins of the leaflets. The period of incubation varies between 2.5 - 6 days (average 4 days), depending on temperature conditions.

Young larvae often penetrate the leaf axis first and at a later stage move to the un lignified young terminal shoot, axils or tips of side branches. Feeding is generally continued on the pith, but consumption of bark, phloem and

leaflets has also been recorded. The number of larval instars may vary from 5 to 7, but most frequently 6 instars have been observed (24). Larvae protect their entrance holes and tunnels by constructing a web, which is covered with plant particles and excrement; these protective structures are also built before moulting. Last instar larvae often spin their cocoon at the upper end of the tunnel, where they pupate. The total life cycle is completed in 4 to 7 weeks (average 5 weeks) depending on climatic conditions and availability of adequate food. Cannibalism has been observed frequently both in the field as well as in the laboratory and affects larvae and pupae.

The average duration of the different stages of H. grandella (at 26°C and 60 percent R.H.) are: egg stage: 4 days, larval stage: 20 days; pupal stage: 10 days; adult stage (till oviposition): 2 days.

The greater majority of adults emerge during sunset, before light intensity has reached its lowest level. Except for a study on mating behaviour of adults in captivity (47) little is known yet about the pattern of nocturnal adult activity. Before mating, the female adopts a calling position by bending the abdomen dorsally upwards between the wings, thereby protruding the ovitubus. Adoption of this posture is generally considered to serve as a means of exposing the glands which produce the sex pheromone, facilitating thus its dispersal.

Courtship activities are minimal; attracted males fly to the females and walk to rear of these. After touching the abdomen of the female with their antennae the males turn around and posterior to posterior copulation is initiated. Adoption of the calling position by females is started about six hours after light intensity approaches its lowest limit, peaks three hours later and ends after approximately 10.5 hours. On the average it lasts 1.6 hours (47). Since any shift of the light-dark cycle (12L:12D) results in an equal shift of the time when the calling posture is adopted by virgin females, it seems likely that the adoption of this position by virgin females follows a circadian pattern.

Mating lasts between 1.5 and 3 hours (47) and may be followed by oviposition immediately afterwards. Under laboratory conditions, up to 1022 fertilized eggs have been obtained from a single female containing one spermatophore. In field plots with trees of approximately 1.60 m height, the number of eggs found on a meliaceous sapling varied from 1 to 48; however,

on approximately 50 percent of these sampled trees only 1 to 3 eggs were oviposited. In this survey, which was executed during the middle of the growing season, 38 percent of the trees were not oviposited upon.

Ramírez and Sterringa (37,52) observed that adults can survive up to 7 days under laboratory conditions without food and water. Depending on the availability of food and climatic conditions the number of generations per year is likely to vary. Under the climatic conditions of the Turrialba area, where high rainfall promotes resprouting of the saplings, H. grandella can be found all year round in young meliaceous plantations. In areas with a pronounced dry season and mature trees the attacks of the shootborer will switch from the shoots to the fruits during the dry period.

1.4.2 General information on the host plants.

Commercial meliaceous tree species in Costa Rica pertain to the genera Carapa, Cedrela and Swietenia. The genus Carapa is represented by C. guianensis Aublet of which the seeds are infested by Hypsipyla ferrealis. However, in Brazil, shoots of the same tree species are reported to be attacked by H. grandella (6).

In Costa Rica, C. guianensis can be found, up to 800 m elevation, in the very humid areas of the Atlantic Plane and the Southern Pacific region. It is a high forest tree which grows well in wet soils, along creeks, in gullies and in swamps.

Of the genus Cedrela, the fruits and shoots of the following native species are attacked by H. grandella: C. odorata L., C. angustifolia Sessé & Moc., C. salvadorensis Standley and C. tonduzii C.DC.

Taxonomically, the nomenclature of C. salvadorensis (51) and C. tonduzii (14) has become confused. Smith (48) in the latest revision of the genus Cedrela at first considered both species conspecific with C. oaxacensis C.DC. & Rose. However, in posterior publications C. tonduzii (49) and C. oaxacensis (50) were redefined and separated again but C. salvadorensis was maintained as a synonym of C. tonduzii.

Since C. salvadorensis and C. tonduzii have distinct morphological differences and occur in completely different ecological regions, these species too have been kept separated here.

Of the Cedrela species, C. angustifolia and C. odorata are widely distributed throughout Costa Rica and can be found from sea level up to 1,200 m. (7). The species require a well drained fertile soil.

C. salvadorensis is relatively rare in Costa Rica, with a restricted distribution. During surveys only 6 trees were located of which four were encountered on the slopes of the Poàs volcano near San Pedro and two near Villa Colón, in the Central Valley. This species which has the largest fruits in the Cedrela genus, grows on fertile volcanic soils, and can be found at altitudes between 800-1200 m.

C. tonduzii is encountered in the higher altitudinal belts of the volcanos Turrialba, Irazù and Poàs, between 1,500 - 2,700m, where it also grows on the fertile volcanic soil of recent origin.

The only species of Swietenia in Costa Rica is S. macrophylla King of which the fruits as well as the shoots are attacked by H. grandella. This tree inhabits the dry forest of the North Western Pacific side of Costa Rica, where it occurs from sea level till approximately 500 m altitude. Scattered in the forest, it is sometimes found in combination with C. odorata along creeks and rivers.

All mentioned Costa Rican Meliaceae are susceptible to borer infestation. Seedlings still in the nursery stage as well as trees over 30 m height are attacked. From a silvicultural point of view, however, the first six years are the most critical.

In this early stage, plants and saplings produce several fresh shoots during the wet season, which are liable to be infested by H. grandella.

Cleaning operations, aimed at providing young plants with as much light as possible, facilitate this frequent production of new shoots and consequently favour a rapid build-up of the insect population. This repeated sprouting, followed by attacks of the borer generally results in branchy trees which are sometimes killed by secondary agents such as fungi and termites, but rarely directly by the borer.

A reduction of Hypsipyla attack often takes place when the trees reach the pole stage (8-10 m); in this stage the frequency of production of new shoots has decreased to once or twice a year. Lateral branching is also less frequent then, because of increased competition for light during the canopy formation. In addition, the Meliaceae are deciduous in the dry season during

which the shoots are harder and more difficult to penetrate for first instar larvae. Moreover, the larval period in trees under moisture stress also increases (46). Together these factors exercise a considerable influence on the possibilities of propagation of the borer.

Mature trees generally produce new flushes of leaves and shoots only once a year. During the dry season, when trees are leafless, the attacks of the shootborer are transferred to the fruits of the trees. Survival during this period, which may last up to 4-5 months in the North Western part of Costa Rica, is further facilitated by individual variability in deciduousness, fruiting and flushing of new leaves and shoots of the Meliaceae. Resprouting of a few individual trees can sometimes be observed in the middle of the dry season. Fructification generally starts at the age of 12 or 13 years (35). It is estimated that a rotation cycle of 35 to 40 years would suffice to produce commercial timber, providing that the planting site is of good quality and attacks of H. grandella could be neglected (35,55).

All Costa Rican Meliaceae are highly desired timber species which can reach diameters up to 2.0 m and heights of over 40 m under optimum conditions. The wood, which is principally used for furniture and veneer, is easily worked and strong for its weight.

1.4.3 Economic importance.

Although several thousands of hectares of pure meliaceous tree species have been established in the past 50 years in Latin America, the literature provides little information on the financial aspects of failures due to H. grandella.

Quantified data about attack percentage, resulting deformation and growth losses are equally scarce and difficult to obtain. On the other hand this problem is aggravated by lack of silvicultural and economical studies on the Meliaceae in Latin America; published records of increment, yields and rentability of these species are virtually absent in the literature. This is explained by the fact that most forest services and forest research institutes in the tropical countries of Latin America have been established after World War II and face budgetarial limitations which hamper the execution of such long-term investigations. However, these studies constitute

an important factor in establishing a proper economical basis for Hypsipyla control and need to be undertaken.

Much information about potential development and yield of Cedrela spp. and Swietenia spp., can be likely obtained from countries in Africa and Asia where these Latin American Meliaceae are planted with more success in view of the fact that they are not or in a lesser degree attacked by the native H. robusta. Thus, tentative economic thresholds for control measures could be obtained. Data on growth of Swietenia macrophylla and S. mahogani Jacq. have been published by Noltée et al (35), whereas information on Cedrela odorata is at present being collected in Nigeria (31).

In the Turrialba area, a survey of 7 opengrown trial plantations of young S. macrophylla, S. humilis and C. odorata revealed that 62 percent of all trees were attacked by the shootborer (45).

Similar generalized data are given for other parts of Latin America. For example, attempts to use C. odorata for reforestation in Puerto Rico were abandoned in view of the severity of H. grandella attack (53). According to Martorell (32) 835,000 mahogany trees (Swietenia spp.) and 1,000,000 Cedrela trees were destroyed between 1935 and 1943 in Puerto Rico. Dourojeanni (16) indicates that in Tingo Maria, Peru, 10 percent of S. macrophylla - and 60 percent of C. odorata - plantations were attacked only four months after planting. In the Petén-area of Guatemala, 250 hectares of S. macrophylla, S. humilis, S. mahogany and C. odorata established in line plantings, are severely attacked by the shootborer. In Cuba, Fors (19,20) and Roig (41,42) evaluated the results of planting of 1,800,000 Cedrela odorata seedlings which were provided by Cuban nurseries to private farmers and concluded that no more than 10 percent had survived.

Contrasting to these failures of which similar negative experiments exist in Argentina, Brazil, Mexico and Venezuela, are a few reports mentioning successful pure meliaceous plantations, which apparently escaped from damage of H. grandella. In the Guayaquil-area of Ecuador, plantations of Cuban origin, established at the farm "La Mina" reached a height of 35 m and had a diameter of 1.12 m at 26 years. Although these plantations were established in the open, no Hypsipyla attack occurred (31). Similarly, several young plantations of C. odorata, S. macrophylla and S. humilis in the Salitre area of Costa Rica have been reported to be without attack, whereas

replications of the same seed origins in other areas were heavily attacked (45). Special mention should be made of the successful plantations of C. angustifolia which have been established in Venezuela and Surinam, notwithstanding the fact that this species is heavily attacked there by the shoot-borer (55). Since this seems to indicate a natural recovery mechanism inherent to this Cedar species, it will be discussed in more detail in chapter 1.4.4.

Concerning the importance of the Latin American Meliaceae on the world timber market, reliable statistics are difficult to obtain since differentiation by timber species is rarely provided. Some examples may, however, illustrate the market situation. Whereas Europe is a principal importer of African Meliaceae, a great part of the export of the Latin American meliaceous timber species is absorbed by the North American market. Brazil is one of the major exporters of meliaceous timber to the United States. Swietenia macrophylla, Cedrela odorata and Carapa guianensis from the Pará and Amazon provinces are exported through Manaus and Belém on the Amazon. In 1969, prices of these timbers varied between US\$ 95-125 per cubic meter of sawn wood (36). Table 2 reflects the steady fall in export of mahogany (Swietenia spp.) from Latin America to the United States.

Table 2. Exports of mahogany (Swietenia spp.) and cativo (Prioria copaifera) from Latin America to the United States, 1960-1968, (21) in millions of Bdft.*

Year	Mahogany	Cativo	all species
1960	25.2	-	25.3
1961	15.5	-	20.3
1962	16.6	-	30.7
1963	13.7	4.5	23.8
1964	23.8	10.0	21.2
1965	12.8	11.4	21.5
1966	16.1	14.7	25.0
1967	10.5	9.7	21.3
1968	8.5	10.2	29.9

* 221 Bdft. = 1 m³.

Increasing scarcity of these Meliaceae has already led to partial replacement of these species by cativo (Prioria copaifera Griseb). A similar substitution of Spanish cedar (Cedrela spp.) by laurel (Cordia alliodora (Ruiz & Pav.) Oken has also taken place on the internal markets of Venezuela and Costa Rica.

Although temporary increases in production of Latin American Meliaceae will occur when inaccessible areas are opened up by major road construction programmes, such as the Trans-Amazonian Highway and the Brasilia-Belém Highway, the long-term trend is likely to be a continuing decline if no suitable methods are developed to grow these timber species.

1.4.4 Possibilities of control.

1.4.4.1 Silvicultural control.

From an ecological point of view, large scale pure plantations of meliaceous tree species, particularly in the humid tropics, represent a highly unnatural situation. The scattered occurrence of these trees under natural forest conditions consequently led to the development of silvicultural methods imitating some of these ecological conditions. Basically, the principal factors taken into consideration refer to: reduction of the number of Meliaceae per hectare, presence of shade and the quality of the planting site. Mechanical control by pruning attacked shoots and branches of trees is considered uneconomical.

The effect of shade is not always a subject of agreement; Chable (15) reports that in Honduras, Hypsipyla damage is complete and widespread regardless whether mahogany trees are located in the open or in heavy shade. Similar high incidence of attack under heavy shaded conditions has been observed in trial plots of mahogany under Gmelina arborea Roxb. in the Turrialba-area. Noltée et al. (35) also indicate that the use of teak as a shelter for mahogany has resulted in an important decrease in growth of latter. On poor soils, mixtures of teak and Cassia siamea Lam. with mahogany showed better results. In India, Beeson (8,9) reports reduction in level of shootborer attack by planting in mixtures and using shade trees. Roberts (40) mentions that attempted control by silvicultural methods in Nigeria, employing Nauclea diderichii (De Wild.&Durr) Merr. and Gmelia arborea as shade trees, were not very successful if the mahogany was planted in pure lines. However, some degree of control has been obtained if the shade trees and the Meliaceae were planted alternately in the same row. In the Ivory Coast, Aubreville(5) employed several African Meliaceae in line plantings to enrich the natural rain forest, emphasizing the need of lateral shade to promote height growth of these tree species. However, no information about shootborer attack is given quantitatively nor qualitatively.

In New South Wales, Australia, about 50 percent of shade is considered necessary to reduce borer infestation so as to permit reasonable growth of Toona ciliata M. Roem. var australis (17).

Huguet and Marie (29), in the French Antilles, indicate that poor soils, excessive isolation and wind should be avoided in mahogany plantations. These authors recommended the establishment of mixtures or small groups in the existing natural forest to reduce Hypsipyla attack. The plants should be laterally protected by leaving brush on the sides.

Reduction or abolishment of maintenance in plantations during the initial stages has sometimes led to a decrease in shootborer attack. Dourojeanni(16) reports about a plantation of Cedrela odorata in Kcosnipata, Peru, in which all cleaning operations were abandoned in view of the high incidence of attack. After some time these Meliaceae proved to have recovered completely and were developing into straight saplings. A similar experience has been recorded in Costa Rica, in two plantations of C. odorata, although form of the trees here, leaves much to be desired.

Imitation of natural forest conditions is most advocated by Holdridge(28) who recommends to bring to maturity no more than 10 cedar trees per hectare, in a mixture with other species. To this purpose, 50 seedlings per ha. should be planted on well drained fertile sites in full sunlight between the other species.

Differences in susceptibility of Meliaceae to attack have also been reported. Most authors (16,44,45) agree that Cedrela odorata is more susceptible to attack than Swietenia macrophylla.

Special reference should be made on Cedrela angustifolia of which successful line plantings and pure plantations have been established in Venezuela and Surinam. Although this rapid growing cedar is severely attacked by the shootborer(37,44,55), it has the property to produce, even under open field conditions, a straight new leader in the immediate vicinity of the attack. Escape from subsequent attack, during the growing season and fast growth of the leader after the dry season in Venezuela and Surinam, provides this species with an advantage over C. odorata, which generally grows less vigorously and has a tendency to produce and develop many side branches after attacks.

Recently an international Cedrela -provenance trial has been initiated by the Commonwealth Forestry Institute, which should provide valuable information about the natural resistance of Cedrela odorata and C. fissilis Vell. in the Ivory Coast, Nigeria and Uganda as well as in Latin America itself, to the native shootborers. Most successful plantations of Meliaceae

have been established by employing exotics. This aspect is dealt with in more detail in Chapter 2.

1.4.4.2 Chemical control.

Attempts to combat Hypsipyla by means of spraying conventional insecticides have repeatedly failed due to high rainfall and to the hidden nature of the insect. At the Experimental Station in Tingo María, Peru, trials employing lead arsenate, DDT and Parathion at 2 weekly intervals were abandoned in view of lack of success and elevated costs (16).

In Barinitas, Venezuela, Ramírez (38) initially reported excellent control of the shootborer with DDT, Aldrin, Fosferno, Telodrin, Parathion, Metasystox, Endrin and combinations of these insecticides, when applied every two days during oviposition periods. However, the short life cycle and overlapping generations of the insect call for very frequent applications of the insecticides. The high costs of these chemical treatments apparently impeded continuation of the trials, since they have never been reported upon again.

However, a new method for chemical control of Hypsipyla is being developed recently by Allan et al. (1,2,3,4,56). In this method a systemic insecticide is chemically or physically combined with a polymer. After insertion of the combination in the soil around the plants, the systemic is gradually released from the polymer by hydrolysis or diffusion and provides a continued supply of pesticide over an extended period to the plant. Five systemics, carbofuran, methomyl, Isolan, phosphamidon and monocrotophos, which had showed to have no phytotoxic effects on Cedrela odorata and offered best protection out of 28 systemics tested, were used in field trials conducted in Turrialba, Costa Rica (3,56). These polymer-systemic combinations were obtained by dissolution of each insecticide at 25 percent concentration in molten polyamide resin and moulding the mixture into cylinders of 1 cm diameter and 8 cm length. Twelve of these cylinders were inserted around each plant, 30 cm from the stem in the soil.

Evaluation of the results indicated that no damage occurred for 90 days on the Cedrela trees treated with the Isolan, phosphamidon and monocrotophos polymer combinations. The methomyl-polymer combination was effective for about 160 days whereas the carbofuran combination protected

the trees for a 340 day period (56). An analysis of the cylinders of the carbofuran-polymer combination showed that only 20 percent of the pesticide had been released.* In view of the climatic conditions in the tropics with respect to precipitation, the controlled release method of insecticides obviously may present economical and ecological advantages when compared with conventional spraying of insecticides (4). However, a number of points will still have to be clarified before larger scale employment of this method might come into effect. In particular, uptake and translocation of the systemic insecticide during transitional dry spells could constitute a difficulty. In areas with a pronounced dry season, resprouting of mahogany and Spanish cedar does not always correlate with the initiation of the wet season. In addition, it can be imagined that repeated increasing dosages of the polymer-systemic combination would become necessary in time when both the root system as well as the stem and foliar area of the trees to be protected increase. To this extent, it should be questioned whether the failure of the systemic-polymer combination to protect the plants in the Turrialba-trials for a period longer than 340 days (although only 20 percent of the systemic was released) is merely due to an inefficient shape of the cylindrical polymer cast, or whether this is due to displacement of the active part of the root system.

Another aspect in need of evaluation is the effect of the systemic-polymer combination on other insects, parasites, and predators.

1.4.4.3 Biological control.

Under ideal circumstances biological control provides a self-perpetuating system, whereby the pest population will fluctuate below an economic threshold.

In tropical forestry, where rotation cycles of meliaceous tree crops may take 25 to 60 years, and the compounded interest of early investments is consequently bound to exercise great weight on the overall rentability of the harvest, biological control could offer advantages when compared for instance with chemical control methods.

* R. Wilkins, personal communication, March 1973.

Although searches for candidate biological control agents of Hypsipyla spp. had started earlier (8,9,33,34) it was not until the 1960's that a major effort to establish a biological control project was initiated by the Commonwealth Institute of Biological Control (CIBC) at Bangalore, India. Rao and Bennett (39) of this institute surveyed and investigated the large complex of natural enemies of H. robusta and listed the smaller number of known parasites of H. grandella. One of their conclusions was that since none of the identified species recorded in India was known in Latin America, reciprocal exchange could greatly enhance the possibilities of biological control.

At the Trinidad Station of CIBC, Bennett and Yaseen (10,11,57) introduced the following Indian parasites: Anthrocephalis renalis Waterston, Tetrastichus spirabilis Waterston, Trichogrammatoidea nana (Zehnt) and an Afrephialtes sp. Rearings of these parasites have been established (11) and releases have been made since late 1960 in Trinidad and other islands of the West Indies, British Honduras and Brazil. However, to date no field recovery of these parasites from H. grandella has been reported.

In India, Africa and Latin America, a parasitic nematode of the genus Hexameris has been reported from larvae of H. robusta and H. grandella (39). Roberts (40) indicates that during the wet season the level of parasitization by this nematode in Ibadan, Nigeria, was as high as 40 percent in some collections of larvae.

With regard to pathogens very few records exist; Myers (33) reports about a fungus of the genus Cordyceps infesting H. grandella, whereas unidentified fungi were observed to attack H. robusta (39). Kandasamy (30) recorded the suitability of H. robusta as a host for Beauveria tenella (Delacroix) Siemaszko.

In Turrialba, Hidalgo-Salvatierra and Berrios (12,13,25,26) investigated the susceptibility of H. grandella larvae for the fungi Metharrhizium anisopliae (Metch) Sorokin, Beauveria tenella and Beauveria bassiana (Bal.) and the bacterial pathogens Bacillus thuringiensis var thuringiensis and B. thuringiensis var entomocidus. These studies, executed under laboratory conditions, showed that the fifth instar of H. grandella is the most susceptible to infection by spores of M. anisopliae when dipped for one minute in a spore suspension of 1.2×10^7 viable spores per ml; mortality obtained was 50 percent. In the experiments with Beauveria, one minute immersion of

of the larvae in a suspension of conidiospores of B. bassiana at 1.4×10^6 viable spores per ml and of B. tenella at 2.9×10^7 viable spores per ml resulted in respectively 13.9 and 12.7 percent mortality. The preliminary experiments with Bacillus thuringiensis indicated that first instar larvae of the shootborer were more susceptible to the variety thuringiensis than the variety entomocidus. In these tests, 91 percent and 20 percent mortality occurred after the artificial diet on which the first instar larvae were reared had been contaminated with an overnight bacterial culture of respectively B. thuringiensis var thuringiensis and B. thuringiensis var entomocidus (26).

With regard to the occurrence of parasites of H. grandella in Costa Rica, none had been registered when the Interamerican Working Group on Hypsipyla embarked upon its programme. However, during surveys and investigations, a considerable number of natural enemies of this insect pest were encountered. They are reported upon in Chapter 2.4.

1.4.4.4 Integrated control.

From the foregoing chapters it is clear that only the first steps have been set on a long road towards economical control of Hypsipyla. Taking into consideration the extended period during which trees have to grow before they can be harvested, it seems unlikely that any method solely will result in adequate protection of the Meliaceae if increased yields as compared to natural forest conditions are to be obtained. Protection of plantations of meliaceous tree species against the shootborer through biological control agents only, may never be obtained on the American continent. However, in combination with silvicultural and chemical control the possibility exists that a system of complementary protection measures could be devised which would not only aim at the desired economical returns, but also maintain the tree species in an ecologically sound equilibrium with its environment

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2. CONTRIBUTIONS TO AN INTEGRATED CONTROL PROGRAMME OF HYPsipyla grandella (ZELLER)

- 2.1. Investigations on the natural resistance of Meliaceae against H. grandella.

Papers:

- 2.1.1. Toona spp., posibles alternativas para el problema del barrenador Hypsipyla grandella de las Meliaceas en América Latina. Turrialba 19(4):531-547. 1969.

This paper has been translated from Spanish into English in this dissertation.

- 2.1.2. Immunity of Toona ciliata M. Roem var australis (F.v.M.) C.D.C. and Khaya ivorensis A. Chev. to attacks of Hypsipyla grandella Zeller in Turrialba, Costa Rica. Turrialba 20(1): 85-93. 1970.

- 2.1.3. Studies on the shootborer Hypsipyla grandella (Zeller) (Lep., Pyralidae) XXVII. Biological and chemical screening for the basis of resistance of Toona ciliata M. Roem. var australis (F.v.M.) C.D.C. Turrialba (24). 1974 (in press).

Toona spp. possible alternatives for the problem of the meliaceous shootborer Hypsipyla grandella in Latin America.*

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ABSTRACT

Toona ciliata and T. ciliata, var australis are fast growing valuable forest trees, which, when planted in forest plantations in their native countries, suffer heavily from attacks of Hypsipyla robusta, a shootborer of Meliaceae. Trials with T. ciliata and its variety australis in Latin America reveal that these exotic Meliaceae, as well as some others, are not attacked by Hypsipyla grandella, present in this continent. Parallel to this experience are findings that Cedrela odorata introduced in other continents is not or is less attacked by Hypsipyla robusta than native Meliaceae. Apparently some preference exists, and selection is made by the native Hypsipyla moth. The first author supposes that this selection is based on the attraction of the Hypsipyla moth by a specific odour of the host tree, which could be different for various Meliaceae. It was noted that when leaves and young shoots of Cedrela odorata were crushed, a strong garlic-like smell was produced, which was not noticed when leaves of T. ciliata var australis were treated in the same way. Of the plots of both species, established in the Puente Cajón Species Trials in Turrialba, Costa Rica, Cedrela odorata is heavily attacked by Hypsipyla grandella, while Toona ciliata var australis growing in the same area is not attacked at all. It is thought that the hypothesis of the olfactory orientation of the moth of Hypsipyla spp. might open new ways toward the solution of the Hypsipyla problem: e.g. by means of (gas) chromatography, the main odorific components of the essential oils in the leaves and the shoots of the Meliaceae could be analysed and at a later stage perhaps be used as attractants against Hypsipyla.

*Received for publication 15 October 1969

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If the hypothesis of olfactory orientation of the Hypsipyla moth is correct, it might also be possible to select and breed Meliaceae, which do not possess or have a low content of the attractant component in the leaves and young shoots.

Crossing of the attack-free species (e.g. Toona with Cedrela) could offer other interesting aspects. The fact that Toona and Cedrela can be propagated vegetatively, is an additional advantage.

This paper further reviews the available botanical, ecological, silvicultural and technological data on T. ciliata and its variety australis. It also includes a short summary of information on Toona sureni and Toona calantata, other species of this genus which may be of very much interest to Latin America.

The authors

Introduction

Mahogany and Spanish cedar are two highly valued Latin American tree species known all over the world for their quality timber. Both, species of the genera Swietenia and Cedrela, pertain to the family of Meliaceae and have their natural distribution limited exclusively to the Neotropics.

Notwithstanding their high economic value for this continent, it has been virtually impossible until now to establish economic plantations of these species in Latin America due to the frequent attacks of the larvae of Hypsipyla grandella (Zeller) a borer which infests several parts of the trees but principally the shoots. The main damage caused consists of the destruction of the terminal shoot, as a consequence of which numerous new shoots are produced resulting in deformation of the main stem. The repeated attacks also cause a decreased growth and in some cases may result in the death of young trees. A similar problem exists in other continents where forest trees of the Meliaceae are attacked by other species of Hypsipyla (24). In Asia and Australia for example, the attacks of Hypsipyla robusta impede the development of Toona plantations, whereas in Africa, larvae of Hypsipyla albipartialis and H. robusta inflict great damage on native Meliaceae (2,3,15, 22,38,50,53).

Chemical control of Hypsipyla is difficult; in the first place because the larvae upon eclosion from the eggs (deposited generally on the stem, on the leaf axis and on the leafaxils) quickly penetrate in the plant tissues. The time during which they would be accessible to insecticides unlikely exceeds a few hours (50). According to Ramirez (45) eclosion mostly occurs during the first hours of the night, which would also constitute a difficulty in the control of the borer. Another problem consists of the high frequency of attacks due to the relatively short life cycle of Hypsipyla. The complete life cycle of this insect takes 35+5 days; since the insect can reproduce itself all year round, chemical control would be very costly.

In order to reduce the attacks of Hypsipyla on the Meliaceae, various recommendations exist, which generally refer to the mixture of the Meliaceae with other forest tree species, shade, soil types to be used and treatments which limit the propagation of the insect. The use of systemic insecticides and of biological control to combat Hypsipyla is also being investigated. In Puerto Rico, a parasite, Calliephialtes sp. has been recorded and in India 11 parasites have been encountered of which Trichogramma minutum may be the most promising since it parasitizes the eggs of Hypsipyla robusta (46,50)

Although the previously indicated methods of control could be of high value in the control of Hypsipyla and consequently could result in an economic solution for the establishment of meliaceous plantations in Latin America, they will not be further discussed here. In this contribution the authors wish to point out that a certain preference of the native Hypsipyla seems to exist for certain representatives of the family of Meliaceae.

Analysing the literature on introductions of exotic Meliaceae in the tropical countries of several continents it is noteworthy that certain species tend to be less attacked by the native Hypsipyla spp.

In Queensland, Australia, the exotic Cedrela odorata from Latin America is considered as a forest tree of great promise in view of its rapid growth and the fact that it is not attacked by Hypsipyla robusta, which destroys Toona ciliata var australis growing next to it (53).

A similar phenomenon has been observed in Turrialba, Costa Rica, in the tree species trials of the Inter-American Institute of Agricultural Sciences,

where Toona ciliata var australis introduced from Australia is free of attacks of Hypsipyla grandella, whereas the native species Cedrela odorata, Swietenia macrophylla and S. humilis in adjacent plots, are frequently attacked.

In Puerto Rico, Geary (27) indicates that Toona ciliata and T. sureni are also free of attack, whereas Cedrela odorata and Swietenia macrophylla in the same arboretum of Ciénaga Alto are severely attacked.

Cedrela odorata does not seem to be susceptible to attacks by the native borer in Africa (44). In Java, Indonesia, this tree species is attacked by Hypsipyla robusta, but damage is not considered to be serious and the species is used to replace Toona sureni which is heavily attacked by the shootborer (3,56).

In the Philippines, plantations of Swietenia macrophylla are free of attack, and this tree species is used in reforestation schemes (50).

In Honduras, Chable (16) observed that the attacks of Hypsipyla grandella are minimal in the following species: Khaya nyassica, K. ivorensis, Toona ciliata and Entandrophragma rederi, all species of Meliaceae provening from other continents. According to his information, Entandrophragma has never been attacked.

In Turrialba, Khaya ivorensis planted next to Swietenia macrophylla is not attacked either, whereas the mahogany is a complete failure due to borer attack.

Notwithstanding this positive information it should be emphasized that a strict specialization of the native Hypsipyla on native Meliaceae apparently does not exist. Various reports mention serious attacks of native Hypsipyla on exotic Meliaceae. In Ceylon and India H. robusta is considered a serious pest of the introduced Swietenia macrophylla (53); in Australia, the introduction of Swietenia mahogani failed due to the attacks of the native Hypsipyla (53) and the French Antilles it was observed that Khaya senegalensis, provening from Africa was attacked by H. grandella (50)

In view of the apparent immunity of Toona ciliata, T. ciliata var australis, T. sureni, Khaya ivorensis and Entandrophragma spp. to attacks of the shootborer H. grandella and considering the high quality of their timber,

these species should receive a high priority in tree species trials in Latin America. Since Toona ciliata and T. ciliata var australis appear to be most promising Meliaceae to be tried in Latin America, a review of the existing literature on this species and the variety australis is provided together with a summary of data of some other Toona species of possible importance.

General

Botanical nomenclature

- a. Toona ciliata M. Roem.
- b. Toona ciliata M. Roem. var australis (F.v.M.) C. DC.

Synonyms

- a. Toona ciliata: Cedrela toona Roxb. ex Rotl.
- b. Toona ciliata var australis: Toona australis Harms; Cedrela australis F.v.M.

Much disagreement has existed between taxonomists on the genus Toona: the species of this Asian genus of forest trees were considered so similar to those of Cedrela in Latin America that De Candolle (11) grouped them together under Cedrela. Earlier, in 1846 Roemer (49) had separated the Asian cedars from Cedrela bringing them together in Toona. In 1896 Harms (18,29) again differentiated the cedars into two genera Toona and Cedrela, however, De Candolle reunited them again in 1908 (12). Recently, Smith (52), in his revision of the genus Cedrela confirmed that the separation of the two genera established by Roemer was correct and recognizes the two genera, Toona in Asia and Cedrela in Latin America, on the several differences indicated below (52):

- a. One of the most important morphological differences consists of the column forming the gynophore, which is present in Cedrela but absent in Toona.
- b. In Toona, the expanded filaments form a pillow-like mass in which the ovary is generally buried, whereas in Cedrela the filaments are adnate to the surface of the gynophore (Fig. 1)*.
- c. The petals of the flowers of Cedrela are adnate to the gynophore by means of a keel on their inner surface. In Toona the petals are connected by their own base to the top of the pedicel far under the mass of expanded filaments.
- d. In Toona the five lobes of the calyx are connected only briefly at the

*The tables and figures which accompany the text are located at the end of this paper.

base. Consequently the calyx will open flat or reflected during flowering; since the petals are only joined at the top of the pedicel, they also open widely. In Cedrela a cup is formed by the joined calyx segments: the connection of the petals with the gynophore only allow their opening above this connection.

A revision of the genus Toona is needed to establish the nomenclature of its species. It is unclear, for instance, if the Toona species of the Australian tropics is a distinct species (T. australis) or only a variety (T. ciliata var australis). It is also uncertain if T. ciliata from the Western Pacific Region (33) is the same species as the one occurring in India. According to some authors (42) 20 varieties of Toona ciliata exist.

Local names:

1. Toona ciliata: Toon tūn, tūni, maha nim (Hindi); Tūni, tūn, tūna, lūd (Bengalī); Maha limbu (Uriya); Mahlum (Satpurus); Drawi (PB.); Tūni, bobich (Nepalēs); Simal (Lepcha); Somso (Bhutia); Poma, Henduri Poma (Assamēs); Goría nīm (Melghat); Grawa (Khond); Mahalimo (Saora); Kujya (Tippera); Katan-gat (Kōl); Madagiri vembu (Madura) Santhana vembu, thevatharam (Tamilēs); Mathagiri vembu (Mal); Vedi vembu (Trav. Hills); Sūli, māli (Salem); Kal kilingi (Nilgiris); Sandani vembu (Tinnevelly); Tundū, kempū gandagheri (Kan); Nogē, chikado, tseetkado (Maghalēs); Shurūzbed (Chakma); Thitkado, tawtama, ni, kashitka (Burmēs); Moulmein cedar, Indian mahogany, Singapore cedar, Sandal neem, Happy Tree, White toon, Yomhom, Burma cedar. In New Guinea, the species has been given the following local names: Red cedar Mafus (Lower Markham Valley), Epi (Suku), Kapere (Vailada), Mufus (Yulu). (5,7,31, 33,47).

2. Toona ciliata var australis: Red cedar, Australian (red) Cedar, Australian Toon (13,14,26,31,59).

Natural distribution:

Toona ciliata and its variety have a wide distribution; the trees are found in India, East Pakistan, Birma, Thailand, South China, New Guinea, Malaya, the Bismarck Archipelago Celebes, the Moluccas, Philippines and in vallies of the Himalaya up to 1,300 m. altitude. It is generally encountered on river-banks, or in shaded gullies from Assam, Bengal, to the Western Ghats. Often, it can also be found in swamps of the Himalayan foot hills. In Southern India it occurs mainly in humid tropical forests (5,30,33,34). Accor-

ding to Kraemer (33), the species can be found scattered in the whole Western Pacific region, where it grows in the tropical lowlands up to 1,700 m. altitude on mountain slopes. Toona ciliata var australis has its natural distribution in Eastern Australia, from Ulladulla, South of Sydney in the state of New South Wales up to Atherton in Northern Queensland (26, 30).

Description

General:

Toona ciliata and its variety australis are large deciduous trees which can reach a height of 50 m and diameters of 1.50 m (15,18,33,38,). The trunk is generally straight and for 75 percent free of branches (15,33); buttresses are frequent, particularly in tropical and subtropical areas (26,33; Fig.2).

Bark:

The bark of mature trees is gray or red brown colored, with a thickness of 6-15 mm. The bark is shed in oblong scales (Fig.2) and consists of an outer reddish layer and an inner white colored layer. Often it contains a dark colored liquid of pleasant smell and bitter taste (5,15,26,33,60).

Leaves:

The leaves are alternate compound, frequently pari-pinnate, 30-50 cm long, with 6-12 pairs of leaflets, mostly 7 pairs. Benthall (5) indicates that the leaves may obtain a length of 100 cm. The leaflets are opposite or nearly opposite, glabrous, ovate-lanceolate, obtuse at the base, apice acuminate, 8-13 cm long and 7-8 cm broad, margins often undulated; the two sides are unequal and curved; mature leaves are brilliantly green, young leaves reddish colored. The petiolules measure approximately 6 mm (5,15, 18,54,58).

The variety australis has alternate, compound, pari-pinnate leaves with 3-8 pairs of leaflets, each having the appearance of an ordinary leaf, unequal sides and petiolules of less than 1 cm long (26, Fig.3).

Flowers:

The inflorescence is a hanging terminal panicle consisting of white, unisexual, fragrant flowers. Calyx, cup-shaped, puberulent exteriorly, with 5 ciliated sepals and 5 oblong ciliated petals; yellow, pubescent disc,

shorter than the ovary; ovary pubescent, style glabrous; 5 stamens with glabrous or pubescent filaments (5,15,18,58, Fig. 3). Francis (26) gives the following description of the variety australis: flowers fragrant, in a large terminal panicle; the individual flowers are approximately 4 mm long the calyx is 5 lobed and 1-2 mm long. On the inner side of the calyx are 5 oval petals of approximately 4 mm length. More towards the centre and shorter than the petals are the stamens, varying between 4-6. The ovary is in the centre of the flower and has a style with a flat, round stigma.

Smith (52) believes that the androecium is derived from a staminal tube of 10 stamens, since many Toona spp. have staminodia alternating with the stamens and because of the existence of the mass of tissue surrounding the ovary (Fig.1).

In Calcutta, India, flowering of Toona ciliata occurs in February-March (5). The variety australis, flowers in September-October. Florescence and fructification generally occur every year.

Fruit and seeds:

Fruit a pedicellate capsule, oblong, woody, 2-2.5 cm long and 0.7-1.0 cm in diameter, splitting open in 5 valves. Seeds with membranous wings on both ends attached to the central column in 5 grooves; 4-5 seeds in each groove (26, Fig.3). Smith (52) indicates that the fruits of Toona and Cedrela are basically similar, the difference being principally a degree of development. E.g. the fruits of Toona are smaller than those of Cedrela and the central column is only angled, whereas it is winged in Cedrela. In Toona the apical area of the column is not sterile, as it is in Cedrela.

Silvicultural aspects

Climate:

In its natural distribution T. ciliata can be found in regions with an annual rainfall of 1,125-4,000 mm (15,17,53); generally the dry season lasts 3-4 months. The species prefers humid sites, but also grows in drier places. Streets (53) indicates that the species can grow under relatively dry conditions if it is irrigated and tended in the early stage (as is done in India). Chevalier (48) observes that it will also grow in a monsoon climate with a prolonged dry season or temperate zones in China. Toona ciliata adapts itself also to very dry conditions (annual rainfall

800 mm) if it is planted in fertile soils and has access to ground water during the dry season (15).

The trees shed their leaves at the beginning of the dry season. In Turrialba, Costa Rica, where rainfall during the driest month still amounts to 50 mm, this deciduousness did not occur until the trees were three years of age. Benthall (5) reports that in Calcutta, India, the trees shed their leaves at the beginning of the cold season.

The species and its variety australis are fast growing and light demanding trees, although they are tolerant to shade in the early stages.

The variety australis can be found in tropical rain forests of the coast of New South Wales and Queensland, Australia, where precipitation is equivalent to or exceeding 1,500 mm (26). The rainfall is uniformly distributed in New South Wales but concentrated in the summer in Queensland.

Temperature in the area of natural occurrence of T. ciliata varies between 43°C (absolute maximum) and -2°C (absolute minimum). Streets (53) indicates that this species tolerates slight frosts. On the Atherton plateau in Queensland, the absolute minimum temperature is -2°C, whereas the absolute maximum is 28°C.

Soils:

T. ciliata and its variety australis grow well on the lower parts of slopes, in fertile soils with good drainage; the trees can also be found frequently on riverbanks. Establishment on compact clays or poor sandy soils generally results in failures. Apparently T. ciliata has certain preference for calcareous soils (15). The root system is superficial, necessitating a good provision of water and nutrients in the upper horizons of the soil. In comparison with Cedrela odorata, Toona ciliata appears to be less exigent with regard to soil-drainage (15). Kraemer (33) indicates that in the Western Pacific region, the species preferably grows on deep, well drained alluvial soils but also is established on mountain slopes up to 1,700 m altitude.

Seed and planting practices

Seed collection: The seeds of Toona ciliata are light; one gram contains between 280-425 seeds (39). The variety of australis contained 306 seeds per gram. In hermetically sealed tins, dry seeds can be stored for the duration of a year (39). According to Letourneux (38) the seeds can be stored in sacks for a year, without losing more than 20 percent of its

viability. Another source (15) reports that the natural viability of seed of T. ciliata does not exceed 1-3 months, but that it will maintain its viability for a year in hermetically sealed tins kept at 4-5°C.

Germination:

Fresh seeds of Toona ciliata germinate well. Letourneux (38) reports an average germination percentage of 90, at 8-12 days after sowing. Magini and Tulstrup (39) indicate that germination starts 9 days after sowing and that a germination percentage of 60-80 is obtained. Under laboratory conditions in Turrialba, 84 percent of fresh seed of the variety australis germinated; apparently a correlation exists between seed weight and germination percentage (Fig. 4). The species can also be propagated vegetatively (53).

In Turrialba, Costa Rica, the seed is germinated in slats (50 x 30 x 10 cm) made of wood or galvanized iron, which are partially submerged in water; humidification of the germinating medium is thus obtained by capillary action. A fine fertile soil is used as medium and seeds are covered with a 2-3 mm layer. Since the seeds are small and light and recently germinated plants can be damaged by rain, the slats are placed under cover.

In tropical Africa (15), seeds are covered with a 2 cm layer of fine soil whereas protection against heavy rains and sunshine is provided by a straw roof. This roof is lifted when germination starts (generally eight days after sowing) and only replaced by partial shade during the warmest hours of the day. Pricking-off* is generally executed when the seedlings are one month of age and have attained a height of approximately 10 cm. In Turrialba, pricking-off takes place two weeks after sowing, when the plants measure approximately 5 cm in height. Direct sowing in the field is generally not employed, only in case seeds are abundantly available. This practice is not recommended since heavy rains destroy the fragile plants (15).

Planting:

Field planting is executed employing stumps, striplings or seedlings from the nursery. In tropical Africa one year old plants of approximately 1.20 m are used, which are successfully planted either during the dry season when the plants are deciduous, or during the beginning of the rainy season;

*Pricking-off: transfer of seedlings from the germination-medium to bags or beds. where they further develop until definite field-planting.

in the latter case, stumps of 7cm length and approximately 25 cm of root are used (15). Stumps are also employed in tropical Asia (36,38). In India, stumps immediately planted gave the best results, however, they could also be stored for 6 weeks if kept humid; in dried condition, the stumps would remain viable only for 3 or 4 days (36); In South-Rhodesia plants of 8-15 cm height are used for planting purposes. In Turrialba, plants of 30 cm height are used for field planting.

Spacing:

Ample spacing seems to be indicated in view of the superficial root system and the need for water and nutrients of this species; in tropical Africa (15) a minimum spacing of 4 x 4 m and an average of 6 x 6 m, is suggested. However, in Puerto Rico it has been noted that the form of Toona ciliata growing in the open is worse than that of Cedrela odorata, and close spacing is recommended (55). Letourneux (38) indicates a spacing of 2 x 2 m. The experience with the variety australis in Turrialba, indicates that plantations of 2 x 2 m form a closed canopy in a year, thus, a more ample spacing of for instance 2.5 x 2.5 m could be recommended.

Treatment of plantations:

Since young plants of T. ciliata and its variety australis are sensible to weed competition, the plantations should be cleaned during the first years (15,53). Generally, pruning is not practiced (15).

In Hawaii, up to 21 percent of trees planted at a spacing of 3 x 3 m needed pruning (Table 1). Bad form of T. ciliata in trial plots is also reported from other countries in tropical Africa (53).

Growth and rotation cycle:

Few data exist on growth of the species and its variety australis in plantations; volume tables are non-existing in the literature. Undoubtedly this is due to the severe attacks of Hypsipyla robusta in the countries where this species and its variety naturally occur. In tropical Africa, it is estimated that plantations on fertile soils could attain an average diameter of 50 cm in 20 years (Table 2).

Letourneux (38) indicates that in tropical Asia a much slower initial development exists: 30cm in the first year, but that subsequent development is fast: Toona ciliata would attain a height of 19 m and a girth of 55 cm at 22 years. In Hawaii, the variety australis is considered the most pro-

missing introduced tree species. A plantation of 22 years had a height which varied between 30-36 m and a diameter of 25-55 cm. On this island plants of 30-60 cm height are employed in a naked root planting system. Apparently this variety adapts itself best in low land zones (13,14).

Geary (27) reports the following on two plots of T. ciliata in the Arboretum of Ciénaga Alto in Puerto Rico (altitude 650 m, annual precipitation 2,500 mm).

Plot 34 A: Age 5.5 years; 9 trees; average height 3.3m (range 1.70-6.70 m); average diameter (D.B.H.):5.3 cm (range less than 2.5-9.5 cm), without Hypsipyla grandella attacks, good form; better than Cedrela spp.

Plot 34 B:Age 5.5 years; 6 trees; average height 3.6 m (range 1.70-6.70 m); average diameter (D.B.H.): 4.0 cm (range less than 2.5 cm -11.0 cm (range less than 2.5 cm-11.0 cm), without Hypsipyla grandella attacks, good form, vigorous.

In Turrialba, Costa Rica, Toona ciliata var australis[‡], proceeding from Hawaii, has been planted in 12 localities and has not been attacked by Hypsipyla grandella. Growth of T. ciliata var australis here is extremely fast and promising (Table 1, Fig.5,6 and 7).

The immunity of T. ciliata var australis against attacks of H. grandella is most convincing in the individual tree plot trials where it is planted at 3 m distance from Cedrela odorata, Swietenia humilis, Swietenia macrophylla and Khaya ivorensis. In these plots, established in 3 localities with 4 replications each, none of the T. ciliata var australis trees has been attacked, whereas Cedrela odorata, Swietenia humilis and Swietenia macrophylla, adjacent to these trees are attacked (Fig. 5,7).

With regards to a possible rotation cycle, insufficient data are available to determine an optimum cycle. Taking into account the existing experience and the most profitable use of the raw material (cabinet wood and veneer wood) the rotation cycle could be estimated at 40-50 years (15). In Turrialba, Costa Rica, it was observed that T. ciliata var australis responds quickly to fertilization. (Table 1) by means of which the rotation cycles could be reduced.

[‡]Additional note: Herbarium material of this taxon has been preserved at Wageningen (WAG) under nrs. Sterringa 40, 41, 42 and 43.

Once a plantation has been established, the second rotation is facilitated by the abundant natural vegetation, which generally proliferates. Many countries, such as South-Rhodesia, Nyassaland and Uganda report that a profuse natural vegetation is established. T. ciliata and its variety australis are tolerant to shade during early stages.

Entomological damage:

In Africa, Asia and Australia, the borers Hypsipyla robusta and Zeuzera coffea (8,15,17,18,22,24,26,38,44,53) are the principal enemies, particularly during the early stages of the plants. As far as T. ciliata and T. ciliata var australis introduced in Latin America is concerned, no attacks of the larva of Hypsipyla grandella has been observed in experimental plantations established in Costa Rica, Honduras and Puerto Rico (16,27).

In Australia, larvae of Pingasa sp. (Geometridae) feed on the leaves of T. ciliata var australis and may cause considerable damage (9). In Turrialba, leaf cutting ants of the genus Atta, can inflict considerable damage in young plantations. During a particularly dry season, attacks of a Planococcus sp. (Cochinilla harinosa) on leaves of T. ciliata var australis were also observed, but the attack did not last long and did not affect the trees appreciably.

Phytopathological damage:

Letourneux (38) reports that plantations of T. ciliata can be attacked severely by the fungus Fomes lucidus.

Mechanical damage:

Herbivores appreciate the leaves of T. ciliata as fodder and may cause damage in young plantations (5,8,15,38). Due to its thin bark, the species and its variety australis do not resist fire (53).

Characteristics and utilization of the wood

General:

Record and Hess (34) indicate that the wood of Toona ciliata can not be distinguished from the wood of Cedrela odorata. The wood of this species is identical to the wood of the Spanish cedar and is used for the same purposes. It has a reddish attractive color, is shiny, has a straight

grain and is often highly figured. It is easy to season and to work; moderately resistant to termites (5,18,20,25,26,53). The wood is moderately durable; experiments executed in Hawaii indicate that the natural durability of posts without treatment would be approximately 4 years (51). Specific weight varies between 0.46-0.64 (20,31,33). Chevalier (18) reports an average specific weight of 0.57 gr/cm³. The color of the sap wood of T. ciliata varies between rose colored to light brown (15) whereas the sap wood of the variety australis has a white-yellowish color; the heartwood of both is reddish.

Anatomy:

Francis (26) provides the following description of the variety australis: the pores of the wood are single and in radial rows of 2-5 pores per row; frequently concentric rings of single large pores can be seen at the beginning of each ring. The rings are likely to be annual rings. Terminal wood parenchyma occurs in concentric circles but is often interrupted by the concentric rows of large pores, which cause the figure of the wood. For T. ciliata the following description is given (19,20): the wood is ring-porous or semi-ring porous (Fig.8). The number of pores varies between 144-368 per cm² (33). Growth rings are present and can be distinguished in cross and tangential cuts; between 2-15 rings can be found per 2.5 cm. Early wood contains large oval pores, without tyloses but often plugged with a dark brown gum. The transition to late wood is gradual. The pores in late wood are smaller and occur solitary or in radial groups of 2-3 pores. Gum ducts are generally absent but can sometimes be found in concentric groups, containing a dark colored substance. Wood parenchyma can be seen with a lens around the pores of early wood. Rays (40 per cm) are moderately wide and can be seen with the naked eye in cross cuts (33). The fibers of T. ciliata var australis have an average length of 0.75cm and 1.37 mm respectively in early and late wood (6).

Wood utilization:

In India and Australia the wood is highly appreciated. Previously, great quantities of timber of T. ciliata were exported from Birma to England. It is principally used for veneers, furniture, fine cabinet-wood, carpentry, cigar and tea boxes, general construction, shipbuilding, matches and fire-wood (1,3,4,5,6,15,18,22,23,25,31,33,47,53,60).

Other uses:

The flowers yield a red and a yellow dye, which is used for coloring cotton in India. The leaves are used as fodder for cattle, whereas the bark of the tree is used as a powerful astringent in the treatment of dysentery; it is also considered a remedy against fever (5). The trees are planted as ornamental shade trees in parks, gardens and avenues.

Other Toona species of silvicultural interest.

Nearly all species of Toona produce a high quality timber. In addition to T. ciliata and its variety australis, Chevalier (18) and Begemann (4) mention the following species: T. calantas, T. fargesii, T. microcarpa, T. mollis, T. multijuga, T. paucijuga, T. serrata, T. serratula, T. sinensis and T. sureni, of which T. calantas and T. sureni are probably of major interest for Latin America. A summary of available information on these species is given below. Of the other species mentioned, Toona sinensis could be an interesting tree species for the subtropical and temperate regions of Latin America, since it was successfully introduced in Paris, France.

1. Toona sureni (Bl.) MerrillSynonyms:

Swietenia sureni Bl., Cedrela febrifuga Bl., Toona febrifuga (Bl.) Roem.
Surenus febrifuga O. Kze, Cedrela toona mult. auct. (2,18).

Local names:

Soerén, laoet, redani (Java); Soren (Madura); Horeni, Linoe (Summa); Suntang putch, incoe, soeren (Malaya); Xúong mót, Zúeng mót, xúong moc, hong dao (Annam); Dham Chharm chancha (Cambodia); Ka xua, sa tam, so banne (dialecto Moi) (2,18,34).

Natural occurrence:

Vietnam: Bienhoa, Phanrang, Province of Baria. Cambodia: Phnon Changor, Royauung, Annam: Blao. Indonesia: Java, Sumatra, Ambón, Sunda islands, Sumba, Madura. Malayan Penninsula and Birma (2,3,18,34).

In Java, T. sureni occurs in the low lands as well as mountains of the monsoon region (3). In Annam, it has also been found at an altitude of 1,020 m in the Djiring mountain range, but it generally is a species of the dense tropical rain forest.

General:

T. sureni is a fast growing, large forest tree which can attain heights of 20-40 m and a diameter of 0.60-2.00 m (3). It has strong branches which are pubescent in early stages but later glabrous. The leaves are 60-80 cm long, compound, generally pari-pinnate with 5-12 pairs of leaflets, frequently 8; the leaflets are 12-16cm in length and 4-5 cm broad, acuminate, glabrous on both sides, sometimes pubescent on the veins; 12-16 side veins; petiolules of 6-15 mm length. Petiole 6-12 cm. Inflorescence a hanging panicle shorter or of the same size as the leaves. Rachis pubescent; pedicel pubescent. White odoriferous flowers of 4mm length; sepals rounded, adnate at the base, petals oblong, pubescent exteriorly, disc pubescent, ovary pubescent at the base; style and filaments of stamens glabrous. Capsule woody, 2 cm long (3,18,34).

The wood of T. sureni is of good quality and highly valued. It is easy to season and to work, attractive, fragrant and has a brown-reddish color; it has a specific weight of 0.39-0.45 and is used for sawnwood, cigar and tea boxes, furniture and interior carpentry (3,18,34).

In Asia, plantations of this species are heavily attacked by Hypsipyla robusta (3). In Puerto Rico, Geary (27) reports that a trial plot of T. sureni in the Cienága Alto Arboretum, is not attacked by Hypsipyla grandella, although adjacent plots of Cedrela odorata and Swietenia macrophylla are heavily attacked. No data are available with regards to growth of this species in Latin America. The following information (27) refers to the plot of this species in Cienága Alto, Puerto Rico (altitude 650 m, annual rainfall 2.500 mm).

Plot 35 A: Toona sureni:

Age 5.5 years; 14 trees; average height 4.3 m (range 2.3-8.3); average diameter 7.0 cm (range from less than 2.5 cm to 13.5 cm); without symptoms of Hypsipyla grandella attacks; some trees badly formed, possibly due to climbers; the majority of trees are straight.

Toona calantas Merrill et Rolfe.

Synonyms:

Cedrela odorata Blanco non L. Cedrela toona F. Vill. non Roxb.

Local names:

Kalantas (Pangasinan, Sambai, Tagalog): Alánagi, alánki, anteng, bakóog, porak (Lloko); Antáng (Ibanag); Kantingen (Iloko, Sambali); lanigda, lanigpa (Bikol); lanigpa (Samar-Leyte Bisaya, Cebú Besaya) (10,18).

Natural occurrence:

The species occurs frequently in the provinces of Mindanao, Palawan Luzón, the island of Batán, Visayas and Mindoro of the Philippines. In its area of natural distribution it can be found generally near rivers and in low lands subject to inundation.

General:

The trees can attain heights of 40-50 m with diameters up to 1.50 m, but frequently the diameter is less. It has a straight and cylindrical trunk, which is free of branches for approximately 50 percent. The bark has a thickness of 5-18 mm and is brownish-red colored. The leaves are compound, alternate and clustered at the end of branches, with 7-11 pairs of leaflets which are pubescent during early stages but later glabrous; 5-13 cm in length and 3,5-6 cm broad (Fig.9). Inflorescence and flowers as in T. sureni. The capsules are larger 3-5 cm, frequently 4 cm (10,18). The wood of T. calantas is highly valued in the Philippines and used for musical instruments, cigar boxes, furniture and carpentry (10,18,34). It contains an essential oil which is very similar to that of Cedrela odorata. Brown (10) citing Brooke, indicates that cadinene is one of the main essential oils. The wood is soft, easy to work and has a red to dark red color. Its specific weight varies between 0.41-0.44 g/cm³. A trial to propagate T. calantas under nursery conditions by means of cuttings, failed in the Philippines (32).

Discussion

The fact that experimental plots of T. ciliata, T. ciliata var australis and other exotic Meliaceae in Latin America are not, or only in a minimal way attacked by Hypsipyla grandella does not only offer good prospects for the establishment of plantations of these fast growing tree species, but it also permits the development of other approaches to solve the problem of Hypsipyla.

Based on the available information one may deduct that the adult of H. grandella obviously selects its host plant to oviposit. How is this selection made? Would it be possible that the typical smell of Cedrela odorata attracts the adult? By crushing the leaves and shoots of this species a strong onion-like smell is obtained, which is not the case when leaves and shoots of T. ciliata var australis are treated in a similar manner. Would it be possible to isolate this constituent (possibly an essential oil) employing gas chromatography, produce it synthetically and use it to combat Hypsipyla? Would it be possible to cross the Toona's which are not attacked with Cedrela spp. and obtain a crossing which will not be attacked either? In Australia, investigations with regard to the problem of Hypsipyla robusta and Toona ciliata var australis indicate that a resistant variety may be obtained (50). The source (50) does not indicate however, in which way T. ciliata var australis would be resistant against the borer.

Note:

By importing seed of exotic Meliaceae for experimental purposes, the grave danger exists that Hypsipyla robusta might be introduced into Latin America also. In order to avoid this, the strictest phytosanitary measures should always be observed.

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Table 1. *Toona ciliata* var *australis*. Summary of data of some experimental plots in Turrialba, Costa Rica and Honaunau Forest, Hawaii (14).

Specifications	Turrialba, Costa Rica					Honaunau Forest, Hawaii		
	Atirro	Bajo Re-ventazón	Puente Cajón	Florencia Sur	Florencia Sur	SP No. 14	SP No. 10	SP No. 8
Plot size (ha)	0,04	0,04	0,04	0,012	0,012	0,4	0,4	0,4
Soil type	clay	clay	sandy loam	sandy clay	sandy clay	A'	P'	A&P'
Precipitation (mm)	2,600	2,600	2,600	2,600	2,600	2,500	2,500	1,250
Age after planting (months)	15	12	17	13	13	12	36	48
Number of trees	100	100	100	20	20	411	302	307
Survival (%)	95	91	94	100	95	86	—	—
Average height (m)	4,1	4,4	5,7	3,0	3,4	1,1	4,0	5,0
Maximum height (m)	6,8	6,1	7,1	4,6	5,0	3,3	14,0	13,0
Minimum height (m)	1,1	0,8	1,9	1,4	1,6	0,3	0,3	0,3
Average diameter (DBH cm)	3,8	4,1	5,7	3,2	3,8	—	—	—
Maximum diameter (DBH cm)	7,4	6,5	8,4	4,7	3,0	—	—	—
Minimum diameter (DBH cm)	1,0	1,0	1,5	1,0	—	—	—	—
Trees pruned ³ (%)	10	13	29	25	30	6	12	21
Diseased trees (%)	0	0	0	0	0	0	0	0
Terminal bud damaged (%)	0	0	0	0	0	0	0	0
Arched trees (%)	0	0	0	0	0	0	0	0
Forked trees (%)	6	11	14	5	5	—	—	—
Fertilization	yes	no	yes	no	yes	no	no	no
Trees resprouting at base (%)	3	5	5	15	15	—	—	—

1.A: Rock with organic and mineral soil P:Pahoehoe rock with thin layer of soil.

2. Not indicated

3. In the Hawaiian plots, all branches up to 4 m height were pruned. In the plots at Turrialba (Atirro, Bajo Reventazón and Puente Cajón) all branches up to 2 m were pruned. For the plots in Florencia Sur, the percentage of trees in need of pruning is indicated.

4. Fertilization in Atirro was initial, treatment consisting of 50 gr 20-20-0 per tree; effected two months after field planting. Fertilization in Puente Cajón and in Florencia Sur was effected every three months with 50 gr and 62 gr of 20-20-0 per tree, respectively.

Table 2. Estimated diameter and height growth of *Toona ciliata* in Tropical Africa (15).

Age (Years)	Diameter (cm, DBH)	Height (m)
1	—	1,20
2	4	3
3	7	5
6	17	10
9	25	14
12	33	18
15	40	22
20	50	25
30	60	30
40*	70	35

* After 40 years, growth decreases considerably.

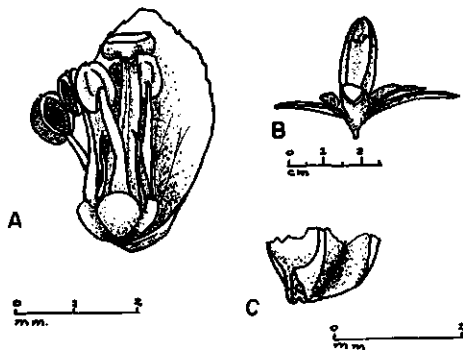


Fig.1. Morphology of a flower of *Toona*. A. Dissected flower of *Toona serrata* (Royle) Roem. showing petal inserted beneath mass of expanded filaments and staminodia alternating with stamens. The ovary base is surrounded by the pillow-shaped tissue formerly described as a disc. B. Fruit of *Toona sinensis* A. Juss. C. Base of a petal showing small area of attachment. From Smith Jr. E. A. (38).



Fig.2. *Toona ciliata* var *australis* in the tropical rainforest in Australia, showing the development of buttresses and aspects of the bark. From Francis, W. D. (26).



Fig.3. Branchlet bearing inflorescence (lower part) and capsules (upper part) of *Toona ciliata* var *australis*. From Francis, W. D. (26).

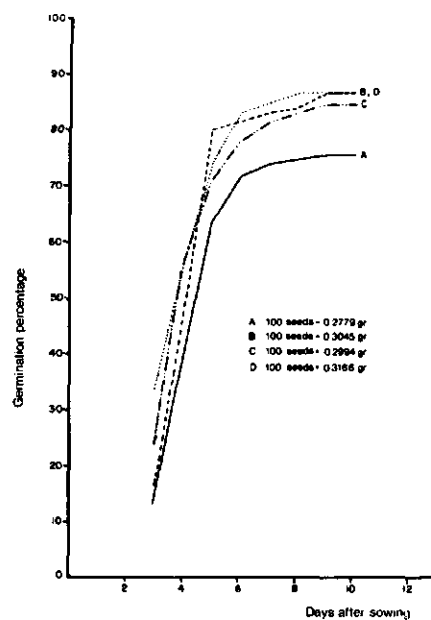


Fig.4. Diagram showing germination percentage and relation between weight and viability of fresh seed of *Toona ciliata* var *australis* under laboratory conditions.



Fig.5. Single tree species trials, Puente Cajón, Turrialba, Costa Rica. Toona ciliata var australis, planted at 3 m distance from Cedrela odorata, is free of attack of Hypsipyla grandella whereas Cedrela is heavily attacked. Toona has been attacked by leaf-cutting ants of the genus Atta. Both species at 13 months after field planting. The pole measures 3 m.



Fig.6. Plot of Toona ciliata var australis 12 months after field planting in the Bajo Reventazón area of Turrialba, Costa Rica. The pole measures 4 m.



Fig.7. Single tree species trials, Bajo San Lucas, Turrialba, Costa Rica. Cedrela odorata planted at 3 m distance from Toona ciliata var australis is heavily attacked by Hypsipyla grandella, whereas Toona is free of attack. Both species at 13 months after field planting. The pole measures 3 m.

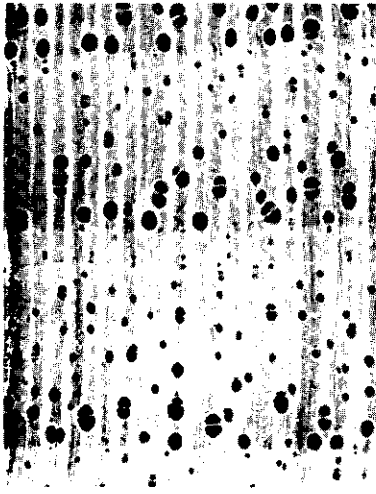


Fig.8. Cross cut of the wood of Toona ciliata showing the difference in size of pores in early and late wood. From Chowdhury, K.A. (19).

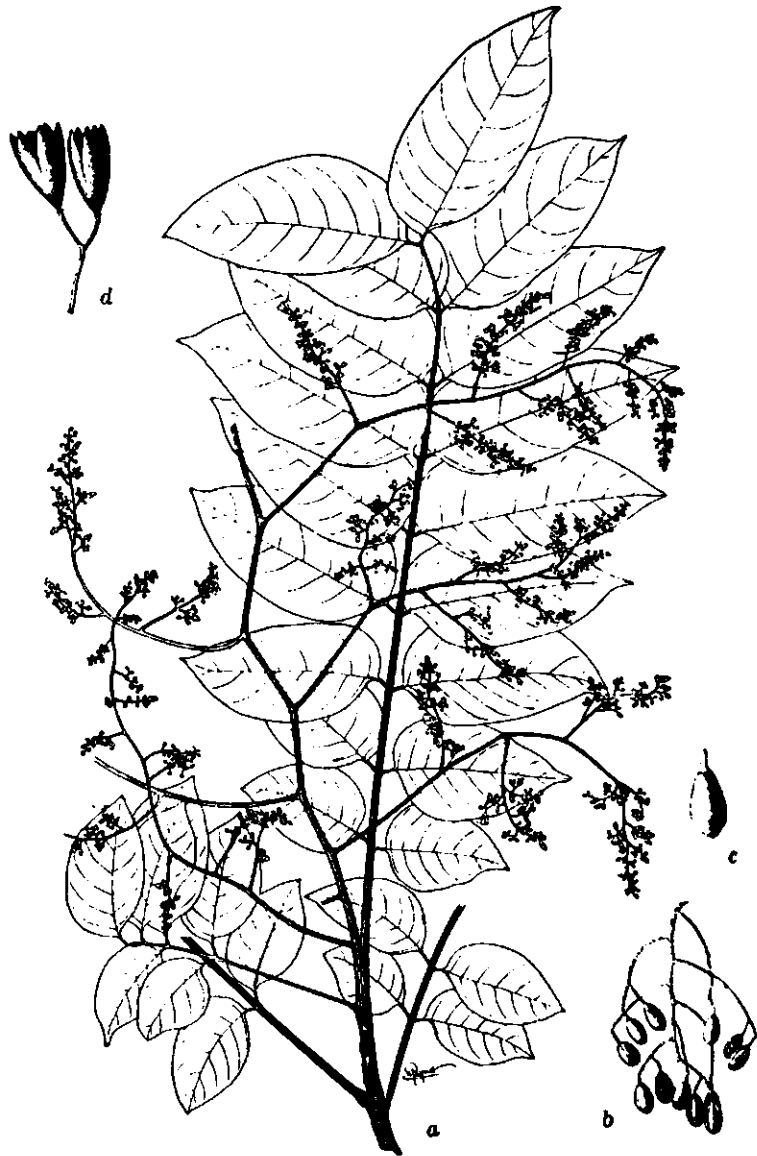


Fig.9. Toona calantas. a. Branchlet bearing inflorescence. b. and c. Capsules. d. Mature capsules. From Brown, W.H. (10).

Immunity of *Toona ciliata* M. Roem. var. *australis* (F.v.M.) C.DC. and *Khaya ivorensis* A. Chev. to attacks of *Hypsipyla grandella* Zeller in Turrialba, Costa Rica* —PIETER GRIJPM**

COMPENDIO

En las parcelas experimentales del Instituto Interamericano de Ciencias Agrícolas, Turrialba, Costa Rica, *Toona ciliata* var. *australis* (*Cedro australiano*) y *Khaya ivorensis* (*Caoba de Nigeria*) no son atacadas por el barrenador de las Meliaceae (*Hypsipyla grandella*), mientras que las Meliaceae nativas como el Cedro (*Cedrela* spp.) y la Caoba (*Swietenia* spp.) son fuertemente atacadas. En muchos países tropicales de otros continentes estas Meliaceae latinoamericanas no son atacadas o son menos atacadas por las *Hypsipylas* nativas, aunque algunos países informan sobre serios ataques.

El autor supone que aceites esenciales volátiles en los brotes y las hojas, los cuales serían diferentes para varias pero probablemente no para todas las Meliaceae, atraen la mariposa de *Hypsipyla* spp. a los árboles huéspedes. Una especialización de la mariposa de *Hypsipyla* sobre ciertos aceites esenciales de las Meliaceae nativas conduciría a la inmunidad de las Meliaceae exóticas que no tendrían estos aceites esenciales como componentes principales. Se proponen algunos proyectos de investigación relacionados con la hipótesis de la orientación por el olfato de la mariposa de *Hypsipyla* a su árbol huésped. En vista de su rápido crecimiento, su valiosa madera y la ausencia de ataques de *Hypsipyla grandella*, la especie *Toona ciliata* var. *australis* parece ser muy prometedora para plantaciones forestales en América Latina. — El autor.

Introduction

THE literature about tree species trials in various tropical countries, indicates that several exotic Meliaceae are not, or are less attacked by the native shootborer of Meliaceae (*Hypsipyla* spp.).

Cedrela odorata from Latin America, introduced in Queensland, Australia, is considered a very promising plantation tree because it is not attacked by *Hypsipyla robusta*, which destroys plantations of *Toona ciliata* var. *australis*¹, growing next to it (21). Lamb (18) and Parry (19) indicate that in Africa, *Cedrela odorata* is unattractive to *Hypsipyla robusta*. In the Philippines,

Swietenia macrophylla is reported to be free of attack and is used for reforestation (17). Damage to this mahogany species is also insignificant in Malaya (20).

In Latin America however, it is impossible at present to establish commercial plantations of these native Meliaceae because of the heavy attacks of *Hypsipyla grandella*, present in this continent.

It should be emphasized however, that apparently the native *Hypsipyla* does not attack the native Meliaceae exclusively; there are reports of native *Hypsipyla* attacks on introduced Meliaceae. For example, in Java, Indonesia *Cedrela odorata* is attacked by *Hypsipyla robusta*, but the damage is not considered serious, and the species is used to replace the native *Toona sureni* in plantations, a species heavily attacked by the borer (1, 15). In India and Ceylon, *Swietenia macrophylla* is reported to be heavily attacked by *Hypsipyla robusta* even though the tree is an exotic (21). Moreover, *Hypsipyla grandella* attacks the introduced *Khaya senegalensis* in Martinique, French Antilles (20).

* Received for publication January 20, 1970.

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¹ Synonyms: *Cedrela toona* var. *australis*; *Toona australis*; *Cedrela australis*.

Although strict specialization of native *Hypsipyla* spp. on native *Meliaceae* is not evident, the native shoot-borers seem to prefer certain meliaceous species. The available information on trials with exotic and native *Meliaceae* in Latin America seems to support this theory.

Chable (6) observed in Honduras that the attacks of *Hypsipyla grandella* on the exotics: *Khaya nyassica*, *Khaya ivorensis*, *Toona ciliata* and *Entandrophragma rederi* are minimal, whereas the native *Cedrela odorata* and *Swietenia macrophylla* are heavily attacked. According to his information *Entandrophragma* was never attacked. In Puerto Rico the exotics *Toona ciliata* and *Toona sureni* are not attacked either by *Hypsipyla grandella* (13).

In the species trials of the Department of Forest Sciences of the Interamerican Institute of Agricultural Sciences in Turrialba, Costa Rica, a similar experience is being observed (14); here *Toona ciliata* var. *australis* and *Khaya ivorensis* are free of any attack of *Hypsipyla grandella*, while plots of *Cedrela odorata*, *Swietenia humilis*, *Swietenia macrophylla* and *Swietenia macrophylla* x *mabogani* are seriously attacked.

Although the species trials in Turrialba are of a relatively recent date, a very prominent difference in attack of the shootborer on the various *Meliaceae* included in the trials exists, so that a report on these observations together with growth data of the plots is justified.

Species Trials with *Meliaceae* in Turrialba, Costa Rica

Presently two types of trials established: Single Tree Plot Trials and Block Trials. The Block Trials vary in size, number of trees per plot and treatment (fertilized and non-fertilized), while the Single Tree Plot Trials only vary in treatment (fertilized and non-fertilized).

Single Tree Plot Trials

These are preliminary selection trials in which usually many species are planted together in a randomized design. The data of each tree are considered as coming from one plot, the "single tree plot". This system of preliminary selection trials was devised by C. B. Briscoe of the Institute of Tropical Forestry in Puerto Rico (5). H. Barres, who worked with Briscoe in Puerto Rico, introduced this design in Turrialba, Costa Rica. The Single Tree Plots have the advantage of offering a better statistical base for comparisons of growth and adaptation of trees to new environments. This experimental design is also less costly to install as less trees of each species are needed and a smaller area is utilized. The Single Tree Plot Trials also have a number of disadvantages, which are discussed in the draft of "A Guide to Tree Species Trials in Tropical America" (12) and will not be elaborated on here.

The Single Tree Plot Trials at the Interamerican Institute of Agricultural Sciences in Turrialba, Costa Rica contain 77 tree-species, varieties and provenances,

planted in 3 locations (Puente Cajón, Bajo San Lucas and Florencia Sur) with 4 replications in each location of which 2 replications are fertilized quarterly with 62 grams of 20-20-0 (250 grams per year), and 2 are not fertilized. Planting distance is 3x3 meters. Among the 77 species, varieties and provenances the following *Meliaceae* have been planted: *Toona ciliata* var. *australis* (Provenance: Hawaii), *Khaya ivorensis* (provenance: Ivory Coast), *Cedrela odorata* (provenance: Costa Rica), *Cedrela odorata* (provenance: Ghana), *Swietenia humilis* (provenance: Costa Rica), *Swietenia macrophylla* (provenance: British Honduras) and *Swietenia macrophylla* x *mabogani* (Provenance: Virgin Islands). These *Meliaceae* were planted in a group, but randomized within the group; the group itself was located at random in each replication. Each replication contained one tree of each species, variety or provenance (Single Tree Plot).

In October 1969, when all trees were 13 months in the field, an evaluation of *Hypsipyla* attack on these *Meliaceae* was made; this information, together with growth data on the trees, is presented in Table 1.

Block Trials

A number of Block Trials containing the following *Meliaceae*: *Cedrela odorata*, *Swietenia macrophylla*, *Swietenia humilis*, *Toona ciliata* var. *australis* and *Khaya ivorensis*, has been established in various locations in the Turrialba area. The size of these plots varies from 0.012-0.040 ha. and the number of trees per plot from 20-100. Fertilized treatment was from non-fertilized to 62 grams of 20-20-0 per tree, applied quarterly. In view of the fact that all plots of the native Latin American *Meliaceae* are so heavily attacked by *Hypsipyla grandella* that growth data are of little value, only three representative plots are included in Table 2.

Conclusions

From the data presented in Tables 1 and 2 the following conclusions may be drawn:

1) All the Latin American *Meliaceae* included in the trials were attacked by *Hypsipyla grandella*, but the exotics *Toona ciliata* var. *australis* and *Khaya ivorensis* were not attacked, although the latter two species were planted at a distance of only 3 meters from the attacked Latin American *Meliaceae*, in the Single Tree Plot Trials (Figs. 1, 2 and 3). In the Block Trials the distance between the plots of the native *Cedrela odorata* and *Swietenia humilis* (both heavily attacked and the exotic: *Toona ciliata* var. *australis* (not attacked) was 55 meters (Figs. 4 and 5).

2) Although only 7 out of 77 trees in the replications of the Single Tree Plots were *Meliaceae*, attacks of *Hypsipyla grandella* occurred. At least for the Turrialba area, this indicates that mixtures of *Meliaceae* with other forest species do not guarantee that *Hypsipyla* attacks will not occur.

Table 1.—Growth data and incidence of *Hypsipyla grandella* attacks on native and exotic *Meliaceae* in Single Tree Plot Trials in Turrialba, Costa Rica. All trees included in these trials were 13 months in the field.

Species	<i>Cedrela odorata</i>		<i>Khaya ivorensis</i>		<i>Swietenia humilis</i>		<i>Swietenia macrophylla</i>		<i>Swietenia macrophylla</i> x <i>maboganii</i>		<i>Toona ciliata</i> var. <i>australis</i>			
	Ghana	Costa Rica	Ivory Coast	Costa Rica	British Honduras	Virgin Islands	Hawaii							
Number of replications (=trees)	6	6	6	6	6	6	6	6	6	6	6	6	6	
Trees attacked by <i>Hypsipyla grandella</i> (%)	100	83	60	80	0	0	20	17	33	33	33	50	0	0
Fertilization	yes ¹	no	yes ¹	no	yes ¹	no	yes ¹	no	yes ¹	no	yes ¹	no	yes ¹	no
Number of surviving trees (out of 6)	5	6	5	5	6	6	5	6	6	6	6	6	6	6
Average height (m)	1.30	1.30	1.30	1.10	1.60	1.50	0.90	1.10	1.20	1.20	1.20	1.40	3.10	3.30
Tallest tree (m)	1.80	1.90	2.20	2.00	2.70	2.30	0.95	2.00	1.75	2.15	1.40	1.95	5.00	5.70
Smallest tree (m)	0.70	0.50	0.75	0.55	1.00	0.90	0.85	0.90	0.80	0.80	0.95	0.95	0.80	1.20
Average diameter (B.H.cm)	1.3	1.3	1.5	1.3	1.3	1.1	1.0	1.0	1.0	1.1	1.0	1.1	3.4	3.3
Biggest diameter (B.H.cm)	2.0	2.0	3.7	2.5	2.5	2.0	1.0	1.0	1.0	1.5	1.0	1.3	6.5	4.8
Smallest diameter (B.H.cm)	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

1) Fertilization consisted of a quarterly application of 62 grams of 20—20—0 per tree (250 grams per year).

3) Of the Latin American *Meliaceae* in the Single Tree Plot Trials, *Cedrela odorata* is attacked most frequently and *Swietenia humilis* the least, although the Block Trials indicate that *Swietenia humilis* (Fig. 4) is also highly susceptible to attacks of the shootborer. There is apparently no difference in susceptibility to attack between the two provenances of *Cedrela odorata* (Costa Rica and Ghana).

4) Of the two exotic *Meliaceae* that are not attacked by *Hypsipyla grandella*, *Toona ciliata* var. *australis* is far more promising than *Khaya ivorensis* in view of its faster growth and better form (Figs. 6 and 7); its valuable wood equals the qualities of *Cedrela odorata* and other Latin American *Cedrela* species.

Discussion

The present available data from the Single Tree Plot and Block Trials clearly indicate a preference of *Hypsipyla grandella* for the native *Meliaceae* included in the trials, and in particular for *Cedrela odorata*. It is also apparent that *Hypsipyla grandella* is able to detect and select these specific hosts from other trees. This host specificity may be due to the moth's ability to seek out and attack trees which emit specific volatile materials. It is interesting to note, that when young shoots and leaves of *Cedrela odorata* were crushed, a strong penetrating, garlic-like smell was produced, which was absent when leaves and shoots of *Toona ciliata* var. *australis* were treated in the same way.

Table 2.—Growth data and incidence of *Hypsipyla grandella* attacks on native and exotic *Meliaceae* in Block Trials in Turrialba, Costa Rica.

Plot location	<i>Toona ciliata</i> var. <i>australis</i> provenance: Hawaii				<i>Cedrela odorata</i> . Provenance: Costa Rica	<i>Swietenia humilis</i> . Provenance: Costa Rica	<i>Kbaya ivorensis</i> . Provenance: Ivory Coast	<i>Swietenia macrophylla</i> . Provenance: Venezuela		
	Atirro	Bajo Reventazón	Puente Cajón	Florencia Sur		Puente Cajón	Puente Cajón	Florencia Sur		Puente Cajón
Plot Size (ha)	0.04	0.04	0.04	0.012	0.012	0.04	0.04	0.012	0.012	0.04
Soil type	river bank clay	sandy river soil	sandy clay loam	sandy clay loam	sandy clay loam	sandy clay loam	sandy clay loam	sandy clay loam	sandy clay loam	sandy clay loam
Drainage	imperfect	good	imperfect	good	good	imperfect	imperfect	good	good	imperfect
Age after field planting (months)	15	12	17	13	13	12	24	13	13	48
Number of trees planted	100	100	100	20	20	100	100	20	20	49
Planting distance (m)	2 x 2	2 x 2	2 x 2	2.5 x 2.5	2.5 x 2.5	2 x 2	2 x 2	2.5 x 2.5	2.5 x 2.5	3 x 3
Survival (%)	95	91	94	100	95	88	81	100	100	70
Trees attacked by <i>Hypsipyla grandella</i> (%)	0	0	0	0	0	100	88	0	0	100
Fertilization*	yes	no	yes	no	yes	yes	yes	yes	no	yes
Average height (m)	4.10	4.40	5.70	3.00	3.40	0.57	0.67	1.43	1.47	1.45
Tallest tree (m)	6.80	6.10	7.10	4.60	5.00	1.20	1.40	2.25	2.30	3.30
Smallest tree (m)	1.10	0.80	1.90	1.40	1.60	0.10	0.10	1.00	1.10	0.60
Average diameter (B.H.cm)	3.8	4.1	5.7	3.2	3.8	**	**	1.2	1.3	3.3
Biggest diameter (B.H.cm)	7.4	6.5	8.4	4.7	3.0	**	**	2.5	2.5	5.6
Smallest diameter (B.H.cm)	1.0	1.0	1.5	1.0	1.0	**	**	1.0	1.0	1.0

* Fertilizer applications:

Atirro: one initial application of 50 grams of 20-20-0 per tree, applied two months after field planting.

Puente Cajón: quarterly applications of 50 grams of 20-20-0 per tree. (200 grams/years).

Florencia Sur: quarterly applications of 62 grams of 20-20-0 per tree. (250 grams/years).

** Trees are too small to be measured for diameters, due to repeated attacks by *Hypsipyla grandella*, and consequent ramification.

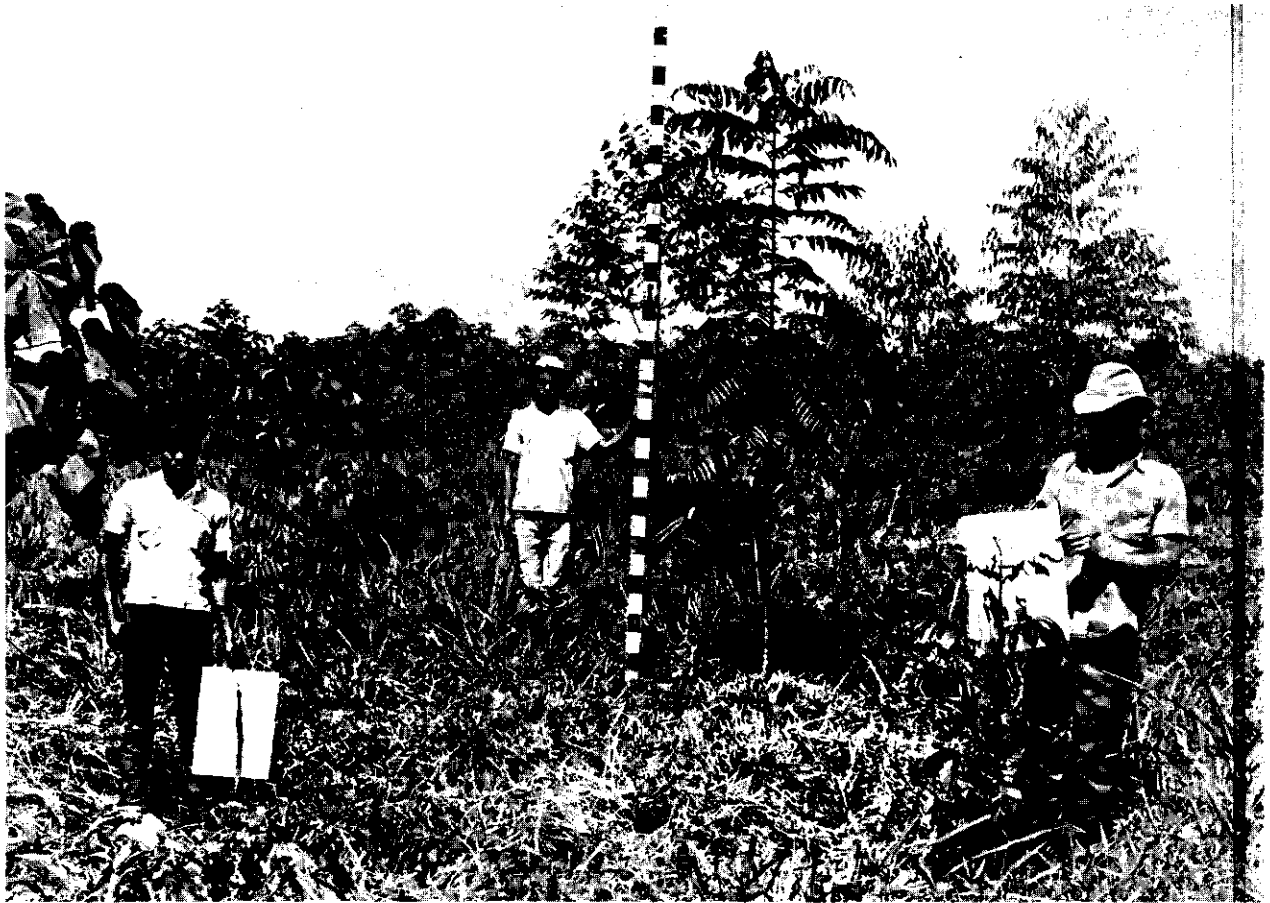


Fig. 1. Single Tree Plot Trials, Puente Cajón, Turrialba, Costa Rica. *Cedrela odorata* (right) and *Swietenia macrophylla* (left) are heavily attacked by *Hypsipyla grandella*, while *Toona*

ciliata var. *australis* is not attacked. Planting distance: 3 m; all trees 13 months in the field. Height of *Toona*: 3.25 m.

It is known that for oviposition some insects select hosts that produce specific essential oils. Ehrlich and Raven (11) discussing the selection of host plants by butterflies, indicate that analysis made it clear that their choices have a chemical basis.

These authors mention that Dethier had noted already several years ago that the apparently unrelated citrus and parsley families, which are both attractive to a group of swallowtail butterflies, had in common certain essential oils (*methyl chavicol*, *anethole* and *anisic aldehyde*) which presumably accounted for the attractiveness to the group of swallowtails. Dethier had also found that caterpillars of the black swallowtail butterfly would even try to feed on filterpaper soaked in these essential oils.

It seems probable that host selection of *Hypsipyla* on the *Meliaceae* may have a similar chemical basis.

Many investigations on essential oils of the *Meliaceae*, of which only a few are cited here, have already taken place, (2, 3, 4, 7, 8, 16) but as far as the available literature could be reviewed, they have not been related to the attacks of *Hypsipyla* spp.

Much research on the essential oils of *Meliaceae* has, for instance, been done in Nigeria by Bevan and collaborators (2, 3, 4). These authors (4) indicate that *anthotocol*, an extractive from *Khaya anthotoca* is related chemically and probably biologically to substances obtained from other *Meliaceae*. This could be the common chemical basis and reason why in all continents *Meliaceae* are attacked by *Hypsipyla* spp. Specialization of the *Hypsipyla* spp. on certain essential oils, might then result in immunity of exotic *Meliaceae* to borer attack if the trees lack or hardly possess these specific chemicals on which the native *Hypsipyla* have specialized.

With respect to the serious attacks of *Hypsipyla robusta* on *Swietenia macrophylla*, introduced into India and Ceylon (21), a comparative study on the essential oils of the shoots and leaves of local and exotic *Meliaceae*, may clarify these and similar cases, e.g. attack of *Hypsipyla robusta* on *Swietenia mahogani* in Australia (21). On the other hand it is also possible that the native *Hypsipyla* spp. may adapt to the new smell or taste of similar essential oils found in exotic *Meliaceae*,



Fig. 2. Single Tree Plot Trials, Puente Cajón, Turrialba, Costa Rica. *Cedrela odorata* (foreground) is heavily attacked by *Hypsipyla grandella*. *Toona ciliata* var. *australis* (left) and *Khaya ivorensis* (right, arrow) are unattacked. Planting distance: 3 m; all trees 13 months in the field. Height of *Toona*: 2.75 m.



Fig. 3. Single Tree Plot Trials, Bajo San Lucas, Turrialba, Costa Rica. *Cedrela odorata* (foreground) is attacked by *Hypsipyla grandella*, while *Toona ciliata* var. *australis* (arrow, above) and *Khaya ivorensis* (arrow, left) are unattacked. Planting distance: 3m; all trees 13 months in the field. Height of *Toona*: 5.00 m.



Fig. 4. Block Trial of *Swietenia humilis*, 24 months after planting, heavily attacked by *Hypsipyla grandella*. In the background

at a distance of 55 m, a plot of *Toona ciliata* var. *australis* (arrow), free of attacks. Puente Cajón, Turrialba, Costa Rica.



Fig. 5. Block Trial of *Cedrela odorata*, 18 months after planting, heavily attacked by *Hypsipyla grandella*. In the background

is the plot of *Toona ciliata var australis*, free of attacks. Puente Cajón, Turrialba, Costa Rica.

which after all, are probably related chemically to those of the native *Meliaceae*. A last possibility which is not very probable, but should not be completely discarded, is that an exotic *Hypsipyla* spp. may have been imported together with the exotic *Meliaceae*.

If the hypothesis of the olfactory orientation of the *Hypsipyla* moth is correct it might open new ways towards the solution of the *Hypsipyla* problem. A number of interesting research projects could then be initiated which ultimately would make it possible to



Fig. 6. Plot of *Toona ciliata var australis*, 18 months after planting, average height: 6.20 m; fertilized quarterly with 50 grams

of 20-20-0; unattached by *Hypsipyla grandella*. Puente Cajón, Turrialba, Costa Rica.



Fig. 7. Appearance of the trees of *Toona ciliata* var. *australis* (unpruned) in the Block trials in Puente Cajón.

establish, on a commercial basis, plantations of the fast growing valuable *Meliaceae* in the tropics.

The following research projects in relation to the *Hypsipyla* problem might be considered.

1) The olfactory orientation of *Hypsipyla* to its hosts. A preliminary investigation by the author is presently underway in Turrialba.

2) Investigation on other reasons why some exotic *Meliaceae* are not, or are less, attacked by the native *Hypsipyla* spp. If the moth of *Hypsipyla grandella* would be given no other choice but to oviposit on seedlings of *Toona* or *Khaya*, would the larvae then enter the shoots? Or are the shoots and bark chemically unpalatable to the larvae? This is also being investigated presently in Turrialba.

3) Analysis of the volatile essential oil(s) in the leaves and shoot of economically important *Meliaceae*,

by means of gas chromatography and N.M.R. and the subsequent determination of the host selection attractant(s) of *Hypsipyla* spp.; such chemicals might be used conceivably in the combat of *Hypsipyla* spp.

4) Selection and breeding of *Meliaceae* which do not have, or only have a low content of the attractant component in the leaves and shoots.

5) Crossing of the attack-free, or little attacked *Meliaceae* with species that are attacked by *Hypsipyla* (e.g. *Toona* with *Cedrela*) might also offer interesting aspects. The fact that *Toona* as well as *Cedrela* spp. can be propagated vegetatively is an additional advantage.

Finally the chemical composition of the essential oils of the *Meliaceae* may also be of interest to botanists and entomologists, who study the evolution and distribution of the *Meliaceae* and the genus *Hypsipyla* in the world.

Summary

Toona ciliata var. *australis* (Australian Red Cedar) and *Khaya ivorensis* (Nigerian Mahogany) included in Single Tree Plot and Block Trials in Turrialba, Costa Rica, are not attacked by *Hypsipyla grandella*, whereas native *Meliaceae* such as *Cedrela odorata* and *Swietenia* spp. are heavily attacked. In many countries of other continents these Latin American *Meliaceae* are not, or are less attacked by native *Hypsipyla* spp., although some countries report serious attacks.

The author supposes that volatile essential oils in the shoots and leaves, which would be different for various but probably not all *Meliaceae*, attract the moth of *Hypsipyla* spp. to its host trees. Specialization of the *Hypsipyla* moth on certain essential oils of native *Meliaceae* would lead to immunity of exotic *Meliaceae* which do not possess these essential oils as main elements. Some research projects related to the hypothesis of olfactory orientation of the *Hypsipyla*-moth to its host trees are suggested. In view of its fast growth, valuable timber and absence of attacks of *Hypsipyla grandella*, *Toona ciliata* var. *australis* seems a most promising plantation tree for Latin America.

Acknowledgements

The author wishes to thank Dr. Robert I. Gara, of the College of Forest Resources, University of Washington, for the critical review of the manuscript and the helpful suggestions. Thanks are also due to Dr. Herster Barres, Department of Forest Sciences, Inter-American Institute of Agricultural Sciences, Turrialba, Costa Rica, for having made available the growth data of the Single Tree Plot Trials.

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Studies on the shootborer Hypsipyla grandella (Zeller) (Lep., Pyralidae).
XXVII. Biological and chemical screening for the basis of resistance of
Toona ciliata M. J. Roem. var australis (F. v. M.) C. DC.*

P. Grijpma,** S. C. Roberts.***

COMPENDIO

La presente investigación fue dirigida a estudiar la base química de la inmunidad del cedro australiano (Toona ciliata var australis) al barrenador de las Meliaceas, Hypsipyla grandella. En plantaciones de campo se constató que el barrenador esta atraído y oviposita sobre el cedro australiano pero que las larvas eclosionadas mueren cuando penetran en los tejidos de esta especie. Experimentos con injertos de Cedrela odorata L. sobre un madriz de Toona resultaron en inmunidad de Cedrela al barrenador. En pruebas empleando compuestos de hojas extraídas por una serie de solventes orgánicos mezclados con los ingredientes de dieta artificial para Hypsipyla se obtuvo una mortalidad de 50, 53, 42 porciento de las larvas del barrenador con las extracciones de acetona, agua y hexano respectivamente.

Utilizando la técnica de cromatografía de capa fina, se estableció que existen probablemente dos componentes tóxicos y polares en la extracción acuosa de hojas del cedro australiano, uno de los cuales es altamente

*Received for publication 18 September 1974.

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polar. En cantidades equivalentes a 50 mg de hojas de Toona, estos compuestos cuando inyectados oralmente en larvas del sexto instar de H. grandella causaron una mortalidad de 80 por ciento de las larvas. En una dosis equivalente a 150 mg de hojas en Toona la fracción purificada del compuesto más polar, resultó en una mortalidad de 100 por ciento de las larvas tratadas.

INTRODUCTION

The Australian red cedar (Toona ciliata var australis; Meliaceae) was introduced in November 1967 in Costa Rica, for inclusion in the tree species trials of the Department of Tropical Forest Sciences of IICA-CTEI. In May 1968, the first field plot was established which soon showed excellent growth and complete absence of attacks of Hypsipyla grandella (Zeller). This absence of attacks was particularly striking since neighboring trial plots of Cedrela odorata L. were heavily attacked by the shootborer. The undisturbed growth and the fact that the leaves and young shoots of the Australian cedar, in contrast to the native C. odorata, did not produce any particular smell led to the hypothesis that H. grandella might orient itself towards native hosts by means of chemo-reception, but that the shootborer would be unable to detect the possibly different volatile compounds of young leaves and shoots of the exotic Australian cedar (5,6).

In May 1971 however, eggs of H. grandella were found on the Australian cedar during a field survey. This finding resulted in a series of investigations on the resistance of T. ciliata var australis against H. grandella attacks, which are summarized below under confirmation, grafting and toxicity trials.

Materials and methods

Resistance confirmation trials.

During field inspections in a mixed trial plot consisting of C. odorata, Pinus massoniana Lamb. and T. ciliata var australis, 100 H. grandella eggs were found on stems of five, approximately 3 m high Toona trees. The eggs were removed from the bark of the trees for laboratory investigations.

Larvae emerging from the eggs were divided into two groups and placed in sealed plastic boxes containing leaves of C. odorata and T. ciliata var australis respectively. Feeding material was renewed whenever necessary, e.g. from once every five days during the first and second instars to once every two days in the last instar of the H. grandella larvae.

Observations with respect to feeding, mortality, pupation and emergence were made and two male and female adults were dissected for species identification.

Average maximum and minimum temperature in the laboratory were 30.3°C and 22.0°C respectively; average maximum and minimum relative humidity were 68.9 and 50.5 percent.

Grafting trials.

In order to determine if chemical compounds present in Toona could be translocated into C. odorata and promote resistance against H. grandella, the native C. odorata was grafted on stems of Toona. The mortality of first instar larvae placed on these grafts was compared with that of larvae placed on seedlings of Toona and Cedrela.

The experiment was conducted in a greenhouse where the average maximum and minimum temperature were 31.4°C and 19.0°C respectively; the average maximum and minimum relative humidity were 96.2 and 78.4 percent.

Larvae provening from H. grandella reared on Cedrela plant material were placed onto the middle of the stem of ten grafts of C. odorata on Toona, ten Toona and ten Cedrela plants of approximately 45 cm height. Each plant received two groups of four larvae, the second group being released three days after the first to enhance survival of the individuals.

The plants were checked for small ants and spiders which predate upon first instar H. grandella larvae. Stickum-Special[‡] was put around the stems at the height of the grafting to impede any future predation and to prevent larvae from boring into the Toona stem.

Survival of the larvae was observed by daily removal of fresh frass from the boring holes. If fresh frass was not produced during two days

[‡]Michel and Pelton Co., Oakland, California.

and no additional boring holes were noted, the larvae were considered dead.

An additional experiment was conducted under laboratory conditions as a control for the greenhouse grafting trial. First instar H. grandella larvae were reared on leaflets obtained from potted plants of C. odorata, T. ciliata var australis and of C. odorata grafted on stems of T. ciliata var australis respectively. The larvae (100/treatment) were subdivided into groups of ten and placed on the leaflets in small, sealed plastic boxes. Survival of the larvae was checked daily under a microscope.

Toxicity tests:

As the previously described tests strongly suggested the existence of chemical toxicity in the plant tissue of the Australian cedar, further experiments were conducted to isolate the responsible fraction(s).

Young shoots and leaves of T. ciliata var australis and C. odorata (for control) were subjected to solvent extraction and subsequent thin layer chromatography (TLC) in order to produce chemical fractions suitable for bioassay. The solvents employed in the extractions; e.g. hexane, ethyl ether, acetone, benzene, chloroform, methanol and distilled water; were selected to include a wide range of solubility parameters, polarities and hydrogen bonding capabilities (4,7). All solvents were reagent grade except acetone and water which were distilled prior to use. Hydrophilic solvents such as acetone, benzene and methanol were dried during the extractions with anhydrous sodium sulfate so that their solvent properties would not change as result of hydration from the water in the leaves.

Extracts of Toona and Cedrela leaves (20g) were obtained by macerating the foliage suspended in solvent (75ml) for approximately five min in an Osterizer blender. The fibrous mass was soaked overnight and subsequently filtered on the foraminous plate of a Buchner funnel. Frequently further clarification with analytical grade filter aid was required. The resulting clear extracts were refrigerated until use.

In the first series of trials, each separate extract (75ml) was mixed with the dry components of synthetic diet (64g) which consisted of commonly

used ingredients (1) except for agar and its corresponding water component. These were omitted since they did not add to the nutritional value of the diet and only would dilute any possible toxic compound present in the fractions. The mixtures were placed in an oven (45°C) for two h to allow the solvents to evaporate. Thereafter the liquid components of the synthetic diet were added and thoroughly mixed with the dry parts which now contained the extractable chemical compounds of Toona (or Cedrela in case of the controls).

When water extracts of Toona or Cedrela were mixed with the dry components of the diet, an equal volume of water was omitted from the normal diet composition, as it was virtually impossible to evaporate the water component of these fractions under the humid ambiental conditions of Turrialba.

The concentration of the extracted chemicals was equivalent to approximately one g of Toona or Cedrela leaves per 8 g of artificial diet. However, the extraction process is not 100 percent efficient nor is it assured that the active components of Toona are chemically stable. Moreover, some chemical interaction (e.g. oxidation or reduction) between the artificial diet components and the Toona extract could result in inactivation of the originally toxic Toona compound(s). As the chemical constituents of the Toona and Cedrela fractions might also be influenced by the acidity of the artificial diet ingredients and consequently influence mortality of the second instar larvae employed in these experiments, the pH of samples of these diets was determined and compared with that of the commonly used rearing medium. For this purpose diet samples (2g) were diluted with distilled water (10ml) and the acidity of the suspension measured with a Beckman Zeromatic pH meter.

Second instar larvae (10-20/treatment) were placed individually in small rearing bottles containing the diet ingredients mixed with the extractives from one of the methanol, benzene, chloroform, hexane, acetone, water and ethyl ether fractions of Toona and Cedrela. Development of the larvae, mortality and time needed to pupate and emerge were recorded.

The bioassay of these diets yielded ambiguous results with respect to the toxicity of the Toona compounds obtained; nonetheless some indication

was provided of which extracts contained possible toxicants.

At this point, additional force-feeding tests (11) were employed: In these experiments sixth instar larvae of H. grandella were force-fed with concentrated water and hexane extracts of Toona leaves (30 ul/larva). The higher concentration was prepared by extraction of a larger amount of Toona leaves (40 g/75 ml solvent). Water and hexane extracts of Cedrelela obtained in identical procedures, were used as controls in these tests.

In order to avoid any effects of the organic solvent on the larvae an aliquot of the hexane extract (13 ml) was evaporated onto the surface of distilled water (2 ml) containing a few drops of a surfactant Tween-20[‡]. Prior to force-feeding the larvae, the extract film was emulsified in the water, so that it could be readily injected.

An "Aglia" micrometer syringe, Burroughs Wellcome & Co., England and a micrometer, Shardlow Micrometers Ltd., Sheffield, England, in combination with a blunted Yale No. 27 hypodermic needle were used in these trials.

For each extract, ten to fifteen sixth instar larvae were individually anaesthetized prior to treatment by placing them in a CO₂ chamber for approximately 60 s. Subsequent force-feeding was facilitated by the use of a stereo microscope to ensure elimination of any larvae that might have been injured during the oral injection. Needle penetration was approximately 3-4 mm into the mouth parts. After treatment, the force-fed larvae were placed in glass jars and mortality during larval and pupal stages was recorded.

Since the aqueous extract of Toona proved to be highly toxic, further separation of its components was obtained through thin layer chromatography (TLC) (12).

The TLC plates (Cellulose 300 G with CaSO₄ binder, Macherey, Nagel and Co.) were prepared using a Desaga type spreader (12) and dried in an oven at 105°C for 15 min. Three plates (20 x 20 cm) were used to separate aliquots of an aqueous extract (T-33) equivalent to 2 g of Toona per plate. The developing solvent and the characteristics of the resultant observable

[‡]ICI America Inc., Atlas Chemical Division, Wilmington, Delaware.

bands (by visual or ultraviolet light) are shown in Table 1[‡]. Three bands from each of the developed plates were removed. The first contained the starting band and the thin fluorescent band (254nm) ($R_f=0.0-0.3$); the second band comprised the middle region with no identifying characteristics ($R_f=0.3-0.7$) and the third contained the rest of the developed region ($R_f=0.7-1.0$) including a green band and fluorescent band (254 nm). The isolated TLC samples were extracted with water (10ml) for 24 h, concentrated appropriately and the resultant aqueous extracts force-fed to sixth instar H. grandella larvae (10-20) as previously described using calculated doses of 50mg of original foliage per larvae.

In the ensuing bioassay the third band was identified as being active; thus, the separation was repeated on a fresh extract (T-34) with a more polar ethyl acetate-methanol solvent (2:3) in an effort to concentrate the mobile components into the final region ($R_f=0.8-1.0$). This band was then removed and rechromatographed with a less polar benzene-ethyl acetate (3:1) solvent and separated again into three sections consisting of the starting band, the middle ($R_f=0.2-0.8$) and the final region ($R_f=0.8-1.0$). These sections were again removed from the glass plates, extracted with water, concentrated as before and force-fed to larvae in doses equivalent to 150mg of original foliage per larvae. It was expected that the less polar developing solvent would effect a better separation of the mobile components by removing the non-polar constituents from the sample.

Results and discussion

Resistance confirmation trials

These experiments resulted in a 100 percent mortality of all first instar H. grandella larvae that were placed on a Toona leaf diet. Actual boring into the leaflets was observed and excrements were found on the leaflets. Fifty percent of these larvae died within 24 hours, 42 percent died within 48 hours and the remainder within 72 hours. The larvae readily accept the offered Toona as food and are apparently unable to detect the toxic properties of the plant material prior to feeding. Several dead first instar larvae could be found with their heads still sticking in the boring holes (Fig. 1). This prompt death suggested the existence of a toxic compound rather than absence of essential food components.

[‡]The tables and figures which accompany the text are located at the end of this paper.

Seventytwo percent of the first instar larvae placed on Cedrela leaflets were reared through to the adult stage; the remainder died due to cannibalism and bacterial infections during the rearing. The dissected specimens were identified as Hypsipyla grandella (Zeller).

Since H. grandella is attracted to the Australian cedar, oviposits on it and its larvae are stimulated to feed on the plant material notwithstanding its toxicity, the tree acts as a natural trap for the insect. Therefore, it might be conceivable to employ the Australian cedar in plantations where this exotic is mixed with native Meliaceae, so as to reduce the Hypsipyla population and keep its damage below a certain threshold. However, several uncertainties ought to be considered before such planting schemes are put into practice. Firstly, development of resistance of H. grandella against Toona could well be promoted if larvae which started to feed on this tree species might continue to feed on Cedrela or Swietenia, e.g. by migration from Toona trees. Other aspects which should still be investigated are, whether the adult has a preference for the different tree species employed in these mixtures and to what degree the shootborer population is effectively influenced by these mixtures. Moreover, a single female can oviposit over 1000 eggs under laboratory conditions and field observations have shown that over 50 percent of the trees in a young Cedrela odorata plantation contained only 1-3 eggs per tree; consequently deficiencies in the effectiveness of Toona as a natural trap for Hypsipyla in mixed meliaceous plantations are expected. Oviposition by lepidoptera on introduced plants closely related to native hosts but toxic to their larvae, is also reported by Dethier, Straatman and others (2,3,10) Straatman (10) suggests that there has been insufficient time for these insects to adapt to the introduced plants, i.e. the adults are unable to discriminate between the introduced plant and the native host, and the larvae have not yet developed the ability to feed on them. Painter (8,9) indicates that the development of host plant preference involves a simultaneous evolution of both the plant resistance mechanisms and of tolerance and host preference of the insect, resulting in the formation of a dynamic equilibrium. In the case of the Australian cedar and Hypsipyla grandella, the lack of this simultaneous evolution of resistance mechanisms may have resulted in the present immunity of the tree to this

insect species. However, as indicated in earlier publications (5,6) a number of reports exist which show the successful attack of native Hypsipyla spp. on recently introduced exotic Meliaceae. For example, of two Meliaceae introduced from India into Puerto Rico, Chukrasia tabularis A. Juss. and Toona ciliata, the former is successfully attacked by H. grandella and the latter not.* Although no explanation has been found yet to account for this difference in susceptibility, it is apparent that resistance does not depend solely on the absence of a simultaneous evolution of the insect and the tree species.

Grafting trials

The results of these trials under both laboratory and greenhouse conditions are shown in Figs. 2 and 3. The grafts of Cedrela on Toona were found to be resistant against H. grandella (Fig. 4, a-d) although not to the same extent as the Toona plants.

The resistance induced in the grafts of Cedrela indicated that the plant constituent(s) responsible for this resistance could be translocated from the Toona understem to the Cedrela graft. However, it should be pointed out that the grafts were only 4 months of age. Further experimentation with older grafts is indicated to confirm the persistence of the induced resistance. In addition, it would be recommendable to include grafts of Toona on Cedrela stems in these trials to determine whether the Toona grafts would become susceptible to H. grandella attack.

Toxicity trials

The highest mortality of H. grandella larvae placed on diets consisting of the commonly used rearing ingredients and the Toona leaf extracts was most consistently found in the water (T-17) and hexane Toona (T-16) extracts (Table 2). Fig. 5 demonstrates the anomaly in the development of larvae feeding on diets containing these extracts. The larvae placed on these diets not only developed more slowly but their mortality was higher (25 and 20 percent respectively) than with other extracts. In particular, initial pupation of the larvae feeding on the mixture of diet ingredients and the aqueous Toona extract took more time than pupation

*Geary, T. F. Institute of Tropical Forestry, Rio Piedras, Puerto Rico. Personal communication, July 1969.

of those placed on any of the other diet mixtures. In addition, in this experiment, mortality during the pupal stage was remarkably high for the treatments in which H. grandella was placed on mixtures of either the water or hexane Toona extracts. In these treatments an additional 25 and 30 percent respectively of the H. grandella died during the pupal stage (Fig. 6). Frequently incomplete wing development was observed in pupae of larvae feeding on these diets.

Pupal weight of H. grandella placed on the mixtures of the Toona extracts with diet ingredients corresponded to a large extent with the mortality percentages documented above. Average weight of pupae reared on CTL (diet ingredients only) C₇, T₁₅, T₁₄, T₁₆, and T₁₇ diet mixtures were respectively 159 mg (range 140-175 mg) 144 mg (range 115-165 mg), 149mg (range 90-185 mg), 144 mg (range 104-180 mg), 113 mg (range 65-170) and 80 mg (range 45-120 mg). In the T₁₇ mixtures only 20.0 percent of the pupae weighed over 100 mg, whereas the corresponding percentages for the T₁₆, T₁₅, T₁₄, C₇ and CTL mixtures (Table 3) were respectively 68.7; 88.9; 100; 100 and 100 percent.

The acidity of the Toona diet mixtures differed little from that of the control and Cedrela mixtures (Table 2) thus, any effect of this factor was discounted.

The only other Toona fraction that caused high mortality of H. grandella larvae, was the acetone extract (T₁₈) (Table 2). However, the mixture of this extract with the diet ingredients resulted in a contaminated (sour) feeding medium. It is unknown whether the contamination per se, or a toxic Toona compound had caused this mortality. Further investigation of this fraction was not pursued in view of the high mortality encountered in the water and hexane extracts of Toona.

The mortality levels observed in the controls which consisted of those larvae reared on either the commonly used rearing ingredients only or the corresponding Cedrela fractions mixed with these ingredients, were considered normal.

Since these diet-mixture tests suggested that the active compound(s) of Toona might be chemically labile, the hexane (T₃₂) and water (T₃₁) extracts of Toona were bioassayed by force-feeding sixth instar larvae.

The results of these tests clearly demonstrated the toxicity of the fresh aqueous Toona fraction, although a certain degree of toxicity was still present in the hexane fraction (Table 4). Moreover, the reduced mortality obtained with an aqueous Toona extract which had been stored under nitrogen for one week at 5°C seems to confirm the suggested instability of the chemical(s) involved.

Both aqueous subfractions T₃₃-TLC-1 and T₃₃-TLC-3, obtained from the thin layer chromatography plates, caused 80.0 percent mortality in the treated larvae, whereas the subfraction T₃₃-TLC-2 had practically no effect (6.7 percent mortality). This finding appears to indicate that two toxic, water-soluble chemical compounds are probably present, one of which is highly polar. Since neither of the subfractions T₃₃-TLC-1 and T₃₃-TLC-3 is as toxic as the original extract T₃₃ in spite of more concentrated dosages force-fed (150 mg vs. 50 mg Toona leaf equivalents) a synergism is suggested.

Confirmation of the toxicity of the highly polar compound in the chromatographed aqueous extract TLC-3(T₃₄) was obtained when this subfraction was rechromatographed in additional tests (T₃₄-TLC-3-1,2,3). The mortality caused by the subfraction T₃₄-TLC-3-2 is probably due to some overloading of the plates (Table 4).

The solubility of the toxicants in water would be in accordance with the results obtained in the grafting trials, where translocation of the toxicant(s) present in the Toona stems induced resistance against Hypsipyla in the C. odorata grafts.

Acknowledgements

The authors wish to thank Mrs. Cathi Roberts for her efficient assistance during the experiments. In particular, appreciation is due to Dr. W. Albertin, Head of the Department of Tropical Forest Sciences and Dr. O. Hidalgo-Salvatierra formerly at IICA/NEP in Turrialba, Costa Rica, for facilitating this research. The critical review of the manuscript by Dr. G.G. Allan, Dr. L.M. Schoonhoven and Dr. J. de Wilde is gratefully acknowledged. The support of this study was provided by the Netherlands Ministry of Development Co-operation.

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Table 1. Characteristics of observable bands of aqueous Toona extracts on cellulose TLC-plates.

Sample Code no.	Developing solvent	R _f values	Characteristics of observable bands
T ₃₃	Ethyl acetate-Methanol (1:1)	0.2-0.3	Fluorescent at 254 nm
		0.8-0.9	Green
		0.95-1.0	Fluorescent at 254 nm
T ₃₄	Ethyl acetate-Methanol (2:3)	0.2-0.3	Fluorescent at 254 nm
		0.8-0.9	Green
		0.93-1.0	Fluorescent at 254 nm
T ₃₄ -TLC-3	Benzene-Ethyl acetate (3:1)	0.92-1.0	Light green

Table 2. Average mortality of H. grandella larvae reared on mixtures of artificial diet ingredients and Toona (T) or Cedrela (C) leaf extracts.

	Sample Code No.	Extracting agent	pH of diet-mixtures	No. of replications	No. of replications with dead larvae	Average Mortality (%)
<u>Toona</u>	T ₉	Methanol	4.98	10	0	0.0
	T ₁₀ , T ₁₄	Benzene	5.06	30	8	26.6
	T ₁₁ , T ₁₅ , T ₁₉	Chloroform	5.00	40	11	27.5
	T ₁₂ , T ₁₆ , T ₂₀ , T ₂₂	Hexane	5.01	50	21	42.0
	T ₁₃ , T ₁₇ , T ₂₁ , T ₂₅	Water	5.01	60	32	53.3
	T ₁₈	Acetone	4.96	10	5	50.0*
	T ₂₆	Ethyl Ether	5.12	20	2	10.0
<u>Controls</u>	(CLT)	Diet ingredients only	5.00	50	7	14.0
<u>Cedrela</u>	C ₃	Methanol	4.95	10	0	0.0
	C ₂ , C ₁₀	Benzene	5.08	30	4	13.3
	C ₅	Chloroform	5.02	10	2	20.0
	C ₄	Hexane	5.04	10	1	10.0
	C ₆ , C ₇ , C ₁₆	Water	5.04	50	9	18.0
	C ₁₈	Acetone	5.06	10	0	0.0
	C ₁₇ , C ₁₉	Ethyl Ether	5.13	30	3	10.0

* Contaminated diet; turned sour.

Table 3. Pupal weight (mg) of *H. grandella* reared on mixtures of artificial diet ingredients and *Toona* (T) or *Cedrela* (C) leaf extracts.

Pupa No.	Control CTL	Water C7	Chloroform T15	Benzene T14	Hexane T16	Water T17
1	140	155	157	154	95	92
2	145	160	148	178	115	58
3	161	159	90	172	120	45
4	174	164	155	180	108	46
5	150	152	180	104	170	80
6	149	141	185	128	112	75
7	162	158	165	160	65	105
8	175	128	155	155	140	85
9	173	165	106	161	90	65
10	165	161	166	155	115	100
11	153	143	105	125	95	95
12	162	163	153	135	125	85
13	146	164	171	108	124	70
14	170	156	185	167	116	120
15	171	139	97	136	98	80
16	116	154	155	133	120.	---*
17	158	157	168	134	---*	---*
18	149	158	149	107	---*	---*
19	152	149	---*	---*	---*	---*
20	---*	---*	---*	---*	---*	---*
Average weight	159	154	149	144	113	80
Percentage \geq 100 mg	100.0	100.0	88.9	100.0	68.7	20.0

*larva died.

Table 4. Mortality of sixth instar H. grandella larvae force-fed with Toona and Cedrela hexane and water extracts and TLC-subfractions of Toona water extracts.

Extracts and code number	N ^o of larvae treated	N ^o of larvae pupated	N ^o of adults emerged	Mortality %
<u>Toona</u> , water (T ₃₁)	12	2	2	83.3
<u>Cedrela</u> , water (C ₂₁)	15	13	11	26.7
<u>Toona</u> , water (T ₃₁)	12	6	6	50.0*
<u>Cedrela</u> , water (C ₂₁)	12	11	11	8.3*
<u>Toona</u> , hexane (T ₃₂)	17	13	11	35.3
<u>Cedrela</u> , hexane (C ₂₂)	17	15	15	11.8
<u>Toona</u> , water (T ₃₃)	15	1	1	93.3
TLC-1	15	3	3	80.0
TLC-2	15	14	14	6.7
TLC-3	15	3	3	80.0
<u>Toona</u> , water (T ₃₄)				
TLC-3-1	12	1	0	100.0
TLC-3-2	12	10	8	33.3
TLC-3-3	12	12	12	0.0

* Same extracts (T₃₁, C₂₁) as used in previous test, but kept for 7 days in refrigerator at 5° C.



Fig.1. Due to a toxic compound in Toona ciliata var australis, first instar larvae of Hypsipyla grandella boring into its tissue frequently die in 2 to 4 h.

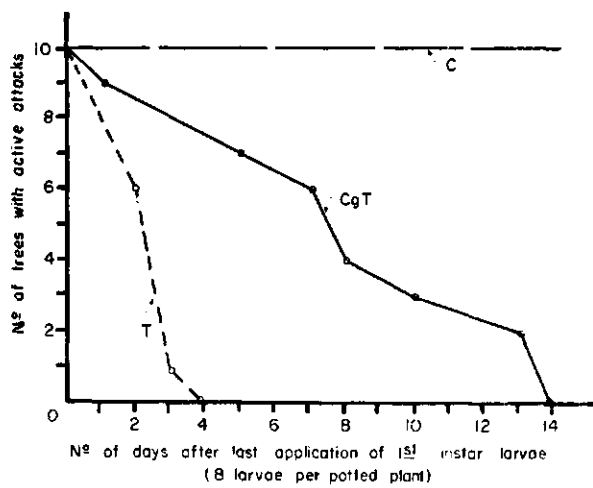


Fig.2. Time dependence of boring activity of first instar H. grandella larvae in plants of C. odorata (C), of T. ciliata var australis (T) and of C. odorata grafted on T. ciliata var australis (CgT).

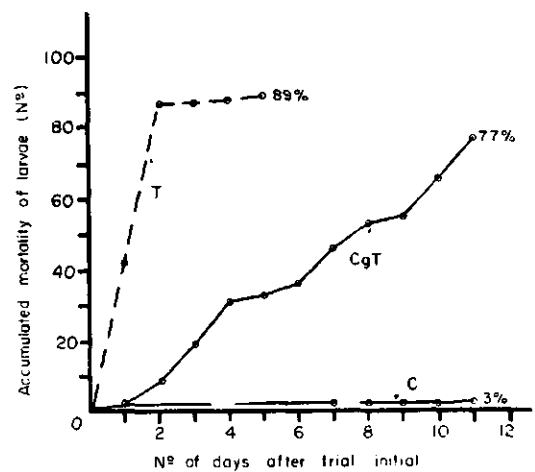


Fig.3. Time dependence of accumulated mortality of 100 first instar H. grandella larvae on leaf diets of C. odorata (C), of T. ciliata var australis (T) and of C. odorata grafted on T. ciliata var australis (CgT).

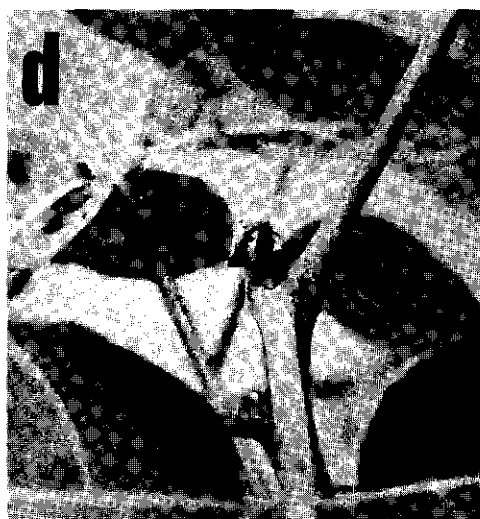
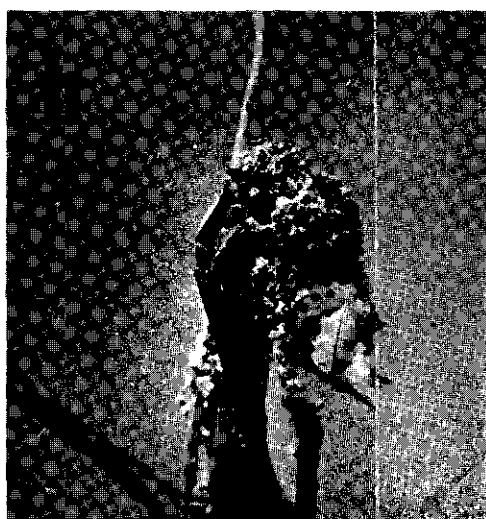
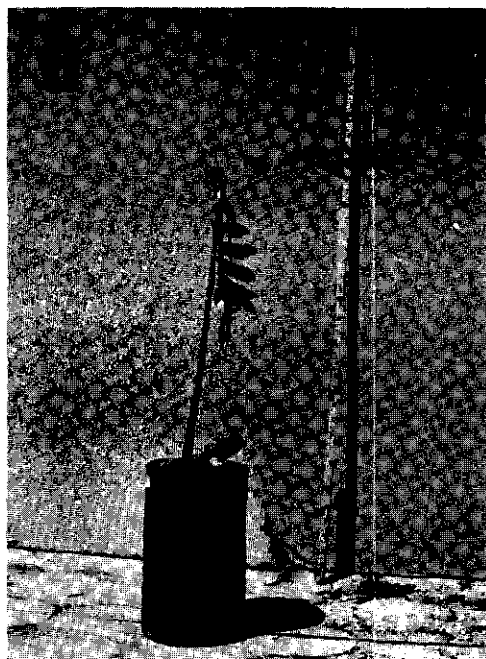


Fig.4.a-d. Effect of H. grandella attack on C. odorata seedlings (a,b) and on C. odorata grafted on T. ciliata var australis (c,d). Pictures taken three weeks after placement of first instar larvae on the plants.

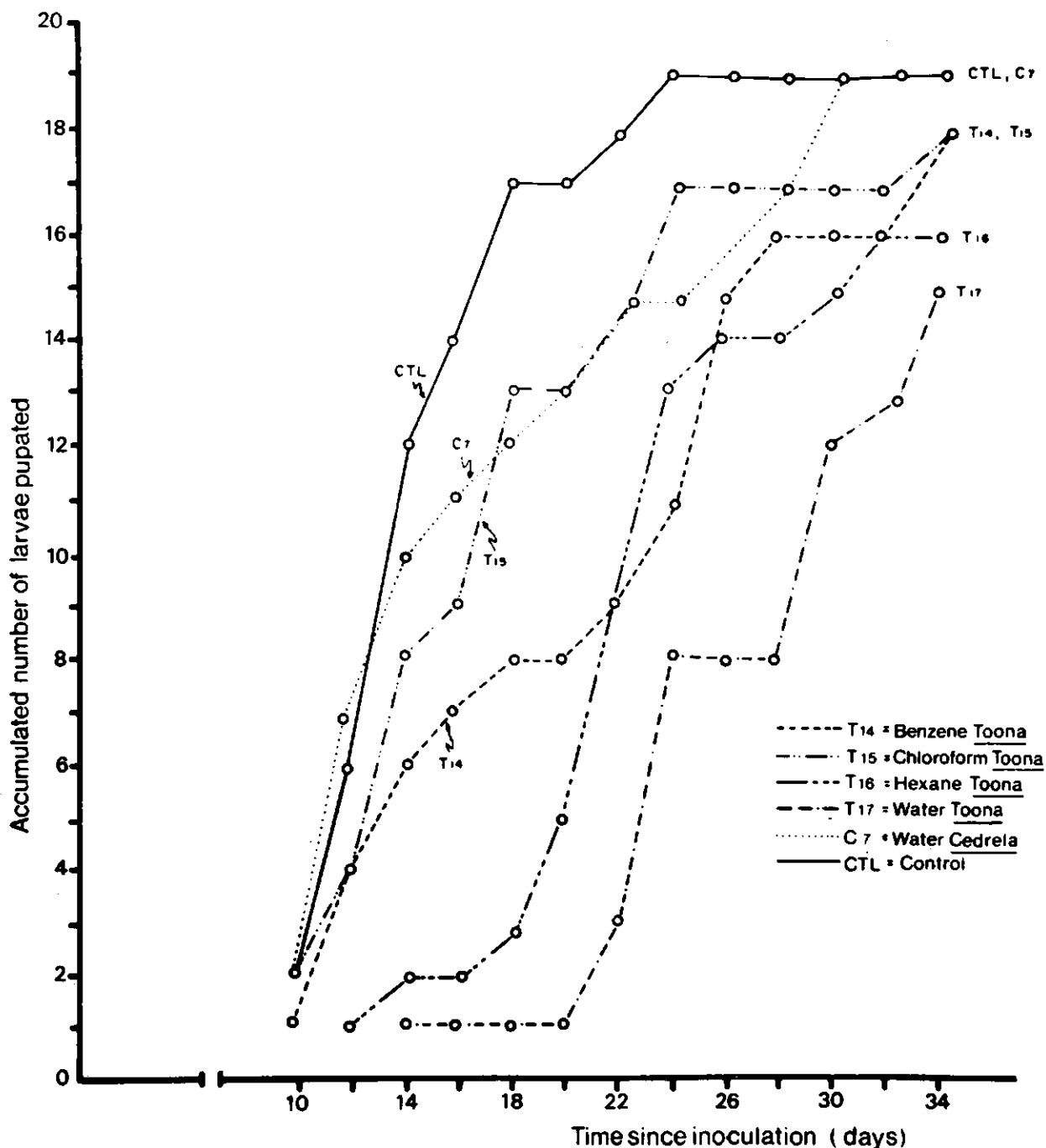


Fig.5. Time required for 20 *H. grandella* larvae of the second instar to pupate after feeding on artificial diet (CTL) and mixtures of artificial diet ingredients with leaf extracts of *Toona* (T₁₄-T₁₇) and *Cedrela* (C₇). Larvae not accounted for died during the experiment.

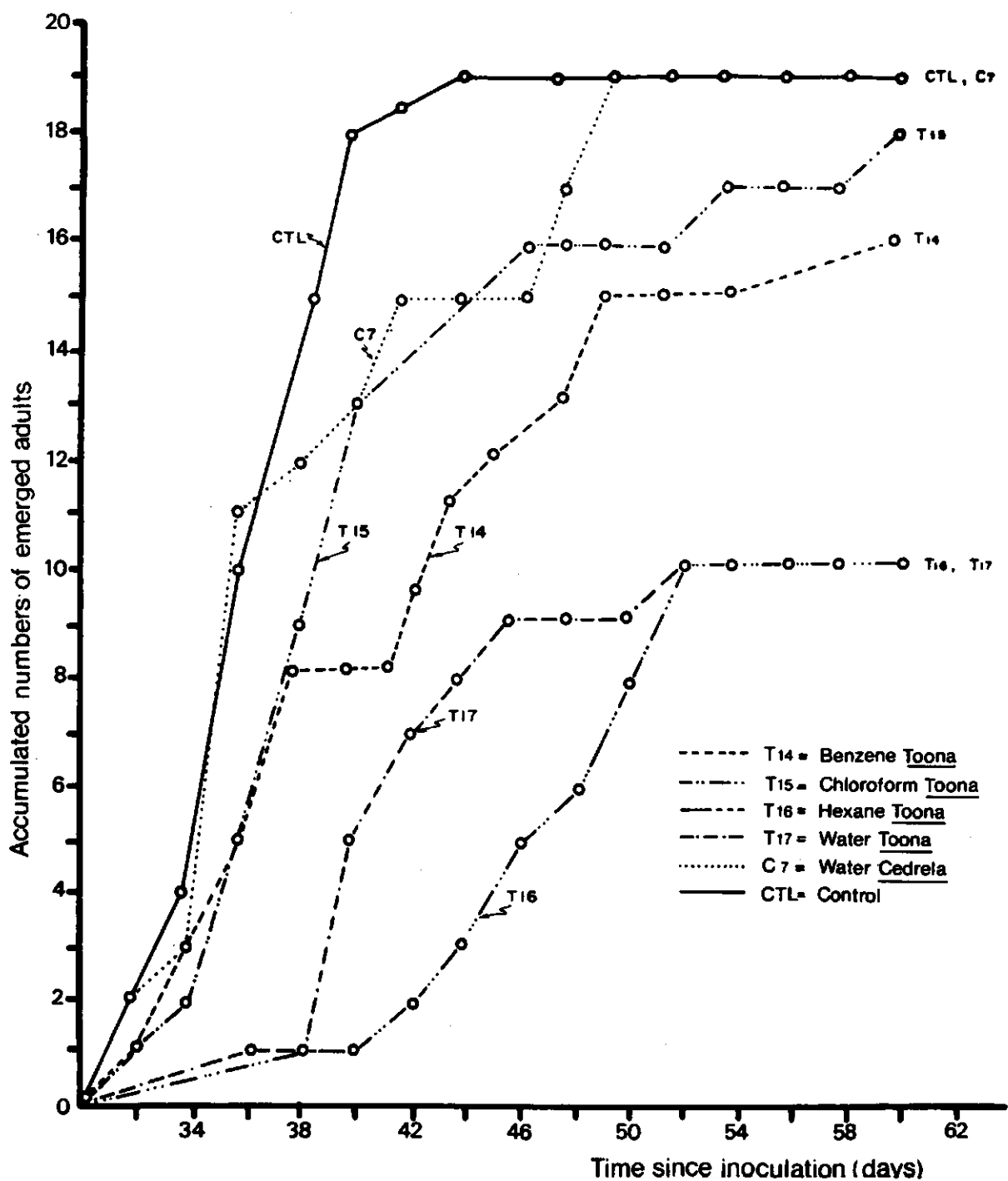


Fig.6. Time required for 20 *H. grandella* larvae of the second instar to emerge as adult after feeding on artificial diet (CTL) and mixtures of artificial diet ingredients with leaf extracts of *Toona* (T₁₄-T₁₇) and *Cedreia* (C₇). Adults not accounted for died during the larval or pupal stage.

2.2. INVESTIGATIONS ON THE HOST SELECTION OF *H. GRANDELLA*.

Papers:

- 2.2.1. Studies on the shootborer *Hypsipyla grandella* Zeller. I.
Host selection behavior. *Turrialba* 20(2):233-240. 1970.
- 2.2.3. Studies on the shootborer *Hypsipyla grandella* Zeller. II.
Host preference of the larva. *Turrialba* 20(2):241-247.
1970.

Studies on the shoot borer *Hypsipyla grandella* Zeller.

I. Host selection behavior* ————— P. GRIJPMA**, R. I. GARA***

COMPENDIO

Este trabajo presenta los resultados de una serie de experimentos relacionados con la selección de los árboles hospederos por el adulto de *Hypsipyla grandella* Zeller. Los objetivos fueron: (1) investigar el comportamiento del adulto en cuanto al vuelo; (2) estudiar las condiciones microclimáticas asociadas con el vuelo; y (3) determinar modelos de los ataques del barrenador en relación a la fenología del árbol hospedante y posibles atrayentes. Los datos obtenidos indicaron que, en una parcela de *Cedrela odorata* L. fuertemente atacada por el barrenador, los adultos volaron a alturas más altas que los arbolitos, los cuales tenían una altura promedio de 0,6 m. También se observó otro modelo de vuelo que consistía en un vuelo corto de los árboles hospederos a la vegetación baja que cubre el suelo y viceversa. En cuanto a la relación entre las condiciones microclimáticas y el vuelo, la duración del estudio fue demasiado corta para llegar a conclusiones definitivas. No obstante se observó que los adultos no volaron cuando la temperatura fue inferior a 17°C. Precipitaciones menores que 11 mm no impidieron el vuelo. La actividad mayor durante el periodo de estudio se registró después de una fuerte lluvia.

Hay indicaciones bastante definidas que el adulto de *H. grandella* se orienta a su hospedero por medio del olfato y que existe una alta correlación entre el número de ataques por árbol y la proporción de hojas frescas. — Los autores.

Introduction

THE shoot borer of Meliaceae, *Hypsipyla grandella* Zeller., is the greatest detriment to the establishment of *Cedrela* and *Swietenia* plantations in the American tropics. The main damage occurs when larvae bore into the growing tips of young plants, thus destroying height growth for a season or more. The biology and distribution of *H. grandella* has been described by Ramirez Sanchez (9).

It is believed that *H. grandella* selects new hosts at night as adults are active during this period. Ramirez Sanchez (9) observed that greatest flight activity occurred after dark and egg eclosion took place from 18:30 h. and on through the night.

Since trees over 6 meters in height are not as heavily attacked as the shorter stems, it is assumed that host selection flights occur mainly at lower levels, i.e., the heights of seedlings and younger stems. Field experience shows that once a plot is invaded by the shoot borer the incidence of infestation augments rapidly and eventually all of the plantation is infested. In time, trees degenerate to such an extent that heavy mortality ensues. Apparently, once a plantation is infested, the moths tend to concentrate within the outbreak.

Unfortunately, little is known on microclimatic and other environmental conditions that influence *H. grandella* flights. The only reports available indicate that heavier attacks occur at the beginning of the rainy seasons, with only minor infestations occurring at the initiation of the dry season (1, 2, 8, 9, 11). In addition,

* Received for publication April 7th, 1970.

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attacks primarily occur in open grown plantations, indicating that temperature among other physical factors may be important in guiding host selection flights. Recent studies (7, 10) indicate that *Hypsipyla* spp. exhibit definite host preferences for certain meliaceous species. In Costa Rica, Grijpma (7) conclusively showed that *H. grandella* preferred *C. odorata* over *Swietenia macrophylla* King, *S. humilis* Zucc. and a hybrid cross of *S. mahogany* (L.) Jacq. \times *S. macrophylla*. However, the insects did not attack *Toona ciliata* M. Roem. var. *australis* (F.v.M.) C. DC. and *Khaya ivorensis* A. Chev. He suggested that the preference of *H. grandella* for *Cedrela* was due to the olfactory response of shoot borers to volatile materials emanating from the plant.

It is believed that a more complete knowledge on the host selection behavior of the shoot borer would provide insights into more imaginative and applicable control methods. In particular, verification of primary attractants could lead to isolation and identification of such compounds; synthesis of these materials could be used in the protection of valuable stands. Identification of these compounds also could lead to a tree breeding program in which less susceptible trees would be developed. Accordingly, the main objectives of the studies described here were to gain insights into the host selection mechanisms of *H. grandella*. Specific objectives were as follows: (1) to investigate the flight behavior of shoot borer populations within a *Cedrela* plantation;

(2) to outline some of the micrometeorological conditions associated with flight; and (3) to investigate patterns of shoot borer attack in relation to host phenology and possible attractants.

Materials and methods

Flight behavior. Preliminary tests, designed to measure the height of *H. grandella* flights, were established in a plot of *C. odorata* in the pure block species trials in the Puente Cajón area, Turrialba, Costa Rica. The plot contained 100 trees, planted at distances of 2 x 2 m. The stand averaged 0.6 m in height and was about 18 months old. The plantation, over the last 12 months, was completely infested and 18 per cent of the trees were dead.

Height of flight was determined by means of 0.75 x 3.00 m wooden frames covered with polyethylene sheeting stretched over the frames. Twelve of these frames were set up in diagonals across the plantation, each 3 m from its neighbor. The frames were then coated with Stickem-Special*, a sticky compound that

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Fig. 1. Two types of sampling barriers used to determine flight patterns of *H. grandella*. The taller barriers sampled height of flight, the others sampled flight in relation to host selection.

remains viscous for a long time. For a period of a week the frames were checked daily and about 90 per cent of the shoot-borers caught were recovered from a height of 1-2 m.

Taking into account results of this preliminary test, the main set of trapping devices was established at a mean height of 1.30 m. These devices, termed trapping barriers (6), were constructed from 0.5 x 1 m polyethylene sheets and covered with Stickem-Special. Eighty barriers were hung from wires in such a manner that most of the surviving trees had a barrier within a meter distance (Fig. 1). A similar set of barriers was established in a non-host stand of *Fraxinus uhdei* and in a stand of *S. macrophylla* that was grown under shade of *Gmelina arborea* Roxb. The barriers were checked nightly and in the morning; shoot borers trapped on the barriers were collected and their position in regards to the individual *Cedrela* trees was noted. Temperature and rainfall were noted and the results correlated with the shoot borer collections.

Temperature relations. Selected Meliaceae trees were also enclosed within a 90 x 90 x 90 cm screened cage. The enclosed trees were infested by shoot borer larvae. As the larval mines extended into the stem the temperature inside the stem was measured by inserting a small thermistor into the larval mine; temperature adjacent to the stems were measured by placing another thermistor next to the stem; resultant temperatures were recorded from a Yellow Springs, model 4256, meter. In practice, one enclosed and infested tree under shade, and another similarly infested tree in open sunlight, were instrumented.

Adult movement. The movements of adults within an infestation also were investigated by means of ground barriers. In this case, 70 x 35 cm polyethylene panels were coated with Stickem-Special and located as follows: (1) two were positioned directly under selected trees, and (2) others in three concentric circles around the trees. The radii of the circles were 0.5,

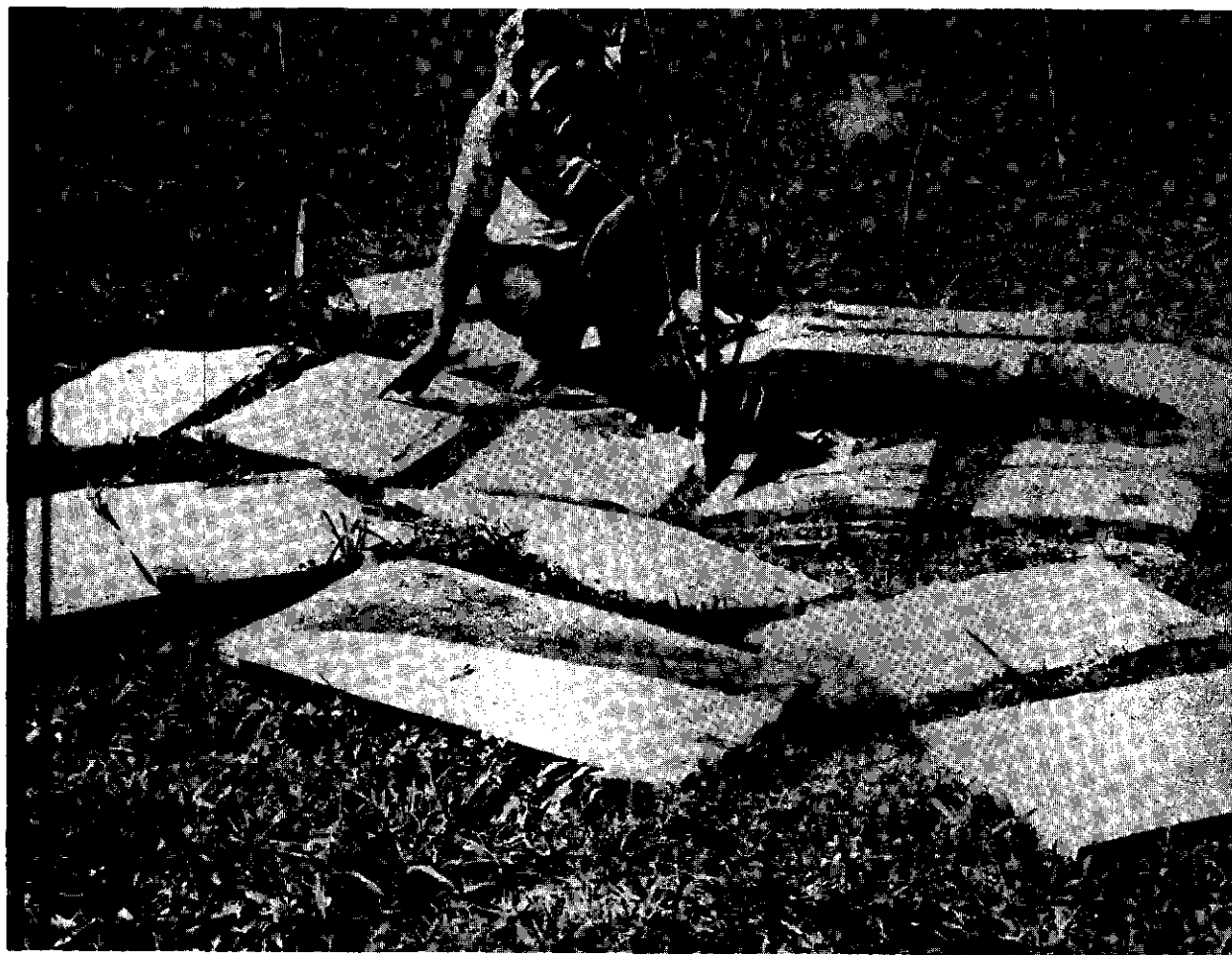


Fig. 2. Ground barriers around a *Cedrela* tree.

1.25 and 2 m respectively (Fig. 2). In the experiment two types of trees were used, one type was flushed with fresh leaves, the other type only had older, mature leaves. Additional barriers (tree barriers) were placed vertically in the form of a cross around one tree with new leaves and another with mature ones.

To further check adult movement, male and female adults were dusted with fluorescent powder. The insects were then released on selected trees and on the ground. Their subsequent activity was followed by observing their fluorescent trails on foliage and on the ground by means of an U.V. light.

Host phenology. In order to relate possible synchrony of fresh leaf production with incidence of attack, periodical surveys were made of the *Cedrela* plantation. Attack frequency was recorded together with the number of fresh and mature leaves.

Attraction. The possibility of primary host attractants was investigated in a series of experiments. Two small tables were constructed, and located adjacent to the *Cedrela* infestation. Four wooden frames, 0.5 x 0.5 x 1 m were placed on the tables, each occupying an equal area. Strips of sticky polyethylene were strung

around the periphery of each frame in effect forming a cage (Fig. 3) for convenience called an olfactory cage.

Various potted meliaceous tree species were placed in frames according to the test in progress.

Results

Flight activity. Flight of *H. grandella* mainly occurred when nightly temperatures were over 17°C (Figure 4). There was not a strict correlation between flight and temperature; however, flight activity took place between 17 and 24°C. Temperature differences between the shaded *Swietenia* and the open grown *Cedrela* only varied between 2° - 3.5°C. in the larval gallery and next to the stem. The open grown trees demonstrated these higher temperatures between the hours of 0900-1500. Ambient temperatures for 24 hour periods virtually were the same under shaded and isolated conditions. Even though ambient temperatures under the shade were equal to the non-shade areas, fewer attacks occurred in the *Swietenia* than in the *Cedrela* plots. Rainfall between 0.5 and 8.0 mm did not hinder flight, but heavier rains, over 11 mm prevented flight.

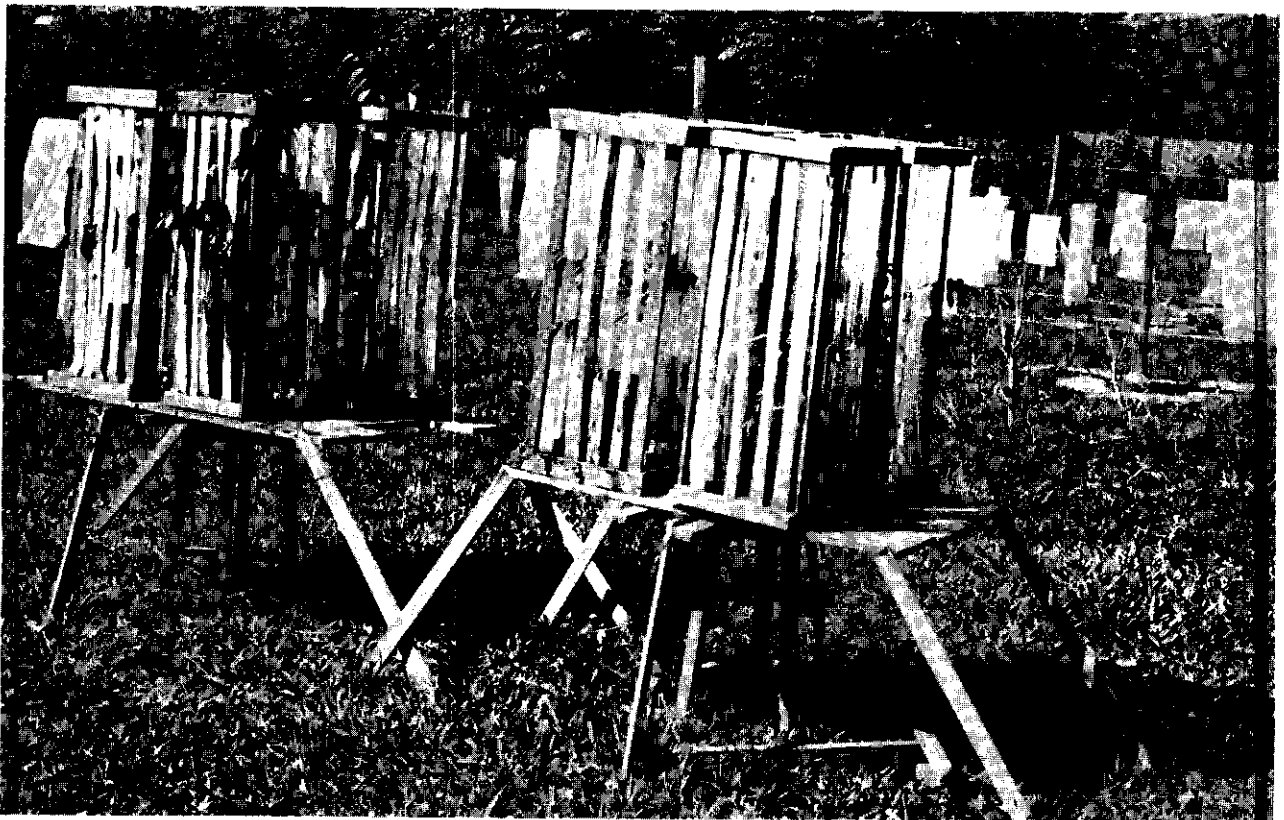


Fig. 3. Olfactory cages containing potted *Toona* (left table) and *Cedrela* (right table).

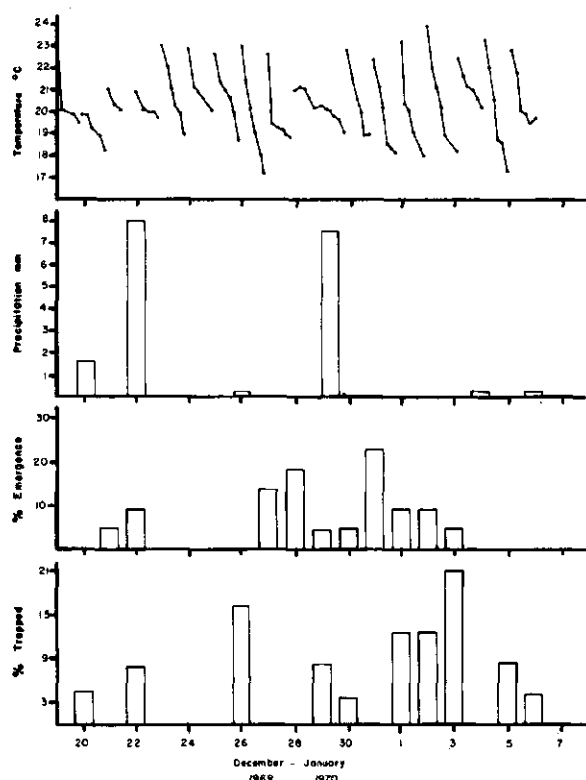


Fig. 4. Relationships between ambient temperatures, precipitation and emergence as well as catches of *H. grandella* on flight barriers.

The emergence of *H. grandella* from pupae placed in outdoor cages correlated with flight activity of the field population as the greater barrier catches occurred within 1-2 days after emergence (Fig. 4). During periods of moth emergence only 4 insects were caught in the non-host stand.

Data from Table 1 indicate that moths are active on the ground near the tree during early night, but invade their host later. The possibility that moths may inhabit ground vegetation during daylight hours is also seen in a cage test where moths were observed resting during daylight (Fig. 5). When moths were dusted with fluorescent powder and liberated on trees and ground, fluorescent trails left by moths indicated that they moved from the ground to the trees and vice versa.

Host selection. During the study it was noted that most of the barrier catches occurred near trees with new leaves (Fig. 6). Periodic surveys of the infestation supported observations that moths preferred to oviposit on trees bearing new leaves. Data from Fig. 7 indicate that the trees most heavily attacked had a predominance of fresh leaves, although trees sustaining a few new leaves among the mature also were attacked. At least during the latter part of the rainy season, just one tree with only mature leaves was attacked.

In tests where *Cedrela* and *Toona* trees were used as potted material in the olfactory cages only the *Cedrela* trees were selected by moths. Similarly only *Cedrela* trees with new leaves were chosen by *H. grandella* when new-leaved *Cedrela* trees were compared to cedar trees with only mature leaves (Table 2).

Table 1.—Accumulated numbers of male and female *H. grandella* caught on ground and tree barriers, near *Cedrela odorata* trees with fresh and mature leaves on the nights of 5/6 January and 5/6 March, 1970.

Time	Barrier Catches							
	Tree Barriers	Fresh Leaves			Mature Leaves			
		Ground Barriers			Tree Barriers	Ground Barriers		
		Inner ring	1.25m	2.00m		Inner ring	1.25 m	2.00 m
19.10	0	5 ♀	2 ♀	1 ♂	No insects caught			
19.15	0	1 ♀	0	0				
19.22	0	1 ♀	1 ♂	0				
19.50	0	1 ♀	1 ♀	0				
20.00	1 ♀	2 ♀	1 ♂	1 ♂				
20.12	0	1 ♀, 1 ♂	0	0				
20.20	2 ♀, 1 ♂	0	0	0				
20.50	1 ♀	0	0	0				
21.17	1 ♂	4 ♀	1 ♂	0				
21.35	0	0	1 ♂	1 ♂				
22.15	1 ♀	0	0	0				
22.30	1 ♀	0	0	0				
22.50	2 ♀	0	0	0				
23.30	1 ♀	0	0	1 ♂				
Totals	9 ♀, 2 ♂	11 ♀, 1 ♂	3 ♀, 4 ♂	4 ♂				



Fig. 5. *A Hysipyla grandella molb resting on vegetation.*

Table 2.—Catches of *H. grandella* on olfactory-cages with different types of potted plant material.

Data Feb-Mar 1970	Host Material	
	<i>Cedrela</i> fresh leaves	<i>Toona</i> fresh leaves
Feb. 23	3	0
24	1	0
25	1	0
26	0	0
27	2	0
	<i>Cedrela</i> -Fresh Leaves	<i>Cedrela</i> -Mature Leaves
Mar. 5	2	0
6	1	0
7	2	0

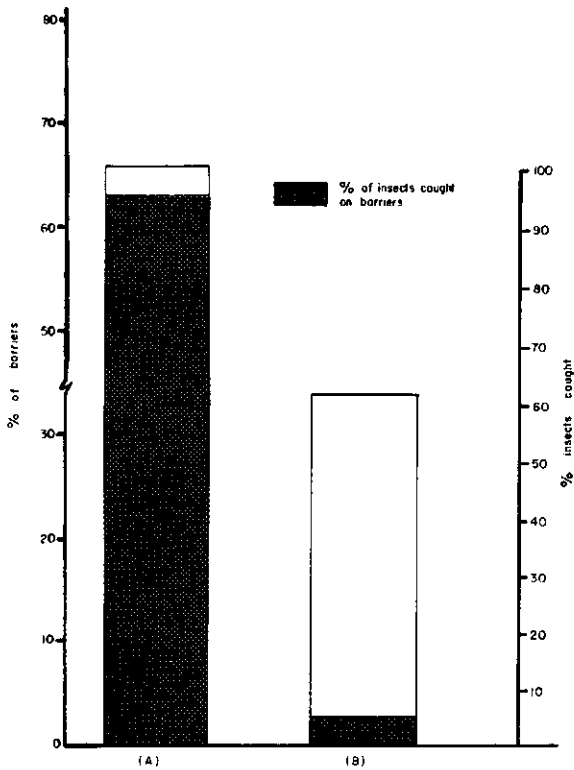


Fig. 6. Percentage of barriers adjacent to *Cedrela odorata* with fresh leaves (A) and without fresh leaves (B), and the respective catches of *H. grandella*, December 20, 1969 - January 7, 1970.

Discussion

Although night temperatures between 17 and 24°C. did not seem to influence *H. grandella* flight, increased flight activity was noted within 4-5 days after rain. It is possible that the additional moisture may stimulate plant growth which in turn may attract more moths. It is also conceivable that *H. grandella* emergence may be induced by periods of higher relative humidity. Tillmanns (11) suggests that after the dry season new attacks by the borer occur soon after the first rains.

The fact that few insects were caught outside of their host area indicated that *H. grandella* do not disperse readily from an active infestation. Within an outbreak, a short distance relationship between emergence and subsequent host selection seems likely. Apparently during the day, adults rest in ground cover at a short distance from their hosts. It also is interesting that the moths' wing and body markings blend in well with herbaceous material.

The results of the experiments strongly indicate that *H. grandella* select hosts by olfactory response to volatiles emanating from fresh leaves. Evidence for this olfactory orientation was supplied by the high percentages of catches on barriers located near fresh-leaved trees and by the response of adults to fresh-leaved *Cedrela* placed in olfactory cages. Further evidence for response to host volatiles was the fact that *H. grandella* detected its host plant outside of the infestation. All these data, however, were taken during the rainy season and most of the trees had fresh leaves. Oviposition on trees without leaves also was observed during the dry season, hence, the presence of new growth can not explain host selection during this season. As it was noted that leafless trees mostly had thin, papery bark, it could be that volatiles responsible for host orientation emanate through lenticels and the bark *per se*. It also is possible that insects may select hosts in response to volatiles emanating from old borings and frass produced by larvae from previous attacks (Fig. 8).

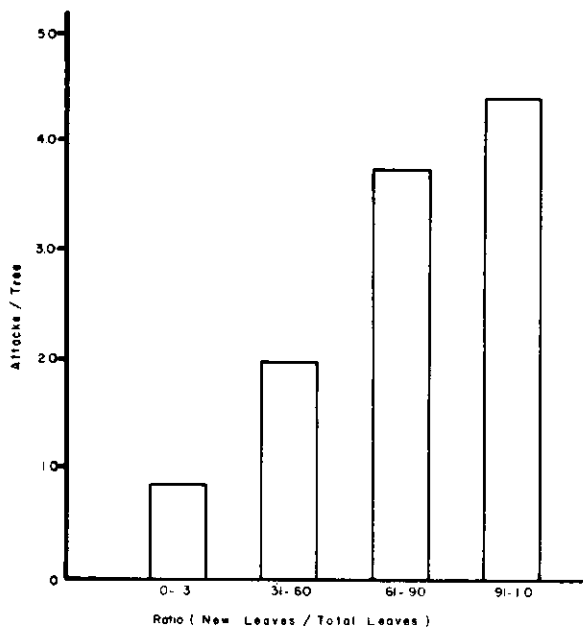


Fig. 7. Relationships between *H. grandella* attack and amount of young foliage available on its host tree, *Cedrela odorata*.



Fig. 8. Egg of *Hypsipyla grandella* oviposited on boring frass of previous attack.

It has been observed that *Swietenia* and *Cedrela* plots often prosper for a short time, then gradually deteriorate as *H. grandella* attacks augment. When one plantation is destroyed, neighboring meliaceous plantations come under ever increasing attack. These observations indicate that flourishing infestations tend to localize *H. grandella* populations within the outbreak areas. It is likely that as long as the emergence of moths is synchronized with the abundance of new growth, the population remains within the infestation. On the other hand, when plantations finally collapse, the moths disperse and become established in new focal centers. Accordingly, the present study shows that insects emerging in the outbreak area did not disperse but rather attacked in synchrony with the production of fresh leaves. It is interesting that during the dry season, when the *Cedrela* plot was leafless, new attacks began in the shaded, neighboring *Swietenia* plot that was fully foliated and unattacked.

It is thought that attacks on Meliaceae are less severe when trees are planted under shade (1, 2, 3, 4, 5, 8, 11). An explanation, in part for this phenomenon may be the lack of suitable ground cover. Another factor may be the differences in temperatures developed under open or shaded stands; possibly larvae boring in the cooler shaded stems emerge when their new hosts are unsuitable for attack. Moreover, present observations indicate that shaded *Swietenia* trees often successfully prevent attacks by exudation of gum.

Although olfactory orientation is indicated, it is not clear whether both sexes are equally responsive to host volatiles. Data from ground and tree barriers show that most catches in immediate vicinity of the trees are females. Perhaps females are more responsive to volatile host material than are the males. Female produced sex attractants could then explain the catches of male *H. grandella* on barriers near fresh leaved trees.

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Studies of the shootborer *Hypsipyla grandella* Zeller.

II. Host preference of the larva* —————P. GRIJPMAN**, R. I. GARA***

C O M P E N D I O

En una investigación previa (Turrialba 20(2):85-93) se informó que el adulto de *Hypsipyla grandella* Zeller, tenía preferencia por las Meliaceae americanas. Sin embargo, muy poco se sabe acerca de los estímulos que inducen a las larvas de *H. grandella* a alimentarse y desarrollarse en forma adecuada.

La presente investigación fue dirigida a estudiar el comportamiento nutricional de larvas de *H. grandella*. Se empleó como fuente de alimento, material vegetal de cuatro especies de Meliaceas, *Cedrela odorata* L., *Khaya ivorensis* A. Chev., *Swietenia macrophylla* King. y *Toona ciliata* M. Roem. var. *australis* (F.v.M.) C.DC., y una especie no-Meliacea, *Aucoumea klaineana* Pierre. Se constató que las larvas de *H. grandella* también tienen preferencia por las Meliaceas americanas usadas en la investigación.

Durante el curso de la investigación, se observó una alta mortalidad en larvas que se alimentaron con material de *T. ciliata* var. *australis*, por lo cual se iniciaron una serie de experimentos complementarios para determinar si el material vegetal de *T. ciliata* var. *australis* tiene alguna sustancia tóxica letal para larvas de *H. grandella*. Los resultados de estos experimentos comprobaron que *T. ciliata* var. *australis* es tóxico para las larvas. También hubo evidencia de que dicha sustancia tóxica tiene características volátiles con lo cual se podría explicar la no oviposición de *H. grandella* sobre *T. ciliata* var. *australis*. Se piensa que esta característica podría ser empleada en el futuro como base para la selección genética de Meliaceas resistentes a *Hypsipyla* spp. — Los autores.

Introduction

STUDIES indicate that *Hypsipyla grandella* Zeller display a definite species preference for the various native Meliaceae (2). Recent observations reveal that *Cedrela odorata* L. trees with a predominance of fresh leaves are attacked more frequently than those with mature leaves (3). It is

believed that the adult *H. grandella* find these preferred *C. odorata* through olfaction (2, 3, 4). Accordingly, the females must have a well developed ability of select a host wherein subsequent larvae will prosper. Little is known, however, on the chain of stimuli and responses that induce larvae to feed and develop properly.

The fact that other Meliaceae, such as *Toona ciliata* M. Roem var. *australis* (F.v.M.) C.DC., are not attacked in Turrialba, Costa Rica, may be attributed to: (a) adults are not attracted to *Toona*, or (b) adults are attracted and oviposit on *Toona*, but the larvae after eclosion soon die. However, recent studies indicate that *H. grandella* are not attracted to *T. ciliata* var. *australis* (3). Investigations in Australia indicate that *T. ciliata* var. *australis* is more resistant to attacks of *Hypsipyla robusta* Moore than are the other Meliaceae (7). No information exists, however, on whether larvae

* Received for publication April 7th, 1970.

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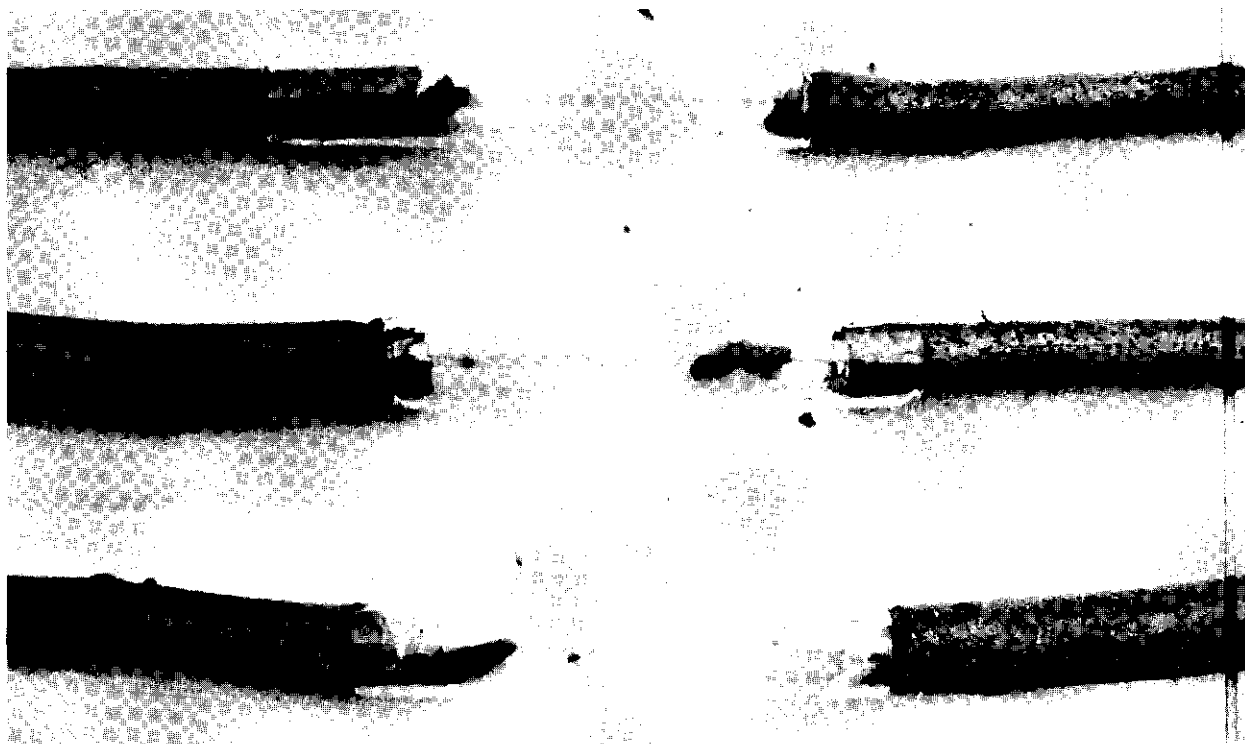


Fig. 1. Host preference test for *H. grandella* larvae, using glass tubes with stems of 4 meliaceous species and a non-host.

of *H. grandella* would be able to complete their life cycle in *Toona*.

The present study was undertaken to determine the behavior of *H. grandella* larvae with respect to food selection and feeding activity.

Materials and methods

Feeding preference. A number of techniques was developed to evaluate the existence of food preference among *H. grandella* larvae. Although it would have been ideal to use instars of equal ages, the tests were performed with larvae of 3rd-5th instars; most were of the 4th instar. Instars were determined by measuring head capsules and were classified in accordance with a table provided by Ramirez Sanchez (6).

To test food preference between four meliaceous species and a non-host, *H. grandella* larvae were placed in the center of glass tubes of about 1 cm in diameter and 8 cm long (Fig. 1). Each tube contained 1 larva and was given the choice of two tree stems which were inserted into the ends of the tube. Normally, the larva selected one of the species as a boring or feeding medium. The experiment was carried out in a cross-treatment design (5). In this design all possible combinations of the 5 species were tested; hence, there

were 15 treatments in total, of which 10 were combinations of distinct species, while 5 were of the same species. The species used were *T. ciliata* var. *australis*, *C. odorata*, *Swietenia macrophylla* King, *Khaya ivorensis* A. Chev. and *Aucoumea klaineana* Pierre, as a non-host. After larvae were introduced into the glass cylinders, their boring was checked 24 hours later. The length of each larval mine was recorded and the amount of boring was assumed to be a measure of host acceptance or preference. About 20 per cent of the larvae soon died within the tubes as a result of a nematode (Mermithidae, probably *Hexameris* sp.*) infestation. These dead larvae were replaced immediately with healthy ones and their boring measured 24 hours later.

In another experiment, larvae were allowed to select a variety of homogenized host materials. In this case 3 plates, 24 cm in diameter, were divided into five chambers by means of plastic separators. (Figure 2). Each chamber contained macerated leaves and shoots of the same meliaceous species and the non-host as described in the previous experiment. However, in one test series only *C. odorata* and *S. macrophylla* were used as choices and larvae introduced into tests were separated as either reared in *Swietenia* or *Cedrela*. On the

* Personal communication from Dr. Calvin L. Massey, Rocky Mountain Forest and Range Experiment Station, Albuquerque, New Mexico, U. S. A.

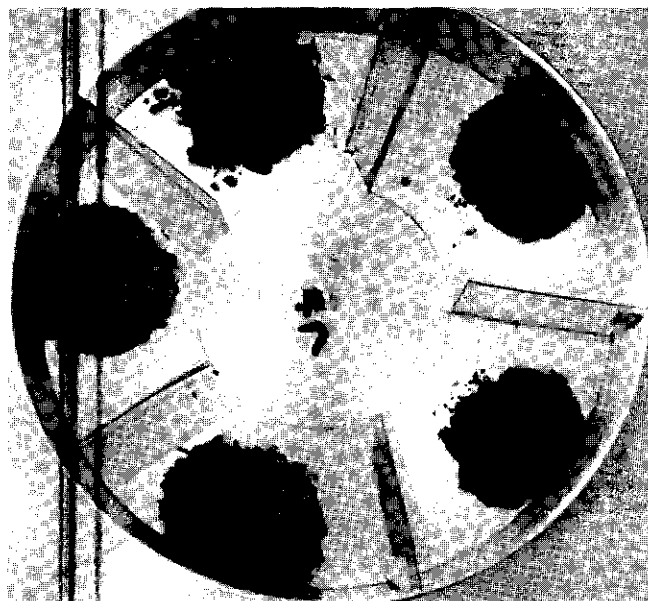


Fig. 2. Host preference test for *H. grandella* larvae using plates divided into 5 chambers containing various host materials.



Fig. 3. Laboratory olfactometer used in establishing host preferences of *H. grandella* larvae. Food choices were placed in the 5 canals, air drawn through glass tube, presented larvae placed in common entrance chamber, with 5 airstreams containing host volatiles.

average, 4 larvae were placed in the center of each plate. Subsequently, the three plates were placed in a darkened growth chamber. The location of each larva was recorded within one hour and 24 hours later.

The possibility that larvae exhibit food preference through olfaction as well as gustation was tested by means of an olfactometer. Basically, the device was made by fastening strips of wood in such a manner as to form 5 distinct canals with a common entrance chamber (Figure 3). By means of a vacuum pump, air was pulled through the 5 canals which, in turn, contained the 5 different host materials used in the previous tests. The air stream passing around the various homogenized host materials would thus contain the different volatiles and transfer them to the entrance chamber. Here, larvae would be able to select the canal of their choice through olfaction. In designing the device, smoke was introduced into the air intakes and demonstrated, in theory, that the technique was usable as five distinct air streams flowed within each canal and then united at the entrance chamber.

Host toxicity. In the host preference tests, as above, it was noted that larvae selecting *Toona*, frequently died. In view of this, another series of tests were designed to determine the possible toxic effects of *Toona* on *Hypsipyla* larvae. In one experimental series, slivers of bark containing eggs of *H. grandella*, collected from a *C. odorata* field plot, were attached to stems of potted *Cedrela* and *Toona* seedlings. In total 10 *Toona* and 5 *Cedrela* seedlings were used; each tree received two bark slivers (with one egg each). All but 4 of the eggs hatched, two of the eggs positioned on one of the cedar plants died, while the other 2 were on 2 different *Toona* plants. During a period of 10 days, observations were made of the first instars' boring activity and associated behaviors.

An additional experiment was designed to study the possible toxic effects of *Toona* on larvae. A standard food medium was created by macerating 16 gr of

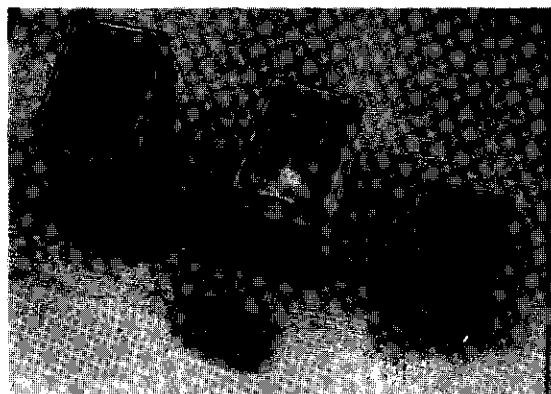


Fig. 4. Containers used to determine toxic effect of volatiles emanating from *Toona*. Larvae prevented from physical contact with macerated leaf material by means of Saran screening.

Swietenia and *Toona* plant material; the control merely contained 16 gr of homogenized *Swietenia*. All of the controls and treatments, in addition, contained 34 gr of water, 1.5 gr of agar, and 0.5 gr of sodium benzoate. Apart from the controls, the remaining 4 treatments contained macerated *Swietenia* and *Toona* in the following proportions respectively: 75-25, 50-50, 25-75 and 0-100 per cent. Thus, the last treatment contained solely *Toona*. The macerated food media were placed into petri dishes; each treatment and the control was replicated 5 times. One larva was introduced into each petri dish and checked for survival and boring activity twice daily during a period of 6 days.

Another experiment was designed to determine if larval mortality induced by *Toona* was a result of toxic volatile compounds or by ingestion of an unsuitable diet. In this case macerated *Toona* material was placed in the bottom of each of 6 containers. Saran™ screening was placed on top of this material so that the larvae would not be in direct contact with the macerated material. A similar series of 6 containers was established, but with *Cedrela* as the host media, and, as a control, 6 additional containers contained water soaked cotton (Fig. 4).

Results and discussion

In the feeding preference tests where *H. grandella* larvae were placed in glass tubes with different host materials as choices, the following represents total boring (cm) into selected choices: *Toona*, 0.00; *Aucoumea*, 1.24; *Khaya*, 9.68; *Swietenia*, 19.26; and *Cedrela* 19.68. An analysis of variance (Table 2) shows that these differences are significant at the 95 per cent level of confidence. A non parametric ranking test confirmed the sequence of these preference. It is clear (Table 1) that the larvae avoided boring into *Toona*, while they readily chose *Cedrela* or *Swietenia*.

The selection of host material by larvae placed in plates with 5 food choices is seen in Fig. 5. It is

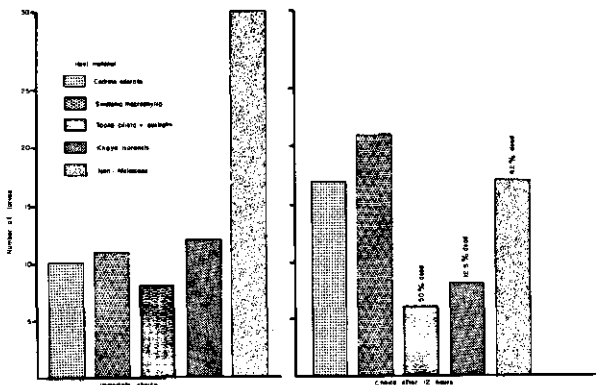


Fig. 5. Selection of macerated host material by *H. grandella* larvae, placed in the centre of plates; subsequent choice expressed by the number of larvae found in chambers containing either *Swietenia*, *Cedrela*, *Khaya*, *Toona* or a non-meliceae species.

Table 1.—Results of feeding-preference test where larvae were placed inside tubes with stems of various hosts inserted at both ends of the tubes; data expressed as distances (cm) larvae bored into different host material: *Toona ciliata* var. *australis*, *Cedrela odorata*, *Swietenia macrophylla*, *Khaya ivorensis* and *Aucoumea klaineana* as the non-host control.

	<i>Toona</i>	<i>Cedrela</i>	<i>Swietenia</i>	<i>Khaya</i>	<i>Aucoumea</i>
<i>Toona</i>	0.00 0.00	2.35 0.00	1.40 0.00	3.29 0.00	0.00 0.00
<i>Cedrela</i>	0.00 0.72	0.00 2.57	0.00 1.05	0.00 2.98	0.00 8.40
<i>Swietenia</i>	0.00 1.65	0.00 1.51	0.00 6.28	0.00 1.15	0.00 1.92
<i>Khaya</i>	0.00 0.41	0.60 1.05	1.19 0.00	2.61 0.90	0.00 1.23
<i>Aucoumea</i>	0.00 1.24	1.01 0.00	4.16 0.00	0.18 0.00	0.00 0.00

Table 2.—Analysis of variance of the influence of host on the boring activity of larvae placed in glass tubes with stems of various hosts inserted in the ends of the tubes.

Source of Variation	D.F.	S.S.	M.S.
Specific vs General	1	.7328	.7328
Specific Preference	4	13.9047	3.47617
General Preference	19	56.9716	2.99851
<i>Toona</i> vs. others	1	7.6452	7.6452*
<i>Cedrela</i> vs. others	1	10.9634	10.9634*
<i>Swietenia</i> vs. others	1	8.8620	8.8620*
<i>Khaya</i> vs. <i>Aucoumea</i>	1	.4970	.4970 N.S.
Remaining components	15	29.0040	1.9336 N.S.
Error	25	66.1917	2.6477
TOTAL	49	137.8008	

*=Significant at 95%
N.S.=Not significant

seen that, within one hour, most of the larvae chose to enter compartments with the non-host material. During the one hour period, the remaining larvae showed approximate equal preferences for *Cedrela*, *Swietenia* and *Khaya*; there was a somewhat lower response for *Toona*. After 12 hours a large proportion of the larval population left the non-host and went into *Swietenia* and *Cedrela*; less were found in *Toona* and *Khaya*. Moreover, many of the larvae remaining in the exotic meliaceae and in the non-host died. The unusually high number of larvae found in the non-host, may have been due to an arresting stimuli (1, 8). The non-host, *Aucoumea* seems to have a high level of strong volatile materials.

Table 3.—Relationship between *H. grandella* larvae reared in either *Swietenia* or *Cedrela* and their subsequent choice of either macerated *Swietenia*, *Cedrela* or non-host plant material.

Plate	Larval Origin	HOST MATERIAL Choices of the larvae				Non-Host	
		<i>Swietenia</i>		<i>Cedrela</i>		Imme- diate	After 12 hrs.
		Imme- diate	After 12 hrs.	Imme- diate	After 12 hrs.		
1	<i>Swietenia</i>	0	1	0	1	6	0
2	<i>Swietenia</i>	1	1	1	1	1	2
3	<i>Cedrela</i>	1	1	2	2	0	0
4	<i>Swietenia</i>	1	1	1	2	1	1
5	<i>Cedrela</i>	1	2	0	0	2	1
6	<i>Swietenia</i>	0	0	0	0	1	1
Totals ¹		4	6	4	6	11	5

¹ Two larvae raised in *Swietenia* made no choice and remained in middle of the plate.

In another test, larvae obtained from either *Cedrela* or *Swietenia* plantations could choose as host material cedar, mahogany, or the non-host. From Table 3 it is

noted that, within an hour, most of the larvae went into the *Aucoumea*. However, after 12 hours, the larvae moved from this non-host to either *Swietenia* or *Cedrela*. In fact, the larvae exhibited no differences in their subsequent choice of these two meliaceous host materials. The olfactometer test (Fig. 6) showed that 85 per cent of the total number of larvae entered the canals with non-host material *Aucoumea* (45 per cent) and the native Meliaceae, *Swietenia* and *Cedrela* (40 per cent). Again the arresting stimulus of *Aucoumea* was observed. Fifteen per cent of the larvae entered the canals with *Toona*, of which 33 per cent died subsequently.

Conclusions from these tests seem to indicate that *H. grandella* larvae prefer their native hosts. It is seen that, although the larvae may be initially stimulated to select an exotic host species, they later leave these hosts and are recovered in native Meliaceae. Frequently, when *H. grandella* larvae were found for protracted periods in non-hosts, they were moribund and died. It is likely that the larvae left the exotic host material because adequate gustatory stimulation was lacking.

The food preference tests showed that a high percentage of larvae that chose *Toona* as a host died. Results of the toxicity test, in which eggs of *H. grandella* were attached to potted *Toona* and *Cedrela* plants

Table 4.—Activity of 1st. instar *H. grandella* larvae on potted plants of *Toona ciliata* var. *australis* and *Cedrela odorata*. Larvae hatched from eggs attached to the seedlings.

Tree No.	Species	No. of Eggs Hatched	Larval Activity			Remarks
			Boring	Dead	Active	
1	<i>Toona ciliata</i> v. <i>australis</i>	2	x	x		Gum exudations; larvae died in 24 hrs.
2	<i>Toona ciliata</i> v. <i>australis</i>	2	x	x		Gum exudations; larvae died in 24 hrs.
3	<i>Cedrela odorata</i>	2	x		x	No gum produced. Larvae active.
4	<i>Toona ciliata</i> v. <i>australis</i>	2	x	x		Gum exudations; larvae died in 24 hrs.
5	<i>Toona ciliata</i> v. <i>australis</i>	2	x	x		No gum, exudation; larvae died in 24 hrs.
6	<i>Cedrela odorata</i>	0	0	0	0	Both eggs did not hatch, attacked by fungi.
7	<i>Toona ciliata</i> v. <i>australis</i>	1	x	x		1 egg did not hatch, attacked by fungi. 1 larva died in 24 hrs.
8	<i>Toona ciliata</i> v. <i>australis</i>	2	x	x		No gum exudation, 1 larva died while boring. other dead in 24 hrs.
9	<i>Cedrela odorata</i>	2	x		x	No gum produced, larvae very active
10	<i>Toona ciliata</i> v. <i>australis</i>	2	x	x		Gum exudations; larvae died in 24 hrs.
11	<i>Toona ciliata</i> v. <i>australis</i>	1	x	x		1 egg did not hatch, attacked by fungi.
12	<i>Cedrela odorata</i>	2	x		x	No gum exudation, larvae very active.
13	<i>Cedrela odorata</i>	2	x		x	No gum exudation, larvae very active.
14	<i>Toona ciliata</i> v. <i>australis</i>	1	x	x		1 egg did not hatch, attacked by fungi; no gum exudation. Larva died.
15	<i>Toona ciliata</i> v. <i>australis</i>	1	x	x		1 egg did not hatch, attacked by fungi; gum exudation. Larva died in 24 hrs.

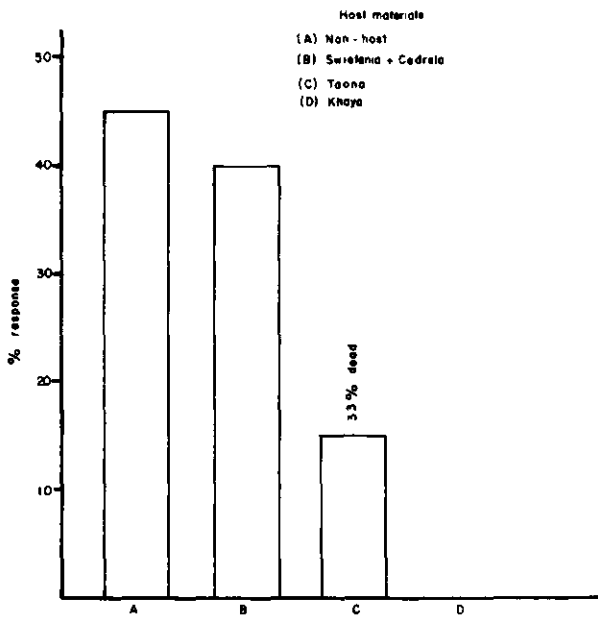


Fig. 6. Choices made by *H. grandella* larvae in olfactometric tests. Larvae were placed within a laboratorial olfactometer containing macerated host material of 4 meliaceous species and a non-host.

(Table 4), indicate that all first instars hatched on *Toona* died within 24 hours after eclosion; larvae hatched on *Cedrela* trees could be reared through their complete cycle. It was interesting to note that 20 per cent of the eggs on both tree species failed to hatch. Accordingly, *Toona* did not adversely affect eclosion. In many cases, the recently hatched larvae, were likely killed by heavy gum exudation of the *Toona*. This, however, may not be the major cause of larval mortality in *Toona*, as several first instars were found dead with only their heads penetrating the plant's epidermis.

Table 5.—Mortality of *H. grandella* larvae placed in petri dishes containing macerated *Toona* and *Swietenia* plant material.

Percentage of Plant Material		Accumulated Mortality (%) Days of Test					
<i>Toona</i>	<i>Swietenia</i>	1	2	3	4	5	6
0	100	0	0	0	0	0	0
25	75	0	0	20	20	40	80
50	50	0	0	20	40	60	80
75	25	20	40	40	80	80	100
100	0	60	60	80	80	80	80

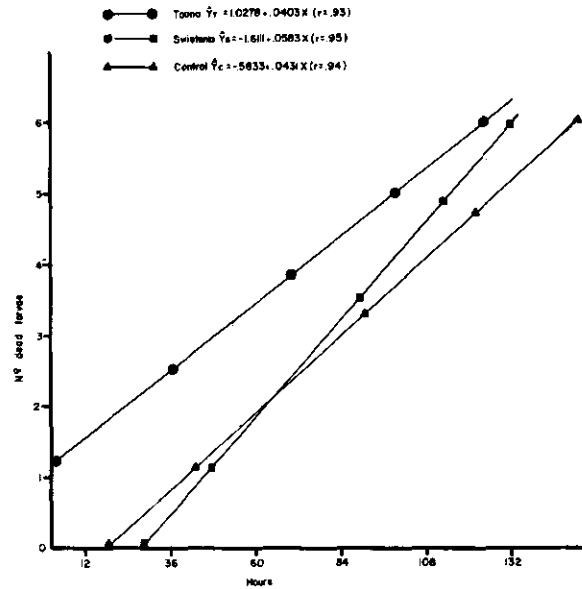


Fig. 7. Regression equations of the death rate of *H. grandella* larvae exposed to volatiles emanating from macerated *Toona* and *Swietenia* leaf material; larvae placed over water soaked cotton were used as a control.

The patterns of larval mortality in the macerated mixture of *Toona* and *Swietenia* material is seen in Table 5. The mortality rate of introduced larvae increased markedly when the proportion of *Toona* increased from 75 to 100 per cent. For example, the response of *H. grandella* to the toxic effects of *Toona* can be noted on the third day of the test when an increasing percentage of *Toona* in the diet resulted in increased mortality rates, ranging from 0 in the control to 80 per cent in the 100 per cent *Toona* medium.

In the final experiment there was evidence that toxic volatiles emanating from *Toona* were responsible for an accelerated mortality rate among the larvae (Fig. 7). The results of the regression analysis revealed a significant difference at the 95 per cent confidence level between *Toona* versus *Swietenia* and control. The difference between *Swietenia* and control was not significant.

From the foregoing results it may be concluded that *T. ciliata* var. *australis* is toxic to *H. grandella* larvae. It is even possible that volatile, toxic compounds from *Toona* may deter *H. grandella* moths from selecting *Toona* for oviposition. These observations may offer prospects for the breeding of resistant *Cedrela* species.

Acknowledgement

The authors wish to thank Dr. Gilberto Pérez, IICA, Turrialba, Costa Rica, for his assistance in the statistical evaluation of the experiments.

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2.3. DEVELOPMENT OF AN ARTIFICIAL REARING TECHNIQUE.

Paper:

- 2.3.1. Studies on the shootborer Hypsipyla grandella Zeller. V. Observations on a rearing technique and on host selection of adults in captivity. Turrialba 21(2):202-213. 1971.

Studies on the shootborer *Hypsipyla grandella* Zeller.
 V. Observations on a rearing technique and on host
 selection behavior of adults in captivity.*—————P. GRIJPMAN**

C O M P E N D I O

Se describe una técnica para la crianza en laboratorio de Hypsipyla grandella Zeller y un método para la producción masiva de huevos del insecto. Con base en los datos observados en dos tipos de dietas, una sintética y otra natural, se estimó una ecuación que relaciona el estado pupal y la emergencia en función del tiempo. De tres distribuciones probadas (Poisson, normal y binomial) la binomial se ajustó mejor a los datos observados.

Las generaciones de adultos de H. grandella criadas con dieta sintética y bajo las condiciones del experimento, continuaron ovipositando en plantas de Cedrela odorata. Se comprobó que los adultos criados con dieta sintética son de mayor tamaño que los adultos criados con dieta natural de hojas y brotes tiernos de C. odorata. El tamaño de la hembra de H. grandella criada con los dos tipos de dietas es significativamente mayor que el del macho. Hembras criadas con ambas dietas vivieron más tiempo que los machos.

Se encontró que adultos de H. grandella criados con dieta natural son atraídos durante la noche por la luz de un bombillo y por pupas u hojas desecadas de C. odorata. Se sugiere un modelo de respuesta para una serie de estímulos que podrían causar la selectividad de H. grandella para las Meliáceas. — El autor.

Introduction

AVAILABILITY of large numbers of adults and other life stages of *Hypsipyla grandella* Zeller, is of importance for research on the lifecycle, host selection behavior, biological control and other related studies. Although an artificial diet for *Hypsipyla robusta* Moore, has been described by Achan (1), a complete rearing technique, which should include mass egg production, has not yet been reported.

In previous studies, executed at the Inter-American Institute of Agricultural Sciences (IICA), Turrialba,

Costa Rica, *H. grandella* eggs were collected from field plots (2, 7). This was cumbersome and inefficient as eggs were not always available. Recent investigations have led to a rearing technique through which all life stages are more easily obtained throughout the year. This paper describes the research related to this method and compares the life cycle of *H. grandella* raised on an artificial diet developed by Hidalgo-Salvatierra (3) with those reared on a natural diet of *Cedrela* leaves and tender shoots.

Material and methods

The research was divided into two stages. In the first stage, oviposition of *H. grandella* in captivity was studied. Two wire screen cages (90 x 90 x 90 cm on

* Received for publication May 31st 1971.

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Fig. 1.—Oviposition cage and frames covered with towel paper. The majority of eggs (circled) on the left frame, is deposited on the upper half of the towel paper.

0.50 m long legs) were placed in the open field at approximately 4 m distance from a building. Location of the cages in the open field was chosen because preliminary experiments, utilizing the same cages in the laboratory had never resulted in oviposition of fertile eggs. Inside the cages, six wooden frames (38 x 85 cm, two per wall) covered with ordinary corrugated kitchen paper towels were suspended on nails in such manner that three of the four vertical walls were covered (Fig. 1 and 2). The fourth wall had a door, wide enough to retrieve the frames. In each of the cages a potted plant of a host tree (*Cedrela odorata* L.) and a non-host (*Cananga odorata* (Lam.) Hook F. & Thoms.) were placed to determine if adults raised on artificial diet would still be host specific (Fig. 2). Periodically, these potted plants were removed for several days to establish if the presence of the plants influenced oviposition.

Unsexed *H. grandella* adults reared on natural and synthetic diets were released nightly at 20:00 hours after emergence in the laboratory in their respective cages. No food was provided for the adults in the cages; during dry spells, however, the paper frames were wetted daily with approximately 30 cc of water to provide adults with moisture.

During a heavy rainy period (from April 4-13, 1971) the oviposition cages were relocated and placed under the eaves of the building in order to protect the towel paper from tearing and breaking at the perforations. The building had a night light (Osram, 50W, 115-125 V, Exc.) located at 3 m distance from, and about 1 m above, the cage containing adults raised on the natural diet. The influence of this light on oviposition was determined during this period by comparing the numbers of eggs oviposited on the one lighted side with the others.

During the period of the rearing experiment (from December 10, 1970 - May 27, 1971), the frames in the cages were replaced every two days, and eggs oviposited on the towel paper frames, screen walls and the potted plants were counted. Sterile eggs were counted every two days. Counting of *H. grandella* eggs on towel paper was facilitated by using a light box containing two fluorescent tubes (Fig. 3). A Munsell Soil Color Chart (9) was used to define the color, under laboratory conditions, of recently deposited eggs and eggs 24 hours old. In the air conditioned laboratory temperature and humidity were recorded continuously.

Mating and oviposition behavior of adults was followed in the cages.



Fig. 2.—Frames and potted host (*Cedrela odorata*, right) and non host (*Cananga odorata*, left) in oviposition cage.

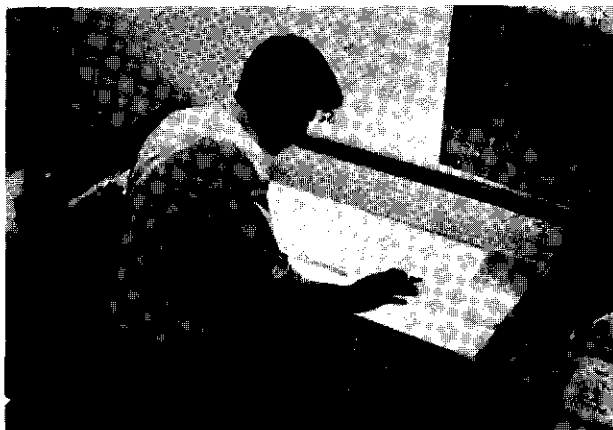


Fig. 3.—Counting of *H. grandella* eggs, facilitated by light box.

In the second stage of the experiment, a comparison was made between the life cycle of *H. grandella* raised in the laboratory on a natural diet (leaves and tender shoots of *C. odorata*) and on a synthetic diet developed by Hidalgo-Salvatierra (3). Fertile eggs, oviposited on the paper of the frames in the cages, were clipped out and put on small sheets of aluminium foil. These sheets were then put in hard, uncompartmented, polystyrene containers (size 28 x 13 x 4 cm) on top of the natural and artificial diets.

Previous trials had shown that if fresh eggs were placed directly on the synthetic diet (Ph=5.7) hatching would not, or only rarely, occur. If soft plastic containers were used larvae bored holes into the lids and escaped.

The number of eggs placed inside each container varied with their availability. In general, between 20 to 60 eggs were used. Forty grams of fresh leaves and tender shoots of *C. odorata* were used each time the natural food was changed. The weight of the synthetic diet was 200 gr, which covered the lower fifth of each container. Synthetic diet often became contaminated with fungi and bacteria. When symptoms of contamination were observed, the larvae were removed and placed in clean containers with fresh diet. Data referring to contaminated containers were excluded from the rearing results. However, the adults obtained from these transferred larvae were used in the oviposition cages in order to maintain the population.

The following data were recorded with respect to rearing: number of days after oviposition needed for hatching, pupation, and emergence.

An embryo was considered hatched, when it had left the chorion. Pupation was recorded as soon as a larva had spun a surrounding cocoon, including thus, the prepupal stage. An adult was considered emerged, when it had left the cocoon surrounding the pupa. When pupae had chitinized, they were removed from the containers and placed in marked glass jars covered

with gauze so that emergence could be traced back to the original batches of eggs.

To compare the yield of the two diets, the following data were noted with respect to each container: number of eggs hatched, number of larvae pupated and number of adults that emerged. These adults were subsequently used in the oviposition cages, to determine fecundity and sex ratio. Separate cages were used for adults reared on each diet. No attempt was made to determine the effect of the diets on the rearing of successive generations. Eggs oviposited in each cage were used for the continuously rearing of new adults on both diets.

To determine the quality of adults reared on both diets, the following properties of the insects were compared: longevity, size, average number of eggs oviposited, per female and percentage of eggs hatched in the containers. In the longevity test, executed in the laboratory, 24 recently emerged adults, of both diets were put in glass jars covered with gauze. No food nor water was provided. In order to avoid the possible influence of factors such as light (windows are only located in one of the walls of the laboratory) on longevity, the jars were placed in a rectangular block of 4 x 12, in which the adults reared on each diet alternated. Mortality, sex and size were determined at 07:45 and 19:45 during this test. The size of the dead adults was established by measuring the distance between the fringes of the wing and the tips of the head with a vernier caliper, which measured to an accuracy of 0.01 cm. If the fringes of the wings or the wing tips were damaged size was not determined. In addition, sex and size were determined on samples of adults of both diets, taken randomly during the whole rearing period. Analysis of variance was used to help interpret results obtained from the rearing experiment and the longevity test. A mathematical equation for the distribution of pupation and emergence of *H. grandella* reared on both diets, with respect to time was determined. At this point Poisson, normal and binomial distribution were tested for best fit. Daily records of pupation and emergence were pooled together into 2-day intervals, so as to facilitate interpretation.

Results and discussion

Oviposition

The described method to obtain fertile *H. grandella* eggs from captive adults reared on synthetic and natural diets resulted in an ever increasing insect population. Egg production of adults from both diets during two periods (one at the beginning and one at the end of this evaluation), is presented in Tables 1-3. Although a strict comparison of these oviposition data cannot be made because of different number of insects, different ambient conditions and possibly different sex ratios, some valid information has been obtained. In none of these periods did oviposition take place until

Table 1.—Number of adults, mortality, sex ratio and oviposition data of *H. grandella* in captivity, during the period of January 11 - February 11, 1971. Adults reared in the laboratory on natural diet.

Date (night of)	N° of adults in cage	N° of adults added	Mortality	N° and sex of dead adults		N° of fertile eggs oviposited	N° of sterile eggs oviposited	Oviposition on potted host and non host trees in the cage*
				♂	♀			
11-12 January 1971	0	1	—	—	—	—	—	
12-13	1	2	—	—	—	—	—	
13-14	3	—	—	—	—	7	2	
14-15	3	2	—	—	—	101	—	
15-16	5	2	—	—	—	37	—	
16-17	7	4	—	—	—	70	—	
17-18	11	9	—	—	—	122	17	
18-19	20	2	2	1	1	125	—	
19-20	20	3	—	—	—	144	49	
20-21	23	2	2	2	—	87	—	
21-22	23	1	2	—	2	127	19	
22-23	22	—	6+2**	3	3	96	—	38 eggs on <i>Cedrela</i>
23-24	14	7	2	—	2	161	9	
24-25	19	3	5	2	3	70	—	
25-26	17	2	1	1	—	392	21	124 eggs on <i>Cedrela</i>
26-27	18	10	4	1	3	94	—	
27-28	24	—	4	1	3	101	4	
28-29	20	3	—	—	—	284	—	
29-30	23	6	3	—	3	86	11	84 eggs on <i>Cedrela</i>
30-31	26	—	2	—	2	89	—	
31-1 February	24	5	—	—	—	147	18	
1-2	29	—	1	—	1	221	—	
2-3	28	—	1	—	1	222	12	
3-4	27	2	4	1	3	65	—	
4-5	25	—	2	1	1	232	—	
5-6	23	—	6	5	1	164	27	
6-7	17	—	4	3	1	16	43	
7-8	13	—	4+2**	3	1	35	—	
8-9	7	—	5	3	2	—	—	
9-10	2	—	1	1	—	—	—	
10-11	1	—	1	1	—	—	—	
Totals		66	66	29	33	3,295	242	264 eggs on <i>Cedrela odorata</i> ; no eggs on <i>Cananga odo- rata</i>

* Potted host and non-host trees were placed in the cages from January 20-31, 1971.

** Escaped or predated.

the third night after release of the first insects in the cages. Only once in the whole rearing period were eggs observed after the second night of release. If oviposition took place on the potted trees, adults of both diets by far preferred *Cedrela odorata*. Oviposition on the non host appears to be accidental and may have been influenced by the nearby host tree. Distance between the potted plants was only 35 cm (Fig. 2).

Location of eggs of synthetic and naturally reared adults on the potted *Cedrela* was similar to location of eggs found on host trees in the field; i.e. on leaf scars, near leaf veins, near lenticels and in small fissures of the bark. Larvae, hatching from these eggs behaved normally and bored into leaf-stems and axils of the topshoot until they pupated and emerged.

Presence of a host tree in the cages was not required to obtain fertile eggs.

The majority of eggs were deposited singly, in the pits of the corrugated towelpaper. Most of these eggs were located on the upper half of the frames (Table 4, Fig. 1 and 4). When female adults became old and were not able to fly or climb anymore, they oviposited fertile and sterile eggs on the wire screening of the cage bottom. This behavior could explain occasional oviposition of fertile *H. grandella* eggs on grass leaves or stones near host trees in field plots.

Freshly deposited *H. grandella* eggs are pale yellow to yellowish brown (Munsell color 2.5Y6/4 - 2.5Y7/4), whereas 24 hours old eggs are red (Munsell color 5R4/8). This difference in color is easily seen with the naked eye and facilitated recognition of fresh and one day old eggs, when the frames were retrieved every other day.

Table 2.—Number of adults, mortality, sex ratio and oviposition data of *H. grandella* in captivity, during the period of March 27 - May 22, 1971. Adults reared in the laboratory on natural diet.

Date (night of)	N° of adults present	N° of adults added	Mortality	N° and sex of dead adults		N° of fertile eggs oviposited	N° of sterile eggs oviposited	Oviposition on potted host and non host trees in the cage*
				♂	♀			
27-28 March 1971	0	4	—	—	—	—	—	
28-29	4	—	1 **	—	—	—	—	
29-30	3	5	—	—	—	10	—	
30-31	8	4	2	1	1	4	20	
31-1 April	10	4	—	—	—	190	—	
1-2	14	9	2	2	—	303	—	
2-3	21	3	1	1	—	82	—	22 eggs on <i>Cedrela</i>
3-4	23	3	3	—	3	274	—	
4-5	22	4	—	—	—	135	—	
5-6	26	5	2	1	1	29	—	
6-7	29	1	4+4**	2	2	78	3	5 eggs on <i>Cedrela</i>
7-8	22	2	5	4	1	138	—	
8-9	19	—	—	—	—	37	1	
9-10	19	—	2	1	1	11	—	
10-11	17	—	1	—	1	75	—	15 eggs on <i>Cedrela</i>
11-12	16	—	9	5	4	18	—	
12-13	7	8	3	—	3	141	—	
13-14	12	—	—	—	—	32	—	
14-15	12	11	1	—	1	17	5	
15-16	22	5	—	—	—	7	—	
16-17	27	4	1	—	1	219	21	23 eggs on <i>Cedrela</i>
17-18	30	5	7	2	5	146	—	
18-19	28	1	6	3	3	75	46	3 eggs on <i>Cedrela</i> .
19-20	23	5	16	6	10	—	—	2 eggs on <i>Cananga</i>
20-21	12	8	—	—	—	57	50	
21-22	20	16	4	1	3	34	—	
22-23	32	23	3	2	1	45	176	
23-24	52	11	10	4	6	63	—	
24-25	53	21	3	2	1	146	161	
25-26	71	7	5	3	2	240	—	
26-27	73	—	8	5	3	454	128	
27-28	65	10	16	9	7	286	—	
28-29	59	21	9	4	5	128	215	
29-30	71	12	21	8	13	355	—	
30-1 May	62	7	8	3	5	312	232	
1-2	61	—	10	6	4	486	—	
2-3	51	10	5	2	3	304	131	7 eggs on <i>Cedrela</i>
3-4	56	9	11	8	3	193	—	
4-5	54	5	7	3	4	75	148	
5-6	52	6	8	4	4	182	—	
6-7	50	8	8	3	5	330	277	5 eggs on <i>Cedrela</i>
7-8	50	16	18	12	6	234	—	
8-9	48	16	7	3	4	495	140	11 eggs on <i>Cedrela</i>
9-10	57	4	11	7	4	349	—	
10-11	50	3	6	2	4	91	165	
11-12	47	3	11	5	6	220	—	
12-13	39	—	5	1	4	191	76	
13-14	34	—	11	6	5	26	—	
14-15	23	—	15	9	6	105	25	
15-16	8	—	—	—	—	59	—	
16-17	8	—	5	3	2	52	—	
17-18	3	—	1	1	—	—	—	
18-19	3	—	1	1	—	—	—	
19-20	2	—	1	—	1	—	—	
20-21	1	—	—	—	—	—	—	
21-22	1	—	1	1	—	—	—	
Totals		299	299	145	148	7,533	2,064	91 eggs on <i>Cedrela odorata</i> 2 eggs on <i>Cananga odorata</i>

* Potted host and non-host trees were placed in the cages from March 28-April 19, and from May 1-May 22, 1971.

** Escaped or predated.

Table 3.—Number of adults, mortality, sex ratio and oviposition data of *H. grandella* in captivity, during the periods of December 14-20, 1970 and April 20 - May 18, 1971. Adults reared in the laboratory on a synthetic diet.

Date (night of)	N° of adults present in cage	N° of adults added	Mortality	N° and sex of dead adults		N° of fertile eggs oviposited	N° of sterile eggs oviposited	Oviposition on potted host and non host trees in the cage*
				♂	♀			
14-15 Dec. 1970	0	2	—	—	—	—	—	28 eggs on <i>Cedrela</i>
15-16	2	—	—	—	—	—	—	
16-17	2	—	—	—	—	13	—	
17-18	2	—	—	—	—	89	—	
18-19	2	—	—	—	—	—	—	
19-20	2	—	—	—	—	18	—	
20-21	2	4	—	—	—	12	—	
21-22	6	1	—	—	—	23	—	
22-23	7	1	—	—	—	93	—	
23-24	8	—	—	—	—	41	8	
24-25	8	—	1	1	—	75	11	
25-26	7	—	1	1	—	162	—	
26-27	6	—	1	—	1	48	—	
27-28	5	—	2	1	1	—	17	
28-29	3	—	2	2	—	—	—	
29-30	1	—	1	—	1	—	—	
Totals		8	8	5	3	574	36	43 eggs on <i>Cedrela odorata</i> no eggs on <i>Cananga odo- rata</i>
20-21 April 1971	0	7	—	—	—	—	—	3 eggs on <i>Cedrela</i>
21-22	7	11	—	—	—	—	—	
22-23	18	4	—	—	—	3	—	
23-24	22	6	2	1	1	3	—	
24-25	26	4	—	—	—	111	157	
25-26	30	—	5	4	1	125	—	
26-27	25	7	4	2	2	176	93	
27-28	28	3	5	3	2	244	—	
28-29	26	6	5	3	2	285	32	
29-30	27	6	1	1	—	127	—	
30-1 May	32	—	6	3	3	128	13	
1-2	26	1	10	5	5	136	—	
2-3	17	17	1	1	—	23	27	
3-4	33	12	4	3	1	34	—	
4-5	41	—	3	1	2	358	138	
5-6	38	—	2	1	1	694	—	
6-7	36	—	3	—	3	947	197	
7-8	33	—	2**	—	—	777	—	
8-9	31	—	6	2	4	549	128	
9-10	25	—	1	—	1	170	—	
10-11	24	—	4	1	3	192	41	
11-12	20	—	5	3	2	181	—	
12-13	15	—	2	1	1	77	27	
13-14	13	—	1	1	—	88	—	
14-15	12	—	6	4	2	—	8	
15-16	6	—	4	1	3	—	—	
16-17	2	—	1	1	—	—	—	
17-18	1	—	1	1	—	—	—	
Totals		84	84	43	39	5,434	861	99 eggs on <i>Cedrela odorata</i> 2 eggs on <i>Cananga odorata</i>

* Potted host and non-host trees were placed in the cage from December 14-18; December 24-30, 1970 and April 29-May 10, 1971.

** Escaped or predated.

Table 4.—Location of *H. grandella* eggs on towel paper, in a oviposition cage located near a common light bulb. Adults raised on natural diet.

Date (night of)	Total No of eggs oviposited	No of eggs located upper half of the frames	Percentage	No of eggs located on lower half of the frames	Percentage	No of eggs located on frames nearest to common lightbulb	Percentage
4-5 April, 1971	113	88	78	25	22	108	96
5-6	29	16	55	13	45	23	79
6-7	56	35	63	21	37	52	93
7-8	125	96	77	29	23	120	96
8-9	37	22	59	15	41	37	100
9-10	6	6	100	—	—	6	100
10-11	77	43	57	34	43	57	74
11-12	20	5	25	15	75	20	100
Totals	463	311	67	152	33	423	91

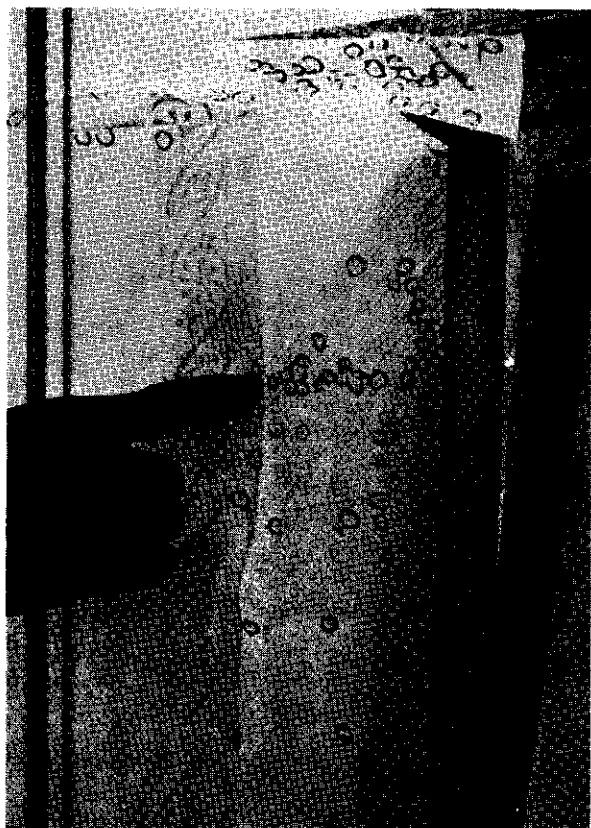


Fig. 4.—One day old fertile eggs on the upper half of the frames. The eggs are located in the pits of the towel paper.

During the heavy rainy period, a remarkable effect of the night light on oviposition was observed. Ninety-one percent of all eggs oviposited during this period were located on the two frames nearest to the light (Table 4). The fact that *H. grandella* is attracted to light was also observed repeatedly during the nightly releases of adults in the cages, when the recently emerged adults could be transferred from the jars to the cage with the help of a flashlight. This attraction to light of a lantern has also been observed by Ramírez Sánchez (10).

Another interesting observation was made during this period. If occasionally a jar containing pupae and desiccated *Cedrela* leaves was left in the cage of the adults raised on natural diet, *H. grandella* adults could be found the next morning on the gauze covering the jar (Fig. 5). If the gauze was removed during the night, the adults could be found repeatedly in the jars again. Although no formal experiment was executed with respect to this behavior, the response of *H. grandella* to the night light and the jars containing pupae and desiccated *Cedrela* leaves could fit into a hypothetical model for the chain of stimuli causing host selection of *H. grandella*.

Callahan (4, 5, 6) developed a theory for the intermediate and far infrared sensing of nocturnal insects. Since common lightbulbs, such as the night light, are known to emit a great quantity of the infrared spectrum, the oviposition behavior of *H. grandella* during this period might well be a response to infrared. The attraction of *H. grandella* to the jars in the cages might



Fig. 5.—*H. grandella* adults in cage, on gauze of beaker containing pupae and desiccated *Cedrela* leaves.

possibly be caused either by an aggregation hormone or wavelength emission of the desiccated (darker) *Cedrela* leaves.

Taking into account these observations, a hypothetical model for *H. grandella* host selection could be the following:

- | | |
|--------------------------------------|---|
| Remote and intermediate orientation: | a: wavelength emission of host |
| Intermediate and nearby orientation: | b: a+chemoreception of host odors and aggregating hormones; sex attractants |
| Landing and oviposition: | c: a+b+copulation and tactile response. |

With respect to mating behavior, observed in the cages during the releases at 20:00, observations gave evidence for the existence of a female sex attractant. *H. grandella* females often remained stationary on the oviposition frames, while lifting their abdomen and "fanning" their wings, supposedly to "fan away" a sex attractant. Fourteen out of 15 "fanning" adults sam-

pled in the cages during the period of the rearing experiment proved to be females. Both males and females made flight exercises however, and also used their wings to climb up the frames.

In early hours of the morning (05:30-06:30) coupled pairs (tail to tail) were observed several times. Coupling itself has not been observed.

With respect to oviposition, a decrease in average egg production and an increase in the average number of sterile eggs per female of each diet can be noticed (Tables 1-3) when the two periods are compared. Average egg production per female reared on natural diet, was 100 fertile and 8 sterile eggs in the period of January 11-February 11, 1971, whereas these figures are 65 and 14 in the period of March 27-May 22, 1971. Average egg production per female raised on the synthetic diet was: 191 fertile and 12 sterile eggs in the period of December 14-30, 1970 and 161 fertile and 22 sterile in the period of April 20 - May 18, 1971.

The main cause for these phenomena could possibly be attributed to the increased number of insects per cage, to sex ratio or to ambient conditions rather than degeneration of the insect population. Evidence regarding the possible effect of sex ratio was obtained when later (May 18-May 27, 1971) 10 sexed adults (5 females and 5 males) raised on synthetic diet, were placed in a cage. These females produced 1062 eggs, of which only 61 were infertile; i.e. an average production of 200 fertile and 12 sterile eggs per female. Sex ratio during the rearing period was approximately 1:1 (Table 1-3)

Rearing

Figure 6 represents the daily temperature and relative humidity fluctuations of the air-conditioned laboratory during the week of May 3-10, 1971. Although minor differences from this regular pattern occurred during the rearing period, daily maximum and minimum temperature never reached over 30°C or below 22°C, respectively. Relative humidity varied between 50 and 68 per cent during the rearing. Maximum temperature and minimum relative humidity in the laboratory occurred at approximately 14:30 hours.

Of three distributions tested, Poisson, normal and binomial, the latter fitted the observed frequencies best.

Figures 8 and 9 show the observed and expected frequencies of pupating larvae (A) and emerging adults (B) of both diets in relation to time (expressed in days after oviposition).

Observed maxima for pupation and emergence of *H. grandella* reared on synthetic diet occurred 26 and 37 days after oviposition, respectively. Observed maxima for pupation and emergence of *H. grandella* reared on natural diet occurred at 25 and 35 days after oviposition.

The difference in time needed for maximum pupation of larvae raised on both diets might be due to the spinning of a sort of "community web" (Fig. 7) which occurred in the polystyrene containers with synthetic diet, but not in the natural diet.

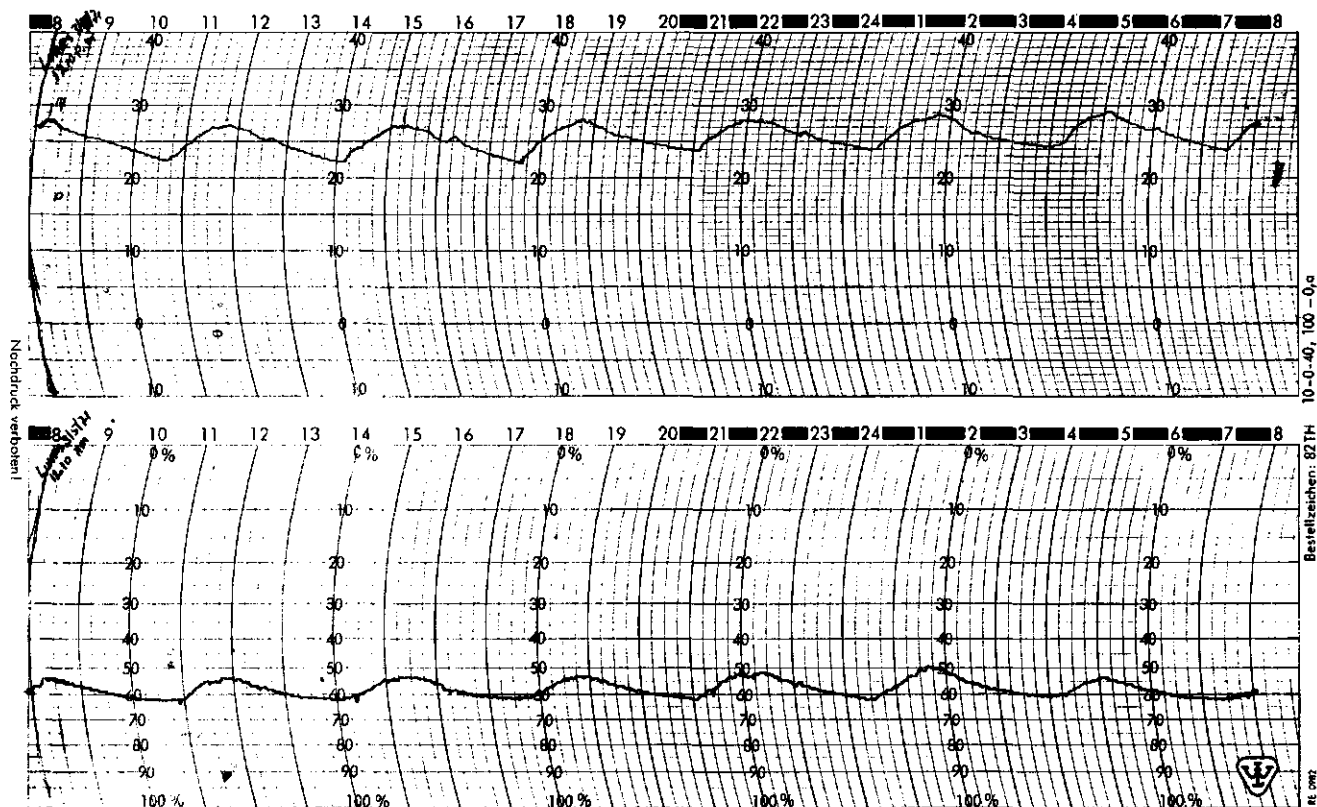


Fig. 6.—Daily temperature and relative humidity fluctuations of the airconditioned laboratory, during the week of May 3-10, 1971. Maximum temperature and minimum relative humidity occurred approximately at 14.30, daily.

This delaying effect, can also be noted from the observed and expected time needed for pupation of larvae from both diets (Fig. 8 and 9). The pupation-curve for larvae reared on artificial diet is flatter than the one for larvae reared on natural diet. Larvae reared on synthetic diet often crowded and bothered each

other. Larval and pupal cannibalism was frequent in the containers with synthetic diet. Yield of adults (Table 5) was higher in natural than in synthetic diets.

Difference in duration of the prepupal and pupal stage in both diets, might be explained by the difference in size of adults reared on both diets. Adults

Table 5.—Yield of *H. grandella* adults, reared under laboratory conditions on natural and synthetic diets in uncompartmented polystyrene containers.

Type of diet	N° of eggs placed in containers	N° of eggs hatched	Percentage of eggs hatched	N° of larvae pupated	Percentage of larvae pupated $\frac{\text{N° pupae}}{\text{N° eggs hatched}} \times 100\%$	N° of adults emerged	Yield (%) $\frac{\text{N° adults}}{\text{N° eggs hatched}} \times 100\%$	Observations
Natural	379	339	89.4	182	53.7	154	45.4	based on data from 11 containers
Synthetic	389	319	82.0	150	47.0	133	41.7	based on data from 8 containers



Fig. 7.—'Community web', spun by *H. grandella* larvae on synthetic diet. Pupae can be observed in the web.

reared on synthetic diet were generally bigger than those reared on natural diet. This could indicate a deficiency in the natural diet of leaves and young shoots, or differences in feeding response to each diet. In natural conditions *H. grandella* larvae will feed mainly on the pith of shoots.

The size of male and female adults reared on synthetic diet was based on 35 measurements for each sex, and ranged from 13.0 - 19.4 mm and 13.0 - 22.1 mm, respectively. Average size of these male and female adults was 16.7 ± 0.8 mm* and 17.9 ± 1.1 mm*, respectively.

The range in size of male and female adults reared on natural diet was from 11.8 - 18.0 mm for males and from 13.0 - 22.1 mm for females, based on 28 and 26 measurements respectively. Average size of these male and female adults was 14.6 ± 0.9 mm* and 15.1 ± 1.1 mm*, respectively.

* $x \pm t \frac{S}{0.01 x}$

In the longevity test (Fig. 10), a significant difference at the one per cent level, was found between sexes; female *H. grandella* of both diets lived longer than males. It should be noticed however, that these observations refer to unmated adults under the specified test conditions. In the cages, where only water was provided (either in the form of rain or offered water during dry spells) longevity of adults reared on synthetic and natural diet ranged from 3-15 and 2-10 days respectively. Adults drinking water could be observed frequently, particularly during the dry spells when water was offered.

Mass rearing

The previously described techniques have led to a preliminary mass rearing program in which larvae are reared on synthetic diet in compartmented polystyrene containers, so as to avoid cannibalism. Oviposition cages are smaller (30 x 30 x 40 cm) and towel paper has been replaced by cheese cloth. Eggs are washed off in a 0.15 per cent solution of sodium hypochlorite which at the same time sterilizes the egg surface. This in turn, reduces contamination of the synthetic diet. Cocoons are removed with a 2.5 per cent solution

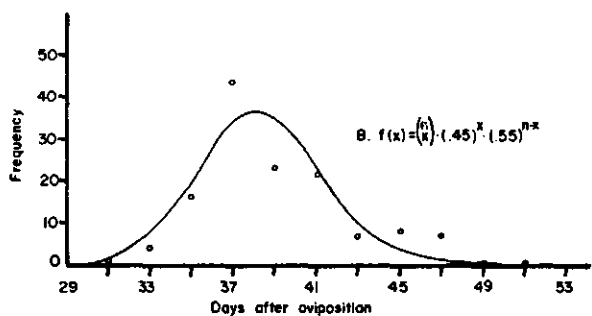
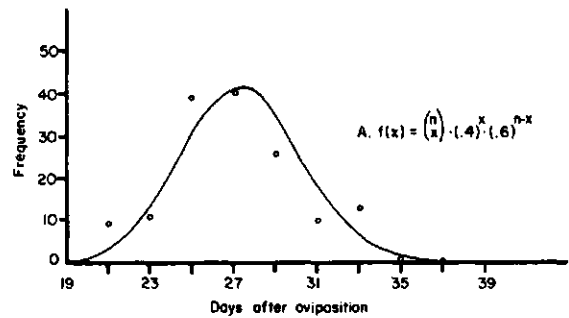


Fig. 8.—Observed and expected frequencies of pupating larvae (A) and emerging adults (B) of *H. grandella* on synthetic diet, in relation to time.

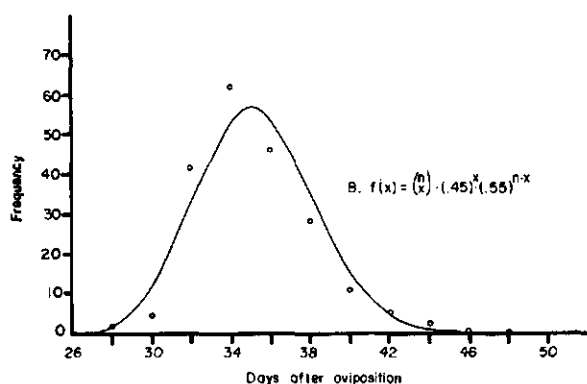
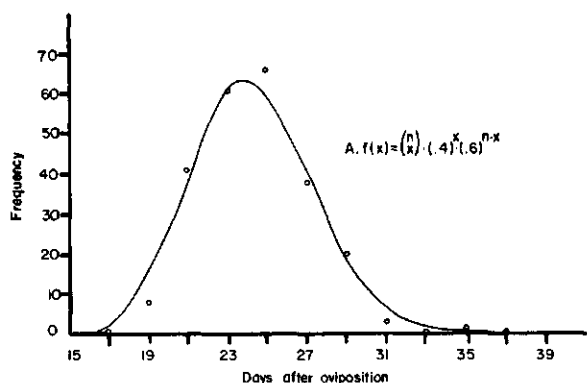


Fig. 9.—Observed and expected frequencies of pupating larvae (A) and emerging adults (B) of *H. grandella* on natural diet, in relation to time.

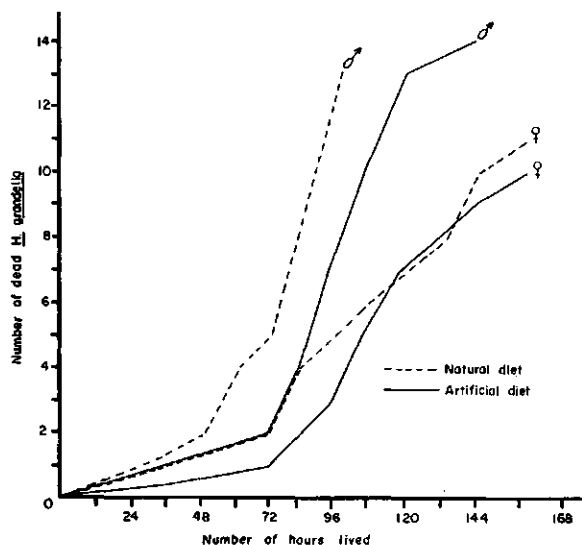


Fig. 10. Comparison of longevity of *H. grandella* adults (males and females) reared on synthetic and natural diet. Accumulated mortality per 12 hours under laboratory conditions; no food nor water provided.

of sodium hypochlorite and pupae are sexed (8). Some steps of the preliminary mass rearing procedures still have to be perfected in order to reach the same level of efficiency as rearing programs for other species of insects (11, 12, 13). Oviposition of fertile eggs in the laboratory has been obtained (at a relative humidity of 65 per cent and 25°C) but the technique needs further investigation. In addition, removal of eggs should be improved and yield of *H. grandella* adults should be increased.

Acknowledgements

The author wishes to thank Dr. Gilberto Páez and Ing. Víctor Quiroga of the IICA-CTEI Computer Center for their assistance in the statistical evaluation of the results. Special thanks are due to Oscar Ovares, foreman of the Department of Tropical Forest Sciences, who dedicated many hours of his spare time on this investigation.

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2.4. INVESTIGATIONS ON THE OCCURRENCE OF PARASITES OF *H. GRANDELLA*.

Papers:

- 2.4.1. Studies on the shootborer *Hypsipyla grandella* (Zeller) (Lep., Pyralidae). XII. Observations on the egg parasite *Trichogramma semifumatum* (Perkins) (Hymenoptera; Trichogrammatidae). *Turrialba* 22(4):398-402. 1972.
- 2.4.2. Studies on the shootborer *Hypsipyla grandella* (Zeller) (Lep., Pyralidae). XVII. Records of two parasites new to Costa Rica. *Turrialba* 23(2):235-236. 1973.
- 2.4.3. Studies on the shootborer *Hypsipyla grandella* (Zeller) (Lep., Pyralidae). XXV. *Hexameris albicans* (Siebold) (Nematoda:Mermitidae) a parasite of the larva. *Turrialba* 24(2):82-86. 1974.

Studies on the shootborer *Hypsipyla grandella* (Zeller) (Lep., Pyralidae). X. Observations on the egg parasite *Trichogramma semifumatum* (Perkins) (Hym.: Trichogrammatidae)*

P. GRIJPMMA**

C O M P E N D I O

En este artículo se hace mención de los siguientes registros nuevos relacionados a los estudios sobre el barrenador de las meliáceas: 1. La oviposición de *Hypsipyla grandella* (Zeller) sobre el cedro australiano *Toona ciliata* M. Roem. var. *australis* (F. v. M.) C. DC. fue observada por primera vez el 20 de mayo de 1971 en una parcela experimental en Puente Cajón, Turrialba, Costa Rica. 2. Mortalidad de larvas del primer instar de *H. grandella* que atacan el cedro australiano. Estas larvas mueren dentro de uno a tres días, sugiriendo la existencia de un compuesto tóxico o la ausencia de un compuesto vital para las larvas en los tejidos del cedro australiano. 3. Parasitismo de *Trichogramma semifumatum* (Perkins) sobre los huevos de *H. grandella*. Esta es la primera vez que se registra la presencia de este parásito en Costa Rica y de un nuevo hospedante *Hypsipyla grandella* (Zeller). 4. Según la determinación del Dr. S. Nagarkatti, del Commonwealth Institute of Biological Control en India, el material original colectado contenía también *Trichogramma pretiosum* Riley y posiblemente una otra especie no registrada *Trichogramma* cerca de *pretiosum*.

Se estableció una cría pura de *T. semifumatum* sobre huevos de *Hypsipyla grandella* y se hicieron observaciones con respecto al ciclo de vida, emergencia, copulación y comportamiento de este parásito.

Un inventario de la plantación recién establecida del cedro australiano reveló un alto porcentaje de parasitación de los huevos de *H. grandella* que podría ser consecuencia de una época seca anormal. — El autor.

Introduction

OVIPOSITION of *Hypsipyla grandella* (Zeller) on the resistant Australian red cedar, *Toona ciliata* M. Roem. var. *australis* (F.v.M.) C. DC., was recorded by the author for the first time on May 20, 1971, in a field plot in Puente Cajón, Turrialba, Costa Rica. First instar larvae of *H. grandella* boring into this species die within 1-3 days, suggesting the existence of a toxic, or the absence of a vital component

for the larvae in the plant tissues of *T. ciliata* var. *australis**

A 100 per cent survey, conducted in a plot of recently planted Australian cedar not only revealed a high incidence of *H. grandella* eggs on the seedlings but also a high percentage of parasitization of these eggs by *Trichogramma*. Subsequent rearing of the *Trichogramma* population on *H. grandella* eggs was initiated and resulted in a series of laboratory experiments on the parasitization of *H. grandella* eggs by this parasite, which are reported here.

* Received for publication September 27, 1972.

** Silviculturist, Forestry Program, Inter-American Institute of Agricultural Sciences, Turrialba, Costa Rica. Attached to IICA through the Dutch Technical Assistance Program. Study to be used by P. Grijpma for Ph. D. dissertation.

* Studies on the shootborer *Hypsipyla grandella* (Zeller) (Lep., Pyralidae). On the resistance of *Toona ciliata* M. Roem. var. *australis* (F.v.M.) C. DC. (in preparation).

Materials and methods

A 100 per cent survey on the incidence of parasitized and non-parasitized *H. grandella* eggs was conducted on December 30, 1971 in a two months old plantation of the Australian cedar. Height of the seedlings was measured and the number of eggs deposited on each was determined. The plantation consisted of 480 trees planted between approximately 1.50 m high *Cedrela angustifolia* Sessé & Moc. ex. DC. trees (provenance Barinitas, Venezuela). Of the Australian cedar seedlings, 432 had been planted with naked roots, the remainder as potted seedlings (4). Precipitation data in the plantation area were recorded. Survival of the *Toona* seedlings was determined and living as well as dead trees were checked for oviposition. Planting distance between seedlings was 1 x 1 m. The plantation was established in an open field, covered with vegetation consisting mainly of grasses and weeds, on property of the Inter American Institute of Agricultural Sciences, Turrialba, Costa Rica. The neighboring vegetation consisted of a pure *Cedrela angustifolia* plantation and an abandoned coffee plantation, heavily shaded by 15 m high *Erythrina* trees. A sugar cane plantation was located at about 100 m distance from the meliaceous plantations, behind the abandoned coffee field. Successful *H. grandella* attacks, indicated by fresh frass, were observed on the *C. angustifolia* plants in the pure plantation as well as in the part of the plantation mixed with the Australian cedar seedlings. Two rows of the pure *C. angustifolia* plantation, consisting of 46 and 41 plants respectively, were also surveyed to determine the incidence of parasitized and non-parasitized *H. grandella* eggs.

Parasitized eggs were removed from the *T. ciliata* var. *australis* and *C. angustifolia* trees with a razor blade and a preliminary rearing method was developed for the *Trichogramma* parasites utilizing *H. grandella* eggs (5). Hereto, the parasitized eggs were put in small polystyrene boxes (12 x 9 x 3.5 cm) and provided with eggs of the shootborer each time upon emergence. Observations were made on the life cycle, emergence, and mating behavior of this *Trichogramma* sp.

An experiment was conducted to determine and compare the pre-emergence and incubation periods respectively of parasitized and non-parasitized *H. grandella* eggs. Fifty parasitized eggs of which the time of parasitization had been recorded and 50 fertile, non-parasitized, fresh *H. grandella* eggs were put in one of the polystyrene boxes. The age of these eggs may have varied between 2-14 hours. Temperature and humidity in the air-conditioned laboratory were recorded continuously. No water was added to the polystyrene box. Upon hatching, first instar *H. grandella* larvae were removed from the box, to avoid consumption of the parasitized eggs by the first instar *H. grandella* larvae which have been observed frequently feeding on *H. grandella* eggs in the absence of other feeding material.

Samples of the original *Trichogramma* population were sent to Dr. B. D. Burks of the USDA Entomology Research Division in Beltsville, Maryland; to Dr. L. De Santis, Museum of La Plata, Argentina, and to Dr. S. Nagakatti of the Commonwealth Institute for Biological Control, Bangalore, India, for determination. Samples of the subsequent rearing were forwarded to Dr. Nagakatti for determination.

Preference of the *Trichogramma* sp. for fresh eggs (1, 6), was tested in an experiment in which 20 fresh, 20 one-day old and 20 two-days old *H. grandella* eggs were exposed simultaneously to 20 female parasites in one of the polystyrene boxes. The three age groups of *H. grandella* eggs had been obtained employing a newly developed technique (8), and were distributed randomly on 9 cm² of towel paper. Behaviour of *Trichogramma* with respect to preference and the parasitization *per se* was followed through a microscope.

The sex-ratio of the egg parasite, reared under prevailing laboratory conditions, was established by counting male and female populations of eight polystyrene rearing boxes after they had died.

Finally, observations were made on the parasitization of unfertilized *H. grandella* eggs by this *Trichogramma*.

Results

The 100 per cent survey for *H. grandella* oviposition in the *T. ciliata* var. *australis* plot of 480 seedlings showed that 123 seedlings planted with naked roots had died. No oviposition of *H. grandella* was observed on these dead seedlings. Of the remaining 357 plants, 93 had a total of 221 *H. grandella* eggs, of which 217 were black, indicating parasitization, and 4 were red. The only other category of *H. grandella* eggs found, consisted of 12 empty, transparent chorions which were collected on 7 seedlings. No further count was made of these hatched eggs, in view of the great difficulties encountered in locating them. No damage to the *Toona* seedlings was noticed, although *H. grandella* larvae had apparently hatched on at least 7 plants. Average height of the Australian cedar seedlings was 55.4 cm.

Microscopic examination of the four red *H. grandella* eggs, showed that they were also parasitized.

The inventory of the two rows of the neighboring *Cedrela angustifolia* plantation presented the same picture. Here, 30 parasitized eggs were found on 13 of a total of 87 plants. Average height of these plants was 1.75 m. Two of the collected eggs were red but also proved to be parasitized when examined under the microscope. The number of parasitized eggs on the *T. ciliata* var. *australis* seedlings varied between 1 and 10, averaging 2.4 per tree. The number of parasitized eggs on *C. angustifolia* plants varied between 1 and 9, averaging 2.3 per tree.

The apparent high incidence of parasitization observed in these meliaceous plantations may have been

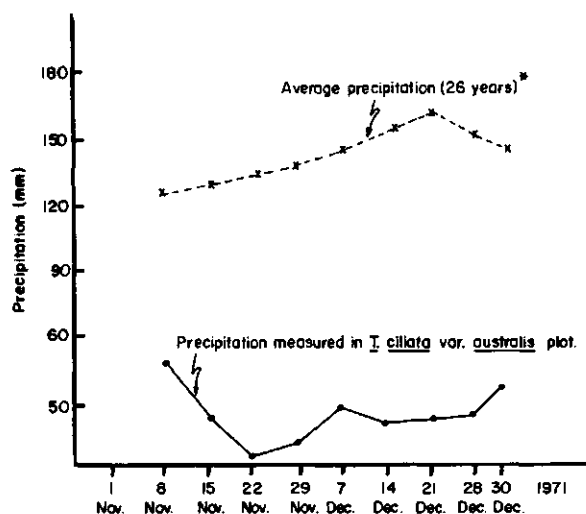


Fig. 1.—Weekly precipitation registered in *T. ciliata* var. *australis* plot as compared to precipitation averages of 26 years (1944-1970).

* Source: Meteorological observation station at IICA-CTEL, Turrialba, Costa Rica. Location approximately 1 km from *T. ciliata* var. *australis* plantation.

influenced by abnormally dry weather conditions. Figure 1 compares the average precipitation of 26 years with the rainfall measured during the first two months after planting of the Australian cedar in the field.

Laboratory rearing of the *Trichogramma* population on *H. grandella* eggs proved to be easy, and was obtained by offering fresh eggs of the shootborer as long as female parasites were alive in each box. About 33 generations have been reared meanwhile and the parasite population is still increasing. The daily fluctuations of temperature and humidity in the air conditioned laboratory varied between 22 and 28°C and 50-60 per cent R.H., respectively.

The incubation period of *H. grandella* eggs and the developmental period of *Trichogramma*, under the indicated laboratory conditions, varied between 84-116 h and 231-240 h, respectively. The greater variability in the incubation period of *H. grandella* eggs is most probably due to differences in time of oviposition. The age of white, "fresh" *H. grandella* eggs may have varied from 2-14 hours under the conditions of this experiment. The *H. grandella* eggs utilized for parasitization by the *Trichogramma* sp. were all exposed at the same time for parasitization by the parasite.

Observations made during this experiment indicated that *H. grandella* eggs become reddish-black approximately 3 days after parasitization and are completely black 4 days after having been parasitized by the *Trichogramma* (Table 1). Since most *Trichogramma* emerged three days after having been collected from the field plot, it can be taken for granted that all *H. grandella* larvae hatching from un-parasitized eggs had already emerged on the seedlings. The empty chorions encountered in the field gave further evidence to this

Table 1.—Development of *Trichogramma semifumatum* in *Hypsipyla grandella* eggs. The most important observable changes in 50 parasitized eggs are recorded in hours after parasitization; parasitization took place between 15.30 and 16.30 h.

Time lapse after parasitization	Observations
29 h	Yellowish "cells" have become visible within red colored <i>H. grandella</i> eggs. One or two dents can be noticed in the egg shell.
38 h	Net like concentration of red pigment in eggs.
45 h	Walls between developing <i>Trichogramma</i> visible; red pigment concentrated near walls.
51 h	Further delineation of walls within <i>H. grandella</i> eggs. Red pigment is concentrated near the walls and edges of the parasitized egg.
68 h	Concentration of red pigment in the developing embryos (reverse situation of the records made from 29 h - 51 h after parasitization). Developing <i>Trichogramma</i> can be easily counted now.
72 h	Individual bumps for each <i>Trichogramma</i> visible. Walls are yellowish colored, red pigment inside.
75 h	Eggs are turning reddish-black; walls are still yellowish colored.
78 h	A few eggs have turned black.
88 h	Majority of the eggs are black.
93 h	All eggs are completely black now. No further changes noticed until emergence.
232 h	First <i>Trichogramma</i> emerged. Cleaned antennae and unfolded their wings employing last pair of legs. Emergence took approximately 10 minutes; cleaning of antennae and unfolding of wings also.

reasoning. It may therefore be assumed that the encountered high percentage of parasitization of *H. grandella* eggs was probably not at all representative of the efficiency of the parasite nor did it give a correct picture of the actual rate of parasitization in this case.

Burks* and De Santis* identified the specimens of the originally collected population as *T. semifumatum* and *T. pretiosum* respectively. Nagarkatti*, y Nagarkatti y Nagaraja (7) indicated that *T. semifumatum*, *T. near pretiosum* and possibly *T. pretiosum* were present in the specimens of the original population. The data presented on the lifecycle, emergence, copulation and behavior only refer to *T. semifumatum*, of which pure populations were established in the laboratory and later identified by Nagarkatti*.

* Personal communication.

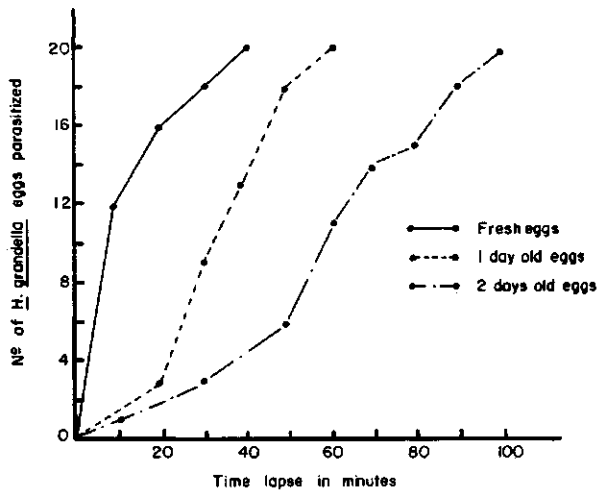


Fig. 2.—Time needed for parasitization of 20 fresh, 20 one day, and 20 two days old eggs of *Hypsipyla grandella* distributed randomly on 9 cm² towel paper and exposed simultaneously to 20 female *Trichogramma semifumatum* (parasitization accumulated in periods of 10 minutes).

The preference of *Trichogramma semifumatum* for fresh *H. grandella* eggs was demonstrated in the preference test (Fig. 2). The lapse of time needed to parasitize 20 eggs of each age group (fresh, 1-day, and 2-days old) by 20 females of *T. semifumatum* was taken as an indication of preference. Microscopic observation of the parasitization of these 60 *H. grandella* eggs demonstrated the preference of the parasite for fresh eggs. The female egg parasite could be seen walking over 1-day and 2-days old eggs to reach and oviposit in the fresh *H. grandella* eggs. This is in agreement with the records of Clausen (1), Hidalgo-Salvatierra and Madrigal (6).

Parasitization of fresh (1-14 h old) 1-day old eggs, age between 26-38 h, was 100 per cent successful, i.e. larval development of *H. grandella* was halted completely whereas parasitization of the 2-days old eggs, age between 50-62 h, still resulted in hatching of 30 per cent of the *H. grandella* larvae.

Superparasitism was observed frequently on fresh and 1-day old eggs, but to a far lesser degree on the 2-days old *H. grandella* eggs.

During the 11-month period in which approximately 33 successive generations of *T. semifumatum* were reared, observations were made on egg development, emergence and behavior of the parasite. Table 1 represents the changes noticed during the pre-emergence period. The number of developing *Trichogramma* per egg was determined on 128 eggs which had been exposed for a period of 24 hours to 79 males and 79 females of this parasite.

A counting of developing embryos of the parasite per *H. grandella* egg, 3 days after initiation of the experiment resulted in 11 eggs containing 1 embryo;

62 eggs containing 2; 36 eggs containing 3; 13 eggs containing 4, and 6 eggs containing 5 developing embryos.

The majority of the adults emerged through one exit. Of 1918 parasitized eggs, 1762 or 91.9 per cent used the same exit hole; 151 eggs or 7.9 per cent had two exit holes and only 5 eggs or 0.2 per cent had three exit holes. Adults when emerging, faced away from the oviposition stratum and were either of the same sex, only males or females, or of mixed sex. All three possibilities were observed during the rearing period. On a number of occasions male parasites could be observed sitting on top of parasitized eggs from which *Trichogramma* were emerging. Mating or mating attempts by these males, took place as soon as a female or male had actually emerged. Occasionally attempted oviposition on empty chorions from which first instar *H. grandella* larvae had already hatched was observed. Form and texture of eggs are probably important factors for parasitization by the female *Trichogramma*. Parasitization behavior is similar to that described by other authors (1, 2, 3).

Determination of the sex of 1742 *T. semifumatum* adults emerging in 8 polystyrene boxes indicated a sex ratio of approximately 1:1 (877 ♂♂ versus 865 ♀♀).

Parasitization of unfertilized *H. grandella* eggs took place any time they were offered. However, the majority of these *H. grandella* eggs collapsed and dried out within a day.

Nevertheless, several well developed egg parasites were obtained from unfertilized shootborer eggs. It is assumed here that unfertilized *H. grandella* eggs are permeable to water and will dry out or swell depending on the availability of water either in the air in the form of vapor or on the surface on which they were oviposited. Successful parasitization of these *H. grandella* eggs may depend on the time needed by the parasite to form the inner layer (1), or may take place in those cases in which the availability of water in the air or on the substrate is enough to permit the normal formation of the inner layer of the parasite in the *H. grandella* eggs. Once this layer has been formed, protection of the egg against changes in its water balance may have been secured and normal development of the parasite may take place.

Some evidence supporting the assumption of the permeability of unfertilized *H. grandella* eggs to water was obtained by moistening the towel paper on which unfertilized eggs had been oviposited. These eggs swelled and collapsed within 24 hours when they dried. Apparently, fertile *H. grandella* eggs do not dry out and collapse.

Successfully parasitized unfertilized *H. grandella* eggs are black with a yellowish tinge, indicating that the black color of parasitized eggs is the result of parasitization by *Trichogramma*.

Acknowledgements

The author wishes to thank Dr. S. Nagarkatti, CIBC, Bangalore, India, for the determination of the *Trichogramma* species and for her valuable comments. Helpful criticism on the content of the paper was also received from Dr. F. D. Bennett, CIBC, Trinidad. The cooperation of Dr. B. D. Burks, USDA Entomology Research Division, Beltsville, Maryland, USA, and Dr. L. De Santis of the Museum of La Plata, Argentina, with respect to the determination of specimens, has also been highly appreciated.

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Studies on the shootborer *Hypsipyla grandella* (Zeller) (Lep., Pyralidae) XVIII. Records of two parasites new to Costa Rica.

Sumario. Se registran dos parásitos del barrenador de las meliáceas, *Hypsipyla grandella* (Zeller), nuevos para Costa Rica. Adultos de *Trichogramma fasciatum* (Perkins) (Hym., Trichogrammatidae) fueron obtenidos de huevos de *H. grandella* recolectados sobre frutos de *Cedrela odorata* L. y de ramas próximas a los frutos, en un bosquecillo ubicado en Santa Cruz, Guanacaste a 200 m s.n.m. Adultos de *Brachymeria conica* (Ashmead) fueron criados de pupas de *H. grandella* recolectadas en frutos de *C. odorata* en el mismo lugar mencionado y en tallos tiernos de *C. tonduzzii* C. DC., *C. odorata* y *Swietenia macrophylla* King en plantaciones jóvenes de estas meliáceas, establecidas en los terrenos del Departamento de Ciencias Forestales Tropicales del IICA-CTEI, Turrialba, Costa Rica, a 650 m s.n.m.

Any biological control program on a specific insect should preferably be preceded by an exhaustive inventory of the biocontrol agents already present in the country. With respect to the shootborer *Hypsipyla grandella* (Zeller) such surveys have been carried out repeatedly in Costa Rica since the establishment of the Inter-American Working Group on this forest insect pest in September 1970. In previous surveys by the author, the larval parasite *Hypomicrogaster hypsipylae* De Santis (4) and three egg parasites, *Trichogramma semifumatum* (Perkins), *T. pretiosum* Riley and a *Trichogramma* sp. near *pretiosum* were found parasitizing *H. grandella* in Turrialba, Costa Rica, at 650 m elevation (2). During more recent inventories two additional parasites were obtained.

The egg parasite *Trichogramma fasciatum* (Perkins) was reared from *H. grandella* eggs which were collected on fruits and small branches adjacent to fruits of *Cedrela odorata* L. trees growing at 200 m elevation in Santa Cruz, Guanacaste. The seed capsules were located at a height of 12 m on trees in open pasture land. Collection took place on January 23, 1973 during the dry season.

Nagarkatti and Nagaraja (3) indicate that *T. fasciatum* attacks *Diatraea saccharalis* (F.) (Pyralidae) in the West Indies, Peru and the USA. This *Trichogramma* species has also been collected in Mexico from eggs of *Heliothis zea* (Boddie) and from an unknown host in Argentina.

The parasite *Brachymeria conica* (Ashmead) was reared from *H. grandella* pupae collected on January 23, 1973 in fruits of *C. odorata* at Santa Cruz, Guanacaste. Adults of this parasite were also reared from *H. grandella* pupae in young shoots of *C. tonduzzii* C. DC., *C. odorata* and *Swietenia macrophylla* King in a two years old mixed forest plantation of IICA-CTEI at Turrialba, Costa Rica.

In addition, *B. conica* adults were obtained from pupae of *Paramyelois transitella* (Walker) (Lep., Phycitinae) found in fruits of a *Forchhammeria* sp. (Capparidaceae) on the beach of Playa Hermosa, Guanacaste. They were also reared from pupae of *Anadasmus porinodes* (Meyrick) (Stenomidae) found in shoots of *Ochroma lagopus* (Bombacaceae) in a forest plantation at IICA-CTEI at Turrialba, Costa Rica.*

It is of interest to note that *B. conica* apparently has a wide ecological range. The Guanacaste area of Costa Rica has a dry period of 4-6 months, whereas the Turrialba region generally has only a one month dry season. Burks (1) indicates that *B. conica* has a distribution from Texas to Brazil. It has also been collected in Trinidad.

Acknowledgements. The author wishes to thank Dr. Sudha Nagarkatti, Commonwealth Institute of Biological Control, Bangalore, India, for the determination of *Trichogramma fasciatum* and Dr. Luis De Santis, Museo de La Plata, La Plata, Argentina, for the determination of *Brachymeria conica*. Thanks are also due to Dr. B. D. Burks, USDA-ARS, Systematic Entomology Laboratory, Washington, USA, for providing the author with documentation on the distribution of *B. conica*.

March 29, 1973.

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Studies on the shootborer *Hypsipyla grandella* (Zeller) (Lep., Pyralidae) XXV. *Hexameris albicans* (Siebold) (Nematoda: Mermithidae) a parasite of the larva

Sumario. Se registra una nueva asociación parasítica entre el nematodo *Hexameris albicans* y el barrenador de las Meliáceas (*Hypsipyla grandella*). Entre 5 y 25 por ciento de las larvas del barrenador, muestreadas en una plantación de Meliáceas del Departamento de Ciencias Forestales Tropicales del CATIE en Turrialba, Costa Rica, murieron debido al parasitismo por el nemátodo. El nivel más alto de parasitismo se encontró en la época de más lluvia y el nivel más bajo al final de la época seca. Las larvas parasitadas fueron recolectadas de ramas de *Cedrela* spp. y de *Swietenia macrophylla* King, encontradas entre 1 y 2 metros encima del suelo. Se incluye una lista de lepidópteros parasitados por miembros del género *Hexameris*.

Research on the control of the mahogany shootborer *Hypsipyla grandella* (Zeller) in Costa Rica, has uncovered an interesting parasitic association between the mermithid nematode *Hexameris albicans* and this pest insect.

Although a mermithid, probably of the genus *Hexameris*, had been collected earlier in 1969 from larvae of *H. grandella* in Costa Rica (8), it had never been identified properly, possibly because no adult stage could be obtained.

Specimens of *Hexameris albicans* were reared from *H. grandella* larvae collected during surveys for biocontrol agents in a meliaceous plantation located in the Florencia Sur forest of the Tropical Agricultural Research and Training Centre at Turrialba, Costa Rica. These insect larvae were obtained from branches of *Cedrela* spp. and *Swietenia macrophylla*, located between 1 and 2 m above the ground. The adult stage of the nematodes was obtained by placing the nematodes for approximately six weeks on moist sand after they had emerged from the *H. grandella* larvae. Figure 1 shows the relative size of the parasite after emergence, as related to the insect larva. The larvae die after the parasite exits from the body cavity.

Some adult nematodes were also collected from the sandy clay loam soil beneath the trees. The percentage of living *H. grandella* larvae which proved to be parasitized by *H. albicans* varied between 5 and 25 per

cent. The highest level of parasitism was found towards the end of the rainy season and the lowest at the end of the dry season.

Measurements of Hexameris albicans from Costa Rica (Fig. 2).

Five males: L = 25.5 mm (11.0 — 33.2 mm). W = 129.0 microns (114.0 — 136.8 microns). Spicule L = 113.3 microns (92.6 — 130.0 microns). Four females: L = 57.7 mm (42.0 — 83.8 mm). W = 187.4 microns (156.8 — 220.4 microns). V = 47.4 per cent (40.2 — 53.7 per cent). Egg = 127.3 x 88.7 microns.

The identification of this nematode as the ubiquitous *H. albicans* follows the redescrptions of this species by recent Soviet workers. It appears to have a very wide host range. Comparison of the Costa Rican specimens with specimens of European *H. albicans* collected by Steined in the early 1920's shows little difference. *Hexameris* spp. are often found parasitic in lepidopterans; some of these are listed in Table 1.

A review of the literature of *Hypsipyla* shows that a *Hexameris* sp. has also been collected from *H. grandella* in Venezuela (20) and British Honduras (3). In India, a *Hexameris* sp. is reported to parasitize larvae of *Hypsipyla robusta* Moore in Kalimpong, Top Slip (Madras) and Dehra Dun. The percentages of

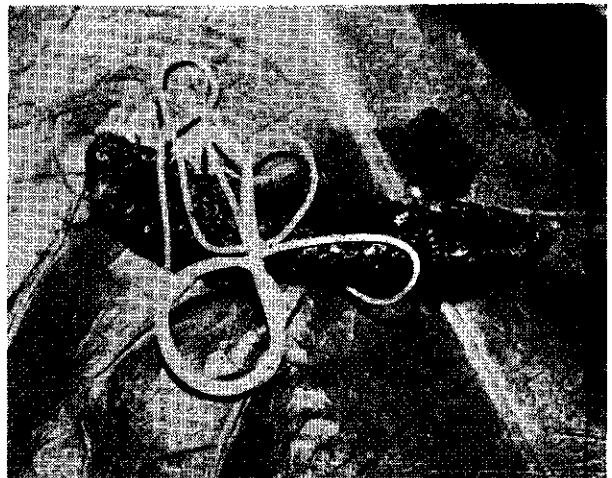


Fig. 1.—Relative size of nematode parasite compared with larva of mahogany shootborer. (Courtesy of Edward Holsten).

Hexameris albicans

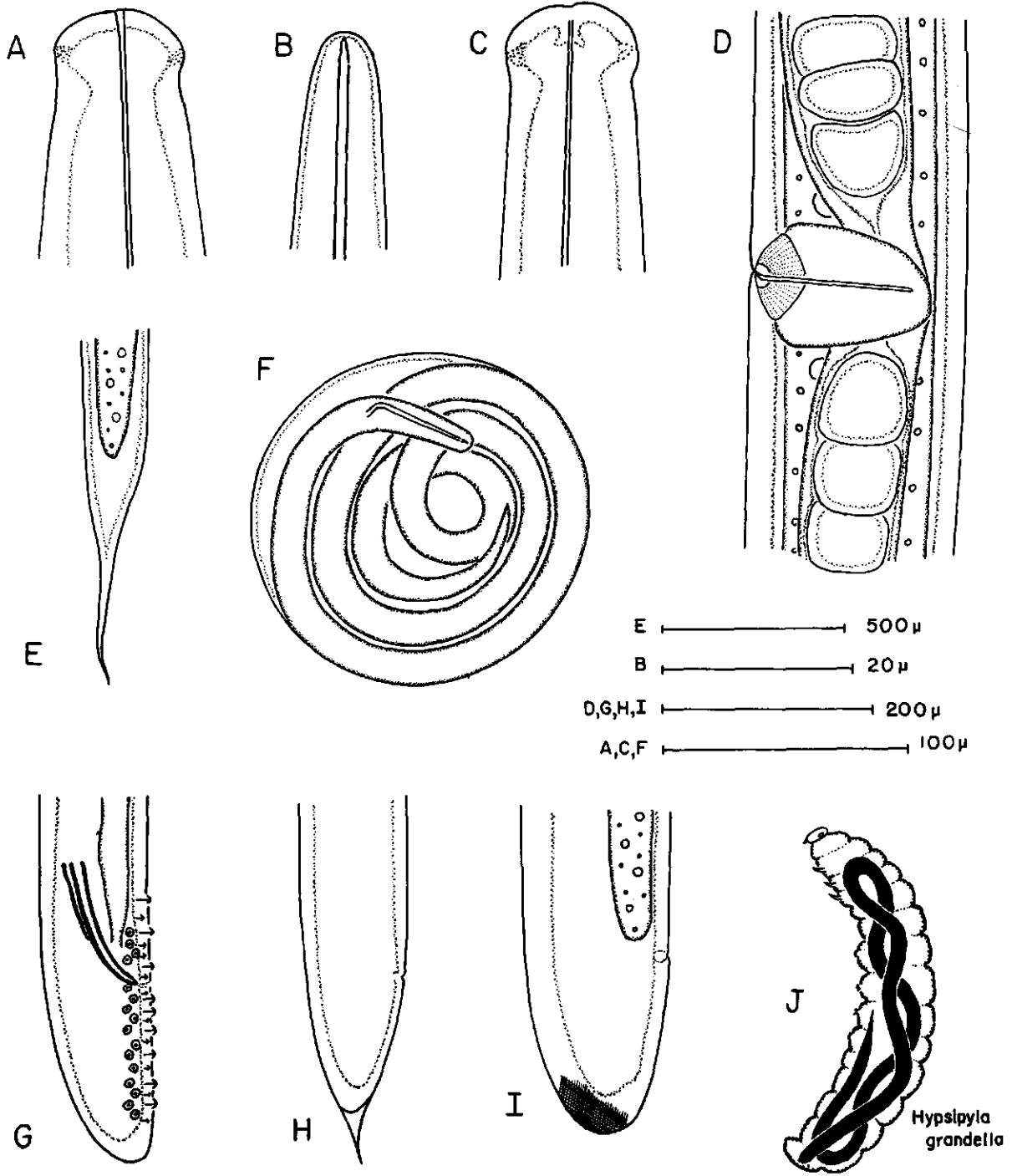


Fig. 2.—*Hexameris albicans*. A. Female bead. B. Head of a parasitic larva, showing tooth. C. Male bead. D. Vulva and vagina. E. Third stage larval tail tip. F. Unbatched egg.

containing preparasitic larva. G. Male tail. H. Juvenile male tail tip. I. Female tail. J. Mabogany shootborer larva *Hypsipyla hosti*.

Table 1.—List of lepidopterans reported parasitized by *Hexameris*.

Host	Region	Authority, year & reference
MACROLEPIDOPTERA		
<i>Pieridae</i>		
<i>Aporia crataege</i> (L.)	Europe USSR	Assmuss, 1958, (2) Artyukhovskiy, 1955, (1)
<i>Nymphalidae</i>		
<i>Inachis io</i> (L.)	Europe Europe, Asia	Siebold, 1853, (24) Linstow, 1898, (14); Schultz, 1900, (22)
<i>Mellicta athalla</i> (Rott.)	Europe, Asia	Schultz, 1900, (22)
<i>Nymphalis antiopa</i> (L.)	Europe, Asia, N. Amer.	Linstow, 1898, (14)
<i>Polygonia c-album</i> (L.)	Europe	Linstow, 1898, (14)
<i>Vanessa</i> sp.	Europe	Siebold, 1853, (24)
<i>Satyridae</i>		
<i>Pyronia tithonus</i> (L.)	Europe, Asia	Linstow, 1898, (14)
<i>Sphingidae</i>		
<i>Mimas tiliae</i> (L.)	Europe, Asia	Hagmeier, 1912, (10)
<i>Arctiidae</i>		
<i>Arctia caja</i> (L.)	Europe, N. America	Siebold, 1855, (25)
<i>Diacrisia</i> (<i>Spilosoma</i>) <i>lubricipeda</i> (L.)	Europe, N. Asia	Schultz, 1900, (22)
<i>Endrosa aurita</i> (Esp.)	Europe	Linstow, 1898, (14)
<i>Noctuidae</i>		
<i>Agrotis infusa</i> (Bois.)	Australia	Common, 1954, (7); Welch, 1963, (27)
<i>Agrotis ipsilon</i> (Hufn.)	USA	Puttler <i>et al.</i> , 1973, (19)
<i>Aletia</i> (<i>Heliophila</i>) <i>pallens</i> (L.)	Europe N. America	Assmuss, 1958, (2); Schultz, 1900, (22)
<i>Apamea monoglypha</i> (L.)	Europe, Asia	Linstow, 1898, (14)
<i>Astoides</i> (<i>Mormonia</i>) <i>sponsa</i> (L.)	Asia	Linstow, 1878, (11)
<i>Autographa gamma</i> (L.)	Europe, Asia, Africa	Assmuss, 1958, (2)
<i>Callierges</i> (<i>Lithocampa</i>) <i>ramosa</i> (Esp.)	Europe	Schultz, 1900, (22)
<i>Catocala nupta</i> (L.)	Europe, Asia to India	Siebold, 1853, (24) Linstow, 1898, (14)
<i>Cerapteryx</i> (<i>Episema</i>) <i>graminis</i> (L.)	Europe, N. America	Siebold, 1853, (24); Linstow, 1898, (14)
<i>Cucullia scrophulariae</i> (Schiff.)	Europe	Linstow, 1878, (11); 1898, (14); Schultz, 1900, (22)
<i>Cucullia tanacetii</i> (Schiff.)	Europe, Asia	Siebold, 1853, (24); Linstow, 1878, (11); 1898, (14)
<i>Cucullia verbasi</i> (L.)	Europe, Asia	Linstow, 1898, (14)
<i>Diloba caeruleocephala</i> (L.)	Europe, Asia	Linstow, 1898, (14)
<i>Ephesia fulminea</i> (Scop.)	Europe	Linstow, 1878, (11)
<i>Epilecta linogrisea</i> (Denis & Schiff.)	Europe, Asia	Schultz, 1900, (22)
<i>Euxoa burnnea</i> (Hufn.)	W. Asia, Europe	Siebold, 1853, (24); Linstow, 1898, (14)
<i>Mythimna</i> (<i>Leucania</i>) <i>l-album</i> (L.)	C & S Europe	Assmuss, 1858, (2)
<i>Noctua orbona</i> (Hufn.)	Europe, Asia	Siebold, 1853, (24); Linstow, 1898, (14)
<i>Polia persicariae</i> (L.)	Siberia	Assmuss, 1858, (2); Schultz, 1900, (22)
<i>Polia</i> (<i>Melanchra</i>) <i>pisi</i> (L.)	Europe	Linstow, 1898, (14)
<i>Scoliopteryx libatrix</i> (L.)	Europe Asia, N. Amer.	Siebold, 1850, (23) Assmuss, 1858, (2); Linstow, 1898, (14)
<i>Geometridae</i>		
<i>Biston betularia</i> (L.)	N. Asia, Europe	Siebold, 1853, (24); Linstow, 1898, (14); Schultz, 1900, (22)
<i>Cidaria berberata</i> (Schiff.)	Europe	Linstow, 1898, (14)
<i>Deilinia exanthemata</i> (Scop.)	Europe, Asia, Canada	Siebold, 1858, (26); Linstow, 1898, (14)
<i>Ennomos alniaria</i> (L.)	Europe	Assmuss, 1858, (2)
<i>Hydriomena coerulea</i> (F.)	Europe, Asia	Schultz (Kriechbaumer), 1900, (22)
<i>Hydriomena furcata</i> (Thun.)	Europe, N. America	Schultz, 1900, (22)
<i>Lomaspilis marginata</i> (L.)	Europe, Japan, Asia	Siebold, 1858, (26)

Table 1.—(Continuation).

Host	Region	Authority, year & reference
Operophtera brumata (L.)	USSR, Europe, N. Amer.	Artyukhovsky, 1955, (1); Linstow, 1898, (14); Schultz, 1900, (22); Polozhentsev, 1955, (17)
Oporinia dilutata (Schiff.) Selenia (Ennomos) bilunaria Esp. Thera juniperata (L.)	Europe N. Asia, Europe Europe	Linstow, 1898, (14) Linstow, 1889, (13) Linstow, 1898, (14)
Dasychira sp. Euproctis chrysoorrhea (L.)	USSR Europe, N. America	Artyukhovsky, 1955, (1) Linstow, 1898, (14); Siebold, 1853, (24)
Lymantria dispar (L.)	USSR	Polozhentsev, & Artyukhovsky, 1953, (16); Polozhentsev, 1955, (17); Po- lozhentsev, Artyukhovsky, & Kharchen- ko, 1964, (18)
Stilpnolia salicis (L.)	Europe Europe, N. Asia	Linstow, 1898, (14) Linstow, 1898, (14)
Gastropacha sp. (Eriogaster) Malacosoma neustria (L.)	<i>Lasiocampidae</i> Europe, Asia Europe, N. & W. Asia	Linstow, 1898, (14) Linstow, 1878, (11); Linstow, 1898, (14)
Odonestis pruni (L.) Philudoria potatoria (L.) Poecilocampa populi (L.)	Italy Europe Europe	Siebold, 1853, (24) Assmuss, 1858, (2) Linstow, 1879, (12); Linstow, 1889, (13)
Notodonta dromedarius (L.) Notodonta ziczac (L.) Phalera bucephala (L.)	<i>Notodontiidae</i> Europe Europe Europe, Asia	Linstow, 1898, (14) Siebold, 1853, (24) Siebold, 1853, (24)
Ptilophora plumigera (Esp.)	USSR Europe	Artyukhovsky, 1955, (1) Linstow, 1898, (14)
MICROLEPIDOPTERA		
Zygaena purpuralis Brünnich	<i>Zygaenidae</i> Europe, W & N Asia	Siebold, 1853, (24); Siebold, 1858, (26)
Heyda salicella (L.)	<i>Tortricidae</i> Siberia Europe	Siebold, 1853, (24) Linstow, 1898, (14)
Laspeyresia pomonella (L.)	Europe, USA, Africa	Siebold, 1853, (24); Linstow, 1898, (14); Schultz (Goeze), 1900, (22); Chittenden, 1905, (6)
Pandemis corylana (F.) Pandemis heparana (D & S)	Europe Europe	Linstow, 1898, (14) Linstow, 1898, (14) Siebold, 1853, (24)
Tinea sp.	<i>Tineidae</i> Europe	Linstow, 1879, (12)
Diatraea saccharalis (F.) Hypsipyla grandella (Zeller)	<i>Pyralidae</i> Cuba, Venezuela British Honduras Venezuela Costa Rica	Guagliumi, 1962, (9) Bennett, 1968, (3) Rao & Bennett, 1969, (20) Nickle, & Grijpma, 1974, (present paper) Chatterjee & Singh, 1965, (5)
Hypsipyla robusta Moore	India	
Cossus cossus L.	<i>Cossidae</i> Europe	Assmuss, 1858, (2)
Hepialus humuli (L.)	<i>Hepialidae</i> Europe	Assmuss, 1858, (2)
Yponomeuta evonymellus (L.)	<i>Yponomeutiidae</i> Europe, Asia	Linstow, 1878, (11); Linstow, 1898, (14)
Yponomeuta padellus (L.)	Europe, Asia	Bugnion, 1878, (4); Linstow, 1878, 1898, (11, 14); Siebold, 1853, 1858, (24, 26)

parasitism during the rainy season at Dehra Dun and Kalimpong were 5 and 9 per cent respectively (20).

Roberts (21) reports a *Hexameris* sp. parasitizing *Hypsipyla robusta* in Nigeria and indicates that this nematode was responsible for the death of as much as 40 per cent of some of the larval samples collected during the wet season at Ibadan. The same author found that of all parasites encountered in *H. robusta*, the nematode has the highest level of parasitism. This information points at the possibility of employing *Hexameris* in a successful biocontrol program of *Hypsipyla*. The most urgent needs with respect to future investigations on insect parasitic nematodes in such biocontrol program are activation of mass production, field release and the establishment of successful field trials (15).

Summary

A new parasitic association between the mermithid nematode, *Hexameris albicans* and the mahogany shootborer *Hypsipyla grandella* from Costa Rica is reported. From 5 - 25 per cent of the insect larvae sampled were parasitized and killed by this parasite. The parasitized larvae were found in branches of *Cedrela* spp. and *Svietenia macrophylla*, located between 1 to 2 m above the ground. Highest level of parasitism was found towards the end of the wet season and lowest level at the end of the dry season. A review of the literature on lepidopterans parasitized by *Hexameris* is included.

Acknowledgements

The authors thank the personnel of the Department of Tropical Forest Sciences of CATIE, Turrialba, Costa Rica, and in particular Oscar Ovares, for their assistance.

April 18, 1974.

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3. ADDITIONAL INFORMATION AND DISCUSSION.

Natural resistance

Apart from being of direct silvicultural importance, the resistance of Toona ciliata var australis also offers interesting aspects of a co-evolutionary nature which enable the analysis of a mechanism by means of which a tree species protects itself against the attacks of an insect which has specialized on this arboreal family.

Various scientists have reported on the effects of a compound and of extracts of the tree species Azadirachta indica A. Juss. and Melia azedarach L. (both Meliaceae) on several insects pertaining to different families which have no relationship with the Meliaceae (2,3).

In 1968, Butterworth and Morgan (2) isolated a substance from Azadirachta indica, which suppressed the feeding of the desert locust Schistocerca gregaria Forsk. In additional research, these authors (3) described the procedure to obtain this chemical (azadirachtin), confirmed its detergency to desert locusts and determined its molecular formula as well as other physical properties.

Gill and Lewis (15) demonstrated the systemic action of azadirachtin and possibly other compounds of A. indica in young bean plants by watering the soil with alcoholic concentrates and aqueous extracts of seeds and of the pure chemical. Apart from repelling the desert locust from the bean plants, these treatments also deterred nematodes of the genus Pratylenchus in barley.

Experiments by Ruscoe (27) and Leuschner (22) showed the ecdyson-like effect which azadirachtin and a methanolic extract have on Pieris brassicae L. and on Antetripsis orbitalis bechuana (Kirk.) In addition, the former author reports an anti-feedant effect and high mortality in Plutella xylostella, Pieris brassicae, Heliothis virescens and some mortality in Dysdercus fasciatus.

Diet mixtures incorporating chloroform extracts of leaves of Melia azedarach also have an anti-feedant and growth retardant action on Heliothis zea (Boddie) and Spodoptera frugiperda (J. E. Smith). Diets containing 10 mg equivalents of M. azedarach, caused 100 percent mortality in both insect species feeding on these diets (24).

The influence of phytoecdysones on growth and mortality of Bombyx mori has been investigated by Shigematsu et al. (30). These scientists found that in diet mixtures ponasterone A had a marked effect on larval growth and mortality, in contrast to ecdysterone and inokosterone.

Recent investigations (Grijpma and Goewie, unpublished results) showed that the toxic, anti-feedant and growth retardant effects of the Australian cedar on H. grandella can also be obtained when dessicated Toona leaves are employed instead of fresh leaves. In these experiments, dry powdered leaves of respectively Toona ciliata var australis and Cedrela odorata (dried for 8 h at 100°C) were homogenized together with the commonly used diet ingredients at a rate of 20 mg per gram of diet. Thirty first instar larvae were placed individually in small jars containing approximately 6 g of each diet mixture and the mortality of the larvae as well as the time necessary to pupate and emerge were observed. The results of this experiment correspond with the earlier conducted diet mixture tests (vide 2.1.3), although the effect of the dried Toona leaves on shootborer larvae was far more pronounced. Eighty percent of the larvae placed on the Toona diet mixture died versus only 10 percent of those placed on the Cedrela mixture. A number of larvae which died during moulting were unable to shed their head capsules. Pupation of the larvae placed on Toona diet mixture started 18 days later than of those placed on Cedrela mixture.

As in the previously conducted test, a large percentage (60%) of the pupae obtained from the Toona diet mixture, was deformed. The most striking deformations consisted of shortened pupal wing sheaths and antennae. However, deformation of the first and last pair of legs as well as of the palpi was also observed.

All sixth instar larvae, force-fed with 30 μ l of aqueous Toona extract (containing the equivalent of 8 mg of dried Toona leaves) died.

Summarizing, Toona compounds appear to have an anti-feedant, growth retardant and toxic effect on H. grandella larvae and in addition seem to upset moults and pupal development of this insect species.

The similarity of the results obtained by the earlier indicated authors (2,3,15,22,24,27) and those obtained with Hypsipyla in grafting trials (systemic action) and in diet mixtures containing dry Toona leaves and aqueous Toona extracts, makes it worthwhile to investigate whether a

phytoecdysone of the Australian cedar might be responsible for these effects.

However, it is interesting to note that sixth instar H. grandella larvae, feeding on the Australian cedar, or force-fed with fractions of it, frequently die within 4-6 h. Another fact to consider is that while shortened pupal wingsheaths are frequent, other characteristics of ecdysone-like activities have not been observed. But it is also of interest to observe that in a preliminary experiment executed in Wageningen, azadirachtin, added to artificial diet, caused the death of fifth instar H. grandella larvae and that this chemical is reported to possess some of the structural features of insect ecdysones (27).

Host selection.

Host selection and the attraction of male insects to females by means of chemoreception are fields of investigation which are receiving increasing attention in the last decade. Of more recent date, however, is the revival of the research on the reception of infra-red radiation by insects which, according to some authors, is presumed to play a role in host-finding and the location of mating partners.

The host selection of Hypsipyla is a subject which has hardly been studied yet. Apart from the research reported in this dissertation, only one additional investigation has been conducted in Puerto Rico by Gara et al (14). The results of that investigation not only confirmed that H. grandella is attracted to the young foliage of Cedrela odorata, but also indicated that an acetone extract of young C. odorata leaves in combination with a potted C. odorata plant having only mature leaves, attracted the shootborer. Neither C. odorata plants with only mature leaves, nor acetone extracts of young leaves of this host alone, attracted any Hypsipyla to the traps. Providing that the information reported by these authors is significant, these findings seem to point at the fact that stimuli other than the olfactory qualities of young host material may also be involved in the host selection of H. grandella.

In complementary experiments, conducted at the Department of Animal Physiology in Wageningen, the attraction of H. grandella to host odours

and infra-red radiation was investigated. First, an electrophysiological study employing the electroantennogram (EAG) method was made to determine whether the receptors on the antenna of the shootborer were stimulated by odours present in extracts of the young leaves of Cedrela odorata. Isolated antennae of female moths were exposed to a puff of air containing scents from the acetone and ether extracts of which the solvents had been evaporated. The volatile compounds of both extracts elicited negative EAG's, indicating that the scents activated the receptors on the antenna. However, similar results were also obtained with volatile compounds of non-hosts, such as Anthocephalus cadamba Miq. As indicated by Schoonhoven (29) negative receptors potentials do not necessarily represent an "attractive" response, but are merely indicative for the excitatory value of the odour. Subsequent olfactometer tests, in which plants and extracts of C. odorata were employed, did not result in the attraction of the shootborer to the scents of this host plants.

The process by means of which monophagous and oligophagous insects locate their host plants is often thought of as a catenary process (20) in which a sequence of stimuli calls forth a sequence of responses. However, it is more likely that the interaction of different external stimuli as well as the interaction of external and internal stimuli influence the behavioural thresholds of the insect.

Since H. grandella is a nocturnal insect, the olfactometer tests were conducted in a darkened room. However, complete darkness immobilized the great majority of the insects and those that did enter the chambers of the olfactometer, through which host and non-host scents were introduced, were distributed evenly over the two compartments. This was also the case when a low intensity, diffuse light was placed at the end of the two chambers. In the latter experiment, however, all females were highly mobile and were attracted towards the light source.

The attraction of nocturnal insects to light is a phenomenon which is little understood yet. Several investigators have suggested explanations; thus, Wigglesworth (33) indicates that these insects orient towards a light source by maintaining a constant angle to it. Although this explains how the insect arrives at the light source and will continue to circle around it,

it does not clarify why the insect is initially attracted to it from a great distance. Mazokhin-Porshnyakov (23) suggests that the light-orientation is a breakdown of a natural mechanism. Field-inhabiting insects would initially fly to a light source because it is an indication of open space. As the insect comes closer to the light, the increasing brightness would decrease the insect's sensitivity for night vision to a point where only the light source is seen. Laidlaw (21) has suggested that the visible radiation of the light is confused with some other invisible stimulus. Verheyen(32) in a detailed study on the attraction of light to animals, considered the trapping effect of light to be a consequence of the re-afference of motoric activity which is constantly matched with the sensory input from the environment.

Theories that insects might observe other parts of the electromagnetic spectrum than the visible portion alone were confirmed when it was shown that bees and other insects can see ultraviolet light (33). The speculation that insects might also perceive infra-red radiation of selective bands of wavelengths was suggested in 1948 by Grant (16) who pointed out that sensillae and sensory pits of certain insects have dimensions which would permit them to sense such radiation.

Since 1964, Callahan (4,5,6,7,8,9) has become the major upholder and investigator of the theory that nocturnal insects respond to electromagnetic radiation in the infra-red region and employ the sensillae and sensory pits on the antennae as a detecting system. The concepts of his research and further developed theories of infra-red reception by insects have been refuted as well as confirmed by several other scientists (10). Hsiao and Hackwell (18) concluded that the eyes of Heliothis zea (Boddie) are the only sensors which mediate the attraction to a Tungsten light source. However, in another publication, Hsiao and Susskind (19) showed the existence of sensillae, similar to the sensilla trichodea on the antenna, at the interstices of facets of the compound eye of this insect. According to this publication, the optimum wavelength at which these sensillae would operate if they were to act as infra-red detectors, would be $4.5 \mu\text{m}$ i.e. exactly in one of the infra-red windows of the atmosphere. The authors reached the conclusion that although the corn earworm does not appear to be attracted to broadband infra-red radiation, the possibility should not be excluded that the insect would

be sensitive to specific wavelengths. In a later article, however, Hsiao (17) ruled out the possibility that infra-red radiation could be involved in the long distance attraction of male Trichoplusia ni moths to females. Neese (25,26) determined in experiments, that the sensilla trichodea on the compound eye of the honey bee take part in the measurement of the sun-angle and in flight control of the bees.

Investigations which confirm Callahan's theories and experiments on the attractive response of insects to infra-red radiation have also been reported by several scientists. Evans (13) established that sensory pits located at the mesothoracic legs of the fire beetle Melanophila acuminata DeGeer sense radiation in the wavelength region of 0.8-2.7 μm . This insect also responded when the antennae were exposed to intense infra-red radiation between 0.8-1.25 μm . This author, who could not establish any attraction of the beetle to smoke, carbon dioxide or carbon particles in olfactometer tests, concluded that the beetle orients itself to fires by detecting infra-red radiation at considerable distances from the heat source.

Bruce (1) determined that the spiny rat mite Laelaps echidnina Berlese responds to incoherent infra-red radiation. In radiation experiments employing wavelengths varying from 1.6-7.0 μm , the mites were most sensitive to a wavelength of 4.5 μm . The setae on the tarsi of the first pair of legs of the mite were proposed to be the infra-red receptors.

Strong attraction to infra-red radiation have been reported by Eldumiaty and Levensgood (11,12) for Heliothis zea, Spodoptera frugiperda (J.E. Smith) and Plodia interpunctella (Hübner). These investigators, who employed a hydrogen cyanide laser emitting at 337 μm , conclude that their results are in agreement with Callahan's theory and that the sensors on the antennae of these insects serve as infra-red detectors.

The attraction of Hypsipyla grandella to a low intensity light source and its favourable effect upon mating and oviposition as compared to mating and oviposition under completely dark conditions, has been observed frequently during the artificial rearing of this insect.

In order to verify if the infra-red portion of the spectrum emitted by this light source was responsible for these effects, an experiment was conducted in which the response of H. grandella to broadband incoherent radiation of wavelengths between 0.8-2.5 μm was compared with the response

of the insect to broadband incoherent radiation of wavelengths between 0.38-2.5 μm of the same light.

The results of this investigation showed that the infra-red radiation alone did not elicit a significant response by the insects, in contrast to the radiation incorporating the visible part of the spectrum (0.38-2.5 μm), which was highly attractive. Moreover, electrophysiological tests, in which isolated antennae of H. grandella were exposed to infra-red and visible radiation of the same light source, did not elicit any negative EAG. From the results of these investigations the conclusion is reached that, under the conditions of the experiments, H. grandella moths appear not be attracted to broadband incoherent infra-red radiation of wavelengths between 0.8-2.5 μm , nor does the antenna seem to mediate in the perception of wavelengths between 0.38-2.5 μm of this light source.

Artificial rearing techniques.

As far as the artificial rearing of Hypsipyla grandella is concerned, several improvements have been effected since its initiation. Samaniego and Sterringa (28) reported on a new method to obtain oviposition of the shootborer in captivity. In this system, mated females are brought to the laboratory and placed individually in small polystyrene boxes containing towel paper on which the eggs are deposited. Instead of obtaining oviposition on large sheets of towel paper in outdoor cages, the eggs which are laid singly normally, are now concentrated on a limited surface and obtained in the laboratory. These authors determined that this new method was more economical than the previously used method and concluded that male and female moths (sex ratio 1:1) should remain for 72 h in outdoor copulation cages to obtain maximum oviposition (210 eggs per female) under laboratory conditions.

Sterringa (31) provided a detailed cost calculation of the artificial rearing of H. grandella in Costa Rica and compared the yield of shootborer adults obtained in four different rearing-treatments. In these treatments respectively one and two larvae were placed on diet in sterilized and non-sterilized glass jars. The results of these investigations indicated that the treatment consisting of two larvae in non-sterilized jars yielded more adults than any of the other treatments. However, the differences

between the treatments were not significant at the 10 percent level.

Survey of natural enemies.

With regard to the survey of biological control agents, two parasites of H. grandella have been recorded in addition to the natural enemies already mentioned in this dissertation. Becker collected a larval parasite of the genus Apanteles in the Turrialba-area and the egg parasite Trichogramma beckeri Nagarkatti. The latter was reared from H. grandella eggs on fruits of Cedrela tonduzii, collected near Santa Cruz on the slopes of the Turrialba Volcano at an altitude of 1,500 m.

Of all Hypsipyla parasites collected in Costa Rica, Hypomicrogaster hypsipylae, Trichogramma spp. and the nematode Hexameris albicans occur most frequently. The ecological range of the nematode and H. hypsipylae is restricted to the wet humid regions of Costa Rica, whereas the egg parasites can be found in the dry as well as the wet areas.

The vast distribution of H. grandella on the American continent where the insect is found at altitudes ranging from sea level up to 2000 m and in dry and wet areas make it improbable that a biological control program alone could be of great effect on shootborer populations. However, as complementary control measure the parasites may well contribute significantly to the overall regulation of this insect pest.

On the other hand the natural enemies of the shootborer could be very effective in biological control program on islands in the Caribbean, such as Jamaica, Trinidad, Cuba and Hispaniola.

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4. SUMMARY

The shootborer Hypsipyla grandella (Zeller) (Lep., Pyralidae) is the main obstacle to the artificial regeneration of valuable meliaceous tree species such as mahogany (Swietenia spp.) and Spanish cedar (Cedrela spp.) in Latin America. On the other hand, the natural regeneration of these species is endangered due to depletion of the naturally existing resources and burning in colonization projects.

This dissertation concerns the development of several fields of research, which when incorporated in a programme of integrated control may contribute to a solution of the Hypsipyla problem.

Chapter 1 contains a general introduction on this insect pest and its host plants in Costa Rica. In addition, a review is provided of the economic importance of the pest in tropical forestry and of the previous and contemporary investigations on the possibilities of its control.

The research carried out in the framework of the Inter-American Working Group on Hypsipyla at the tropical Research and Training Centre of the Inter-American Institute of Agricultural Sciences at Turrialba, Costa Rica, is dealt with in Chapter 2.

These investigations refer to the natural resistance of Meliaceae, host selection, development of an artificial rearing technique for H. grandella and to a survey of parasites in Costa Rica which might be employed in a biological control of the shootborer.

The main results are:

- a. Two exotic Meliaceae, African mahogany (Khaya ivorensis) and the Australian cedar (Toona ciliata var australis) were introduced and were found to be immune against attacks of the shootborer. Biological and chemical screening for the basis of resistance of the Australian cedar led to the location of two toxic components in the aqueous fraction of young leaves and shoots of this tree species. The toxicity of Toona can be translocated to Cedrela odorata grafted on the Australian cedar.
- b. Experiments on the host selection of H. grandella point at the existence of a host selection mechanism in which the female adult orients itself towards the host by means of olfaction. Fourth instar larvae of the borer prefer native hosts to exotic species as food sources.
- c. An artificial rearing technique was developed for H. grandella. A diet (Vanderzant) used for rearing Heliothis zea appeared to be a suitable medium for mass rearing Hypsipyla. Although initially mating of adults could only be obtained in outdoor cages in Costa Rica, subsequent rearing in Wageningen, under completely artificial conditions, proved to be perfectly feasible. Larval and pupal periods of H. grandella reared on artificial and natural diets were determined and compared. Female adults are generally larger than males and live longer. Artificially reared females still restrict oviposition to meliaceous host plants.

- d. A survey of biological control agents of the shootborer resulted in the following new records of H. grandella parasites in Costa Rica: Trichogramma fasciatum, T. pretiosum, T. near pretiosum, T. semifumatum, Hypomicrogaster hysipylae sp. n., Brachymeria conica and Bracon chontalensis; an Agathis sp. has to be identified yet. In addition the nematode Hexameris albicans was found to parasitize larvae of the shootborer in Swietenia macrophylla and Cedrela spp. The egg parasite Trichogramma semifumatum could be reared easily on eggs of H. grandella.

5. SAMENVATTING

Terwijl de kunstmatige verjonging van waardevolle Meliaceeën soorten in Latijns Amerika, zoals mahonie (Swietenia spp.) en ceder (Cedrela spp.), enerzijds wordt tegengehouden door de schade welke de topboorder Hypsipyla grandella (Zeller) (Lep., Pyralidae) aanricht, wordt anderzijds de natuurlijke verjonging van deze soorten in gevaar gebracht doordat de bestaande voorraden worden uitgeput en door branden ten behoeve van kolonisatie projecten worden vernietigd.

Dit proefschrift op artikelen, handelt over de ontwikkeling van verscheidene gebieden van onderzoek over deze topboorder welke, in een geïntegreerd bestrijdingsprogramma opgenomen, een bijdrage vormen tot de oplossing van het Hypsipyla probleem.

Hoofdstuk 1 bevat een algemene inleiding over dit schadelijke insect en haar waardplanten in Costa Rica. Tevens wordt een overzicht gegeven van het economisch belang van de plaag voor de bosbouw en van eerder uitgevoerd en contemporain onderzoek naar de mogelijkheden van haar bestrijding.

In het tweede hoofdstuk worden de verschillende onderzoeken behandeld welke in het kader van de Interamerikaanse Hypsipyla Werkgroep in het Tropisch Onderzoeks- en Opleidings Centrum van het Interamerikaans Instituut voor Landbouwwetenschappen te Turrialba, Costa Rica, werden uitgevoerd. Deze onderzoekingen hebben betrekking op de natuurlijke resistentie van exotische Meliaceeën, waardkeuze, ontwikkeling van een kunstmatige kweek methode voor H. grandella en op een inventarisatie van in Costa Rica voorkomende parasieten welke in een biologisch bestrijdingsprogramma zouden kunnen worden opgenomen. De belangrijkste resultaten hiervan zijn:

- a. Twee Meliaceeën, de Afrikaanse mahonie (Khaya ivorensis) en de Australische ceder (Toona ciliata var australis) werden in Costa Rica geïntroduceerd en immuun bevonden voor aantasting door de topboorder. Biologische en chemische onderzoekingen naar de oorzaak van de resistentie van de Australische ceder leidden tot de localisering van twee componenten in de waterfractie van bladeren en jonge scheuten welke toxisch zijn voor larven van H. grandella. Enting van de inheemse, voor aantasting vatbare Cedrela odorata op onderstammen van Toona, bleek tot resistentie van de inheemse ceder te leiden.
- b. Proeven met betrekking tot de waardkeuze van Hypsipyla adulten duiden op een orientatie-mechanisme waarbij de vrouwelijke vlinder gebruik maakt van in de waardplant voorkomende vluchtige geurstoffen. Als voedselbron prefereren larven van het vierde stadium inheemse Meliaceeën boven exotische.
- c. Een kunstmatige kweekmethode werd ontwikkeld voor de topboorder. Een Vanderzant dieet voor Heliothis zea bleek tevens geschikt te zijn voor de massakweek van Hypsipyla. Hoewel in Costa Rica copulatie van vlinders alleen in in de buitenlucht geplaatste kooien gunstig verliep, bleek dit in Wageningen onder volledig kunstmatige condities mogelijk. De larvale

en pupale periode van op kunstmatig dieet gekweekte H. grandella werden bepaald en vergeleken met die van op natuurlijk dieet gekweekte exemplaren. Vrouwelijke vlinders zijn over het algemeen iets groter dan mannelijke en leven langer. De waardkeuze van op kunstmatig dieet gekweekte vlinders blijft zich tot de Meliaceeën beperken.

- d. Het onderzoek naar het voorkomen van parasieten van de topboorder leidde tot de volgende nieuwe registraties:

Ei parasieten: Trichogramma fasciatum, T. pretiosum, T. semifumatum en een Trichogramma soort nauw verwant aan T. pretiosum.

Larvale parasieten: Hypomicrogaster hypsipylae, Bracon chontalensis, Brachymeria conica en een Agathis soort nauw verwant met A. albispina.

Tevens werd de nematode Hexameris albicans verzameld welke larven van H. grandella in Cedrela en Swietenia macrophylla parasiteert.

De eiparasiet Trichogramma semifumatum bleek gemakkelijk op eieren van H. grandella gekweekt te kunnen worden.

6. CURRICULUM VITAE

The author received his university training at the State Agricultural University in Wageningen, Holland, where he specialized in forest management, forest exploitation, aerial surveying and road construction. After receiving his degree in 1961, he was temporarily employed at the Department of Forest Sciences of the University in the field of wood technology, investigating physical and mechanical properties of Surinam timber species. That same year he accepted a 3-year assignment at the FAO Regional Office for Latin America in Santiago, Chile, during which he was responsible for the collection, analysis and evaluation of the Latin American forest statistics published in the Yearbook of Forest Products Statistics by the European Office of FAO.

From 1965-1973 he was employed by the Netherlands Bureau of Development Cooperation and stationed in Turrialba, Costa Rica, at the Tropical Research and Training Centre of the Inter-American Institute of Agricultural Sciences of the OAS, where he lectured on tropical forest regeneration at the Post graduate school of this centre and conducted silvicultural research. During this assignment he introduced several promising tree species into Costa Rica, among which the Australian red cedar (Toona ciliata var australis).

The resistance of this tree species against the notorious shoot-borer Hypsipyla grandella (Zeller) resulted in a series of investigations on this forest insect pest.

With a few colleagues he established in September 1970, the Inter-American Working on Hypsipyla in which he served as Coordinator from 1970-1974. In 1972, this Working Group had grown to 68 members in 26 countries and had become an International Working Party under the auspices of the International Union of Forest Research Organization. An International symposium on integrated control of the shootborer, was held in March 1973 in Costa Rica to acquaint the participants from developing countries with several promising aspects of Hypsipyla control.

The author is editor of "Studies on the shootborer Hypsipyla grandella (Zeller) (Lep., Pyralidae)" and has published a selected bibliography of the Meliaceae in collaboration with Dr. B. T. Styles of the University of Oxford.