A COMPARATIVE STUDY ON THE SUSCEPTIBILITY OF TWO SPECIES OF *LEUCAENA* TO *HETEROPSYLLA CUBANA* CRAWFORD (HOMOPTERA:PSYLLIDAE)

by

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A COMPARATIVE STUDY ON THE SUSCEPTIBILITY OF TWO

SPECIES OF *LEUCAENA* TO *HETEROPSYLLA CUBANA*

CRAWFORD (HOMOPTERA:PSYLLIDAE)

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ABSTRACT

The exotic psyllid, *Heteropsylla cubana* Crawford, became a pest of *Leucaena leucocephala* (Lam.) de Wit, in the Southeast Asian and South Pacific Islands Regions in 1985. Experiments were conducted to compare susceptibility and/or resistance in *L. leucocephala* with that in the reportedly resistant species *Leucaena collinsii* Britton & Rose. When the growth of infested plants was compared, *L. leucocephala* lost 3 and 7 times more of its potential height and diameter increment, respectively, than did *L. collinsii.* The numbers of alighting adults were 5 times higher in *L. leucocephala* than on *L. collinsii* in both pure and mixed species stands. Only 35% of *L. collinsii* plants were reinfested, while all *L. leucocephala* plants were reinfested. About 1.9 and 2.6 times more eggs were laid on *L. leucocephala* than on *L. collinsii* in the field and laboratory, respectively.

Colored card traps reflecting in the yellow spectrum (550 nm) attracted more adults than those reflecting at $<$ 500 nm, consistent with a peak reflectance in the same range from young leaves. About twice as many adults responded to the caged *L. leucocephala* than to the caged *L. collinsii.* In a two-choice olfactometer, females readily responded to the hexane leaf extract of *L. leucocephala.* At a concentration of 1×10^{-3} g. equivalent of leaf material, females were attracted to *L. leucocephala* extract but not to *L. collinsii* extract. However, at a 10 times lower concentration, *L. collinsii* extract became attractive.

First and 2nd instar nymphs settled equally on leaves of both *Leucaena* spp. Stylet penetration successfully reached the vascular bundles in both species. On excised leaves, there was 4% more egg mortality in *L. collinsii* than in *L. leucocephala*, and on potted plants survivorship to the 5th instar was about 5-fold less on *L. collinsii* than on *L. leucocephala.* About 11 times more adults eclosed on

L. leucocephala than on *L. collinsii*. Adults that developed on *L. collinsii* were significantly smaller than those on *L. leucocephala*. Ten days after infestation, about 16% of the leaflets of *L. collinsii* abscised, but none in *L. leucocephala* did. Both antixenosis and antibiosis were concluded to operate in *L. collinsii* against *H. cubana*, with antibiosis causing high nymphal mortality in the first 2 instars and smaller adults, and both ultimately contributing to much lower production of adults.

To my loving wife, Aida
my twin sons, Michael Mark
Jerome Matt and
my lovely daughters, Melissa Joy
Jennifer Marie

....and **God** said to them (man and woman), "Be fruitful and multiply; fill the earth and subdue it; have dominion over the fish of the sea, over the birds of the air, and over every living thing that moves on the earth."

And **God** said, "See, **I** have given you every herb that yields seed which is on the face of all the earth, and every tree whose fruit yields seed; to you it shall be for food."

Also, to every beast of the earth, to every bird of the air, and to every creature on earth, in which there is life, **I** have given every green herb for food", and it was so. **(Genesis 1:28-30)**.

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CHAPTER I

GENERAL INTRODUCTION

Introduction

In 1976, experts from the U.S. National Academy of Sciences and the Philippine Council for Agriculture and Resources Research covened to evaluate the potential of *Leucaena leucocephala* (Lam.) de Wit (Leguminosae) in the tropics (PCARR-USNAS 1977). This move was made in response to the need to increase agricultural and forest productivity in tropical rural areas. Both government agencies and private organizations promoted the use of this fast-growing tree as a source of fodder, fuelwood and other wood products, as a nurse tree for some industrial tree crops, and for land rehabilitation and soil improvement. In the Philippines, its wood was also designated to provide the primary fuel for dendrothermal power plants to generate electric power.

Since 1977, the use of *L. leucocephala* has greatly expanded throughout Southeast Asia and the Pacific Region. In Australia more than 8,000 ha of rangeland were planted to this tree (Bray and Sands 1987). In Indonesia and the Philippines, more than a million ha of *L. leucocephala* were planted in reforestation and land rehabilitation programs (McCauley 1986). By 1985, Taiwan had 13,000 ha of leucaena plantations (Jen 1986) to serve as a source of raw materials for pulp and paper (Pan 1987).

The accidental introduction of a minute psyllid, *Heteropsylla cubana* Crawford, has completely disrupted the use of *L. leucocephala* throughout Southeast Asia and the Pacific Region. It has caused rapid and extensive damage and mortality to *L. leucocephala.* As a result, a moratorium was recommended on the planting of *L. leucocephala*, except for research, until seeds of resistant varieties or crosses and more information about the pest could become available (McFadden 1986; NFTA 1987). While the development of resistant varieties has proceeded with dispatch (Othman and Prine 1984; Glover 1987; Pan 1987; Sorensson and Brewbaker

1987; Wheeler et al 1988), no research has been done on the nature of resistance. This thesis represents the first study designed to provide this information.

Brief History of the Introduction of *Leucaena leucocephala* into the Philippines

Leucaena leucocephala, the economically most important of the 12 known species of *Leucaena*, was distributed from Central America, beginning about 400 years ago, to countries outside its natural geographical range (Pound and Cairo 1983; Brewbaker 1986). It is believed to have been introduced into the Philippines from Mexico through the Spanish Galleon trade (Alferez 1977). *L. leucocephala* has two varieties, *L. leucocephala* var. *leucocephala* (the common type) and *L. leucocephala* var. *glabrata* (the giant type) (Brewbaker 1987). Although the common type was already growing in the wild, it was not until the early 1960 that the giant variety was introduced from Hawaii into the Philippines where it is known as giant ipil-ipil (Bawagan and Semana 1977). This variety may grow as high as 20 m, while the common type grows only to 12 m. *L. leucocephala* is cross-fertile with other *Leucaena spp.*, but it is also highly self pollinated.

The giant variety grows very fast. Based on the growth rate of 2.3 year-old trees, as reported by Bawagan and Semana (1977), it can put on an average of 5.2 m of height increment per year. At a density of 44,000 plants/ha, plantings of 4 different strains of giant *L. leucocephala* at the University of the Philippines at Los Baños (UPLB), Philippines, had mean annual volume gains of 203.9 to 311.92 m^3/ha/yr.

The wood of giant ipil-ipil is of excellent quality. The trunk has a specific gravity of 0.50 to 0.59. The fibers are about 1.2 mm long and have other desirable characteristics which make them useful for paper manufacture. The heating value of the wood ranges from 4,167 to 4,445 calories/kg or 7,500 to 8,000 BTU/kg, making it satisfactory for fuelwood.

Giant ipil-ipil also has good herbage yield. At UPLB, it produced from 10.6 to 24 tons/ha/yr of dry matter with cutting frequencies of every 8 to 12 wk (Alferez 1977). Its leaves are superior to other *Leucaena* spp. as animal feed in terms of quality and yield. As cited by Benge and Curran (1976), the leaves contain 275 ppm carotene, 22.2% protein and 29% crude fiber. The protein and carotene content is comparable to that of alfalfa which contains 20-25% protein. Labadan (1977) estimated that the 10 leading feedmills in the Philippines required about 30,000 metric tons of dried ipil-ipil leaves annually. Thus, growing ipil-ipil for leaf meal became a cottage industry for many families.

The species can also grow in barren areas, e.g., in denuded areas (Dalmacio 1977). Its aggressive and deeply-penetrating root system breaks up and aerates impervious soils (Djikman 1960), increasing water infiltration. Surface run-off and soil erosion are thus decreased, and water quality is improved.

Ipil-ipil is also planted as a pioneer species to improve soil conditions in order that other tree species may be established (Dalmacio 1977). While enriching the soil by nitrogen fixation, it also provides shade needed in the early stages of development of interplanted tree species. Because of these qualities, giant *L. leucocephala* became the most widely planted variety of *Leucaena*.

History of ***Heteropsylla cubana*** Infestation in Southeast Asia and the South Pacific Region

Heteropsylla cubana is believed to be native to the Caribbean (Mitchell and Waterhouse 1986). It was first discovered by Crawford in Cuba and reported in 1914 (Yang and Fang 1986). In 1917, collections were made in the Virgin Islands and later in neighboring countries. These collections were used by Brown (1985) to describe the Psylloidea of Panama. Outside its natural geographical range, the psyllid was reported first in Florida in August 1983 (Othman and Prine 1984) where it infested *Leucaena* spp., causing die-back (Brewbaker 1986). By April 1984, the species was found on koa haole (leucaena) in Hawaii (Nakahara and Lai 1984). In February 1985, the insect was reported to be damaging leucaena in Western Samoa on the islands of Upolu and Savaii (Hollingsworth et al. 1985), and in late 1985, it was observed in Fiji, Tonga, Niue and New Caledonia (McFadden 1986). It is possible, however, that it was introduced earlier but remained unnoticed. Also during 1985, farmers in Cebu, Philippines, observed the psyllid in small numbers in February although serious defoliation did not start before March (McFadden 1986; Lapis 1986a). It was found in southern Taiwan the same year (Hsieh et al. 1987). In Indonesia the psyllid was first recorded in Bogor in March 1986 and, within 3 months, was found in several regions of the country (Oka et al. 1987). It was also during that year that the psyllid was found in Australia (Donaldson 1986) and Malaysia (Tho 1987). *H. cubana* also crossed over to the Indian Ocean basin, reaching Sri Lanka in 1986 and India in 1988 (Singh 1988).

The spread of *H. cubana* across the Pacific Ocean occurred very rapidly. How the psyllids dispersed so far in less than one year has puzzled entomologists. It is doubtful that the transport of seeds, which are not fed upon by the psyllids, or of living plant materials could have been the source of the pest. Leucaena is easily propagated by seed, hence the introduction of living plant material into a country is unlikely. Beardsley (1987) hypothesized that adult psyllids were transported by aircraft. Because adults are strongly attracted to electric lights and because leucaena grows wild around many airports throughout the Pacific, he suggested that psyllids attracted to the lights of night-loading aircraft probably served as the most important innoculum of the pest. It was also hypothesized that the insects were carried by large air currents, such as the jet stream, at high altitudes. However, evidence is lacking to confirm either hypothesis.

Biology of *Heteropsylla cubana*

Description of the pest

Species in the genus *Heteropsylla* are endemic to the tropics and subtropics in the New World. However, the systematics of this group of psyllids is confused because the species often very closely resemble each other (Beardsley 1987).

Adult *H. cubana* are 1-2 mm long. The wings are held roof-like over the abdomen, causing them to resemble miniature cicadas. They have stout hind legs which are adapted for jumping. Although winged, the adults are not known to be strong fliers. The general body color is yellowish brown throughout, eyes are black, and antennae are brown, with apices of the 4th to 5th and the whole last 5 segments black (Yang and Fang 1986). The immature stages are much smaller than the adults and resemble aphids. Fifth instar nymphs are elongate-ovoid, with general body color brown, eyes red, antennae pale brown, with apices of 5th to 6th and whole last 4 segments black, wing-pads and sclerites on dorsal surface black (Yang and Fang 1986). Both adults and immature stages feed by means of an elongate, hair-like stylet which is inserted into the vascular tissues of their host.

Life cycle, behavior and feeding damage

The white to yellow-orange eggs of *H. cubana* are laid in large numbers on the new growing tips of the host plant (Stechman et al. 1987). With few exceptions, the eggs are deposited between the folded leaflets which must be parted for the eggs to be seen. The eggs are elongate-ovoid and bear a filamentous prolongation near one end which apparently serves to anchor them to the plant and which may also play a role in the uptake of water from the host (Beardsley 1986). Hatching occurs after 3 to 4 days at 29°C (R. Lucero[1], pers. comm.). The emergent nymphs search out a suitable site to feed, usually on young and succulent tissues. They are not known to feed on old mature leaves and twigs. The nymphs undergo five molts before reaching the adult stage. The total developmental period, from egg to egg, reportedly takes 28 to 31 days (Stechman et al. 1987). Similarly, R. Lucero found the eggs to develop into adults in 16 to 21 days. Adults survive from 35 to 42 days on their host. In the Philippines and in most tropical countries, it is estimated that there may be as many as 8 or 10 generations per year (V.J. Calilung[2], pers. comm.).

Damage to leucaena trees may take several forms depending on the density of the feeding insects and on prevailing climatic conditions. Withdrawal of plant juices causes stunting and rosette-formation of new growth when the density of feeding psyllids is moderate (Calilung 1986). Repeated attacks lead to severe defoliation and eventual necrosis (Lapis 1986b). In addition, the rust-colored honeydew, copiously excreted by the insect, sticks on the plant terminals and drips onto the lower older leaves, encouraging growth of sooty molds, which inhibit photosynthesis. When psyllid populations are very high and during extended periods of drought (i.e.,during the dry season) most attacked leucaena trees die. New shoots on surviving trees are further attacked, as are shoots sprouting from the surviving roots and stumps of some defoliated trees. When such attack extends until the following dry season, the trees usually die.

Host range

In general, psyllids are highly host specific in that a species usually successfully breeds on only one or a few closely related species of host plants

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(Beardsley 1987). Species feeding on more than one plant species are rare. Adults may feed on other groups of plants, especially during outbreaks, but they usually do not oviposit on these plants or, if they do, their offspring do not develop successfully. Species of the genus *Heteropsylla* have a narrow host range, and all of those for which host associations are definitely known are confined to the species of Leguminosae (Beardsley 1986). However, because *Heteropsylla* spp. closely resemble each other, published host records may not always be reliable.

H. cubana feeds mainly on *Leucaena* spp. However, Nakahara et al. (1987) reported that they successfully reared the species on *Samanea saman* (Jacq.)Merr., a legume on which *H. cubana* is not found in nature. Not all species of leucaena are suitable hosts for *H. cubana*. While detailed studies have not been done, some species reportedly harbor only few eggs and immature stages of the psyllid and some do not support successful development of the insect (Pan 1987). Its most preferred hosts are some cultivars of *L. leucocephala*. However, preliminary experiments in Hawaii, Australia and Taiwan show patterns of resistance among *Leucaena* species. Of the different species tested, *Leucaena pallida* Britton & Rose and *Leucaena collinsii* Britton & Rose (used in this study) are reported to be highly resistant (Sorensson and Brewbaker 1987). *L. leucocephala* and *L. collinsii* are quite different from each other in morphology and growth habits (Brewbaker 1987). For example, leaflets of *L. leucocephala* are about 4.5 mm wide while those of *L. collinsii* are only about 2.2 mm in width. The biomass potential of *L. leucocephala* is also much higher than that of *L. collinsii*. *L. leucocephala* can grow to as high as 22 m with a diameter at breast height (dbh) of 41 cm, while *L. collinsii* grows only 15 m high with a dbh of 20 cm. Both species, however, regrow rapidly following coppicing.

Bases for the Outbreak of *Heteropsylla cubana*

Lapis (1986a) enumerated four possible factors that could explain the unrestricted growth of the psyllid populations in the Philippines and other countries. These are:

1) favorable climate,
2) lack of competition with other insect pests,
3) absence of efficient local natural enemies, and
4) readily available hosts.

Because giant *L. leucocephala* was erroneously thought to be tolerant to most insect pests, except to insects attacking their pods and seeds (Zabala 1977), it was propagated extensively. Hence, in almost all areas, susceptible leucaena was available to the psyllid. Thus, the pest population expanded unchecked (McCauley 1986), and caused severe defoliation, die-back and often death of the host trees.

Mechanisms of Plant Resistance to Insects

Resistance phenomena in plants to insect pests has been classified into two major categories (Horber 1980). One expresses the relative success or failure of an insect species to survive, develop, and reproduce on a plant species. The other measures the relative damage of an insect on the host plant in qualitative and/or quantitative terms. Snelling (1941), in his definition of plant resistance, included the characteristics of a plant that enables it to avoid, tolerate, or recover from insect attacks under conditions that would normally injure other plants of the same species. Painter (1951) described resistance as the relative amount of heritable qualities that influence the ultimate degree of damage done by the insect. Beck (1965) limited his definition to the success or failure of an insect to use a plant as a host, excluding the ability of a plant to recover or repair losses after injury occcurs. In practical agriculture, on the other hand, plant resistance is synonymous with the ability of certain varieties of a plant species to produce a larger crop or harvest than other varieties under the same pest population pressure. In addition to these definitions, the concept of resistance used in this paper conforms with the concept of Horber (1980) that plants classified for resistance ordinarily belong within the host range of the insect species and that "host plant" and "immune" exclude each other. Immunity in this context represents complete inability of the insects concerned to use a plant for food or oviposition sites. Therefore, a host plant can be more or less resistant but not immune and an immune plant is not a host plant.

Resistance categories used consistently throughout this paper are based on the definition and fundamental mechanisms proposed by Painter (1951) and, Kogan and Ortman (1978).

As defined by Painter (1941) preference or nonpreference "denotes the groups of plant characters and insect responses that lead to or away from the use of a particular plant or variety, for oviposition, for food, or for shelter, or for combinations of the three." Because of some restrictions in the use of the term "nonpreference", Kogan and Ortman (1978) proposed the term "*antixenosis*" to substitute for nonpreference. The definition of Kogan and Ortman (1978) proposes that "antixenosis" should convey the meaning that resistance factors present in the plants trigger a negative behavioral response in the insect, i.e., nonpreference. Antixenosis would thus promote a behavior leading to the avoidance of the plant by the insect for any use.

Antibiosis includes all "adverse effects on the insect's life history which result when the insect uses a resistant host-plant variety for food" (Painter 1951). Based on this definition, antibiosis includes chemical and physical defences of the plant that could, alone or in combination, kill the insect or affect its development. Hence, even such factors as early cessation of leaf development, premature leaf abscission or rapid senescence of foliage, which may reduce the nutritional resources of the plant and affect larval growth (Felton et al. 1989) are considered to be a form of antibiosis.

Tolerance was defined as a "basis of resistance on which a plant shows an ability to grow and reproduce itself or to repair injury to a marked degree in spite of supporting a population approximately equal to that damaging a susceptible host" (Painter 1951). It has no direct effect on the insect's life history or the development of its population. It refers to the plant's ability to survive and recover from damage caused by insect attack.

These categories are arbitrary and vaguely delineated (Horber 1980). Not all resistance phenomena can be assigned unequivocally to one or the other of the three major categories. For example, antixenosis may be mistaken for antibiosis and *vice versa*, when young immature insects reject a plant as a host, unless an in-depth investigation is made.

General Objectives

My research was divided into three general phases. The objective of the first phase was to assess the impact of *H. cubana* infestation on two *Leucaena* spp.: the giant ipil-ipil, *L. leucocephala*, and a presumably resistant species, *L. collinsii*. The second objective was to investigate any semiochemical-based communication between the host plant and the psyllid as a basis for antixenotic resistance. The third objective was to examine other host traits affecting insect responses that could impart resistance/suceptibility to *H. cubana*. Objectives 2 and 3 were achieved by comparing the behavior and growth response of the psyllid when presented with both the more susceptible host, *L. leucocephala*, and the less susceptible host, *L. collinsii*, and also by comparing the response of the two host plants to oviposition and feeding by the psyllid.

General Materials and Methods

Source and Culture of Host Plant Materials

Seeds of *L. leucocephala* were collected at Los Baños, Laguna, Philippines from plants of an unknown cultivar that have been previously heavily attacked by *H. cubana*. Seeds of *L. collinsii*, Mexico provenance, were provided by the Nitrogen Fixing Tree Association, Waimanalo, Hawaii.

Unless otherwise stated, all plants were grown in the greenhouse at Simon Fraser University, at 27-30°C under a 12:12h L:D cycle. Except during summer, the source of light was from ordinary fluorescent lamps attached to the ceiling of the greenhouse. Plants were watered whenever necessary. They were fertilized every 60 days with Green Earth (Alberto-Culver Canada Inc., Ontario) slow release fertilizer spikes (N-P-K = 10-8-5). Depending on the plants' size, they were grown in capacity pots. When more than 60 cm tall, the plants were cut 15 cm from the growing point to encourage branching.

Collection and Rearing of Insects

H. cubana were collected from infested *L. leucocephala* in the Philippines. They were transported to Simon Fraser University in June 1988 and again in October 1990, when the culture previously established from the first importation had been killed by diesel fumes accidentally introduced into the rearing facility. Psyllids were reared on potted ipil-ipil in 51 x 56 x 91 cm Saran-screen cages inside a quarantine room held at 24-28°C, R.H. $> 60\%$ and a 13:11h L:D cycle. Every week after the start of adult eclosion, uninfested plants were introduced into the cage for the adults to oviposit on. Infested plants were cut about 15 cm above the root collar, returned to the greenhouse, and allowed to recover and coppice for future use.

CHAPTER II

GROWTH IMPACT OF INFESTATION BY *HETEROPSYLLA CUBANA* ON TWO SPECIES OF *LEUCAENA*

Introduction

Feeding by *Heteropsylla cubana* is more or less confined to different species of the genus *Leucaena*. The wide range of variability in *Leucaena* spp. is reflected in the variable reactions by the species and their hybrids to feeding by *H. cubana*. Neither common nor giant *L. leucocephala* has shown resistance to the psyllid (Brewbaker 1987), except for partial tolerance in certain "giant" types (Anon. 1986; Wheeler et al. 1988). Hence, resistant species of *Leucaena* could serve as the genetic source of resistance for *L. leucocephala* to justify further cultivation of the species (Brewbaker 1987).

There are 12 recognized species of *Leucaena*; more than 900 accessions of these are grown and are flowering in Hawaii (Brewbaker 1987). These species have been crossed in a number of combinations resulting in over 50 viable interspecific hybrids (Pan 1985; Sorensson 1987). *L. collinsii* Britton & Rose, *L. pallida* Britton & Rose, *L. retusa* Benth. and *L. esculenta* (Moc. & Sesse) Benth. have shown high levels of resistance against *H. cubana* (Sorensson and Brewbaker 1987). In Taiwan, *L. greggi* S. Watson was also found to be highly tolerant (Pan 1987). Some provenances of generally susceptible species were moderately tolerant, but some individuals of these provenances were completely defoliated and sufferred some die-back.

In Hawaii, evaluations of the differential susceptibility among species were made from flowering trees $\geq$ one-year-old, and an empirical score of 1-9 was applied. This score integrated data on psyllid populations, reproduction, and damage on young vegetative shoots (Sorensson and Brewbaker 1986). Low scores mean high levels of resistance of the plant. On the other hand, the damage evaluation method of Othman and Prine (1984) and the relative abundance of psyllids on young shoots were followed in Taiwan to evaluate leucaena resistance according to a rating score from 0 to 10, corresponding to increasing levels of defoliation (Pan 1987).

Wheeler et al. (1988) used populations of first instar *H. cubana* to evaluate *L. leucocephala* varieties for resistance. The Nitrogen Fixing Tree Association (NFTA) International Leucaena Psyllid Trial (LPT) Network, which was initiated in 1987, used standardized guidelines and common germplasms provided by NFTA for 12 trials established in seven countries (Glover 1987). Seven more trials in 1988 and nine more in 1989 were completed in 16 countries (Wheeler and Brewbaker 1989). In these trials comparisons of the average fresh weights per plot of 40 trees were used to indicate resistance of the test plants. This biomass criterion had not been used in the past to evaluate the quantitative impact of the psyllid on leucaena.

Although *L. collinsii* was reported to be highly resistant to *H. cubana* (Pan 1987; Sorensson and Brewbaker 1987; Bray and Woodroffe 1988), the damage inflicted on the plant by the psyllid has not been quantitatively assessed. Hence, my objective was to compare the impact of psyllid infestation on the growth of seedlings of *L. leucocephala* and *L. collinsii* based on three criteria: height increment, diameter increment and above-ground biomass yield.

Materials and Methods

Experimental Plants

Fifty seven-month old seedlings of each of *L. leucocephala* and *L. collinsii* were grown outdoors in 25 cm diameter terra cotta pots near infested *L. leucocephala* stands in Los Baños, Philippines. To promote development of root nodules, seedlings of both species were innoculated with an isolate of *Rhizobium* (isolate L_6), a nitrogen-fixing bacterium, by pouring the rhizobium-solution at the root collar of the seedlings. One week before the experiment began, when the *L. leucocephala* and *L. collinsii* plants were approximately 25 and 50 cm tall, respectively, the plants were sprayed with fenvalerate, at 0.05% a.i., to kill any psyllids that might have infested them. During the course of the experiment the plants were watered regularly.

Experimental Layout

The 50 plants of each species were divided each into two groups to represent the two major treatments, i.e., sprayed and unsprayed. These groups were then further subdivided into two smaller groups of 12 and 13 plants. The resulting eight groups of plants were then randomized in two straight rows, either of the rows for one species, along the periphery of an infested leucaena stand, facing the northeast slope, at the back of the Ecosystems Research and Development Bureau building. Each group was 1.5 m away from its nearest neighbor. Two treatment groups were chosen for each species. Plants in these groups were sprayed with monocrotophos, at 0.05% a.i., every two weeks until the termination of the experiment. The insecticide solution was sprayed by means of a half-liter plastic aerosol dispenser. The spray was directed to the shoots and young open leaves of the plants and was done until wetting was obvious. Plants in the two control groups for each species were sprayed with water alone. Care was taken to minimize spray drift between groups by placing large pieces of cardboard between them during spraying. Each pot was numbered and labelled by treatment. Predation on psyllids in the unsprayed plots was very low during the course of the experiment, and any noticeable predators on the plants were removed by hand.

Data Gathering

The height and diameter of each plant in each treatment were measured at the start of the experiment. Height was taken from the ground level to the terminal node which was measured to the nearest 0.5 cm. The diameter was measured at 2.5 cm above ground with a Vernier caliper (Japan Micrometer Mfg. Co. Ltd.) to the nearest 0.1 mm. Measurements thereafter were done every week for 14 weeks.

After the final measurements of the height and diameter, the plants were uprooted. The upper biomass was separated from the roots by cutting the plant at the root collar. The leaves and stems were separately cut into small pieces and separately wrapped in aluminum foil. They were oven-dried at 70°C until their weight was constant, about 3 and 7 days for the leaves and stem, respectively. The dried samples were individually weighed on a triple beam balance.

Statistical Analysis

Because uninfested *L. collinsii* inherently grew taller and larger than uninfested *L. leucocephala*, only intra-specific growth parameters were compared. To correct for heteroscedasticity, the data on height and diameter were transformed using $\log_{10} X + 1$ and $\sqrt{X + 0.5}$ transformations, respectively, before statistical analysis (Zar 1984). For mean height and diameter increment in relation to time after initial infestation, the slopes or elevations of the regression lines between experimental treatments, i.e., sprayed and unsprayed, for each species were compared for homogeneity of two regression coefficients by *t*-test (Zar 1984). The final heights and diameters were compared by *t*-test using the two-sample hypothesis for testing for difference between two means after determining equality of treatment variance (Zar 1984). The biomass yields between sprayed and unsprayed plants for each species were also compared by the two-sample hypothesis test.

Results

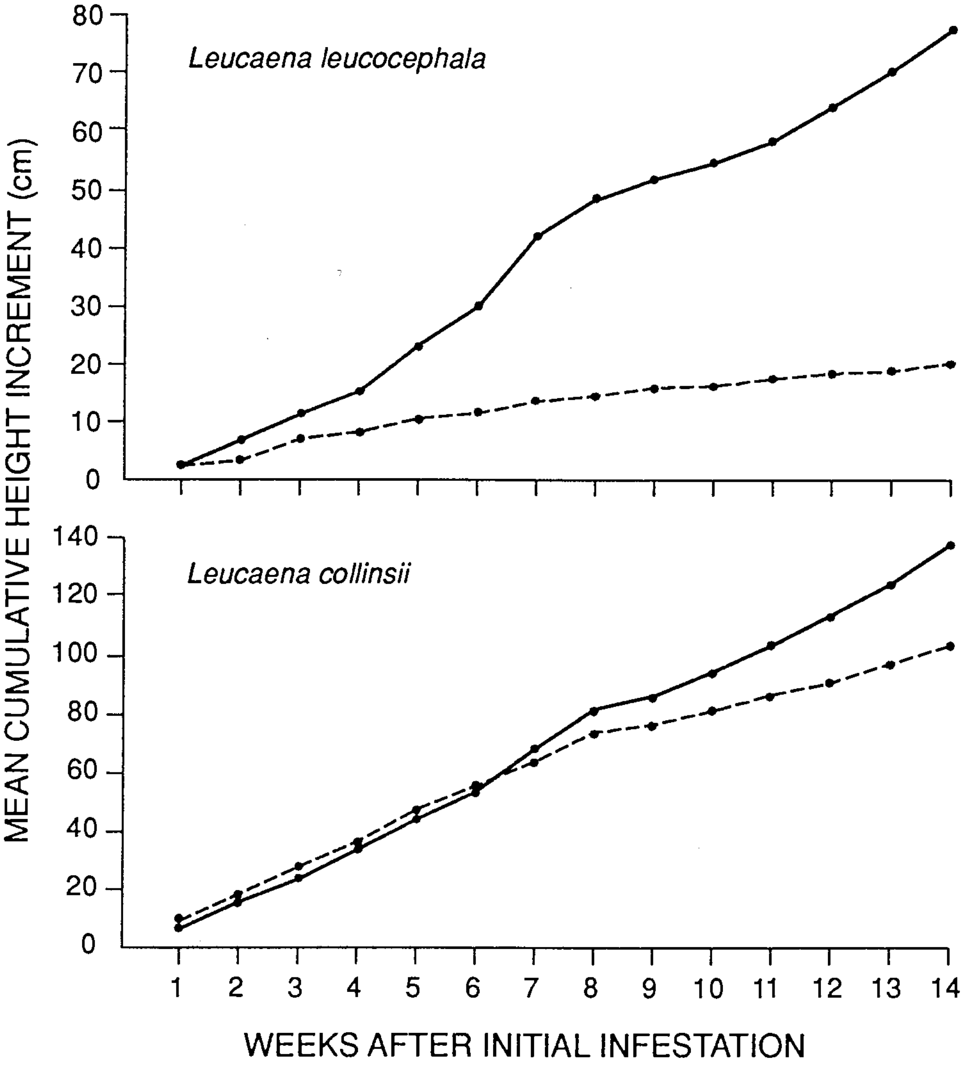
Observed Infestation Characteristics

Sprayed *L. leucocephala* and *L. collinsii* were almost free of psyllids, except for a few adults that were sporadically observed on *L. leucocephala.* Numbers of pioneer adults on individual unsprayed *L. leucocephala* plants were higher than on unsprayed *L. collinsii.* Likewise, *L. leucocephala* plants supported much larger populations of nymphs than those of *L. collinsii.* While all *L. leucocephala* plants were infested by adults, the mean percent infested *L. collinsii* plants recorded for each observation period was only 52% (SE = 19.98). Heavy infestation on *L. leucocephala* resulted in shoot die-back and arrestment of terminal growth. Any regrowth was readily infested. Hence, there was continuous adult and nymphal infestation on unsprayed *L. leucocephala* plants. In contrast, the period of adult infestation on *L. collinsii* was discrete, and nymphal infestation was brief, since most nymphs died before reaching maturity. Reinfestation on these plants also took longer than for *L. leucocephala* giving all but a few plants time to recover and produce new healthy shoots.

Height Increment

The slopes of the regression lines for height increment over time between sprayed and unsprayed *L. leucocephala* or *L. collinsii* were significantly different ($P < 0.001$), indicating that psyllid infestation severely reduced height growth rate of infested plants (Fig. 1). Sprayed and unsprayed *L. leucocephala* had mean height increments of 5.5 and 1.4 cm per week, respectively. Sprayed and unsprayed *L. collinsii*, on the other hand, had 9.8 and 7.4 cm increments per week, respectively. After 14 weeks, sprayed *L. leucocephala* were almost five time taller than the

Fig. 1. Cumulative height increment of sprayed (solid lines) and unsprayed (broken lines) *L. leucocephala* and *L. collinsii* seedlings. Regression equations for the four treatments and significance of slopes between two treatments within species are: *L. leucocephala*, sprayed, $Y = 0.11 + 1.58X$, $r^2 = 0.979$, and unsprayed, $Y = 0.20 + 1.01X$, $r^2 = 0.952$, $P < 0.001$; *L. collinsii*, sprayed, $Y = 0.52 + 1.41X$, $r^2 = 0.989$, and unsprayed, $Y = 0.75 + 1.12X$, $r^2 = 0.977$, $P < 0.001$. In no case was the SE of any mean height increment > 14% of the mean.


Leucaena leucocephala
Leucaena collinsii
MEAN CUMULATIVE HEIGHT INCREMENT (cm)
0
10
20
30
40
50
60
70
80
0
20
40
60
80
100
120
140
1
2
3
4
5
6
7
8
9
10
11
12
13
14
WEEKS AFTER INITIAL INFESTATION

unsprayed group, a highly significant difference (t-test, $P < 0.001$). Sprayed *L. collinsii* grew only about one-third taller than the unsprayed trees (Fig. 1), also a highly significant difference (t-test, $P < 0.001$), but much less than for *L. leucocephala*. Unsprayed *L. leucocephala* lost 74.1% of their potential height increment, three times more than did infested *L. collinsii* (Fig. 2).

Diameter Increment

The slopes of the regression lines for diameter increment of sprayed and unsprayed *L. leucocephala* were significantly different ($P < 0.001$), indicating a severe reduction in girth growth rate resulting from psyllid infestation (Fig. 3). Between sprayed and unsprayed *L. collinsii*, however, there was no significant difference between the slopes ($P > 0.10$) or the elevations ($P > 0.5$) of the regression lines. Sprayed and unsprayed *L. leucocephala* had a mean weekly diameter growth of 0.54 and 0.25 mm, respectively, while the corresponding rates for sprayed and unsprayed *L. collinsii* were 0.49 and 0.45 mm, respectively. While sprayed *L. leucocephala* had a final girth increment twice as great as the unsprayed plants, a highly significant difference (t-test, $P < 0.001$), the difference in final diameter between sprayed and unsprayed *L. collinsii* was almost negligible (t-test, $P > 0.10$). Unsprayed *L. leucocephala* lost 54.2% of their potential diameter increment, seven times more than infested *L. collinsii* (Fig. 2).

Fig. 2. Comparative growth loss caused by *H. cubana* in unsprayed *L. leucocephala* and *L. collinsii* seedlings afters 14 weeks.

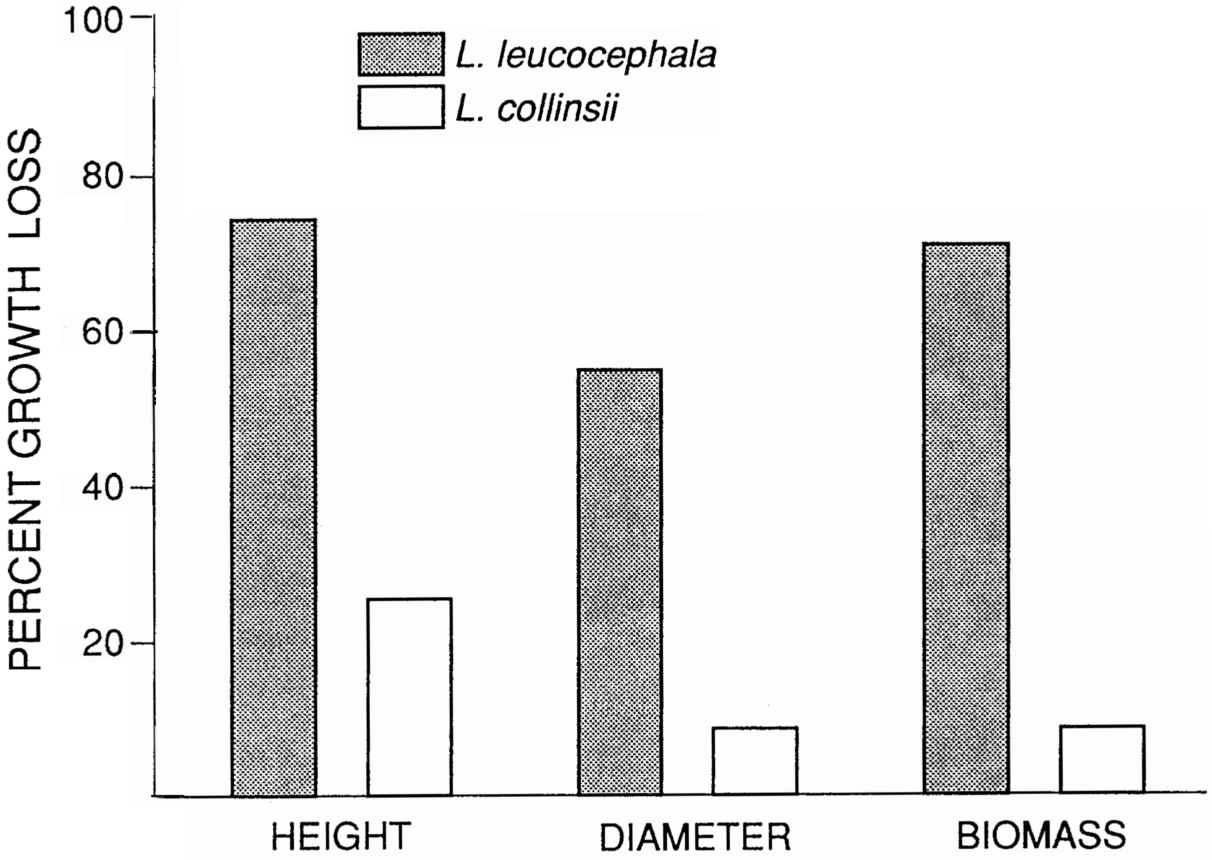
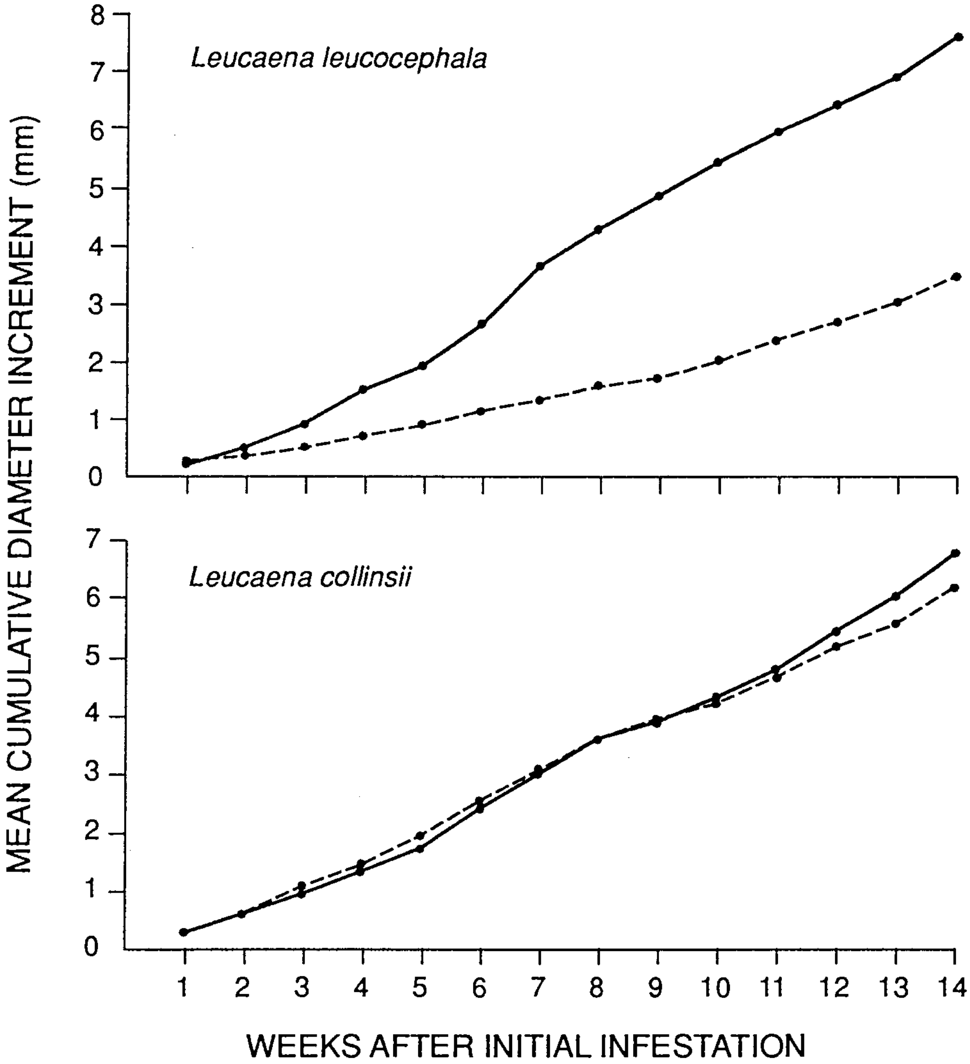

PERCENT GROWTH LOSS
100
80
60
40
20
L. leucocephala
L. collinsii
HEIGHT
DIAMETER
BIOMASS

Fig. 3. Cumulative diameter increment of sprayed (solid lines) and unsprayed (broken lines) *L. leucocephala* and *L. collinsii* seedlings. Regression equations for the four treatments and significance of slopes or elevations between two treatments within species are: *L. leucocephala*, sprayed, $Y = -0.29 + 0.83X$, $r^2 = 0.991$, and unsprayed, $Y = 0.24 + 0.43X$, $r^2 = 0.972$, $P < 0.001$; *L. collinsii*, sprayed, $Y = -0.10 + 0.71X$, $r^2 = 0.993$, and unsprayed, $Y = 0.001 + 0.68X$, $r^2 = 0.997$, $P > 0.05$. In no case was the SE of any mean diameter increment > 17% of the mean.


Leucaena leucocephala
Leucaena collinsii
MEAN CUMULATIVE DIAMETER INCREMENT (mm)
WEEKS AFTER INITIAL INFESTATION
0
1
2
3
4
5
6
7
8
1
2
3
4
5
6
7
8
9
10
11
12
13
14

Biomass Growth

Unsprayed *L. leucocephala* that were heavily infested by *H. cubana* were about four times lighter in above-ground biomass (dry weight) than sprayed plants, a significant difference, and again indicating a severe impact of infestation (Table 1). In comparison, unsprayed *L. collinsii* were almost as heavy as the sprayed plants. On a pecentage basis, infested *L. leucocephala* lost as much as eight times more biomass than unsprayed *L. collinsii* (Fig. 2).

Table 1. Above-ground biomass of sprayed and unsprayed *L. leucocephala* and *L. collinsii* seedlings after 14 weeks.

Species	Treatment	Biomass (g) ($\bar{x}$ ± SE)[a]
L. leucocephala	Sprayed	39.6 ± 0.85a
	Unsprayed	11.2 ± 0.83b
L. collinsii	Sprayed	55.3 ± 6.83a
	Unsprayed	50.6 ± 4.73a

[a] Means for each species followed by the same letter are not significantly different (n = 25), *t*-test, $P < 0.05$.

Discussion

My results, compiled for 14 weeks on seedlings, are consistent with observations that *H. cubana* infestation has a very severe long-term impact on the growth of those *L. leucocephala* that survived infestation. Although *L. leucocephala* can withstand repeated defoliation, either through cutting or grazing (Plucknett 1977), the degree and frequency of defoliation affect the plant's productivity (Alferez 1977). When infestation occurs during the first year of development, especially if the canopy is not sufficiently developed to shade out weeds, *L. leucocephala* will suffer greatly from interspecific competition (Plucknett 1977). Since *L. leucocephala* is shade-intolerant, it can not compete successfully with taller competitors (Moomaw 1977). Hence, even if infested trees were to survive repeated attacks by psyllids, they would be very unlikely to put on significant growth.

My results confirm those of others that *L. leucocephala* is sensitive to *H. cubana*, while *L. collinsii* is more resistant to the pest (Sorensson and Brewbaker 1984; Hollingsworth et al. 1985; Sorensson and Brewbaker 1986; Bray and Sands 1987; Sorensson 1987; Bray and Woodroffe 1988). However, care must be taken in interpreting the results because the numbers of infesting psyllids and the duration of infestation were not the same for plants of the two species. All unsprayed *L. leucocephala* plants were infested, whereas not all *L. collinsii* plants were infested at any one time, suggesting that antixenosis may have been expressed. In addition, the duration of infestation on individual *L. collinsii* plants was intermittent while all *L. leucocephala* plants were continously infested throughout the duration of the experiment. Hence, the low damage sustained by *L. collinsii* may be due, in part, to low initial and succeeding infestation level, and short infestation period on each individual plant. This results emphasize the importance of exposing the test plants to natural infestation, in contrast to artificial infestation, in that the method allows both antixenosis and antibiosis to operate naturally against the insect pest. The variable response observed among individual *L. collinsii* plants to the psyllid infestation may be due to the genetic variability in the seed lot I used in the experiment. Bray and Woodroffe (1988) found differential responses among accessions of *L. collinsii* to the psyllid infestation.

Wheeler et al. (1988) found differences in total tree damage ratings, i.e., defoliation, between the K8 and K636 varieties of *L. leucocephala*, but no significant differences in mean numbers of first instar nymphs. This result suggests a differential reaction of the two varieties to the same attacking insect population. It further suggests that number of attacking insects alone is not a good index in measuring resistance. In such cases, quantitative damage ratings, e.g., height and diameter growth, and biomass yield, could assume importance in assessing resistance to *H. cubana*. While such methods would be difficult for large trees, my experiment indicates that quantitative damage ratings could be used to assess young plants in resistance comparison experiments. In addition, the use of seedling plants could facilitate layout of experiments and speed up resistance screening trials. Resistance by *L. collinsii* that were $<$ 1-yr old appeared to be expressed clearly in our experiment and that of Bray and Woodroffe (1988). Experiments should be done to confirm the same response in other *Leucaena* spp. and varieties. Although plant height can affect initial infestation in other insect species (Cartier 1963; Tingey and Leigh 1974), field observations strongly suggest that *H. cubana* adults readily infest young shoots of tall trees and young epicormic shoots of short coppiced trees.

My experiment clearly show significant differences in the response between *L. leucocephala* and *L. collinsii*, and between infested and uninfested plants of *L. leucocephala*, indicating a greater impact of *H. cubana* infestation on infested *L. leucocephala* than on *L. collinsii*.

CHAPTER III

FEEDING AND OVIPOSITIONAL PREFERENCE OF *HETEROPSYLLA CUBANA* BETWEEN TWO SPECIES OF *LEUCAENA*

Introduction

Differences in the damage sustained by plants of different species or varieties when attacked by insects reflect the plants' relative susceptibility or resistance. The degree of damage is most often dependent on the size of insect population that becomes established. Thus, even "tolerant" plants could be severely damaged when the population of infesting insects exceeds a certain limit. Hence, resistance could be determined, in part, by host-insect interactions that reduce the probability of successful establishment.

Most phytophagous insects have specialized feeding habits, i.e., feeding on a narrow range of taxonomically related plant species and even restricting themselves to feed on particular plant parts (Beck and Schoonhoven 1980). Host plant selection by insects in their feeding stages could be divided into three distinct behavioral phases: 1) attraction to a potential food plant; 2) arrestment or cessation of locomotion; and 3) stimulation (or deterrence) of feeding on that plant (Hanson 1983). Orientation, feeding and oviposition are determined by physical and chemical characteristics of the host (Saxena 1969). Hence, phytophagous insects are said to be adapted to the metabolic/physical properties of their host plants and are, therefore, capable of identifying the chemical composition of plants that they encounter in their environment. Plants contacted by an insect elicit a corresponding behavior from the insect. Some plants are rejected while others are accepted.

In nature insects usually search for host plants on which to feed or oviposit. However, even within their range of host plants insects have shown differential preferences. Beck and Schoonhoven (1980) termed this behavior as "host-plant preference" and refer to the "insect's predilection to select some plants in preference to others, within its host-plant range." Some insects are known to alight and feed more on one plant than on another related plant species. Compared to barley, *Hordeum vulgare* L., different species of warm-season grasses were not as attractive to 4 species of alate aphids (Kieckhefer 1984). Adult foliar beetles, *Ootheca bennigseni* Weise, prefer some cultivars of *Phaseolus vulgaris* L. over others (Karel and Rweyemamn 1985). Wheat, *Triticum aestivum* L. ex Thell., with pubescent leaves attracted lower numbers of *Rhopalosiphum padi* (L.) than the glabrous-leaved cultivars (Roberts and Foster 1983). Adults that were unable to feed left the plant. Likewise, feeding preferences have been demonstrated in the stem weevil, *Cylindrocopterus adspersus* (LeConte), on species of sunflower (*Helianthus* spp.) (Rogers and Seiler 1985), and by the chinch-bug, *Blissus leucopterus leucopterus* (Say), on different varieties of wheat (Stuart et al. 1985).

Feeding does not necessarily lead to oviposition in some insects. Adults are still discriminating when selecting a plant for oviposition. Pickleworms, *Diaphania nitidalis* (Stoll), and melonworm, *Diaphania hyalinata* (L.), laid fewer eggs on glabrous mutants of two *Cucurbita* spp. than on plants with normal pubescent foliage (Day et al. 1978; Elsey and Wann 1982; Elsey 1985). The sorghum midge, *Contarinia sorghicola* (Coquillett), laid 17 times more eggs on one variety of *Sorghum biocolor* (L.) than on others (Rossetto et al. 1984). Similar behavior was reported for other insect species, i.e. *Lygus hesperus* Knight on bean cultivars (Bosque-Perez 1982), *Heliothis viriscens* (F.) on *Nicotiana tabacum* L. introductions (Jackson et al. 1983), *Aphis fabae* Scopoli on *Vicea fabae* L. cultivars (Holt and Wratten 1986), *Empoasca kraemeri* Ross & Moore on several bean lines (Kornegay et al. 1986), and *Rhopalosiphum padi* (L.) on varieties of oats and barley (Weibull 1988).

While several studies have been done to compare the reaction of different *Leucaena* spp. and cultivars of *L. leucocephala* to *H. cubana* infestation (Pan 1987;

Sorensson and Brewbaker 1987; Bray and Woodroffe 1988; Wheeler et al. 1988; Wheeler and Brewbaker 1989), none has dealt with the behavioral response of *H. cubana* to their host plants. This study aimed to determine if differential selection for feeding and oviposition by *H. cubana* adults occurs between *L. leucocephala* and *L. collinsii.*

Materials and Methods

Host-plant Preference

Two experiments were conducted in Los Baños, Laguna, Philippines. Seedlings of *L. leucocephala* and *L. collinsii* were grown for 5 months in terra cota pots with ordinary forest soil. The average heights of the seedlings at the start of the experiment were 18.9 and 12.8 cm for *L. leucocephala* and *L. collinsii*, respectively.

The first experiment assessed adult *H. cubana* colonization of *L. leucocephala* and *L. collinsii*, either separately by species or with plants of both species intermixed. When the plants were grouped separately, there were 25 plants of each species in each of the two blocks. The nearest infested leucaena trees were about 2 m from the group of potted plants. The distance between species groups was about 3 m while the individual plants within blocks were spaced 30 cm away from each other. When plants were intermixed, the set-up was similar to that when they were separate, except that equal numbers of plants of the two *Leucaena* spp. were mixed randomly together in each block.

Before the start of the experiment, all the plants were sprayed with fenvalerate, a synthetic pyrethroid, to remove any *H. cubana*. Four days after spraying, the numbers of reinfesting adults on individual plants were noted. At this time no adult mortality, due to insecticide treatment, was observed on the plants. Fenvalerate is a contact insecticide and although relatively persistent is not strictly systemic. Plants having small or poorly developed shoots, i.e., < 4 developed raches, at the time of observation were excluded. This procedure resulted in unequal sample sizes. Adults that were not on the young shoots were considered transients and, therefore, regarded as not truly attracted to the plant. There were 4 and 5 experimental replicates, i.e., groups, set up for the single and mixed-species groups, respectively. Each replicate was done during different 4-day periods.

ANOVA for a Randomized Complete Block design with unequal subsamples was used to analyze between numbers of psyllids on the plants, both within and between species (Gomez and Gomez 1984).

After the first experiment was completed, the same plants were used in the second experiment. Twenty-five plants of one species were arranged in a 5 x 5 square grid, with 30 cm between plants. A grid of plants of the other species was about 3 m distant. Four days after pesticide application, the numbers of plants infested by adult *H. cubana* were noted. As in the first experiment, only those plants with developed shoots were sampled. The experiment was replicated 20 times over an 80-day period, with the location of the species and individual plants in each grid re-randomized for each replicate. The data were transformed by arcsine and tested for equality of treatment variance before the differences between means were compared by *t*-test using the two-sample hypothesis (Zar 1984).

Ovipositional "Preference"

Three days after adults were counted in the final data gathering of the second experiment above, 24 pairs of infested shoots were selected from each species of *Leucaena*. An infested shoot was defined as a developed shoot or unopened leaf with no fewer than 2 adults on it. For each pair, the shoots of each species were of the same stage of development, but shoots of *L. collinsii* were almost always longer than those of *L. leucocephala*. All the eggs on the shoots were counted under a dissecting microscope.

Another experiment was done in the laboratory at Simon Fraser University to test the psyllid's ovipositional preference on the two *Leucaena* spp.. Paired *L. leucocephala* and *L. collinsii* plants were placed inside a 51 x 56 x 91 cm Saran-screen cage. As in the field experiment, shoots of the plants were of almost the same stage of development. Ten pairs of female and male *H. cubana* were introduced into the cage. After 3 days, the plants were removed and the eggs on the shoots counted. The experiment was replicated 13 times with new psyllids and plants on different 3-day periods.

The means in each experiment were tested for equality of treatment variances before comparison by *t*-test using the two-sample hypothesis (Zar, 1984).

Results

Host-plant Preference

Significantly more adult *H. cubana* settled on *L. leucocephala* than on *L. collinsii* in both pure and mixed species stands (Table 2). Even in a mixed stand, 5 times more adults settled on *L. leucocephala* than on *L. collinsii.*

Every *L. leucocephala* plant was reinfested within 4 days of insecticide treatment, whereas significantly fewer *L. collinsii* plants were reinfested (Table 3). Reinfestation rates for *L. collinsii* ranged from 5 to 65% ($\bar{x} = 35\%$).

Ovipositional "Preference"

Significantly more eggs were laid by *H. cubana* on *L. leucocephala* than on *L. collinsii* in both field and laboratory experiments (Table 4). About 1.9 times more eggs were laid on *L. leucocephala* than on *L. collinsii* in the field. Assuming that all the 10 female psyllids in the laboratory experiment laid eggs on both species, the mean number of eggs laid per female for 3 days on *L. leucocephala* and *L. collinsii* is 20.2 and 7.5, respectively.

Table 2. Infestation by adult *H. cubana* on pure and mixed stands of *L. leucocephala* and *L. collinsii.*

Species	Pure Stand		Mixed Stand	
	No. reps	No. adults per shoot ($\bar{x} \pm$ SE)[a]	No. reps	No. adults per shoot ($\bar{x} \pm$ SE)[a]
L. leucocephala	4	7.4 ± 1.37a	5	5.6 ± 0.58a
L. collinsii	4	1.8 ± 0.62b	5	0.9 ± 0.36b

[a] Means within a column and within a row followed by the same letter are not significantly different, ANOVA, $P < 0.05$.

Table 3. Reinfestation by *H. cubana* adults on *L. leucocephala* and *L. collinsii* plots 4 days after pesticide application.

Replicate number	n	*L. leucocephala* % plants reinfested	n	*L. collinsii* % plants reinfested[a]
1	15	100	15	60.0
2	10	100	14	21.4
3	20	100	19	31.6
4	19	100	20	5.0
5	15	100	17	11.8
6	14	100	16	18.8
7	24	100	16	12.5
8	21	100	16	6.3
9	10	100	10	60.0
10	10	100	10	50.0
11	14	100	13	30.8
12	17	100	9	0.0
13	11	100	11	63.6
14	11	100	11	63.6
15	10	100	10	10.0
16	9	100	10	40.0
17	20	100	20	65.0
18	20	100	20	65.0
19	25	100	25	32.0
20	25	100	25	52.0

[a] Mean reinfestation level for *L. collinsii* = 35%, significantly lower than for *L. leucocephala*, *t*-test, $P < 0.05$.

Table 4. Number of eggs laid by *H. cubana* on *L. leucocephala* and *L. collinsii* in the field and in the laboratory.

		Field		Laboratory
Species	n	No. eggs per shoot ($\bar{x}$ ± SE)[a]	n	No. eggs per shoot ($\bar{x}$ ± SE)[a]
L. leucocephala	24	706.6 ± 91.6a	13	201.9 ± 35.2a
L. collinsii	24	381.1 ± 54.3b	13	74.5 ± 20.6b

[a] Means within a column followed by the same letter are not significantly different, *t*-test, $P < 0.05$.

Discussion

The higher numbers of *L. leucocephala* than *L. collinsii* plants that were infested (Table 3) and the higher numbers of adult psyllids settling on *L. leucocephala* (Table 2) indicate that *H. cubana* is highly discriminating while foraging for food and/or oviposition sites. The much higher numbers of eggs laid on both species in the field than in the laboratory (Table 4) may suggest that multiple landing and oviposition occurred in the field. It is very probable that most adults left the plant after ovipositing. This phenomenon was observed for alate *Aphis fabae* Scopoli and *Metopolophium festucae* (Theobald) *cerealium* (Kidd and Cleaver 1984; Dent 1986). However, it is also possible that most adults stayed longer on *L. leucocephala*, either to feed or oviposit, which could explain the higher numbers of eggs laid on *L. leucocephala*. Alate aphids were reported to stay longer and reproduce more on suitable than on less suitable host plants (Müller 1958; Kring 1972). Although my data on adult colonization on both *Leucaena* spp. may be an underestimate (Table 2), the conclusion that they indicate a true difference in host preference is most probably valid. This differential preference by the adults explains, in part, why unsprayed *L. collinsii* were less damaged than unsprayed *L. leucocephala* (Chapter II, Fig. 2 and Table 1).

The computed numbers of eggs oviposited per female, assuming all 10 females laid eggs, under laboratory conditions (Table 4) may also be an underestimate. Not all of the 20 adults that were released inside the cage were observed to have settled on the shoots. Also, among those that settled it was not known how many were females and how many laid eggs. In contrast, the plants in the field were exposed to a very large number of potential psyllid invaders which might explain the higher numbers of eggs laid on both species of leucaena compared with those in the laboratory (Table 4).

As there was differential attraction by alighting adult psyllids between the two leucaena species, it appears that such difference in the numbers of alighting psyllids (Table 2) subsequently contributed to the difference in the numbers of eggs laid between the two leucaena species (Table 4). The factors responsible for the weak preference of *H. cubana* adults to *L. collinsii* are not yet known, but are probably chemical in nature. *Leucaena collinsii* might contain either volatile or non-volatile chemicals that repel alighting or feeding adults. Alternatively, it might lack sufficient chemical attractants for the insect.

CHAPTER IV

BASES FOR HOST-PLANT SELECTION OF *HETEROPSYLLA CUBANA*

Introduction

Host selection in insects is composed of a sequence of behavioral responses to specific stimuli. Each response brings the insect to the next situation in which another set of stimuli will release another set of activities. For a plant to be infested, an insect must be able to recognize and reach a plant. Orientation and oviposition in most insects are both governed by physical and chemical characteristics of their host (Saxena 1969). Many studies have demonstrated that insects are highly discriminating while foraging for food or oviposition sites using visual or olfactory stimuli (Thorsteinson 1960; Beck 1965).

Of the potential visual cues, color is the most well studied (Prokopy and Owens 1983). Most insects studied respond well to spectral reflectance ranging from 350-650 nm (Menzel 1979). The Caribbean fruitfly, *Anastrepha suspensa* (Loew) is attracted by orange and yellow, which are colors of many fruits they attack (Greany et al. 1977). The initial landings of the aleyrodid, *Trialeurodes vaporariorum* Westw., appear unrelated to the suitability of the plant as a host, but are strongly related to color (Vaishampayan et al. 1975a,b). In their flight phase, adults orient towards the sky which reflects at 400 nm but will tend to land on green plants that reflect maximally at 550 nm (Coombe 1982). Whiteflies and aphids show strong landing responses to yellow-reflecting surfaces (Kring 1972), as in green leaves that reflect peaks in the yellow portion of the visible light sprectrum.

Physical features are rarely unique to a single plant species. In contrast, chemical characteristics are often typical to a plant species and play a major role in host-selection for ovipositing or feeding adult insects. Hence, though attention has been given to the role of visual stimuli (Prokopy and Owens 1983; Judd et al. 1988) numerous works have also been done to emphasize the chemical aspects of host-plant discrimination by phytophagous insects (Dethier et al. 1960; Hsiao 1969; Dethier

1980; Dethier 1982; Bell and Carde 1984). Volatile chemicals usually influence the initial orientation of insects to their host from a distance (de Wilde et al. 1969; Hawkes and Coaker 1979; Dindonis and Miller 1980; Fein et al. 1982; Visser 1986; Judd and Borden 1989). However, chemical stimuli also stimulate probing, biting and oviposition once the insect is in contact with the plant. The plant chemicals that affect insect behavioral responses are classified according to their influence on sensory responses (Hsiao 1969). Chemical stimuli that elicit positive responses are called attractants, arrestants or stimulants, while those that evoke negative responses are called repellents or deterrents.

Egg-laying females identify suitable plants by their chemical and physical characteristics (Miller and Strickler 1984; Harris and Miller 1984). Secondary compounds typical of a given plant may be oviposition stimulants for insects which feed on that plant (Gupta and Thorsteinson 1960; Rodman and Chew 1980; Renwick and Radke 1983), while others are oviposition deterrents when occurring at high levels in unsuitable plants but not in suitable plants (Tingle and Mitchell 1984; Mitchell and Heath 1985; Tabashnik 1987). Plants suitable for a particular insect may also contain compounds that deter oviposition by that insect (Weins 1978; Renwick and Radke 1981, 1985). The acceptance and rejection of a plant by an insect may, therefore, depend on the balance of positive and negative stimuli within the plant (Renwick and Radke 1987).

Even within populations of plant species, differential host selection by insects has been demonstrated. Mitchell (1977) found that *Brassica oleracea* L. subsp. *oleracea* plants with the greatest release of a volatile compound, allyl nitrile, elicited a stronger positive behavioral response by *Pieris brassicae* L. than plants which release small amounts of the volatile. The oviposition behavior and distribution of egg masses of *Ostrinia nubilalis* Hubn. in the field differ in various maize varieties

(Anglade et al. 1981). Thus, Stockel et al. (1987) classified the different hybrids as "favorable" or "non-favorable" for oviposition by *O. nubilalis.* They hypothesized that the choice is mediated by a chemical communication system using volatile compounds active at a distance from the insect and active when in contact with the insect. Andersen and Metcalf (1987) related the preference of *Diabrotica undecimpunctata howardi* Barber to blossoms of *Cucurbita maxima* Duchesne over those of other *Cucurbita* spp. to the high volatile release rates and high cucurbitacin levels found in *C. maxima.* Minor differences in chemical characteristics between two varieties of soybean also caused significant differences in their relative susceptibilities to *Trichoplusia ni* (Hubn.) (Khan et al. 1987).

To date, practically no research has addressed the role of vision or olfaction in host preference by *H. cubana.* My objectives were to determine if color and/or host odor influence the differential preference displayed by *H. cubana* adults between *L. leucocephala* and *L. collinsii.*

Materials and Methods

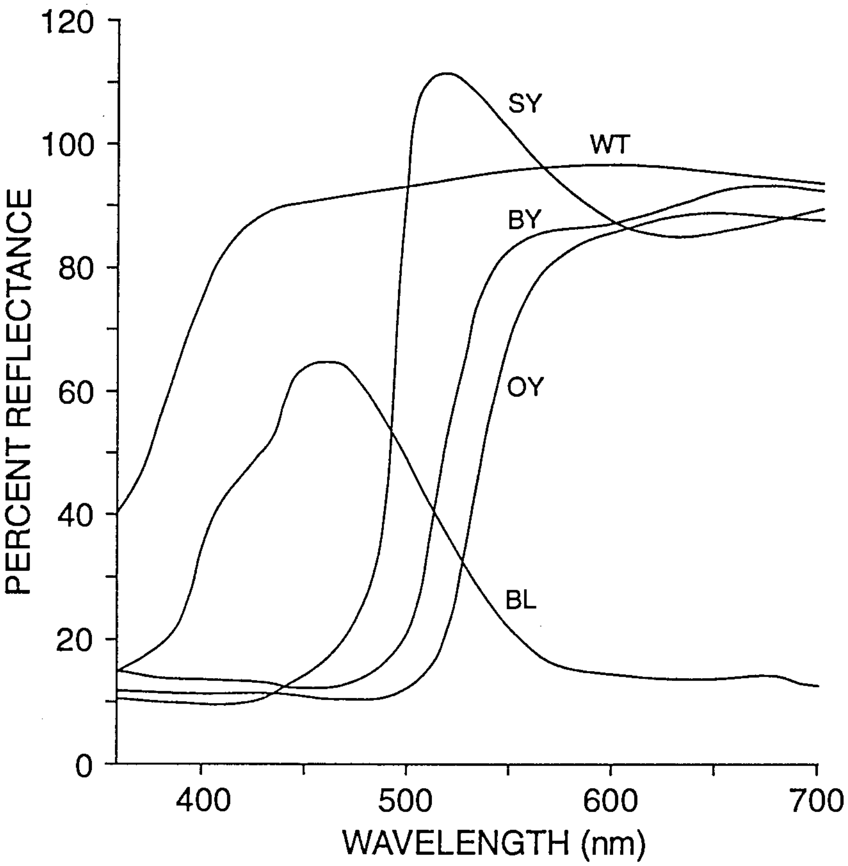
Color Response

Chrome-line card traps (Phero Tech Inc., Delta B.C.) of the following colors were compared for their relative attractiveness to adult *H. cubana* in the field: non-UV white, blue, bright yellow, orange yellow and super yellow. Visible wavelength reflectance curves for the five colored board traps are shown in Fig. 4. The different colored cards were randomly hang vertically, but evenly spaced, from a horizontal string suspended 1.5 m above ground inside an infested stand of *L. leucocephala* in Los Baños, Philippines. After 24 h, the traps were collected and the number of adults that were caught were counted under a dissecting microscope. The experiment was replicated 36 times over 9 days, with 4 replications per day. In 5 of these days, the numbers of males and females caught were also counted.

Reflectance measurements were also made using a Cary 17 recording spectrophotometer on leaves of different ages, i.e., unexpanded young leaf, 1st fully expanded leaf and 3rd mature leaf, of the two species of *Leucaena*. Because of their small size, the pinnules of the leaf were laid side by side and sandwiched between 24 x 50 mm glass slides. Only the upper leaf surface light reflectance was measured. The intensity of visible light (350-700 nm) reflected from the leaf surfaces was compared with a magnesium oxide standard curve (=100% reflectance).

The trap catch data were transformed using $\sqrt{X} + 0.5$ and the data for all the experimental days were tested for homogeneity of variance before analyzing the means by ANOVA and Duncan's multiple range test (Gomez and Gomez 1984). Data on sex response to color were tested for homogeneity of ratio before testing by X^2 for a fixed-ratio hypothesis.

Fig. 4. Spectral reflectance curves of 5 Chrome-line card traps; SY = super yellow, WT = non-UV white, BY = bright yellow, OY = orange yellow, BL = blue. Data obatained from Phero Tech Inc., Delta, B.C.


PERCENT REFLECTANCE
0
20
40
60
80
100
120
400
500
600
700
WAVELENGTH (nm)
SY
WT
BY
OY
BL

Odor Response

Field Experiment

To test if volatiles from the host plants influence the orientational response of *H. cubana* adults, three 6-month-old seedlings, about 40 cm tall, each of *L. leucocephala*, *L. collinsii* and a non-host, *Amaranthus spinosus* L. (age not known), were placed inside separate Saran-screen cages. The screen obstructed clear color refectance of the leaves of the test plants when viewed from the outside. All the plants used had well-developed shoots. The cages were pentagonal and measured 30 cm on each side and 100 cm in height. The cages were placed along the periphery of an infested *L. leucocephala* stand in Los Baños, Philippines.

White cardboard traps coated with Stickem Special (Seabright Enterprises, Emeryville, CA), measuring 15 x 15 cm, were clipped on the middle portion of all the sides of the screen cage. After 24 h, the traps were collected and replaced with clean traps, and the total number of *H. cubana* adults for all the traps for each species was recorded. The cages together with plants were re-randomized every collection time, usually in the morning. The experiment was repeated for 15 days as replicates. Plants were replaced with new plants when they did not produce well-developed shoots.

The data were analyzed using multisample hypothesis analysis of variance after $\log_{10}(X + 1)$ transformation, and the means were ranked by Tukey's test at $P = 0.05$ (Zar 1984).

Laboratory Bioassays

Plant extract. Extracts were prepared by placing excised unexpanded leaves of both *Leucaena* spp. in screw cap vials with hexane (HPLC grade) for 24 h, after which the solute was transferred into another vial and stored in the freezer for future use. For every gram of plant tissue a corresponding 5 mL of hexane was used as solvent. Hexane was used because it is a good solvent for most extractables, including leaf surface wax on which volatiles could be entrapped.

Insects. *H. cubana* used in the bioassay were from cultures maintained on *L. leucocephala* plants in the laboratory. The test insects were adults of undetermined age but were all green to orange-green in color. They were held individually in gelatin capsules for at least 30 min before each test; each insect was used only once.

Bioassay procedures. The attractiveness of extracts of *L. leucocephala* and *L. collinsii* to adult *H. cubana* was tested using the still-air olfactometer similar to that developed by Smith (1989) for the pear psylla. It was made from opaque plexiglass, 5 x 5 x 12 cm in dimension, and divided crosswise into 3 equal parts. A circular chamber, 25 mm in diameter and 10 mm deep, was made in each of the 2 lateral parts while a 6 mm deep chamber was made in the middle portion. A straight canal, about 6 mm deep and 12 mm wide, connected the 3 chambers to each other. The 2 lateral chambers were both 2.5 cm distant on either side of the central chambers. A transparent plexiglass, about 4 mm thick, covered the top of the device. The cover was pegged to one corner of each lateral part to fit and secure all the parts of the olfactometer together as a bioassay was in progress, but still allowing full view of the insect inside the olfactometer. This set-up allowed easy access to all 3 chambers by sliding the bottom parts out, either singly or simultaneously.

A bioassay was done by putting the extract and solvent each on a circular white filter paper, about 15 mm in diameter, placed on an 18 mm-diameter microscope cover glass in either of the lateral (test) chambers, while the insects were introduced individually into the central (release) chambers. A response was defined as movement of the test insects into either of the test chambers. Observations were terminated after the test psyllids completed their response, or 10 min after release if no response had occurred. During the bioassay, a white cardboard cylinder, measuring 25 cm in diameter and 30 cm tall, and open on both ends enclosed the olfactometer. A lamp with white-light was placed 10 cm above the top open end of the cylinder to provide uniform lighting. The cylinder housed two olfactometers that were observed simultaneously. Bioassays were conducted between 1300 and 1800 h.

Several experiments were conducted to test the response of adult *H. cubana* to host volatiles. The first experiment compared the responses of males and females to extracts of the susceptible *L. leucocephala*. Succeeding experiments compared the responses of females to solvent or extracts of *L. collinsii*, to a choice of *L. leucocephala* and *L. collinsii* and to the hexane solvent or a *L. leucocephala*/*L. collinsii* extract mixture. In all experiments 5 *u*L of the prepared extract (1 x 10^{-3} g. equivalent of plant material) and control solvent was used as stimulus. A final experiment tested *L. collinsii* extract at 4 concentrations ranging from 1 x 10^{-3} to 1 x 10^{-5} g. equivalent. Data were analyzed separately for each set of bioassays using the fixed-ratio hypothesis X^2 test (Gomez and Gomez 1984).

Results

Color Response

Flying adult *H. cubana* showed a hierarchical preference for card traps colored super yellow, orange yellow, bright yellow, white and blue, in that order (Fig. 5). However, there were no significant difference in the responses of males and females to the different colored traps (X^2, $P < 0.05$).

The reflectance intensity (RI) of the leaves differed between ages and between *Leucaena* spp. (Fig. 6). The fully expanded leaf of *L. leucocephala* had the highest overall RI of 51%, followed by the unexpanded leaf at 47%. In comparison, the maximum RI of the fully expanded young and unexpanded leaves of *L. collinsii* were 46.5% and 46%, respectively, slightly lower than that of *L. leucocephala.* The mature leaf of *L. collinsii* had a maximum RI of 41.5%, higher than that of *L. leucocephala* at 34%.

Leaves of all ages of both species reflected maximally at similar wavelengths, i.e., 550 nm (yellow). There was a pronounced rise in reflectance at about 500 nm (Fig. 6), coinciding with a similar rise in reflectance of the most preferred super yellow cards (Fig. 4). The rise in reflectance at 500 nm was steeper and the peak at 550 nm was higher in *L. leucocephala* than in *L. collinsii* (Fig. 6). As the leaves matured, the yellow peak became less pronounced.

Odor Response

Field experiment

There were significant differences in the number of adults caught on sticky cardtraps on cages containing *L. leucocephala*, *L. collinsii* or the non-host, *A. spinosus*, with the degree of preference in that order (Fig. 7).

Fig. 5. Numbers of adult *H. cubana* caught on colored Chrome-line card traps of different light reflectances. Bars topped by the same letters are not significantly different, Duncan's multiple range test, n = 9, $P < 0.05$. (SY = super yellow; OY = orange yellow; BY = bright yellow; WT = non-UV white; BL = blue).

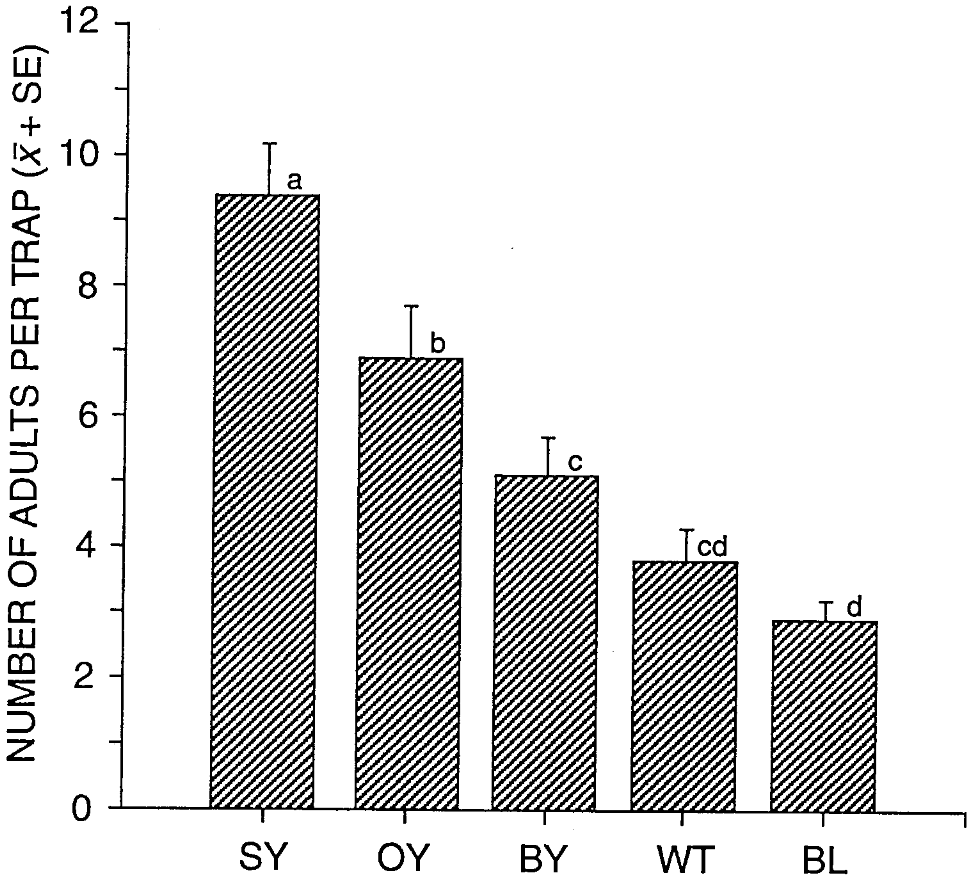

NUMBER OF ADULTS PER TRAP ($\bar{x}$ + SE)
0
2
4
6
8
10
12
a
b
c
cd
d
SY
OY
BY
WT
BL

Fig. 6. Spectral reflectance curves of young-expanded, young unexpanded, and mature leaves of *L. leucocephala* (solid line) and *L. collinsii* (dashed line).

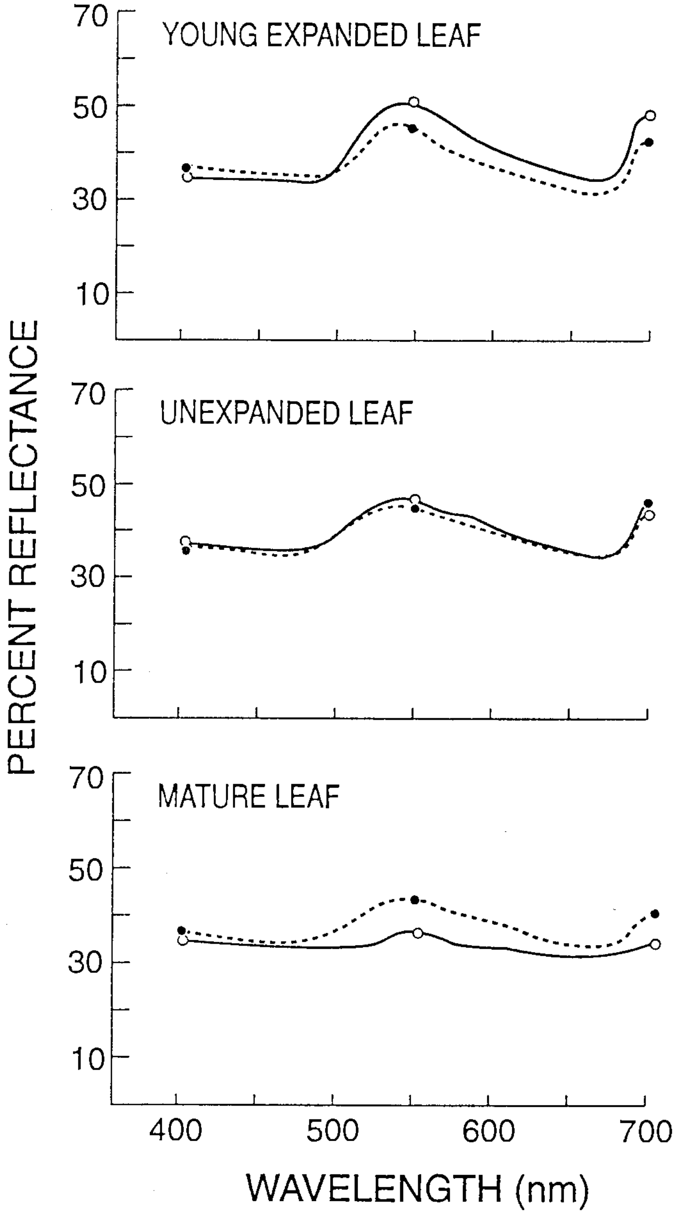
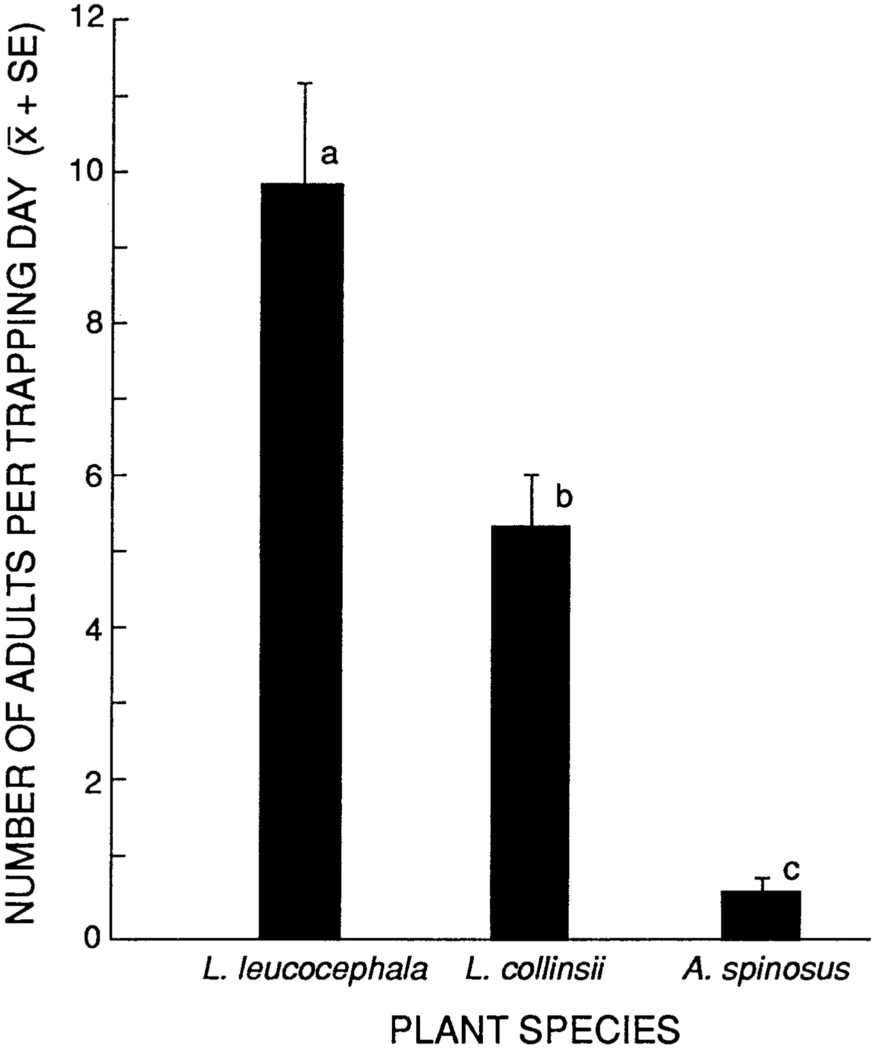

YOUNG EXPANDED LEAF
UNEXPANDED LEAF
MATURE LEAF
PERCENT REFLECTANCE
70
50
30
10
400
500
600
700
WAVELENGTH (nm)

Fig. 7. Comparative numbers of adult *H. cubana* caught on white sticky card traps in response to caged host and non-host plants. Means topped by the same letter are not significantly different, multisample hypothesis ANOVA, Tukey's test, $n = 15$, $P < 0.05$.


NUMBER OF ADULTS PER TRAPPING DAY ($\bar{x}$ + SE)
0
2
4
6
8
10
12
a
b
c
L. leucocephala
L. collinsii
A. spinosus
PLANT SPECIES

Responses of H. cubana to L. leucocephala and L. collinsii leaf extract

Significantly more females responded positively to the hexane extract of *L. leucocephala* leaves than to the solvent control (Table 5). There was no significant difference between the numbers of males responding to the two stimuli, although 68.8% of the responsive individuals contacted the filter paper impregnated with leaf extract.

Significantly more females were attracted to *L. leucocephala* extract than to hexane (Table 6). On the contrary, the females were not attracted to *L. collinsii* extract when tested against the solvent control. Likewise, when *L. leucocephala* was tested against *L. collinsii*, there was no significant difference between the numbers of females contacting the two extracts. However, when equal amounts of extracts of *L. leucocephala* and *L. collinsii* were mixed, significantly more females went to the mixture than to the solvent control.

When tested against a series of *L. collinsii* extracts at graded, low concentrations, H. *cubana* females responded positively to a stimulus of 1×10^{-4} g. equiv., but not to stimuli at higher or lower concentrations (Table 7).

Table 5. Responses of male and female *H. cubana* to extracts of *L. leucocephala* leaves in a two-choice olfactfometer. Experimental stimuli presented as 1 x 10^{-3} g. equiv. of plant material in 5 *u*L of solvent.

Sex	n	Number of responders	Percent response (responders only)		Chi-square value[a]
			Extract	Solvent	
Male	41	32	68.8	31.2	3.78ns
Female	33	24	76.9	23.1	6.50 *

[a] ns = not significant; * = significant, $P < 0.05$.

Table 6. Responses of female *H. cubana* to extracts of *L. leucocephala* and *L. collinsii* leaves in a two-choice olfactometer.

Experiments	n	Number of responders	Percent response (responders only)			Hexane	Chi-square value[a]
			Leucaena leucocephala	*Leucaena collinsii*	Both species		
L. leucocephala vs. hexane	33	28	75.0	-	-	25.0	6.04*
L. collinsii vs. hexane	30	26	-	50.0	-	50.0	0.04ns
L. leucocephala vs. *L. collinsii*	32	28	42.9	57.1	-	-	0.42ns
Both species vs. hexane	39	35	-	-	74.3	25.7	7.31*

[a] ns = not significant; * = significant, $P < 0.05$.

Table 7. Responses of female *H. cubana* to different concentrations of extracts of *L. collinsii* leaves in a two-choice olfactometer.

Stimulus strength (g. equiv.)	n	Number of responders	Percent response (responders only)		Chi-square value[a]
			Extract	Solvent	
1×10^{-3}	32	28	50.0	50.0	0.04ns
5×10^{-4}	34	31	54.8	45.2	0.13ns
1×10^{-4}	32	27	74.1	25.9	5.33 *
1×10^{-5}	33	26	65.4	34.6	1.88ns

[a] ns = not significant; * = significant, $P < 0.05$.

Discussion

My results suggest that wavelength-specific reflectance intensity (RI) can influence the magnitude of color attraction to *H. cubana* in the field (Fig. 4-6) but does not affect attraction between sexes. Wavelength-specific reflectance intensity is defined as the total reflected light of a specific or defined band of wavelengths (Vernon 1986). Hence, although traps of yellow hue are preferred by adult *H. cubana* compared with blue and white, maximum preference occurs at wavelength above a peak RI of 100% (i.e., super yellow at 510 nm with RI = 110%) (Fig. 4). In the onion fly, *Delia antiqua* Meigen, Ishikawa et al. (1985) found vivid yellow, with RI peak of 40%, to be 6 times more attractive than pale yellow, with RI peak of 20%. Vernon (1986) showed violet or blue with peak RI above 30% to be much more attractive than the same spectral wavelength below RI of 30% to *D. antiqua.* This could explain, in part, why alighting adult *H. cubana* congregate on the young leaves and shoots of leucaena, which have higher RI, than on old mature leaves which had a much lower wavelength reflectance intensity, and which also reflected maximally between 500 and 550 nm (Fig. 6). Prokopy and Owens (1983) also noted that some aphids are more attracted to more highly reflective young developing leaves, the yellow color of which was correlated with high nitrogen content of the sap, than to the mature green leaves of the same plant, which had a lower reflectance.

It is surprising that relatively few adults were caught on the traps when there were tens of thousands of adult psyllids on the host trees during the experiment. The low numbers of captured *H. cubana* may be due to the small number of adults in their dispersive behavior during the experiment. Moreover, those that were caught were flying within the host canopy, and probably did not easily distinguish between the cards and the foliage. It is also possible that the psyllids use yellow hue also to guide them back to crop level after flight. In aphids, Kennedy et al. (1961) suggested that the primary function of color is to distinguish plants from the sky. They found that the predominantly long-wave emission from both leaves and soils (= 540-560 mμ) contrasts sharply with shorter wavelength of the light from clear or clouded skies (<500 mμ). Coombe (1982) was able to show that the whitefly, *T. vaporarorium*, is more likely to take off when illuminated with shorter (400 nm) than when illuminated by longer (550 nm) wavelengths which Coombe (1981) found earlier to stimulate the whiteflies to land. The reflectance peak of young expanded leaves between 500 and 550 nm probably allows the psyllids to distinguish the yellow reflectance of those leaves from shorter wavelength colors which could have interferred with a landing response. This hypothesis would explain the low response to white and blue cards (Figs. 4,5). Similarly, Judd et al. (1988) found ultraviolet reflectance to interfere with response by *D. antiqua* to reflectance between 350 and 400 nm.

The low numbers of adults caught also mean that color is a weak stimulus for host selection and that other stimuli (e.g., host odor) play a greater role. Beck (1965) concluded that color by itself probably does not account for an insect's host specificity, although it frequently influences early stages of orientation. In addition, Thorsteinson (1960) found shape, size and color to be "too variable and lacking the identifiable uniqueness required to explain the obvious discriminatory power of insects".

When plants were caged outdoors in such a manner as to obstruct color perception, adult *H. cubana* preferentially oriented to the cage containing the more susceptible *L. leucocephala* than to the cages holding either the less susceptible *L. collinsii* or the non-host plant (Fig. 7). This result suggested that *H. cubana* had responded to host plant volatiles. This hypothesis was further supported by laboratory experiments using two-choice olfactometer, although females responded more strongly than males to volatiles from *L. leucocephala* leaf extracts (Table 6). Such differential response between sexes to plant volatiles has also been demonstrated in the parasitic braconid, *Microplitis croceipes* (Cresson), and ichneumonid, *Netelia heroica* Townes (Whitman and Eller 1987), and in the flea beetle, *Phyllotreta cruciferae*, to allyl isothiocyanate (Vincent and Stewart 1984).

The stronger response by *H. cubana* females to leaf extracts of *L. leucocephala* than to extracts of *L. collinsii* (Table 6) and the positive response to *L. collinsii* extract only at one low concentration (Table 7), suggest that *L. collinsii* has only a weak olfactory attraction. The possibility of a strong repellant is negated by the lack of a preference when *L. leucocephala* was tested against *L. collinsii*, and the strong response to the mixture of *L. leucocephala* and *L. collinsii* extracts (Table 6). If the active chemicals are the same in both species, it is possible that in nature *L. collinsii* produces so much of these chemicals that *H. cubana* do not normally respond positively. In the two-spotted strawberry mite, *Tetranychus urticae* Koch, the "standard essential oil mixture" (SEOM) containing low concentrations of the volatile methyl salicylate attracted females but repelled them at high concentrations (Rodriguez et al. 1976). Otherwise, it is also possible that at high concentrations of *L. collinsii* extract, some volatiles are present at sufficient concentrations to mask the activity of an attractant. Visser and Avè (1978) explained this phenomenon as a "disturbance of the attractive complex by artificially changing the relative proportions of the components". However, in interpreting these results one should be wary of the possibility that "Hopkins host selection principle" (Beck and Schoonhoven 1980) may be operational in *H. cubana*. All the insects used in the bioassays were reared on *L. leucocephala* which could influence the adult's predilection to prefer the plant species on which they were reared during their nymphal stages (Yamamoto et al. 1969; Eijackers and van Lenteren 1970).

Heteropsylla cubana is oligophagous and restricts its host range within the genus *Leucaena*, but with varying degrees of preference. Leaves of both *Leucaena* spp. reflected at the yellow spectrum although with slight differences in reflectance intensity. Since spectral quality of the foliage of the different *Leucaena* spp. and some non-host species is most likely to be similar, it is doubtful that *H. cubana* uses color primarily in host selection. Prokopy and Owens (1983) cautioned that plant spectral quality is unlikely to constitute a host-plant specific character for herbivorous insects because of its similarity among most plants, except for some exceptions, e.g., red and green cotton plants (Stephens 1957), red and green Brussel sprouts (Dunn and Kempton 1976) and red and green cabbage (Prokopy et al. 1983). However, the difference in the attractiveness of the extracts of the two *Leucaena* spp. to female *H. cubana* at the same concentration strongly indicates that such differences contribute substantially to the preference of *H. cubana* adults for *L. leucocephala*. It is likely, however, that *H. cubana* uses combined visual and chemical information to locate its more preferred host, *L. leucocephala*.

CHAPTER V

EVIDENCE FOR ANTIBIOSIS IN *LEUCAENA COLLINSII* TO *HETEROPSYLLA CUBANA*

Introduction

When an insect has successfully located and accepted a host, it must then contend with the host's suitability. The influence on food consumption and on post-ingestion of host suitability determines larval survival and growth which subsequently will also affect the fertility, fecundity and longevity of adults of the next generation. Host suitability was described by Painter (1951) as the "antibiotic" modality of resistance of plants against herbivores. A brief resume of the possible bases for antibiosis in plants was given by Panda (1979). These include a) the presence of toxins in resistant plants; b) the presence of growth inhibitors; c) the absence of some nutritional materials, such as vitamins, vitamin-like substances, sugars or essential amino acids in the particular part of the resistant plant eaten by the insect; d) the deficiency of certain nutritional elements in the host plant; e) nutritional imbalance; f) tissue proliferation or increased secretion known to cause death of eggs or young larvae; and g) presence of phytoecdysones.

The presence of toxic compounds in plants, such as in leaves of resistant plants (Dimock et al. 1986; Khan et al. 1987), toxic exudates from leaf hairs (Thurston and Webster 1962) and from silk of some lines of resistant corn (Walter 1957; Knapp et al. 1967), were reported to cause mortality in larvae of some insects. Other chemicals found in less susceptible plants inhibited larval growth and development and adult fecundity (Lukefahr et al. 1966; Klun et al. 1967; Tingey et al. 1975; Berenbaum and Feeny 1981; Mooney et al. 1981).

Inadequate supply or deficiency of certain nutritional elements affects the growth and reproductive capacity of insects feeding on resistanct plants. Low concentrations of amino acids (Knapp 1966), lack of thiamine, nicotinic acid, folic acid, or choline (Hagen 1958), low concentrations of N, P, K or Fe (Allen and Sellman 1957) and/or lack of Zn (Raccah et al. 1971) have been shown to reduce larval growth rate and larval weight, and induce wing formation in several insect species. Nutritional imbalance in host plants can also cause metabolic derrangements, and can affect larval development (Beck 1956; House 1965).

Hairs on leaves of some plants constitute a defence against herbivores. Eggs of the cereal leaf beetle, *Oulema melanopus* (L.), laid on the leaf surface of pubescent hosts were more susceptible to dessication and newly-hatched larvae sufferred higher mortality than when laid on glabrous hosts (Schillinger and Gallun 1968; Schillinger 1969). Glandular trichomes on the surfaces of some plants entrap and immobilize some insects with their exudates (Gentile and Stoner 1968; Gentile et al. 1968; Gibson 1971; Tingey and Gibson 1978; Tingey and Laubengayer 1981; Lapointe and Tingey 1986). Toxic glandular secretions can also cause insect mortality (Thurston et al. 1966; Shade et al. 1975; Williams et al. 1980; Kennedy et al. 1981; Dimmock and Kennedy 1983).

Phytoecdysones, e.g. α- and β-ecdysone, that cause premature maturation to non-functional adults are widely distributed among the plant kingdom (Panda 1979). Although less frequent in occurrence, juvenoids that cause supernumerary molts or disrupt reproductive development and embryogenesis also impart unsuitability to certain hosts (Bowers et al. 1966). Similarly, chemicals that have anti-juvenile hormone activity can determine host plant suitability (Bowers et al. 1976).

One often overlooked cause of mortality for folivorous insects is early leaf abscission. Faeth et al.(1981) have demonstrated that early leaf abscission by *Quercus* spp. can substantially reduce survival of leaf miners. Also, mined leaves of holly, *Ilex aquifolium* L., falling in June-February were found to contain live larvae of *Phytomyza ilicis* Spencer, which die as the fallen leaves dry out and begin to decompose (Owen 1978). Center (1987) hypothesized that eggs of *Neochetina eichhorniae* Warner deposited in the very oldest leaves of waterhyacinth are lost as the senescent leaf tissue breaks loose from the shoot or becomes water-logged.

The lower numbers of eggs laid on *L. collinsii* than in *L. leucocephala* (Chapter III) could not account for the much lower nymphal and emerging adult populations observed on the former species. Other resistance mechanisms must be operating on *L. collinsii* against the eggs and/or nymphs of the psyllid. Leaves serve as a medium on which eggs are deposited and may, therefore, affect egg development. There might be physical barriers on the leaves that influence nymphal settling and feeding. Leaf phenology might also affect success of nymphal establishment. Hence by comparing the developmental biology of *H. cubana* on *L. leucocephala* and *L. collinsii*, my objective was to investigate the hypothesis that one or more mechanisms of antibiosis impart resistance to the latter species against *H. cubana*.

Materials and Methods

Hatchability of Eggs

Ten potted plants of each of *L. leucocephala* and *L. collinsii* were exposed to oviposition by female psyllids inside Saran-screen cages in the quarantine room at Simon Fraser University. Three days after infestation, samples of leaflets with eggs on them were detached from the plant and allowed to float on demineralized water in 2.5-cm diameter polyethylene disposable cups. This technique prevented rapid drying of the leaflets and possible dessication of the eggs. Eggs that were prone to fungal infection because they were on the margins of the leaflet and would have been in constant contact with the water were plucked out. Excised eggs were also examined for the presence of "pedicel" under a dissecting microscope.

The number of nymphs that hatched on both *Leucaena* spp. were recorded daily, until the fifth day, after which no more nymphs hatched. The data were tested for equality of treatment variance before comparing their means by a *t*-test using the two-sample hypothesis (Zar 1984).

Survival of Nymphs

Twenty-five potted plants each of *L. leucocephala* and *L. collinsii* were allowed to be infested by *H. cubana* in the field in Los Baños, Philippines. The date of infestation was recorded for each plant. Two days after infestation, the plants were cleaned of adult psyllids and brought inside the laboratory where reinfestation by adult *H. cubana* was prevented. Nymphs were allowed to develop, under room temperature of about 27-29°C and lights supplied by fluorescent and incandescent lamps about 45 cm above the plants' canopy, and a 13:11 L:D cycle, until the 5th and last immature instar. Since the eggs hatch in 3-4 days and the five stadia last for 2, 2, 2.5, 3 and 3.5 days, respectively (R. Lucero[1], pers. comm.), the shoots and

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young leaves of sample plants were detached within the time corresponding to these durations. The shoots and leaves were then examined under a dissecting microscope and the numbers of living and dead nymphs in each instar were recorded. Since most dead nymphs remain attached to the leaves and raches, these counts were used to evaluate nymphal mortality. Nymphs in each instar could be distinguished by their relative body size and wing pad length.

The above methods were used because attempts to introduce newly hatched nymphs manually onto young leaves of potted plants were unsuccessful. There was very high mortality due to handling, and many nymphs failed to settle and establish on the leaves on which they were innoculated. Destructive sampling of shoots was also necessary, because counting nymphs under a microscope is difficult without damaging the leaves or young shoots. Using the excised-leaf technique also failed. Because leaves had to be replaced daily as they dried rapidly, the nymphs had to be transferred and handled frequently which resulted in very high mortality.

The data were transformed using arcsine and tested for equality of treatment variance before the differences for each instar between *Leucaena* spp. were subjected to a t-test using the two-sample hypothesis (Zar 1984).

Nymphal Settling

Nymphs were introduced onto the abaxial (lower) surface of newly-detached leaves of *L. leucocephala* and *L. collinsii*. The time from innoculation until the nymph has settled was recorded. The nymph was considered to have settled and to have begun feeding if there was no further movement within 1 min after the nymph ceased walking. For each *Leucaena* species there were 32 replicates for each of instars 1-3.

To determine if pubescence affected nymphal settling, a similar experiment was done to compare the time taken by 2nd instar nymphs to settle on *L. collinsii* leaves having varying degrees of pubescence. There were 20 replicates for each class of leaves.

Histological studies of the feeding sites between the two *Leucaena* species were also made. Young leaves on which psyllid nymphs were feeding were collected from the laboratory cultures and fixed for 24 h in formalin-acetic acid-alcohol (F.A.A.). They were dehydrated in alcohol series, embedded in paraffin and sectioned to a thickness of 10µ (Johansen 1940). All sections were stained with safranin-O and fast-green. Feeding tracks in leaves of both species of *Leucaena* were measured. The thickness from the adaxial (upper) and from the abaxial epidermis to the vascular bundles of the leaflet and the rachis were also measured. These measurements were taken at the middle vein of the leaflet. Thickness of the leaflet was measured at the nearest possible point to the middle vein and at approximately 100µ from the distal part of the leaflet .

The data on nymphal settling by the 3 nymphal instars and length of feeding tracks on the two *Leucaena* spp. were tested for equality of treatment variances before comparing their means by *t*-tests using the two-sample hypothesis (Zar 1984), while data on settling time of 2nd instar nymphs on the different classes of leaves of *L. collinsii* were compared using the multisample hypothesis single factor analysis of variance (Zar 1984).

Leaflet Abscission

Twenty-five potted plants each of *L. leucocephala* and *L. collinsii* were exposed to *H. cubana* infestation in the field in Los Baños, Philippines. Two days later, uninfested and infested plants of both species that were cleaned of adults were brought inside the laboratory. After 10 days, the numbers of abscised and intact leaflets of the young primary leaf, from 18 infested and 18 uninfested plants of each *Leucaena* spp., were recorded. The data were converted to percent leaflet fall, and transformed to their arcsine values before comparing their means by a *t*-test using the two-sample hypothesis (Zar 1984).

In another experiment, 15 9-month old seedlings of each *Leucana* sp. were grown inside the greenhouse at Simon Fraser University. They were arranged randomly on a bench. Fertilization and watering were the same for all plants. Temperature was maintained at 25-27°C. For each plant, the date when the shoot opened was recorded. The shoots were inspected daily and the date when the first leaflet(s) become yellow and fell was recorded. The data for yellowing and abscission were tested separately for equality of variance before comparing the means between the two *Leucaena* spp. by a *t*-test using the two-sample hyposthesis (Zar 1984).

Adult Production

Nine 7-month old potted seedlings of each *Leucaena* sp. were allowed to be infested in the laboratory for 4 days, after which the adults were mechanically killed. The newly-hatched nymphs were allowed to develop until maturity. The adults were collected and counted every day from individual plants until no newly eclosed adults were found for 4 days.

Immediatley after the adults were collected, their length was measured from the anterior part of the head to the tip of the genitalia for both sexes, while their width was measured at the widest part of the thorax.

The data on numbers of adults produced and on adult size were tested for equality of treatment variance before comparing the means between the two *Leucaena* spp. by *t*-tests using the two-sample hypothesis (Zar 1984).

Results

Hatchability of Eggs

The hatching success was very high for eggs laid on both species of *Leucaena* (Table 8). Even on the resistant species, there was only about 10% mortality. Nevertheless, there was a significantly lower rate of hatch (4%) on *L. collinsii* than on *L. leucocephala.*

The egg of *H. cubana* (Fig. 8) was elliptical, with a distinct pedicel that is inserted into the tissue of the leaflet and/or rachis of the host plant.

Survival of Nymphs

Significantly more nymphs developed successsfuly on *L. leucocephala* than on *L. collinsii* (Fig. 9). Survivorship to the 5th instar was about 4-fold less on *L. collinsii* than on *L. leucocephala.* Mortality rates for the first 2 instars were 57.7% and 20.3%, respectively, on *L. collinsii*, and 24.1% and 8.1%, respectively, on *L. leucocephala*, both significantly different between host species (*t*-test, $P < 0.001$). There was no significant difference for the 3rd instar between plant species (*t*-test, $P > 0.10$). On both species, there was no mortality of the last two instars. Mortality of nymphs due to being trapped in their honeydew was relatively uncommon.

Nymphal Settling

There were no significant differences (*t*-test, $P > 0.05$) in the time of settling for the 1st, 2nd, or 3rd instar nymphs feeding on detached leaves of *L. leucocephala* and *L. collinsii* (Fig. 10). On both species, younger instars took longer to settle than the older instars. Taking the average time for each instar on both *Leucaena* spp. the 1st, 2nd and 3rd instars settled on their hosts in about 94, 76 and 50 sec, respectively, after they were placed on their hosts.

Table 8. Hatchability of eggs of *H. cubana* on excised leaflets of *L. leucocephala* and *L. collinsii.*

Species	No. rep	No. eggs per replicate ($\bar{x}$ ± SE)	Percent eggs hatched ($\bar{x}$ ± SE)[a]
L. leucocephala	18	108.2 ± 50.2	93.7 ± 0.8a
L. collinsii	18	75.2 ± 31.5	89.7 ± 0.8b

[a] Means significantly different, *t*-test, $P < 0.05$.

Fig. 8. Drawing of an egg of *H. cubana* showing the "pedicel" or "stalk" (arrow). Longitudinal and transverse axes of typical eggs measure approximately 0.27 and 0.12 mm, respectively.

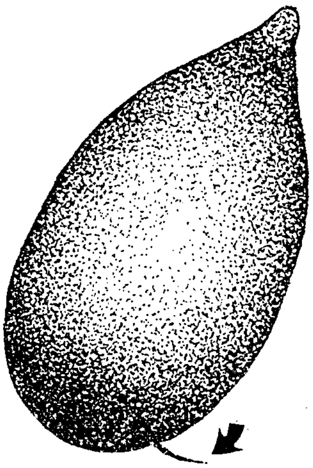


Fig. 9. Cumulative percent survival of *H. cubana* nymphs feeding on *L. leucocephala* (bold line) and *L. collinsii* (broken line) seedlings in the laboratory. Nymphal survival between *Leucaena* spp. significantly different for 1st and 2nd instars, *t*-test, $P < 0.001$.

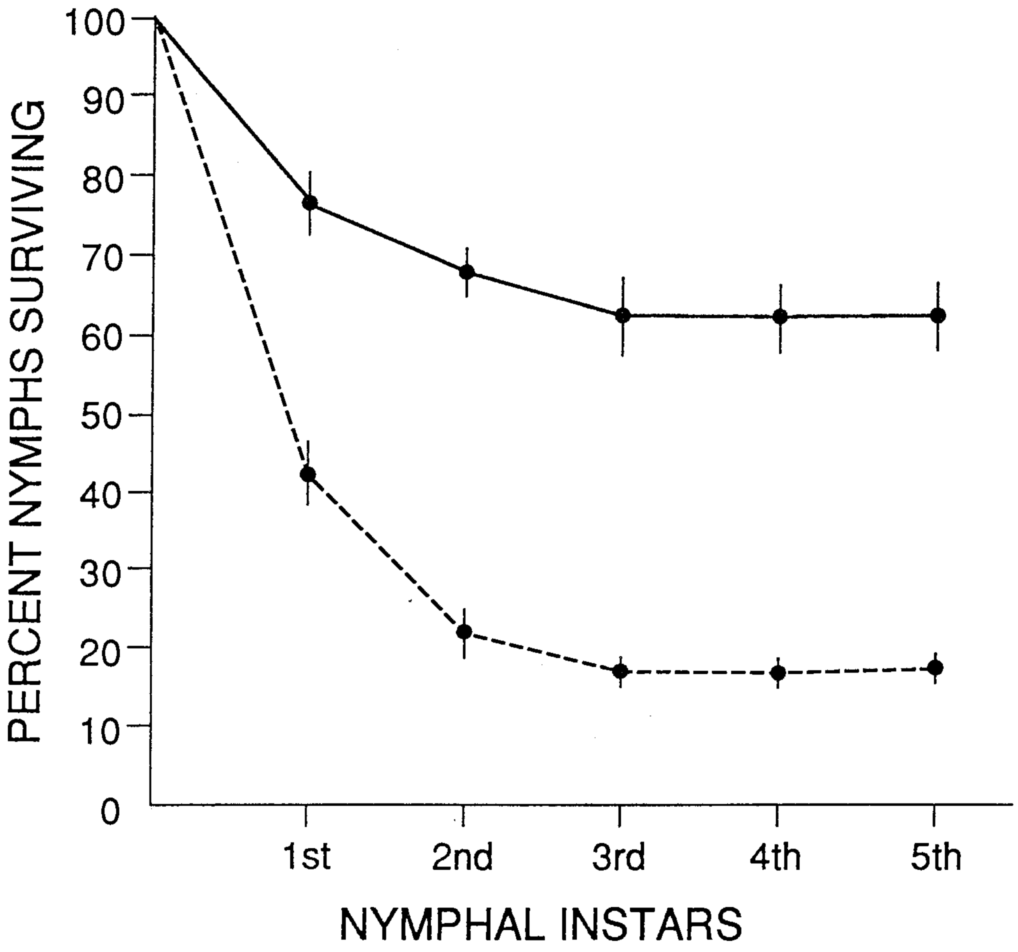
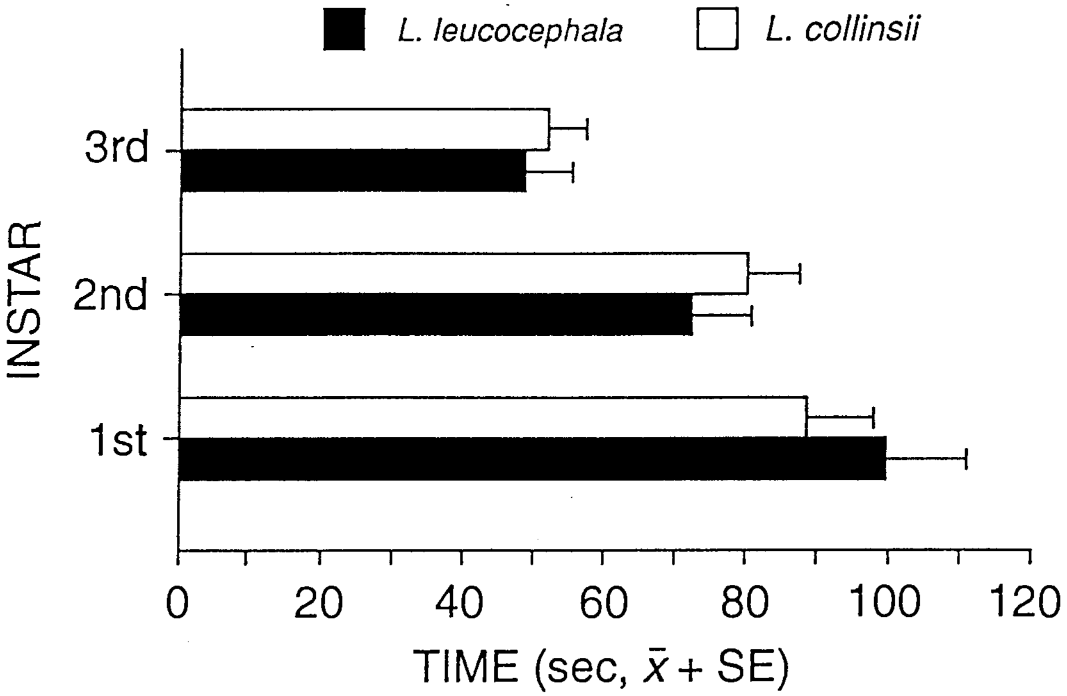

PERCENT NYMPHS SURVIVING
100
90
80
70
60
50
40
30
20
10
0
1st
2nd
3rd
4th
5th
NYMPHAL INSTARS

Fig. 10. Settling time of *H. cubana* nymphs on excised *L. leucocephala* and *L. collinsii* leaflets. Means for each instars between species not significantly different, *t*-test, $n = 32$, $P > 0.05$.


L. leucocephala
L. collinsii
INSTAR
3rd
2nd
1st
0
20
40
60
80
100
120
TIME (sec, $\bar{x}$ + SE)

There were 3 kinds of leaves found in *L. collinsii* according to location and density of hairs. Some plants had leaves with numerous hairs, some plants had leaves with no hairs on the upper surface, and some had leaves with hairs only on their margins/edges (Table 9). However, there was no significant difference in the settling time among 2nd instar nymphs that were introduced on leaves in the different pubescence classes. The nymphs readily settled on leaves in all 3 classes.

The feeding "tracks" or stylet sheaths produced by the nymphs could be easily seen since they were stained bright red by safranin (Fig. 11). The feeding tracks were either branched or unbranched and were usually pushed between cells of the mesophyll and into the region of the vascular bundles. Some, however, terminated in non-vascular cells. The lengths of the feeding tracks of nymphs feeding on *L. leucocephala* and *L. collinsii* differed significantly (Table 10), but appeared to be influenced by the morphology of the leaflet. The distances from the epidermis to the vascular bundles and leaflet thickness between *Leucaena* spp. were significantly different between species (Table 10). The leaflets of *L. leucocephala* were about one-third thicker, and in most cases their vascular bundles were twice as distant from the epidermis, than those of *L. collinsii*. Nevertheless, in both species the nymphs were easily capable of reaching their feeding site within the leaf tissue.

Leaflet Abscission

An average of 16% of leaflets of *L. collinsii* abscised after 10 days of psyllid feeding, while none of the leaflets of *L. leucocephala* abscised within the same time span (Table 11). When the leaves were left undisturbed, yellowing and abscission in *L. collinsii* started significantly earlier than in *L. leucocephala*. On *L. collinsii*, infested leaves that were still attached to the plant became yellow and senesced, while uninfested leaves of *L. collinsii* as well as infested leaves of *L. leucocephala* showed no signs of advanced senescense and abscission (Fig. 12).

Table 9. Density of pubescence and 2nd instar nymphal settling time on three classes of leaves of *L. collinsii*.

			No. hairs per leaflet ($\bar{x}$ ± SE)			
Class	n	Adaxial surface	Abaxial surface	Margin	No. nymphs tested	Settling time (sec) ($\bar{x}$ ± SE)[a]
1	34	27.8 ± 1.9	56.9 ± 3.6	97.1 ± 3.2	20	49.20 ± 4.3
2	31	0.0	9.5 ± 0.5	40.5 ± 0.4	20	53.75 ± 5.2
3	31	0.0	0.0	37.1 ± 1.0	20	57.45 ± 6.6

[a] No significant differences in settling time, ANOVA, $P > 0.05$.

Fig. 11. Sections of the leaflet (A, 800x) and rachis (B, 400x) of *L. leucocephala* showing the feeding tracks (indicated by arrows) produced by the nymphs of *H. cubana*.

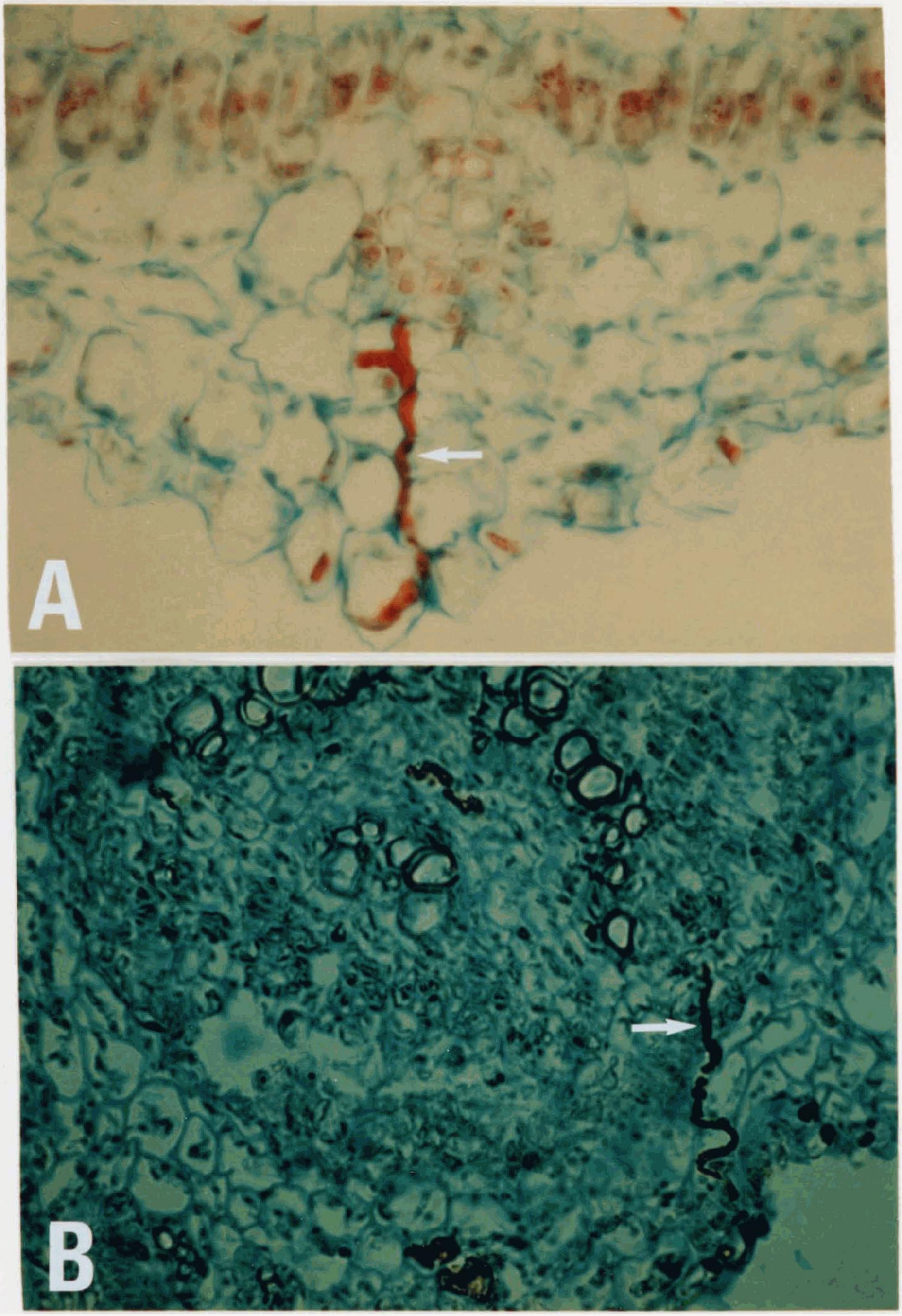

A
B

Table 10. Length of feeding track of *H. cubana*, and morphological characteristics of leaves of *L. leucocephala* and *L. collinsii*.

Species	n	Length of feeding track (u) ($\bar{x}$ ± SE)[a]	n	Thickness from epidermis to vascular bundles (u)[a]				Leaf thickness (u)[a]	
				leaf		rachis			
				abaxial surface ($\bar{x}$ ± SE)	adaxial surface ($\bar{x}$ ± SE)	abaxial surface ($\bar{x}$ ± SE)	adaxial surface ($\bar{x}$ ± SE)	middle ($\bar{x}$ ± SE)	margin ($\bar{x}$ ± SE)
L. leucocephala	25	42.9 ± 5.3a	15	67.1 ± 4.9a	39.7 ± 2.6a	182.9 ± 11.1a	98.7 ± 8.2a	88.3 ± 3.4a	56.5 ± 3.4a
L. collinsii	27	36.7 ± 3.7b	15	39.3 ± 1.9b	22.7 ± 1.5b	155.7 ± 4.1b	59.2 ± 2.6b	56.5 ± 1.5b	45.7 ± 1.5b

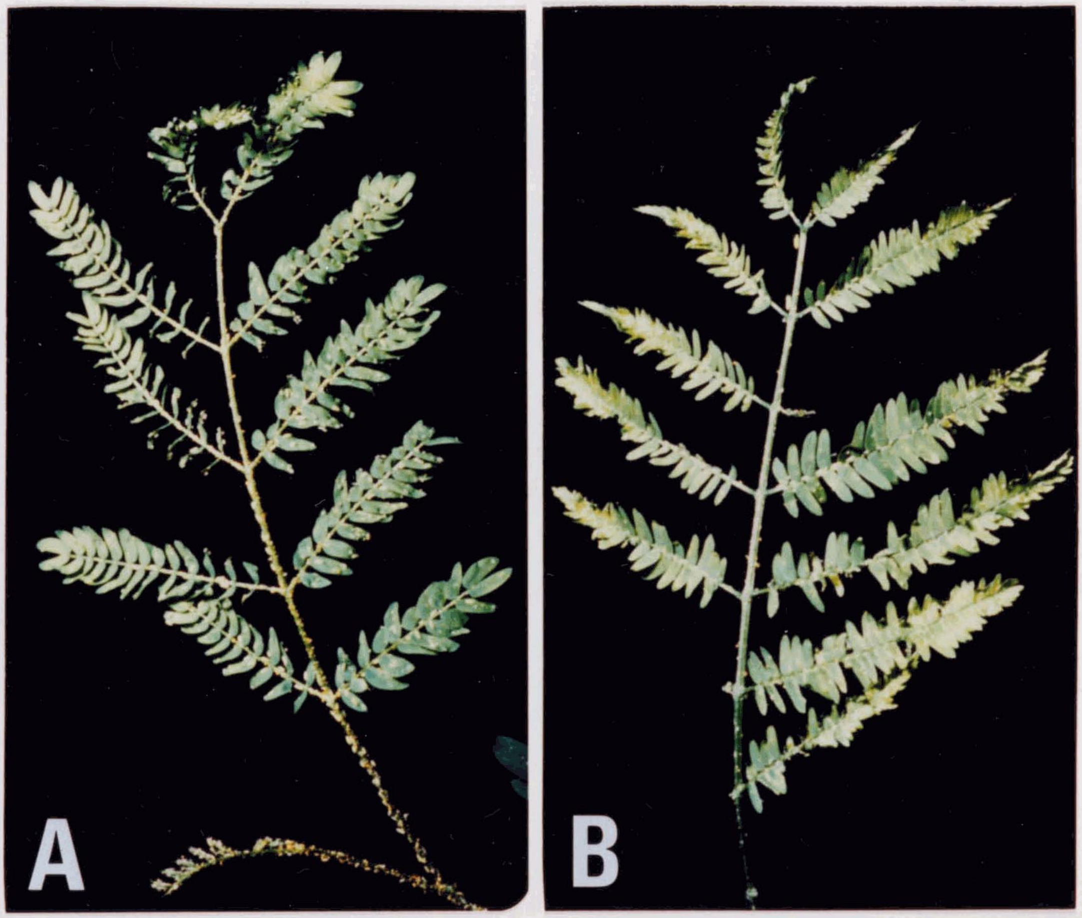
[a] Means within a column are significantly different, *t*-test, $P < 0.05$.

Table 11. Leaflet abscission and yellowing on *L. leucocephala* and *L. collinsii*.

Species	n	Percent leaflet abscission after 10 days infested ($\bar{x}$ ± SE)	 uninfested	n	No. days from leaf opening to natural yellowing ($\bar{x}$ ± SE)[a]	No. days from leaf opening to natural abscission ($\bar{x}$ ± SE)[a]
L. leucocephala	18	0.00	0.00	15	61.6 ± 2.8a	68.60 ± 3.3a
L. collinsii	18	16.08 ± 3.38	0.00	15	25.4 ± 3.8b	34.27 ± 3.9b

[a] Means within a column followed by the same letter are not significantly different, *t*-test, $P > 0.05$.

Fig. 12. Response of young expanded leaves of the two *Leucaena* spp. 10 days after commencement of feeding by *H. cubana* nymphs: A) *L. leucocephala* showing no apparent advanced senescence (0.50x); B) *L. collinsii* with secondary and tertiary leaves already abscised (0.75x).


A
B

Adult Production

Significantly more adults emerged from nymphs that fed on *L. leucocephala* than from those that fed on *L. collinsii* (*t*-test, $P < 0.001$) (Fig. 13). Approximately 11 times more adults were produced on *L. leucocephala* than on *L. collinsii*. Adult *H. cubana* that developed on *L. collinsii* were generally significantly smaller than those on *L. leucocephala* (Table 12). However, there was no significant difference in the body width of females.

Fig. 13. Comparative numbers of adult *H. cubana* eclosing on *L. leucocephala* and *L. collinsii* seedlings. Means significantly different, *t*-test, $P < 0.05$.

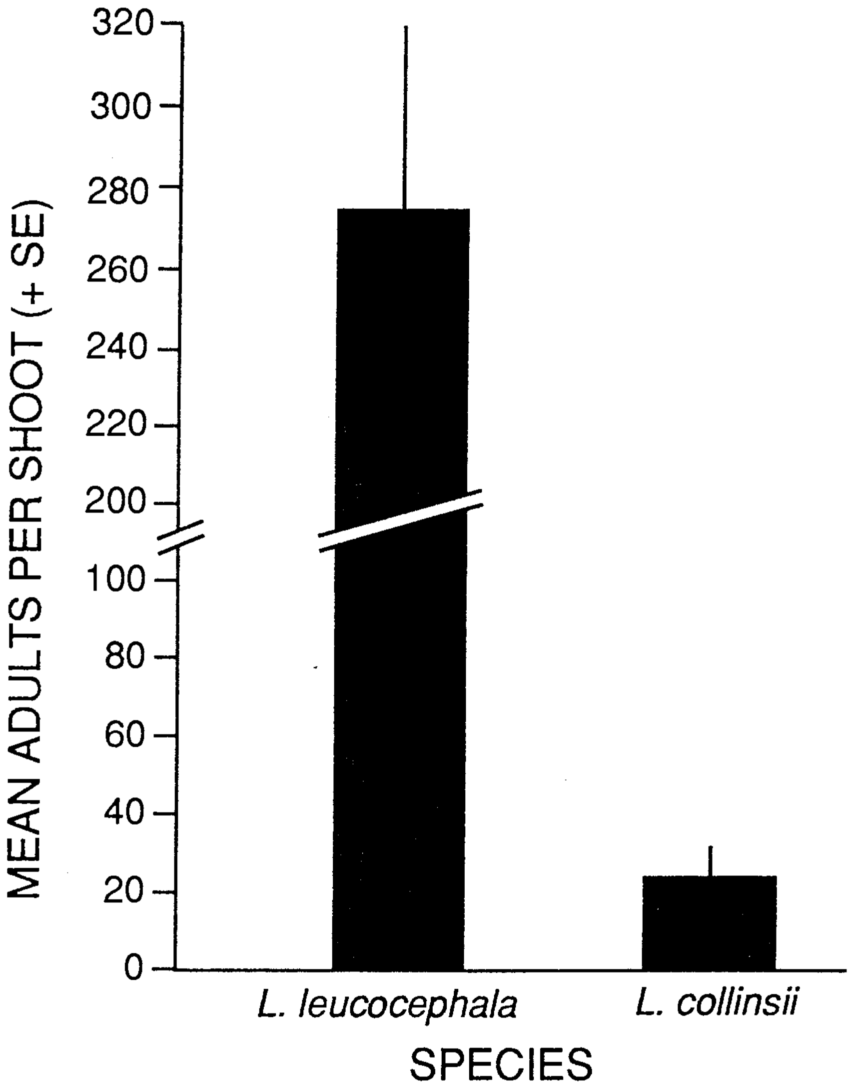

MEAN ADULTS PER SHOOT (+ SE)
320
300
280
260
240
220
200
100
80
60
40
20
0
L. leucocephala
L. collinsii
SPECIES

Table 12. Dimensions (mm) of adult *H. cubana* that developed on *L. leucocephala* and *L. collinsii*.

Host	n	Males[a] length ($\bar{x}$ ± SE)	width ($\bar{x}$ ± SE)	n	Females[a] length ($\bar{x}$ ± SE)	width ($\bar{x}$ ± SE)
L. leucocephala	32	1.49 ± 0.01a	0.48 ± 0.01a	32	1.73 ± 0.01a	0.52 ± 0.01a
L. collinsii	20	1.42 ± 0.01b	0.46 ± 0.01b	18	1.65 ± 0.03b	0.51 ± 0.01a

[a] Means within a column followed by the same letter are not significantly different, *t*-test, $P > 0.05$.

Discussion

The pedicels of the eggs of *H. cubana* (Fig. 8) are very similar to those of *Cardiaspina densitexta* Taylor. White (1968) found that *C. densitexta* eggs removed from a leaf could develop normally, provided that the pedicels were kept immersed in water. He also experimentally showed that the psyllid's eggs actively take up water through the pedicel. Most probably, the pedicels of *H. cubana* also function to take up water from the leaf tissues. Although significantly more eggs hatched on *L. leucocephala* than on *L. collinsii* (Table 8), the over-all percent hatchability of the eggs in the resistant leucaena was too high to conclude that any allellochemics from the resistant host were taken up by the psyllid's eggs that affected their development. It is most probable that *H. cubana* eggs extract only water from the leaf tissue for their normal development and do not take up other chemicals. If they do and if there are toxic allelochemics in *L. collinsii*, a much higher egg mortality than in Table 8 should be expected. Because of the small size and relatively large surface area of the leaflets of *L. collinsii*, water might have been lost faster than from leaflets of *L. leucocephala* during the experiment, even when the excised leaflets were provided with water. This difference in water loss could have caused the slight decrease in hatching rate observed in eggs laid on *L. collinsii* leaflets. It is doubtful that this phenomenon occurs in nature, except perhaps during critically low soil moisture conditions. In the field, the eggs of *H. cubana* appear to be well adapted to develop on different *Leucaena* species, and profound resistance of *L. collinsii*, as observed in Figs. 1-3, could not be expressed through an antibiotic effect on egg development.

In contrast, antibiosis in *L. collinsii* appeared to have a striking effect on the development of *H. cubana* nymphs, especially on the first two instars (Fig. 9). My experiments did not determine if the high mortality of the 1st and 2nd instar nymphs was due to any toxic allellochemic. However, phloem contains neither the variety nor the concentration of potentially noxious phytochemicals found in leaf tissue (Raven 1983). Since *H. cubana* is a phloem feeder, it is doubtful that toxic allelochemics were the primary factor in the early nymphal mortality. Moreover, the young nymphs accepted the resistant species as readily as they accepted the susceptible species (Fig. 10), at least on excised leaves, suggesting that there was no antixenotic or antibiotic effect of *L. collinsii* on nymphal feeding. There remains a possibility, however, that excised leaves are not physiologically similar to attached leaves (Yardwood 1946; Barrs and Weatherly 1962), which might affect the nymph's ability to settle and feed compared to what happens in nature. In addition, on both host species stylet penetration was successful. There were no apparent morphological or physical barriers present in *L. collinsii* leaves that could hinder settling and feeding of the nymphs. In fact, the leaves of *L. leucocephala* were thicker and the distance from the epidermis to the vascular bundles in both its leaves and raches was comparativley much longer than in *L. collinsii* (Table 10). Neither did the pubescence on leaves of some individuals of *L. collinsii* affect nymphal settling or feeding (Table 9). There was also no indication of a trichome-based deterrent as found in wild potato, *Lycopersicum pennelii* Corr. (D'Arcy), against the potato aphid, *Macrosiphum euphorbiae* Thomas (Goffreda et al. 1989), or of any exudate, e.g. from glands on the leaflets, that could trap the nymphs. The nymphs were quite mobile on the pubescent leaves, as the smaller instars walked between the hairs while the larger instars walked over them. The long settling time exhibited by some nymphs on either *Leucaena* spp., sometimes as long as 4 min, may be because of difficulties encountered in locating their preferred feeding site, as evidenced by some branched feeding tracks (Fig. 11). In the pear psylla, *Psylla pyricola* Foerster, Ullman and McLean (1988) found that when the nymphs and adults ingested from the xylem, phloem or bundle sheath cells the probe was always uninterrupted. But when ingestion was made from the mesophyll and dermal cells, ingestion was frequently terminated and new probes were initiated. This means that the conducting cells were the preferred feeding site of the psyllid.

One possible explanation for the high mortality of early instar *H. cubana* on *L. collinsii* (Fig. 9) is that, at high populations of newly hatched nymphs, competition for space and feeding sites, becomes a limiting factor, since the total flat surface area per leaflet of *L. collinsii* was much smaller than that of *L. leucocephala.* In *C. densitexta*, first instar psyllid nymphs tend to disperse from overcrowded leaves (White 1970). Since young nymphs of *H. cubana* feed only on very young leaves and shoots, access to favorable feeding sites during the early instars is very critical. It is logical that settling times should be much longer when the nymphs are more crowded because of competition for feeding sites, than when nymphs are allowed to feed individually on a detached leaf (Fig. 10). It is, therefore, possible that young nymphs that were denied access to a suitable feeding site succumbed to water loss (Clark 1963), as suggested by their shrunken appearance. Phloem is also a source of abundant water which is very important to phytophagous insects (Scriber and Slansky 1981).

One interesting response of *L. collinsii* to psyllid infestation, which also supports the above discussion, was the premature abscission of infested secondary leaves and leaflets. The phenomenon of premature leaf-fall caused by leafminer attack has been documented in apples, *Malus sylvestris* Miller (Pottinger and LeRoux 1971), holly, *I. aquifolium* (Owen 1978) and in alfalfa, *Medicago sativa* L. (Hendrickson and Dysart 1983). Although some endophagous species might survive abscission and possibly benefit from it (Kahn and Cornell 1983), *H. cubana* nymphs are external feeders and any nymphs present in falling leaves will undoubtedly die from dessication, starvation or predation on the ground.

On *L. collinsii*, feeding by *H. cubana* apparently induced premature chlorosis and senescence on intact leaves. *Cardiaspina densitexta* has been shown to produce chemicals that induce early senescence around psyllid feeding sites (White 1970), possibly inducing breakdown of tissues that results in the liberation at the feeding site of greater amounts of soluble nitrogen (Kennedy and Stroyan 1959; Fennah 1963; Woodburn and Lewis 1973). Some lepidopterans in the families Gracillariidae (Miller 1973) and Tischeriidae (Osborne 1973) and some scale (cochineal) insects (Moran 1981) induce "green islands" around feeding sites, presumably in response to enzymes secreted during feeding. These areas remain green and nutritionally suitable even after leaf senescence and abscission. Following the procedures of White (1970) I was unable to show the presence of any toxic chemicals produced by the feeding nymphs of *H. cubana*. Cold-water extracts of the 5th instar nymphs of *C. densitexta* caused dead patches and discoloration on disks of mature *Eucalyptus fasciculosa* (F. Muell.) leaves, similar to the feeding damage of the psyllid in the field (White 1970). Histological studies also did not reveal visible cell damage within the vicinity of the feeding locus (Fig. 11). This difference might be due to the fact that unlike *C. densitexta*, *H. cubana* is not a lerp-forming psyllid that settles in one spot and remains there until adult emergence (White 1969). White (1970) suggested that the quality of food available to the nymphs of *C. densitexta* determines their chance to survive and grow. Nymphal mortality soon after settling was attributed to insufficient nitrogen in the leaves, because only in times of persistent water stress is the amount of soluble nitrogen in the leaves very high (Fennah 1965). On the contrary, *H. cubana* apparently relies on nymphal mobility in locating suitable feeding sites. Hence, the young nymphs concentrate on the developing shoots, young leaves and young stem of their host where there is a higher total concentration of free amino acids than in mature foliage, with some notable differences in particular amino acids (Journet and Cochrane 1978). For this reason, actively growing plant tissues are the preferred and optimal feeding sites of many species of phloem-feeding aphids (Kennedy et al. 1950; Mittler 1953). Early feeding by caterpillars of the winter moth, *Operohptera brumata* L., coincides with maximum leaf protein content and minimum leaf sugar content, suggesting that availability of nitrogen, rather than carbohydrate, may be a limiting factor for spring-feeding larvae (Feeny 1970). During senescence and the early stages of abscission of foliage, nitrogen, phosphorous and potassium are lost from leaves (Oland 1963). *Heteropsylla cubana* is a phloem feeder and it is probable that it also responds to levels of amino acid in the sap. The smaller size of the adult psyllids that developed on *L. collinsii* might be a response to the low level of nutrients in the senescing leaves. While suboptimal amino acid nutrition would reduce the growth rate of phloem feeding insects (Mittler 1958), high 1st and 2nd instar mortality would not be expected. It could then be hypothesized that most *H. cubana* nymphs in their early instars did not survive because they failed to settle and feed on the phloem tissue due to intraspecific competition and consequently starved, as mentioned above. This could be supported by the fact that even in *L. leucocephala* a significantly high 1st and 2nd instar mortality occurred. The relatively lower mortality on *L. leucocephala* compared with *L. collinsii* could be attributed to the differential response of the two *Leucaena* spp. to *H. cubana* infestation. Even though high nymphal intraspecific competition was present, *L. leucocephala* was able to support a higher nymph population because their leaves did not senesce and abscind as early as in *L. collinsii*. Premature senescence and abscission would have denied access to food for young nymphs at a time that is of critical importance for their early survival and establishment.

Also, it would not be of adaptive advantage for *H. cubana* to secrete a chemical that triggers senescence or abscission of leaves and in fact at moderate nymphal populations, such effects do not occur on the susceptible host, *L. leucocephala* (Table 11). Hence, leaf senescence and abscission on *L. collinsii* may be due to feeding damage *per se* (Addicott and Lynch 1955) or to the rapid up-take of water from the leaves (Hough and Pimentel 1978). The induction of abscission by the psyllid is clearly suggested in Table 11. Although *L. collinsii* naturally abscind their leaves earlier in comparison with *L. leucocephala*, induced abscission in infested *L. collinsii* was obvious after 10 days of infestation which was earlier by as much as one-half the time taken for natural abscission. Damage by the psyllids on *L. collinsii* starts when adults feed on the unopened leaves before and during oviposition, and by take-up of water by the eggs (White 1968). The area around the oviposition site usually discolors and becomes chlorotic and sometimes gall-like after a few days, on both *Leucaena* species.

The differential response of the two *Leucaena* species to psyllid feeding may simply be a function of leaf size. Leaflets of *L. collinsii* are about one-half the size of that of *L. leucocephala*. Faeth et al. (1981) postulated that if there were some damage threshold for abscissing leaves, large leaves should be less likely to abscind than small leaves with the same absolute area damaged by herbivores. In support of this hypothesis, I observed that when the population of feeding *H. cubana* nymphs was very high, newly opened leaves of *L. leucocephala* also abscind.

It is clear from my experiments that there are some antibiotic mechanisms in *L. collinsii* working against *H. cubana*. These could include (1) water stress, rather than allellochemics, in *L. collinsii* leaves causing slight mortality of eggs, (2) smaller flat leaf area in *L. collinsii*, resulting in competition for food and space during the 1st and 2nd instars when nymphal density is very high, but which is more pronounced in *L. collinsii* than in *L. leucocephala*, and (3) premature senescence and abscission of the leaves of infested *L. collinsii* resulting in the deterioration of the nutritional quality of the leaves and reduction in the availability of both space and food resources for the feeding nymphs, subsequently affecting the insect's development.

More experiments are needed to elucidate further the modality of these apparent resistance mechanisms of *L. collinsii* against *H. cubana* and to determine the presence of secondary plant chemicals in *L. collinsii* that might affect the growth, survival and development of *H. cubana* nymphs and the fitness of the subsequent developing adults.

CHAPTER VI

GENERAL DISCUSSION AND CONCLUSIONS

The fast-growing, high-yielding varieties of ipil-ipil, *L. leucocephala*, have drawn the interest of many people in the Philippines since the 1960's. There were two types of ipil-ipil introduced: the Hawaiian giant ipil-ipil which is more of a tree type cultivar, and the Peruvian ipil-ipil which is more of a bushy type because it produces more branches on the lower bole. Initially the giant cultivars were grown for wood and leaves as a source of fuelwood and pulp, and fodder for cattle and feed meal for poultry. Later, they were used for innumerable purposes, ranging from erosion control to fuel for dendrothermal electric generators. Besides loans granted by the government to farmers, the tremendous market available for ipil-ipil products served as incentives for many farmers to get invloved in ipil-ipil production, with the hope of raising their economic status. In addition, elaborate and expensive cultural practices were not required. For many decades ipil-ipil had no serious pest and disease problems.

When *H. cubana* suddenly became established in the Southeast Asian Region, the South Pacific Islands and Australia in 1985, nearly all plantations were wiped out, except for very small isolated plantings and sporadically-planted individual trees. This disaster resulted in an indefinite moratorium on the planting of this species all over the region, until species or cultivars resistant to the psyllid, but which are of comparable use to the formerly planted ipil-ipil cultivar, become available, .

The search for efficient natural enemies in South America, ipil-ipil's origin, is still on-going. Although a complex of predators and fungi have been reported attacking *H. cubana*, none is effective enough to reduce the pest's population. Selection of resistant species to replace the susceptible ipil-ipil was also done by many workers in different countries. Consistently, *L. diversifolia*, *L. pallida*, *L. esculenta* and *L. collinsii* showed some resistance to the psyllid. However, these studies evaluated plant resistance based only on estimates of psyllid damage, adult psyllid populations and/or ratings on egg and nymph density on the plant. None dealt with the mechanism(s) of resistance exhibited by any of the four resistant species.

Resistance breeding programs are on unsound grounds unless particular mechanisms of resistance are identified. Hence, my research aimed to determine the possible resistance mechanisms observed in *L. collinsii* against *H. cubana*, by comparing both its response to the psyllid and the psyllid's response to *L. collinsii*, with that in the susceptible species, *L. leucocephala*. Only *L. collinsii* was used in the evaluation because of the difficulty in procuring the seeds of the other species at the start of this research.

My results confirm other workers' reports that *L. collinsii* is resistant to the psyllid. Compared with *L. leucocephala*, growth loss in infested *L. collinsii* was much less than in infested *L. leucocephlala*. Also differences in growth response between infested and uninfested *L. collinsii* were not as large as those between infested and uninfested *L. leucocephala*.

Field tests reveal that fewer adult *H. cubana* alighted on and less eggs were oviposited on *L. collinsii* than in *L. leucocephala*, which could explain in part why there was less damage on *L. collinsii* than on *L. leucocephala*. That this preference behavior of the psyllid is governed by chemical volatiles from the host, was illustrated by the field cage experiment. Results in laboratory bioassay experiments supported both field experiments, in that female *H. cubana* were more attracted than the males to volatiles of *L. leucocephala* even at higher leaf extract concentrations. However, like *L. leucocephala*, *L. collinsii* was also found to be attractive, but only at a low concentration of the extract. Hence, it is very possible that the antixenotic characteristic of *L. collinsii* in the field was the result of its higher production of volatiles.

Antibiosis was clearly demonstrated in *L. collinsii* against the psyllid, based on significantly lower survival rates of the 1st and 2nd instars, and smaller numbers of adult psyllids eclosing on *L. collinsii* compared with those on *L. leucocephala*. Whether this mortality was chemically inflicted was not investigated in my research. I suggest, however, that premature leaf senescence caused water deficiency and deterioration in the nutritional quality of the feeding site. Premature abscission, on the other hand, contributed to artificial reduction of available space on the leaf, resulting in high intra-specific competition for food and space, which subsequently resulted in starvation of deprived nymphs. The latter phenomenon seems very likely to be a major contributing factor in high nymphal mortality. I was not able to show any morphological plant characteristics, e.g. trichomes, that could affect nymphal feeding and movement on the plant. As on the preferred species, *H. cubana* was also mobile and capable of reaching and feeding on the vascular bundles, the preferred feeding site, in *L. collinsii*. I deliberately did not include studies on "tolerance" as it was practically difficult to maintain the same nymph populations between the two *Leucaena* spp., since most nymphs on *L. collinsii* die early. My experiments, nevertheless, showed that the resistance mechanisms in *L. collinsii* are based on both antixenosis and antibiosis. This is summarized in Table 13. Thus, the resistance must be based on more than one gene, i.e. horizontal resistance, and is very likely to be stable (Gallun and Khush 1980).

Results of my studies represent one step toward the incorporation of one or more resistance mechanism traits in the breeding of *Leucaena* spp. against the psyllid, *H. cubana*. These findings also open new areas of further research. More work is needed to study in-depth the chemistry of the resistant *L. collinsii* and other species, and its specific role in the host selection, host acceptance behavior of and host suitability to *H. cubana*, and to determine its place in psyllid population management.

Table 13. Attributes of *L. collinsii* likely to influence establishment of *H. cubana*.

Resistance mechanism	Event	Insect response	Plant characteristics influencing insect response
Antixenosis	orientation	weak attraction/ repulsion	repellency of volatiles at high concentration or presence of repellent overriding attractant
	oviposition	fewer eggs deposited	weak attractant, hence fewer alighting and ovipositing adults
			ovipositional unsuitability in response to physical/chemical plant attributes (?)
Antibiosis	egg survival	less hatch	low leaf moisture content (?)
	nymphal probing	stylet penetration	suitability of plant tissue for penetration and feeding
	nymphal survival	high mortality in 1st and 2nd instars	premature leaf abscission, hence reduced space/food resources for the insect resulting in competition
			toxic leaf chemicals (?)
	adult eclosion	few adults developing	combined effect of antixenosis and antibiosis
		smaller size	poor nutritive quality of senescing leaves

The main avenues used to find or develop psyllid-resistant ipil-ipil (Bray 1987) are: (1) Selection within *L. leucocephala.* Most provenances, however, were susceptible to *H. cubana* except those from Northeast Mexico which showed tolerance. Its stability when planted in another environment has not been tested though; (2) Selection among species other than *L. leucocephala.* About 4 species of *Leucaena* were found resistant to the psyllid. They were rarely grown elsewhere outside their native habitat and their potential for fuel and forage is not known; and (3) Interspecific hybridization. This involved the direct use of sterile F_1 hybrids between species other than *L. leucocephala.* Their usefulness as fuel and forage is also uncertain. It also involved hybridization and selection in progenies of succeeding generations. This aims to obtain sufficient resistance against the psyllid and have optimal fodder and wood yield by transfering the resistance observed in other *Leucaena* spp. into *L. leucocephala.* Breeding programs of this nature, however, are long term.

Until now selection for psyllid resistance is based on empirical methods and relied mostly on the performance of the plants in the field. The mechanisms of resistance is not well understood, identified and incorporated in the breeding and screening programs. Hence, selection was based on the assumption that resistant plants were accurately identified. With this method, there is a big possibility that the identified supposedly resistant plants do not have the full complement of the resistance mechanisms present in the parent plants. Unknowingly, plant breeders may be selecting for only one resistance mechanism which could be easily broken by a variant psyllid. Knowledge of resistance mechanisms operating in resistant parent *Leucaena* spp. could lead to the development of a rapid, more accurate screening technique which could also be applicable to seedlings. Understanding the genetics of resistance could also facilitate genetic improvement of *L. leucocephala* against the psyllid without risking the possibility of modifying its desirable traits. This could now be accomplished using the gene-transfer technique.

It could not be discounted that a biotype(s) of *H. cubana* exist. However, since species of *Leucaena* other than *L. leucoephala* were never planted in commercial scale in Southeast Asia and the Pacific Islands regions, except for experimental purposes only, it is assumed that if a more aggressive biotype exists it is present only in trace amounts. Nevertheless, this warrants that development of resistant *Leucaena* plants must be aimed at producing plants with broader genetic base and at augmenting the number of genes conferring resistance. As such, higher levels of resistance could be attained and the chances of breaking down plant resistance by any biotype that could develop later will be minimized. Besides the different resistance mechanisms displayed by *L. collinsii* against *H. cubana*, there may be other types of resistance on other *Leucaena* spp.. Sorensson and Brewbaker (1987) postulated that resistance in *L. pallida* and most *L. esculenta* is related to the transparent and sticky exudate which coats the young leaflets, while resistance in *L. retusa* may be due to its coriaceous leaflets. These species could serve as additional sources of genes conferring resistance to *H. cubana*.

The development and use of resistant *Leucaena* plants against *H. cubana* is justifiable for several reasons. Until now, there is no single plant species that can replace the innumerable uses provided by *L. leucocephala*. No species has gained the popularity or recognition from farmers as *L. leucocephala* has. Hence, there is no doubt that the development of a *Leucaena leucocephala* hybrid resistant to the psyllid would restore its status as a commercial crop. Although a complex of natural enemies are associated with *H. cubana* none is effective enough to reduce the psyllid's population. *Leucaena leucocephala* is not a high-value crop and therefore the use of high-cost control methods, e.g. chemical control, is not economical. The use of resistant plants against *H. cubana* will prove less costly in the long run.

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