Banana plants regulate larval feeding site for leaf feeding moth: *Ceramidia butleri* (Ctenuchidae, Lepidoptera).

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LES BANANIERS, SITE HABITUEL DE NOURRITURE POUR LA CONSOMMATION DE FEUILLES DE LA LARVE DU LEPIDOPTERE *CERAMIDIA BUTLERI* (CTENUCHIDAE, LEPIDOPTERA).

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RESUME - Une étude de la biologie et du comportement de *Ceramidia butleri* MOESCHLER (Ctenuchidae, Lepidoptera) à Coyoles, Honduras, aide à élucider les relations entre *C. butleri* et son hôte. Dans les interactions hôte-herbivore, les larves de *C. butleri* se limitent aux tissus physiologiquement plus âgés des bananiers. Ce mode de distribution est le résultat des facteurs de mortalité en post-émergence affectant les premiers stades larvaires (instar).

INTRODUCTION

Frequently when plants are attacked by phytophagous insects, new foliage receives the major impact of the feeding destruction. 'Cavendish' banana plants have reversed this pattern, limiting leaf feeding by *Ceramidia butleri* MOESCHLER to the older leaves. Through a combination of rapid growth and host induced differential survival of the first instar *Ceramidia* larvae, banana plants protect their new foliage from their most serious pest in the New World. This relationship represents an example of an introduced plant which exhibits an effective defensive mechanism against a native insect herbivore. The effects of this defensive mechanism influence feeding tolerance limits and have ramifications applicable to pest management planning.

HARRISON (1959) discusses the life history and habits of *Ceramidia butleri* in Costa Rica. The morphology and biology of a closely related species, *Ceramidia viridis* DRUCE from Ecuador is discussed in two papers by TOURNEUR (1967 and 1969). The ecology of *Ceramidia* in Costa Rica is discussed by HARRISON (1964) and in Ecuador by TOURNEUR (1967). The parasites of *C. butleri* in Central America are discussed by HARRISON (1964 and 1965) and BURKS (1962).

METHODS

Populations of *C. butleri* were studied in Standard Fruit Company farms in the Aguan Valley of Honduras. Farms are located near the town of Coyoles in the State of Yoro. Field populations of eggs and larvae were monitored by cutting the required leaf from selected plants and making counts from the entire under surface of the leaf. Leaf number 1 is the newest leaf and higher numbers represent older leaves.

Laboratory evaluations were done at La Ceiba, Honduras. Eggs and larvae used were collected from field popula-

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tions in Coyoles. Caged feeding studies were done on a small research planting of bananas in La Ceiba. One first instar larvae was placed on the underside of a leaf inside a round cage made of clear plastic 25 mm in diameter and 40 mm high. A fine cloth was placed over the top of the cage. Larvae were checked daily for a period of 6 days. Five cages were placed on each leaf and the experiment was replicated 10 times.

Egg parasitism was determined by collecting eggs from banana plants and caging them in size «0» gelatin capsules. After 10 days they were observed and the number of parasites recorded.

RESULTS AND DISCUSSION

Ceramidia butleri generations are strongly cyclic. Larvae

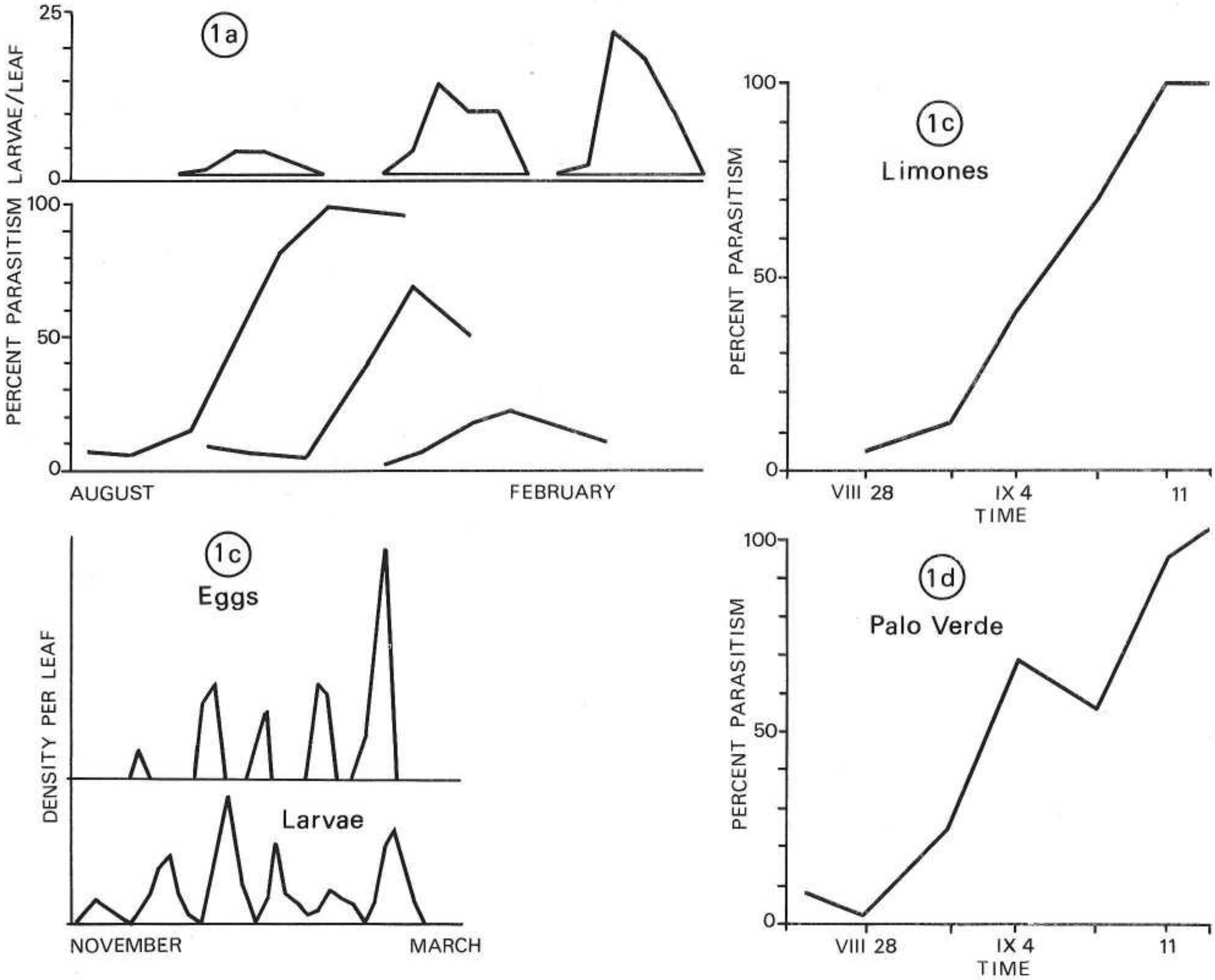

Figure 1 a - RELATIONSHIP OF PERCENT EGG PARASITISM TO LARVAE POPULATIONS IN THREE SUCCESSIVE GENERATIONS.

Figure 1 b - FREQUENCY OF EGG AND LARVAE DENSITY OF *CERAMIDIA* ON LEAF EIGHT OF BANANA PLANTS IN COYOLES, HONDURAS.

Figure 1 c - PERCENT PARASITISM OF *CERAMIDIA* EGGS BY *TRICHOGRAMMA* SP. IN THE LIMONES FARM OF COYOLES, HONDURAS.

Figure 1 d - PERCENT PARASITISM OF *CERAMIDIA* EGGS BY *TRICHOGRAMMA* SP. IN THE PALO VERDE FARM OF COYOLES, HONDURAS.

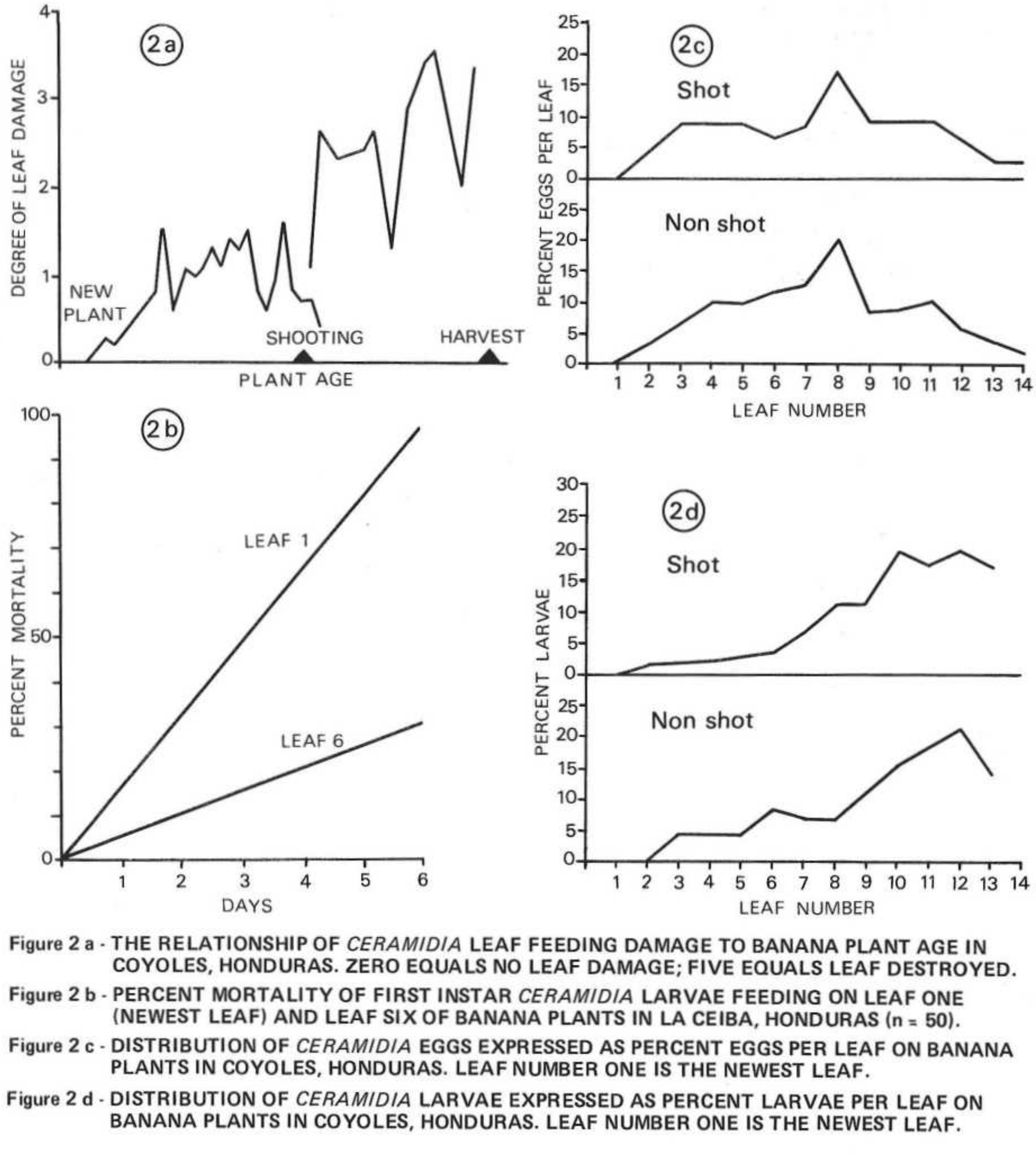

Figure 2 a - THE RELATIONSHIP OF *CERAMIDIA* LEAF FEEDING DAMAGE TO BANANA PLANT AGE IN COYOLES, HONDURAS. ZERO EQUALS NO LEAF DAMAGE; FIVE EQUALS LEAF DESTROYED.

Figure 2 b - PERCENT MORTALITY OF FIRST INSTAR *CERAMIDIA* LARVAE FEEDING ON LEAF ONE (NEWEST LEAF) AND LEAF SIX OF BANANA PLANTS IN LA CEIBA, HONDURAS (n = 50).

Figure 2 c - DISTRIBUTION OF *CERAMIDIA* EGGS EXPRESSED AS PERCENT EGGS PER LEAF ON BANANA PLANTS IN COYOLES, HONDURAS. LEAF NUMBER ONE IS THE NEWEST LEAF.

Figure 2 d - DISTRIBUTION OF *CERAMIDIA* LARVAE EXPRESSED AS PERCENT LARVAE PER LEAF ON BANANA PLANTS IN COYOLES, HONDURAS. LEAF NUMBER ONE IS THE NEWEST LEAF.

appear in sharply peaked waves 6 to 7 weeks apart, depending on the season (Figure 1 B). Since young larvae do not feed through the leaf, heavy leaf damage is limited to a 2 or 3 week period for each generation.

An important factor contributing to the natural collapse of populations is egg mortality due to parasitism by *Trichogramma* sp. (Trichogrammatidae, Hymenoptera) (Figure 1 A). Characteristically *Trichogramma* parasitism starts at a low level at the beginning of the *C. butleri* egg cycle but increases rapidly. By the end of the *C. butleri* egg production cycle nearly all the eggs may be parasitized (Figure 1C and 1D). The strong cyclic nature of the *C. butleri* populations probably tend to keep the parasite population low at the beginning of each egg cycle because most of the adult *Trichogramma* do not survive until the next cycle of egg production.

A tightly grouped adult emergence pattern with an initial thrust of egg production is important to *C. butleri*.

When *C. butleri* egg production starts out slowly, by the time the peak of egg production is reached, *Trichogramma* has the ability to parasitize a high percentage of the egg population. The relationship of the two populations during the first few days of each egg generation plays a major role in determining the level of parasitism.

Ceramidia butleri larvae feed mostly on plants after flowering and on older leaves of plants which have not flowered (Figure 2 A). Old or older leaves in this paper may also be interpreted as dying leaves. This suggests that *C. butleri* populations are sensitive to the physiological state of the host.

When the levels of larvae feeding damage on old and new leaves were compared on banana plants before flowering, the older leaves always received the most severe damage. 90 % of the *C. butleri* larvae are located on leaves 6 through 12 and 60 % are located on leaves 9 through 12 (Figure 2 D). This relates directly to the amount of leaf damage to the leaves in these various positions. Egg oviposition does not follow the same pattern (Figure 2 C). No difference was noted in egg levels on leaves 3 through 12. Since egg oviposition on the banana plants is random, the progressively increasing number of larvae on the older leaves is dependent on post-oviposition factors.

A similar relationship was observed when eggs and larvae were compared on plants before flowering (non-shot plants) with plants after flowering (shot plants). (Since banana plants do not produce additional leaves after flowering, plants which have flowered contain only old leaf tissue similar to leaves 6 through 12 on non-shot plants). When egg oviposition was compared between shot and non-shot plants, no significant differences were found. When larvae numbers were compared between shot and non-shot plants, a significantly ($P = 0.01$) larger number of larvae were collected on shot plants ; 439 compared to 269. This is consistent with feeding data presented in figure 2 A showing more feeding on leaves after flowering (shooting).

Since egg oviposition is random both in respect to leaf position and plant age within a plantation, the higher concentration of larvae on the older foliage is viewed as being caused by post emergence factors. This differential distribution in density of *C. butleri* larvae could be related to leaf orientation, resulting in increased or decreased exposure of the larvae to physical or biological mortality factors such as wind, rain, sun or parasites. It muy be also related to chemical composition or the physical characteristics of the leaf at different physiological stages.

Results of feeding tests in the field with larvae caged on leaves 1 and 6 indicate that first instar larvae suffer increased mortality when caged on the first leaf of non-shot banana plants as compared to leaf 6 of the same plant (Figure 2 B). During six days of feeding 100 % of the larvae caged on leaf 1 died compared with 16 % of the larvae caged on leaf 6.

Only under high larvae density levels were leaves 1 through 5 damaged. This occurred only when larvae levels reached the range of 60-80 larvae per leaf or above. At levels of 60 larvae per leaf and above, damage may result to the new leaves as a result of two factors ; one, even though the percentage is low, enough larvae are able to live on the younger leaves to cause damage, and two, migration of the older instar larvae to the young foliage due to crowding and competition for food on the older leaves. Larvae in the third instar and older appear to be able to develop normally on the young leaves on banana plants. Field observations show that in high density infestations new leaves show mostly feeding damage caused by fourth and fifth instar larvae.

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