THE BIOLOGY AND ECOLOGY OF THE MACADAMIA
NUTBORER *Ecdytolopha torticornis*
IN COSTA RICA

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. Ph.D. Thesis

UNIVERSITY OF EDINBURGH

1994

DECLARATION

I declare that the work presented in this thesis is my own unless stated otherwise.

ACKNOWLEDGMENTS

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INTRODUCTION

Nut trees of the genus *Macadamia* spp. (Proteaceae) grow naturally in the rain forests of Australia and New South Wales (Ironside, 1987). Macadamia trees have been introduced and planted in many parts of the world, particularly Hawaii, South Africa, Malawi, Guatemala and Costa Rica. At present new plantations are being established in Colombia, Brazil, Venezuela and Ecuador. Production in Australia and Hawaii accounts for more than 70 % of the world nut crop. The Hawaiian production increased from 4762 tonnes in 1989 to 7077 tonnes in 1993, while the Costa Rican production rose from 136 tonnes in 1989 to 726 tonnes in 1993, a five fold increase in four years (Lucas, 1994).

The macadamia was introduced to Costa Rica in 1952, but it was not until 1965 that it started to be grown commercially as an alternative cost crop to coffee. The orchards were situated in plantations previously devoted to coffee (50-1200 masl) (González, 1978).

Macadamia exceeded all expectations in productivity. New orchards started to proliferate and soon it became a highly remunerative, non traditional export crop. At the present time, Costa Rica is the world's third largest producer of macadamia, behind only Hawaii and Australia.

With the excellent ecological conditions that Costa Rica offers for nut production, and the attractiveness of its international price, various government agencies as well as private banks have adopted generous incentive schemes to stimulate macadamia nut production. As a result of this, the area planted with macadamia increased from 2000 ha in 1982 to 8000 ha in 1993 (Alberto Montero, personal communication).

Macadamia production in Costa Rica is under the responsibility of nearly 600 macadamia producers, 86 % of these having small plots under ten hectares, representing nearly 30 % of total area planted with macadamia. The remaining farmers own medium size plantations (11 - 99 ha) and large size plantations (over 100 ha) (Müller, 1989).

There are six processing plants in the country. Macadamia de Costa Rica, a company situated in Turrialba, owns the principle processing plant for macadamia in Costa Rica and is also the largest producer with over 700 hectares. Until recently, all nut production of the country was processed by this processing plant.

As the area used to grow macadamia has increased, so have reports by producers of pest damage. One of the causes of damage to the nuts is *Ecdytolopha torticornis* (Meyrick) (Lepidoptera: Tortricidae) which tunnels into the nut and feeds on the kernel. Although an increase in nut damage has been reported from 16 % in 1987 (Lara, 1987), to 28 % in 1990 (Masís and Campos, 1990), and 39 % in 1992 (Blanco *et al.* in press), chemical control has not yet been thought necessary. However, with the increase in the number and the size, of existing macadamia orchards and new plantations coming into production (six years), the insect will undoubtedly increase in number and in its significance as a pest. Therefore, effective methods of managing this pest must be found.

Appropriate pest management usually consists of a combination of two or more techniques (e.g. introduction or augmentation of biological control agents, the development of sampling methods, the correct timing and dosage of insecticides, cultural practices), which diminish the pest population without producing problems in the environment (Horn, 1988). As *E. torticornis* is relatively new to damaging macadamia nuts, an intimate knowledge of the biology and ecology of this species and its relationship to its host is needed to devise management strategies for this pest.

Initially, the insect was identified by the Commonwealth Institute of Entomology (CIE), United Kingdom as *Cryptophlebia leucotreta* (Meyrick). Subsequently it was reidentified as *E. torticornis*, which is closely related to *C. leucotreta*. It has been reported as a cocoa pest in the West Indies and on banana and oranges in South America, but until now not as a macadamia pest (Chamberlain, 1989).

Although the present research focuses only on *E. torticornis*, general information on *Cryptophlebia* spp. is presented, since there is a lack of information on the former pest and a similarity in the damage by both pests to nuts.

There are three species of macadamia: *Macadamia integrifolia*, *M. tetraphylla* and *M. ternifolia*. Present commercial varieties are mainly grafted Hawaiian selections of *M. integrifolia*. The *tetraphylla* types are inferior in nut quality and are not accepted by processors, and the *ternifolia* types have a small and bitter nut (Montero, 1991).

Of the many Hawaiian varieties developed, the most commonly grown in Costa Rica are clones Keahou (Haes 246), Kau (Haes 344), Kakea (Haes 508) and Keaau (Haes 660). Density of planting is affected by the combination of clones planted. The clones 344 and 660 exhibit an upright tree growth (orthotropic) while clones 246 and 508 present a spreading and semiupright growth (plagiotrophic) (Queensland Department, 1984).

The aim of this research was to study the biology and ecology of the macadamia nutborer, *E. torticornis*, in a macadamia orchard in Turrialba, Costa Rica.

The specific objectives were:

1. To determine the life cycle and fecundity of *E. torticornis*.

2. To investigate the factors affecting its abundance and distribution.

3. To study management practices which affect insect abundance.

SECTION I. BIOLOGY OF MACADAMIA NUTBORERS
Cryptophlebia spp AND *E. torticornis* .

Distribution and dispersal

Cryptophlebia ombrodelta (Lower) has been reported damaging nuts in the Northern territory of Queensland, New South Wales and its surroundings (Ironside, 1974), while *C. leucotreta* (Meyrick) and *Cryptoplebia batrachopa* (Meyrick) are known from Malawi, Zimbabwe, South Africa and other parts of Africa (La Croix and Twinda, 1986; Ironside, 1992). *Cryptophlebia illepida* (Butler) and *C. ombrodelta* are the most common nutborer species in Hawaii (Jones and Tome, 1992). Damage to macadamia nut by *C. illepeda* in Hawaii has been reported since 1919 (Namba, 1957).

The distribution of macadamia nutborers varies from one genera to the other. In Costa Rica, *Ecdytolopha* was reported as a pest in 1986 in Turrialba, Province of Cartago, and Guápiles, Province of Limón, two of the main macadamia planting areas (Masís and Soto-Manitú, 1989). From 1990 onwards, its presence, but low damage, has been reported in San Vito de Coto Brus, Province of Puntarenas, in San Carlos, Province of Alajuela, and in Tilarán, Province of Guanacaste (personal observation).

Description and habits

The eggs of *C. batrachopa* are flat and ovoid and have a pitted corion. They are laid individually on young fruits (preferably on nuts already infested with larvae), normally three eggs per fruit. Ironside (1974) reported that up to 15 eggs may be laid on the green husk of one nut. Most of the eggs are laid on the upper half of the fruit; fruits of over 24 mm in diameter being preferred. Jones and Tome (1992) found that, in Hawaii female *Cryptophlebia* moths did not lay eggs on nuts smaller than 20 mm in diameter. There appears to be no preference for oviposition at different heights of the trees. After hatching, the larvae burrow into the husk and feed on the kernel. The last instar larvae leaves the nut to pupate. Studying *C. batrachopa* life cycle at a mean temperature of 27 °C, La Croix and Thindwa (1986)

found that it took the eggs 8.4 (± 1.6) days to hatch, and 24.4 (± 3.5) days for complete larval development on an artificial diet; and adult emergence occurred after 9-14 days. Ironside (1981) reported a duration of the life cycle of *C. ombrodelta* (from egg laying to moth emergence) of 5 weeks during the summer.

Cryptophlebia may leave the nut tree by dropping on a thread from the outer branches or by crawling down the branches and trunk. Pupation can occur in the soil, and on axils on branches. Most pupae in the ground are found at a depth of 2-5 cm (La Croix and Thindwa, 1986). Namba (1957) observed that pupation in *C. illepida* occurred in the tunnel near an exit hole in the husk, and that sometimes, when the husk splits before pupation, the cocoon was built along the edge of the crack.

E. torticornis is a grey moth of about 10 mm in length. The eggs are ovoid and elongated (Masís and Soto-Manitú, 1989; Masís *et al.* 1989). They are normally laid on the husk of immature nuts, as this allows the larvae to penetrate the shell and feed on the kernel. Once the larvae has almost completed its development in the kernel, it emerges from the nut and opens an exit hole through the carpel. If the eggs are laid on mature nuts (shell hardened), the larvae feeds only on the carpel and do not cause any damage to the kernel (Chamberlain, 1989).

Pupation in *E. torticornis* is reported as probably occurring in the leaf litter at the base of the tree (Chamberlain, 1989).

Ecdytolopha infestation of trees within an orchard is patchy, which could indicate that it is a poor flier or that trees vary in susceptibility to pest attack (Chamberlain, 1989). Masís (1990) found differences in susceptibility to *E. torticornis* within macadamia clones. Clone 246 was found to be the most susceptible, followed by 344, 660 and 508 in a one year study in Turrialba, Costa Rica.

Host plants

Alternative hosts for *Cryptophlebia* spp. include several economic food plants and numerous species commonly grown as ornamentals. *C. batrachopha*, *C. ombrodelta* and *C. leucotreta* have *Litchi chinensis* Sonner (Sapindaceae) as a common alternative host, while *C. ombrodelta* and *C. leucotreta* have *Cassia* spp. (Leguminosae) and *Citrus*

sinensis L. (Rubiaceae) as an alternative host. The following host plants are specific for each pest species: *C. ombrodelta* (Australia and Hawaii) also feeds on *Acacia farmesiana* (L)., *Bauhinia galpinii*, *Poipiona pulcherrims* L., *Phaseolus lunatus, Tamarindus indicus* and *Cupeniopsis anacardioides; C. batrachopa* feeds on *Caesalpinia decapetala, Azanza garckeana* and *Feijoa sellowiana* Berg; and *C. leucotreta*, a very polyphagous species, feeds on over 50 species of plants including cotton (*Gossypium* sp.), maize (*Zea mays*), citrus, sorghum, okra, *Psidium guajava, Courbonia glauca, Thylaceum africanum, Ziziphus mucronata, Terminalia sambessiaca* and many other plants. *C. leucotreta* is a pest on citrus, especially on navel oranges in Southern Africa, and on cotton (Ironside, 1974; La Croix and Thindwa, 1986; van der Geest *et al.*, 1991). *C. illepida*, a species native to Hawaii, is found frequently on *Acacia koa, A. confusa, A. farnesiana, Sapindus oahuensis* and other hosts (Namba, 1957).

In Costa Rica, *Ecdytolopha* seems to have only macadamia as a host. However, in other countries of tropical America, *Ecdytolopha* has been reported attacking other trees. For example, *E. puntipiciana* has been reported as a cocoa and cotton pest in the West Indies (Entwistle, 1976), and as a banana and citrus pest in South America (Chamberlain, 1989). In the Dominican Republic, an unidentified species of *Ecdytolopha* is responsible for the failure of the guava (*Psidium guajava*) paste industry (Abud, A. personal communication).

CHAPTER 1

LIFE CYCLE AND BIOLOGY OF

Ecdytolopha torticornis

The aim of this study was to determine the life cycle of *E. torticornis* and its biology.

1.1 MATERIALS AND METHODS

Field work was carried out at the Oriente Farm, Macadamia de Costa Rica, Turrialba, 09° 53' N, 83° 41' W, 620 to 700 m above sea level. The mean annual rainfall during the period 1991 - 1993 was 2600 mm; the mean temperature 22 °C, and the relative humidity around 80 %. The Oriente Farm is one of the oldest macadamia orchards of the country. It is a 225 ha orchard divided into eighteen plots which vary in size and age (from 20 years old to newly planted), in height and in the proportion of clones per plot. The surrounding area comprises sugarcane and coffee plantations, macadamia and coffee intercropped, pasture lots, and untouched forests.

Laboratory work was carried out at the Integrated Pest Management Project's laboratory (23 °C, 80% RH) at CATIE (Centre for Tropical Agricultural Research and Education), Turrialba, Costa Rica.

An attempt was made to obtain the duration of each stage of the life cycle by following the development of the larvae from the eggs produced in the laboratory. However, first and second instars died, perhaps due to excess heat from the lighting on the stereoscopic microscope or by handling when checked. Consequently, a laboratory colony was initiated in April 1991 from larvae found in damaged nuts and fertile eggs brought in every two weeks from the Oriente Farm. Efforts were made to rear the larvae on an artificial diet. However, the medium became contaminated with fungi, and it was decided to feed the larvae with immature (shell not hardened) macadamia nuts (0.8 - 1.5 cm in diameter) from clone 344, which appeared to be the most susceptible to the nutborer attack (Blanco *et al.* in press). The eggs and larvae were individually reared in plastic

cups (160 cm^3) containing moistened absorbent filter paper added to the bottom, and the lids were perforated with hot needles to provide ventilation. Records of larval development were taken every two days. Food and water (by moistening the filter paper) were placed every two days.

Head capsule width and body length of the larvae were measured with a stereoscope microscope (Olympus) fitted with an ocular micrometer. Instar number was ascertained by measuring the discarded head capsules or moults found on the nuts.

The number of *E. torticornis* eggs per nut and the number of holes per nut were obtained from observations on the vertical distribution of the nutborer (Chapter 6).

Observations on other aspects of the life cycle of the nutborer, such as larval feeding behaviour and adult activity, were made on nuts collected every two weeks from the field and on further occasions in the field.

1.2 RESULTS

Eggs laid in the field were placed individually on the middle half of the macadamia nuts, most in the narrow space between adjacent fruits. Oviposition was only found on fruits with diameters over 8 mm, but mature nuts (with a hard husk) seem not to be attractive for oviposition. It was possible to find up to 8 eggs per nut {0 (65 %), 1 (11 %) 2 (9 %), 3 (6 %), 4 (3 %), 5 (3 %), 6 (1 %)}, with a mean of 0.8 eggs (n=201 nuts). Eggs were found to have a flat, circular to ovoid shape and ranged from 1.1 to 1.34 mm (mean 1.2, SE = 0.01) in length (n = 33). When first laid, they were pale white but darkened to a red-brownish colour with embryological development. No eggs were found on fruit petioles, leaves or branches.

The egg incubation period of the nutborer averaged 5 - 6 days (Table 1.1). The incubation period was approximate, therefore no mean and standard error are included. Four larva instars were found. The length and head capsule width of each instar are presented in Table 1.1. The duration of the first, second and third instars ranged

Table 1.1: Measurements of the length and size of the developmental stages of *E. torticornis* reared in the laboratory.

Stage		Days		Head capsule width (mm)			Length (mm)	
	n	Range	Mean ± SE	Range	Mean ± SE	n	Range	Mean ± SE
Egg	33	5 - 6	-*			33	1.1 - 1.3	1.2 ± 0.01
Larvae								
L1	8	3 - 4	3.3 ± 0.18	0.4 - 0.5	0.4 ± 0.02	7	1.2 - 1.6	1.4 ± 0.04
L2	8	3 - 4	3.8 ± 0.16	0.6 - 0.9	0.7 ± 0.02	9	3.0 - 6.4	5.0 ± 0.35
L3	8	3 - 4	3.4 ± 0.31	1.1 - 1.3	1.2 ± 0.02	5	7.0 - 9.6	8.6 ± 0.35
**L4	23	3 - 9	6.3 ± 0.27	1.6 - 1.8	1.7 ± 0.02	19	8.4 - 19.5	13.9 ± 0.56
Pupae	37	7 - 15	13.2 ± 0.26		Female	34	7.4 - 12.7	9.9 ± 0.24
					Male	38	6.0 - 10.3	8.5 ± 0.13

*approximate value
**including prepupae

from 3 to 4 days, while the duration of the fourth instar (+ prepupa) ranged from 3 to 9 days.

The newly emerged larva wanders on the nut surface until it finds an appropriate place to bore into the nut. It took one larva, observed in the field, around fifty minutes from the time of emergence from the egg to the time it disappeared into the husk. In the case of *C. ombrodelta*, Ironside (1981) reported that a newly hatched larva may search for a feeding site for as long as 24 hours before entering a nut. *E. torticornis* larvae did not noticeably feed on or bite the chorion of the eggs from which they hatched. Damaged nuts at this time are difficult to find since the entry hole is very small (similar to a pinhead). As the larvae grow, the entry/exit hole is enlarged and is more clearly visible, and damaged nuts can easily be identified by frass accumulation on and around the exit hole.

Once the larvae have bored inwards the husk, they tend to bore towards the top and bottom of the nut, where husk width is at its greatest. The number of holes per nut varied from 1 to 6. One hole per nut accounted for 67 %, while two holes accounted for 25 %, and three holes 6 % (n=882). Most of the larvae fed mainly on the husk, but if the shell had not hardened they continued boring through into the kernel. Damage to the surface of the shell was often found due to the attempts of the larvae to bore through into the kernel. Larvae were found mostly singly, but when *E. torticornis* were abundant, it was possible to find up to 3 - 4 larvae in a nut. When more than one larvae per nut were found, they were usually in different instars. No cannibalism was observed.

Larvae were found to be negatively phototactic, and shelter wherever they could.

When larvae were close to molt, they stopped feeding and entered a period of quiescence. The head capsule and skin of first instar larvae were found inside the nut, while head capsules and skins from the second and third moults were usually found outside the nuts, probably as a result of larvae cleaning their exit holes and tunnels. The head capsule and skin of the last instar were found attached to the pupae exuviae.

As the larvae neared pupation, feeding stopped and they entered a period of inactivity. Silken webs were sometimes spun between two or more nuts in a single cluster. The larvae spun

coccoons attaching debris found nearby, and after six days, pale-yellow pupae were observed. Newly formed pupae were pale-yellow, but darkened to a brown colour as their chitin hardened. The pupal period ranged from 7 to 15 days (Table 1.1). Female pupae were 15 % larger (n = 34) than male pupae (n = 38). Pupae can be sexed by using the genital apertures located on the ventral surfaces of the ninth abdominal segment, where female pupae lack the knobs characteristic of males (Tortós, 1991). When pupae were near to eclosion, they were found with almost a third of their body protruding from the nut.

Pupae were mostly found in the nuts, but they were also present in lichens and moss on the main stem and petioles of the tree, although not in the leaf litter at the base of the tree as reported by Chamberlain (1989). Ironside (1974) reported that *C. ombrodelta* pupae were also found on the side branches, but in *E. torticornis*, this was not observed. In the laboratory, pupation took place in or on almost any substratum (close to the nuts, on the floor, on erasers, on papers, on curtains, etc.) *E. torticornis* adults generally emerged during the day, although a few emerged during the night or early hours of the day. Chamberlain (1989) reported that females are the first to emerge, and that males emerged a few days later. This result was not observed in the present study. The most active period observed for adult emergence was 13:00 - 14:30 h. Adult activity in the laboratory increased during dusk, probably due to mating behaviour. Moths inside the cages moved their wings repeatedly and made short flights. For other tortricids, an increase in adult activity is reported as part of the mating courtship (Palaniswamy *et al.* 1979; Daiber, 1976). Females started laying their eggs two days after emergence.

In the field, adults were rarely seen during the day. Moths were observed resting on macadamia leaves, but not elsewhere, perhaps because of their colour against the lichens on the leaves or moss on the tree trunk. The adults do not fly when it is windy and show very limited flight activity in general; even short distance migration has not been observed. During this study, most of the moths noted were noted around 13:00 h. Namba (1957) found the *Cryptophlebia* adults during the day among fallen leaves and in crevices of the trees. *Cryptophlebia* spp. are crepuscular moths, whose

activity is at the highest point very late in the afternoon and early evening (Daiber, 1980).

Seventy two pupae were taken at random from the laboratory colony and sexed. The 38 male and 34 female pupae had a sex ratio which did not differ significantly from 1:1 (X^2 = 0.22, 1 df).

No alternative hosts were found during the three year study, although a search was made on some tropical species within the macadamia orchard (*Acacia* spp., *Citrus* spp., bananas, cocoa) which are alternative hosts to *Cryptophlebia* spp. and *E. punctipiciana* (Ironside, 1974; La Croix and Thindwa, 1986; Entwistle, 1976)

1.3 DISCUSSION

There are substantial similarities between *Cryptophlebia* and *Ecdytolopha*. However, they differ in their hosts ranges and in the number of instars in each species. Although no alternative hosts were found for *E. torticornis*, it is likely that this species is indigenious to Costa Rica or to tropical America. It could be that its host (s) are some unknown forest species, but under the attractiveness of a crop being in monoculture, they switched to macadamia. *C. illepida*, which is native to Hawaii, has been reported as switching to macadamia during periods when the pods of *Acacia koa*, its native host, dry up (Namba, 1957). *E. torticornis* is different to the *Ecdytolopha* spp. reported in other American tropical countries since it does not feed on banana, cocoa, guava and citrus, crops normally grown in the zones where the macadamia plantations are established. The presence of five parasitoid species, two of them reaching high levels of parasitism, also indicates that *E. torticornis* has been in Costa Rica for a long time.

The life cycle from egg to adult of the nutborer lasts nearly 36 days, so it is possible it could produce ten generations per year. The actual number of generations per year, however, will depend on food availability and its quality. Chamberlain (1989) suggested that there might be only two generations per year, or that the insects moved onto another host plant after the main nut harvest.

Macadamia trees flower heavily and frequently abort most of the ovules soon afterwards. The fact that the moth prefers to oviposit

on nuts over 8 mm in diameter, but not on mature nuts although large in size, implies some form of adaptive behaviour by the moth to protect their offspring. It is suggested that food quality decreases in mature nuts and that larvae emerging in them will fail to survive. In addition, oviposition of the moths on nuts already containing eggs or larvae could give the new larva the disadvantage of an increased risk of intraspecific competition for food and space.

CHAPTER 2

FECUNDITY OF *E. torticornis*

This chapter reports observations on mating behaviour, fecundity and the longevity of the moths.

2.1 MATERIALS AND METHODS

Moths were reared from cocoons collected at random in the field at approximately weekly intervals and from cocoons from the parasitism study (see Chapter 4). On the day of emergence, moths were transferred to the cages or jars used in the study.

Three wooden frame, mosquito net cages of different sizes (A) and 5 jars (B) were used to study mating and oviposition.

(A) Each cage (35 x 35 x 35 cm; 40 x 40 x 50 cm; 80 x 40 x 50 cm) contained a water - filled jar with macadamia nut clusters, flowers and twigs. Access to the interior of the cage was through two muslin sleeves or a hinged door in the front. The number of female - male adults per cage was varied, and the cages were left either in the laboratory or outside. Adults were fed on honey and water. Two weed flowers commonly found on the orchard, *Emilia sonchifolia*, and *Impatiens balsamina* were added to see whether the adults would feed on them.

(B) Each jar (Plate 1.1) was lined at the bottom with absorbent filter paper which was moistened with water as required, in order to maintain a high relative humidity. Two nuts (approx 1.5 cm diameter, shell soft), a small lid containing cotton with honey and water and a strip of folded wax paper were included. The jars were covered with mosquito netting fastened with a rubber band.

Records were taken on the number of eggs laid, egg viability (fertility) and adult longevity. The eggs were counted daily. At the beginning, jars and nuts were changed daily in order to avoid confusion with the number of eggs laid. Later the eggs were circled with different marker colours (one for each day: black, red, blue, green) since it was observed that moths tended to lay eggs on nuts or surfaces already containing eggs.

15
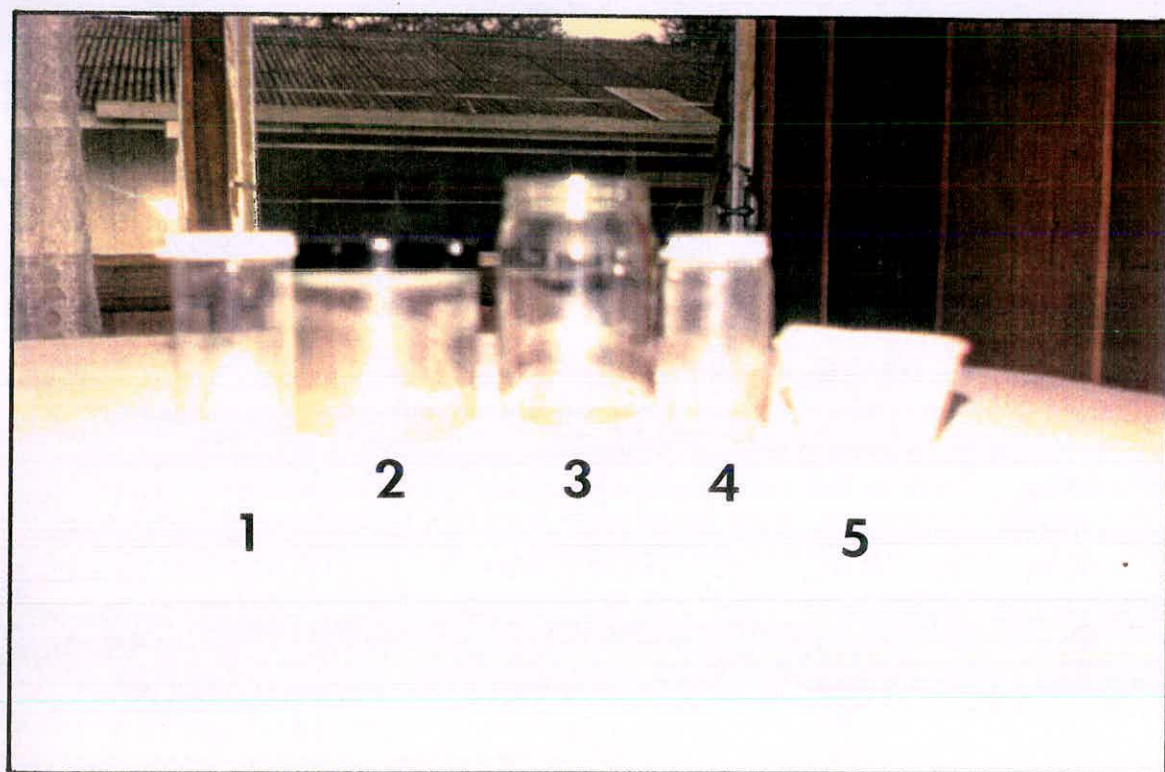
Plate 1.1:   Jars used in the fecundity study of
               E. torticornis.

               _____ 5 cm

2.2 RESULTS

Moths were not seen to feed on or be attracted to the flowers included, but were attracted to honey.

The acts of mating and oviposition were never observed, but occurred between evening and early morning, since eggs were usually discovered in the mornings. An increase in adult activity was observed near dusk; adults made a series of short flights inside the cage, and females raised their abdomen as if they were in a calling position.

Very few eggs were obtained from the cages and jar types one, two and four; however, jar types three and five were successful for egg laying. A total of 1117 eggs were obtained from 34 females in jar type 3 and 5 (Table 2.1). The number of eggs laid per female ranged from 2 to 74, with a mean of 37.2 eggs. Eggs were laid mainly on the jar wall on jar type 3 and on the nuts on jar type 5, although they were also laid on filter paper and wax strips. The number of infertile eggs was about 35 % of the total laid.

Under laboratory conditions, moths lived up to 16 days.

2.3 DISCUSSION

E. torticornis oviposited in jar type 3 more regularly, perhaps because of its shape and type of glass. Jars 1, 2 and 4 were straight-sided and their glass was thick (laboratory jars and diels), while jar type 3 had a curved shape and its glass was thinner. As with jar type 5, it was a white opaque, plastic jar which might have induced the moths to lay eggs because of the low light level inside the container. It is probable that females need a curved surface similar to that of the nuts as a stimulus for laying their eggs, and that the bright light which passed through the jars with thick walls had a negative influence on egg laying. An effect on light intensity during oviposition on parasitoid production was studied by Kolodny-Hirsch (1988). He found an increase of four fold in the mean number of coccoons produced when light intensity increased from 0 to 1,452 lux (2.12 w /m^2).

Table 2.1: Number of *E. torticornis* eggs laid in jar types 3 and 5 in the laboratory, at CATIE, Turrialba, 1992.

Replicate	No of adults female	male	Egg condition fertile	infert	Σ	Eggs/Female
1	1	1	26	47	73	73
2	1	1	43	21	64	64
3	1	2	35	21	56	56
4	1	2	19	23	42	42
5	1	2	38	28	66	66
6	1	2	58	16	74	74
7	1	2	62	8	70	70
8	1	2	43	19	62	62
9	1	2	4	3	7	7
10	1	2	5	1	6	6
11	1	2	48	15	63	63
12	1	2	0	3	3	3
13	1	2	2	0	2	2
14	1	5	27	22	49	49
15	2	2	7	14	21	10.5
16	2	2	12	4	16	8
17	2	3	8	3	11	5.5
18	2	3	35	12	47	23.5
19	3	6	31	1	32	16
20	3	1	18	47	65	21.6
21	3	2	112	65	177	59
22	3	8	91	20	111	37
			724	393	1117	
mean	n=22		32.90	17.86		37.2
SE						5.13

Factors such as temperature, relative humidity and the effect of food quality during the rearing could have influenced the number of eggs laid. High variability on the number of eggs laid and in the number of infertile eggs (Table 2.1), suggests that an external factor could have affected the potential of the moth to lay all its available eggs and their fertility. Weston and Miller (1987) studied the effect on ovipostion of host-deprived seed corn fly. A decrease in the number of eggs was found due to a decrease in egg maturation, indicating that lack of exposure to highly acceptable plants may result in decreased fecundity in the field. They suggested that this change in number of eggs laid might represent an adaptive compensatory mechanism to conserve gamet in the absence of host plants suitable for larval development. Danthanarayana (1975) found that the fecundity of *Epiphyas postevittana* (Walker) (Tortricidae) was influenced by the type of food as well as by temperature. Fecundity in other tortricids (*Cryptophlebia ombrodelta* and *C. leucotreta*) has been reported to be variable: being 230 per female (Ironside, 1974; Daiber, 1980), while Geier (1963) reported a mean of 33 eggs per female in *Cydia pomonella*. However, Powell (1976) found that one female (*Synnoma lynosyrana*) in a breeding jar with two males laid an average of 29 eggs, while various females exposed to the host laid an average of 92 eggs per female implying that laboratory conditions may affect oviposition adversely. In this study, fecundity of *E. torticornis* was found to be 37 eggs per female, which relates to that reported for the other tortricids.

Variability in fecundity may contribute significantly to population trends. Despite the success in obtaining eggs for this insect in the laboratory, it is felt that the results obtained may still not reflect the actual fecundity of *E. torticornis* in the field. Therefore, more and accurate studies of the fecundity of the nutborer should be carried out using these data as a base reference.

SECTION II. FACTORS AFFECTING THE ABUNDANCE OF *Ecdytolopha torticornis*.

Insect populations are integral parts of ecosystems. Their ecological interactions determining their distribution and abundance in the field are very complex as their populations and their environments are continously changing often as a result of men alterying nature. Population densities of insects fluctuate in response to intrinsic and extrinsic factors (Horn, 1988).

As a way of recording and accounting the effect of these factors on the population changes in the life of a species in its natural environment, a life table technique was developed (Varley *et al.*, 1973; Southwood, 1978; Horn, 1988).

A life table is an intergenerational summary of the mortality that affect each stage of an insect species. In this technique it is necessary to record the survival rates of each stage, the longevity of the adults, the female fecundity level, the female-male ratio and the external factors that may diminish the population level (Varley *et al.*, 1973; Southwood, 1978; Horn, 1988).

Life tables are important as they allow researchers to check if an insect population is stable and if so, the level at which the population stabilizes. This is done by reducing a very large body of data to a form which can be readily analyzed. Life tables can also help the researcher in the planning of pest control strategies and can aid in determining and enhancing the effectiveness of parasitoids in controlling host populations (Varley *et al.*, 1973; Southwood, 1978; Horn, 1988).

There are two types of life tables: an age specific (generation, cohort or horizontal) and the time specific (vertical) life tables. In an age specific life table a single cohort of individuals (traditionally 1000) born within the same interval of time is followed from birth to death. Most of the insect life tables constructed are age specific, since insects of temperate climate are seasonal. When generations overlap or where there is a substantial developmental delay, the population should be divided into age classes and analyzed in other ways (Horn, 1988; Begon *et al.*, 1990).

A time specific life table is based on the age grouping of a population with overlapping generations collected at a single

instant of time. The entire population is usually sampled several times during the season and the life table is infered from the individuals alive in each age class (Horn, 1988; Begon *et al.*, 1990).

Detailed knowledge of the insects' life history and biology is necessary for the construction of a life table in order to assess the importance of the different types of mortality (Varley *et al.*, 1973).

A typical insect life table consists of a series of columns in which the first column (x) sets out the interval or life stages that have been distinguished and that are not equal in calendar time. The second column (lx) refers to the number of survivors entering an age interval. The mortality column (dx) referes to the number of individuals dying during the age interval x to x + 1 (qx=dx/lx). Survivorship and mortality are subdivided into components (dxF and d'x) to separate the impact of different causes of mortality (Horn, 1988; Begon *et al.*, 1990).

The sources of mortality are expressed in terms of killing power or k-value which is obtained from the difference between the logarithms of the population before and after mortality acts. The sum of each k-value provides the generation mortality (K). k-values may also be used (by plotting them against log (N) to determine the population density dependency on each mortality factor (Varley *et al.*, 1973).

When consecutive life tables have been constructed for an insect, it is possible to estimate the contribution of each separate mortality (k) to the overall generation mortality (K) and to determine the factors that cause the largest fluctuation in the population (key factor). Varley and Gradwell (1968) designed a graphical method to obtain the key factor by selecting the (k) plot that looks most similar (amount and direction of (k)) to that of total mortality (K).

The key factor is not always easy to identify by the graphical method. Hassell and Huffaker (1969) determined the key factor by calculating the correlation coefficients between the values of the total mortality (K) and each submortality (k), a high correlation indicating the key factor. However, Podoler and Rogers (1975) indicated that it is not always possible to identify the key factor by using only the value of the correlation coefficient and developed a quantitative method that overcomes this problem. They suggested that individual submortalities should be plotted as (k) values on the y-axis against

total mortality on the x-axis, and that the submortality that gives the greatest value of the slope (the regression coefficient b) is the key factor. On the other hand, Southwood (1978) indicated that Podoler and Rogers' method is not a precise statistical test for the importance of each mortality, since the sampling error incorporated in (k) will also appear in (K) and therefore it only gives an estimate of the contribution of each mortality to changes in the (K) value.

Thus key factors are sources of mortality which contribute the most to population instability. Density dependence factors: diseases, parasitism and predation, and competition, are those that tend to occur proportionately more heavily at higher densities, thus stabilizing a population (Varley et al., 1973). Other factors: weather, insecticides, soil tillage, burning of crop residues, etc. present a density-independent effect and are not considered capable of regulating a population about an equilibrium (Horn, 1988)

Factors that affect the dynamics of a population are diverse, varying in intensity within periods of data collection and within localities. Some of these factors are fecundity, natural enemies, competition, weather and climate, diseases, dispersal and migration and food quality (Varley et al., 1973; Southwood, 1978; Horn, 1988).

Fecundity

All animals must produce a certain number of offspring in order to, with the effect of natural selection, maintain the species. The size of young will depend on intrinsic and extrinsic factors which vary with each species. Among these factors are: fertility, the number of viable eggs laid by a female; fecundity (r), the mean number of eggs per female; and the net reproductive rate (Ro = lxmx), the number of female offspring per female (Varley et al., 1973).

Failure of females to realize their potential fecundity can be a major factor contributing to changes in numbers of insects between generations. Reduced reproduction of a population may result from failure of adults to deposit their full complement of eggs or offspring because of the effect of weather or the direct action of natural enemies. Additionally, changes in plant characteristics such as those resulting from water stress or level of plant fertilization can affect

fecundity (Andrewartha and Birch, 1974; Southwood, 1978), while nitrogen content of the food is an important determinant of insect growth, survival and reproductive rates (Matton, 1980). Iheagwam (1981) studied the effect of weight of insect, leaf age, leaf hardness and nitrogen content of leaves of cabbage on the fecundity of the cabbage whitefly, *Aleyrodes brassicae*. He found that the fecundity of whitefly was directly proportional to her weight, that young leaves which had a higher nitrogen content induced the greater number of eggs, and that leaf hardness was inversely related to fecundity. The effect of switching hosts on the longevity and fertility of *Lygus hesperus* was studied by Al-Munshi *et al.* (1982). Their results showed that the second host had a highly significant effect on longevity; insects which switched from alfalfa and broad bean to wheat and green bean lived longer than those who switched to tomato and mustard, thus had the time of laying more eggs. The rate of oviposition is influenced by temperature and the extent to which the potential fecundity is realized, is influenced by the longevity of the females (Southwood, 1988). High temperature favors rapid immature development resulting in a shorter adult life expectancy in *Corythucha* spp. (Neal and Douglas, 1990). The effect of temperature and different food sources on the development, the fecundity, and the longevity of the tobacco budworm, *Heliothis virescens*, was studied by Nadganda and Pitre (1983). Their results showed that more eggs were laid at 20 °C than at 25 or 30 °C. Since females lived longer at lower temperatures, they had more time for egg laying. The shortest developmental time was found on larvae fed on artificial diet, but developmental times varied with temperature when larvae were fed on cotton or soybean.

May (1976) found that morpho butterflies have a high adult survival and lay few eggs at a time, but that the total eggs laid during their life span is not dissimilar to that of related species. The wide distribution of eggs in space and time allows these species to compete successfully in habitats where there is heavy competition from predators or where resources are limitted.

The speed of development, longevity and fecundity of a population is affected by the insect innate capacity of increase and by the environment. Under favorable conditions, the insect's innate capacity of increase is positive and the population increases, while

under adverse conditions, the rate of increase will be negative and the population will decrease (Andrewartha and Birch, 1974; Horn, 1988; Bellows *et al.*, 1992).

Parasitoids and predators

The nature of parasitoids and predators affect their role in the regulation of pest populations. Parasitoids require one host for their complete development, while predators need more than one prey individual to complete their development. Parasitoids also differ in that some are specific parasitoids to a host, thus their searching efficiency needs to be very accurate. Generalist parasitoids are less efficient in regulating a specific pest, but have the advantage of switching to various hosts. The impact of parasitoids and predators on the pest population also differ: parasitized larvae continue damaging their host until the parasitoid larva is nearly fully grown, so there is a longer delay in the control achieved. Predators on the other hand, kill and consume prey at much faster rates than parasitoids, and are also more likely to survive periods of host scarcity by switching to alternative foods (Varley *et al.* 1973; Horn, 1988).

The effect of parasitoids and predators on the abundance of pest populations are considered to be mainly density-dependent processes (Varley *et al.*, 1973; Dempster, 1983). Hirose *et al.* (1980) considered that *Papilio xuthus* populations were regulated by *Trichogramma* spp. in a density-dependence response, although the response relationship was not clear when egg densities were low. Varley *et al.* (1973) reported the winter moth, *Operopthera brumata*, to be regulated by the density-dependent attack of polyphagous predators on its pupae.

Lastres (1990) studied the predation of *Doru taeniatum* and *Solenopsis geminata* on *Spodoptera frugiperda*. Her results indicated that *S. geminata* at a density of 10 ants/m² or less, is an important source of mortality to *S. frugiperda*, reducing its population by 20% during the first four weeks after the emergence of corn. *D. taeniatum* was found to be an important predator of second instar of *S. frugiperda* at a density of one *Doru* per plant.

Nakamura and Ohgudhi (1981) studied the regulatory mechanisms on the population dynamics of *Henosepilachna pustulosa* in a cool temperate forest. They found that mortality during egg stage mainly due to arthropod predation was 64.4 %, first to third instar larval mortality due to arthropod predation was 84 % and fourth instar mortality due to wasp parasitism was 4 %.

Weather and climate

Weather, the annual, seasonal and diurnal changes in temperature, humidity, precipitation, wind and sunshine, and climate, long term averages of the above measurements, affect insect physiological processes and survival rates. Weather acts as a density-independent factor and is said to be a catastrophic mortality factor (Andrewartha, 1966; Varley *et al.*, 1973).

The effect of rainfall varies with its duration and intensity, the size and stage of the insects and the availability of a place to shelter. Harcourt (1966) found that during heavy rainfall, small *Pieris rapae* caterpillars were disloged and fell to the ground where they perished in small puddles or were drowned in the leaf axils. He also observed that larger larvae were not easily disturbed by rainfall, and when dislogged, they were usually able to regain the plant.

Heavy rainfall also affects the performance of biological control agents. Moran and Hoffmann (1987) found that cochineal insects, *Dactylopius opuntiae*, which feed on the cactus *Opuntia ficus-indica*, were ineffective as biological control agents in wet areas since many of the colonies were washed from the host plants and that many of the individuals remaining in the colonies were killed by heavy rainfall.

Temperature has a direct effect on insect development and survival. For example, Regniere (1987) oberved the egg development of *Choristoneura fumiferana* at eight constant temperatures and found that the fastest egg development ocurred at 30 °C. Langor and Raske (1988) found that the most important abiotic factor causing mortality of *Dendroctonus simplex* in Newfoundland was low autumn temperature, causing a 14 % mortality among immature instars and a 7.8 % mortality of adult overwintering. Aphid population may

increase in cool wet weather which slows or stops their natural enemies (coccinelids and hymenopteran), activity (Horn, 1988).

Dispersal and migration

Most animals have a stage in their life cycle that is specialized for dispersal (Horn, 1988).

Dispersal, is defined by many authors as the movement of insects by drifting with air currents or water, by swimming, walking or flying and by clinging to some moving object, plant or animal. Some scientists relate dispersal to adverse conditions in the habitat, such as food shortage or overcrowding, but as in migration, dispersal is closely related to the insect life cycle and behaviour (Andrewartha, 1966; Den Boer, 1990). Dispersal increases outbreeding and genetic recombination, resulting in greater evolutionary plasticity (Horn, 1988).

Dispersal can be either density-dependent or density-independent processes. Aphids start the dispersal process when overcrowded or at a certain stage of development of their host. During this period, mortality in aphids can be caused by heavy winds, by landing on a non adequate host or by exposure to natural enemies. Hodgson (1991) proposed that dispersal in *Myzus persicae*, *Brevicoryne brassicae* and *Megoura viciae* was governed by the growth pattern of the plant, food quality. Mason (1976) found that a large proportion of early instars of Douglas-fir tussock moth was apparently lost during dispersal by wandering or dropping off the foliage on silk threads either through predation or landing on non-host species. He thus stated that dispersal is a self-regulatory process which apparently occurs in response to overcrowding and food stress.

In the migratory locust, *Schistocerca gregaria*, migration takes place as a response of crowding. As the food supply improves, locust population increases, and juvenile hormone production is reduced, allowing the development of wings and flight muscles. The overcrowded population then migrates in search of a larger food supply and thus protecting the other locusts from starvation (Dempster , 1963).

Dispersal influences the distribution pattern and hence the size and location of sample units and of the selected study plots (Clark *et al.*, 1967).

Food quality

For most insect herbivores, the quantity of the host plant resource appears not to be limiting (Hairston *et al.*, 1960). Individual hosts plants and plant populations are highly heterogeneous in space and time (Whitham, 1981). As host plants vary in quality, insects have the option of avoiding less suitable food, or concentrating in the more nutritious tissues of the plants. Nitrogen, in the forms of aminoacids and proteins, is the plant nutrient which influences at the major extent feeding by herbivores (Horn, 1988). McClure (1980) indicated that the availability of nitrogenous food limit animal abundance. Many authors relate the availability of nitrogenous food to insect fecundity, survival and growth (van Emden, 1966; Feeny, 1970; McClure, 1977; Horn, 1988). Ohmart *et al.* (1985) found that the concentration of nitrogen in the foliage of *Eucalyptus blakelyi* influenced the number of eggs laid and the rate of production of eggs by female *Paropsis atomaria*. Females fed on leaves with lower nitrogen concentration laid fewer eggs and at a more slower rate than when fed in leaves containing more nitrogen.

Plants defend from herbivory by quantitative or qualitative defensive adaptations. Qualitative compounds are usually present in low concentrations and include alkaloids, glucosinolates, cardenolides and cyanogenic substances, many of which interfere with internal metabolism of herbivores (Rhodes, 1983; Barbosa and Krischik, 1987). These defenses prevail among early-successional plant species unapparent and ephemeral in phenology and location, whose rapid growth and reproduction are favored (Horn, 1988). However, Barbosa and Krischik (1987) suggested that qualitative allelochemicals such as alkaloids may be common in persistent plants such as trees. Herbivores feeding on early-successional plant species are mainly specialists and must evolve specializations to avoid or overcome qualitative defenses (Horn, 1988). For example, insects that feed on tobacco plants have developed three different mechanisms

for avoiding nicotine toxicity: a) by selective feeding on phloem which does not contain nicotine b) by developing a barrier to absorption from the digestive tract or to penetration into the nervous system, and c) by enzymatic detoxification (convertion to cotinine (Robinson, 1979). Morris and Thompson (1964) found the flavones tricin and orientin and their glycosides which are toxic to insects, in the wings of the butterflies *Coenonymphia pamphilus* and *Melanargia galathea*. They suggested that the ingested flavonoids are not detoxified, but instead are stored in the body and wings.

Quantitative defenses such as tannins, silica, lignins, etc. are effective against nearly all herbivores and are considered typical of plants in later stages of ecological succession (Horn, 1988). Tannins and lignins are phenolic compounds that are found, often in high concentrations in vascular plants. One possible defensive function of tannins is precipitation of protein in the herbivore's digestive tract. Precipitated protein would presumably be less digestible than soluble protein, and the herbivore would thus obtain inadequate dietary protein from tannin-rich plants (Rhodes and Cates, 1976).

Host suitability may change seasonally and in response to stressors such as other insects, pathogens and drought (Horn, 1988). The quality of food decreases as tissue ages since nitrogen and water occur in lower concentrations (Feeny, 1970; Mattson, 1980). McQuate and Connor (1990) examined the preference of larvae of the Mexican bean beetle, *Epilachna varivestis* for foliage of soybean grown under various levels of water deficit. They found an increase of free amino acid concentrations in foliage grown under water deficits. Larvae prefered to feed on foliage under mild water deficits than on well-watered controled plants or on plants with severe water deficits.

Secondary compounds have also shown to be oviposition stimulants in some families of insects. For example, the cabbage butterfly, *Pieris rapae*, is stimulated to oviposit by sinigrin and a synergy of chemicals present in cruciferous plants (Renwick and Radke, 1983), while female butterflies of *Papilio protenor* are stimulated to egg-laying by water soluble substances (naringin, hesperidin) present in *Citrus* plants (Honda, 1986). The diamondback moth, *Plutella maculipennis*, is stimulated to oviposit by the presence of mustard oils (Rausher, 1983). Secondary compounds also play an important role in the detection of plant hosts. Andersen and Metcalf

(1986) demonstrated the effect of indole, a floral odor component present in male blossoms of cucurbits, in the attraction of *Acalymma vittatum* and *Diabrotica virgifera* to *Cucurbita maxima*.

Competition

Competition may occur either among members of a single species or between species utilizing the same resource (Horn, 1988). Intra or interspecific competition is a density-dependent process. In general, as population size increases, there is a struggle amongst the insects for food and space, resulting in a smaller birth rate and increase death. Intraspecific competition may produce fewer and smaller individuals or cannibalism might occur (Polis, 1981); it can also have an effect on the prolongation of the immature stages, thus increasing the time to first reproduction (Horn, 1988). Intraspecific competition has long been regarded as one of the principal density-dependent mortality factors affecting insect populations (Cole, 1981). Knutson and Gilstrap (1990) reported cannibalism as an expression of intraspecific competition among larvae of *Diatraea grandiosella* prediapausing, because only one larvae overwinters in each stalk corn. The larch casebearer lays one egg per needle, but under high population pressure, they can lay more than one. However, only one will survive the competition for food and space (Long, 1990).

Interspecific competition may lead to the extintion of a species or to the coexistence of two or more species depending on the host, environment and insect habits (Cole, 1981; Horn, 1988).

Competitive displacement of one species by another was reported by Bess *et al.* (1961). *Opius longicaudatus* was introduced into Hawaii for the control of the fruit-fly *Dacus dorsalis*, but although it was established, parasitism of *D. dorsalis* was low. *O. vandenboschi* and *O. oophilus* were subsequently introduced. The population of *O. oophilus* increased rapidly, and eliminated the two other braconid species.

Diseases

Diseases caused by fungi, bacteria and viruses are considered density-dependent mortality factors (Varley *et al.* 1973; Horn, 1988). Myers (1988) has speculated that short-term genetic changes in susceptibility to pathogens may account for the cyclic pattern of population densities of many forest insects, although there is no direct evidence for this. Siegel *et al.* (1986) found that infection by the microsporidian, *Nosema pyrausta*, of both the parasitoid, *Macrocentres grandii*, and its host, *Ostrinia nubilalis*, resulted in fewer parasitoids surviving to adulthood.

Virus diseases have been reported as important mortality agents for insect populations. The collapse of a population of *Cnepharia* spp. larvae in summer barley caused by *Cnephasia granulosis* virus was reported by Glas (1986). He found that larval density decreased from 3200 per m ^{2} to 51 larvae per m ^{2} due to *C. granulosis*.

CHAPTER 3

DYNAMICS OF MACADAMIA NUT DAMAGE BY
Ecdytolopha torticornis

The purpose of this study was to characterize the seasonal changes in nut damage by *E. torticornis* in relation to nut production.

3.1 MATERIALS AND METHODS

Field work was carried out in a 222 ha macadamia estate located at Turrialba, Costa Rica, at elevations ranging from 620 to 700 m. The mean annual rainfall is 2600 mm, the mean temperature is 21 °C, and the relative humidity is around 80 %.

Every two weeks, for a total of 62 sampling dates, from May 1991 to September 1993, all the nuts which had fallen naturally from 40 trees were removed. Nuts were collected from trees of the four most commonly planted clones: 246 (11 trees), 344 (10 trees), 508 (10 trees) and 660 (9 trees). From April 1992, the sample size was increased to 100 trees (5 trees from each of 4 clones at 5 sites), and 100 nuts per tree were examined. Site 4 only had one tree of clone 508 due to errors during the selection of the trees. The remaining nuts from each tree were weighed in order to estimate the total number of nuts (see later).

Five sites (Plate 3.1) were chosen according to the age of the macadamia trees, availability of clones per site, and surrounding habitats. Site 1 was composed of lots 4 and 3A-B; site 2, by lots 1, 2 and 15A-B; site 3, by lots 10 and 11; site 4, by lots 7 and 14; and site 5, by lot 16. Site 1 had a flat topography, and was located at the entrance of the macadamia orchard, close to the main road and the Pejibaye River. Due to its proximity to the main road, much of the macadamia husk from the processing plant was deposited there. Site 2 also had a flat topography, but was situated on the lower slopes of a hill, close to the Pejibaye River. There were *Cassuarina* sp. trees planted along an internal road nearby. Site 3 was on a slight slope, situated at the mid-altitude of the farm. Site 4 had an irregular shape, with a steep slope, and was surrounded by *Cassuarina* sp. trees,
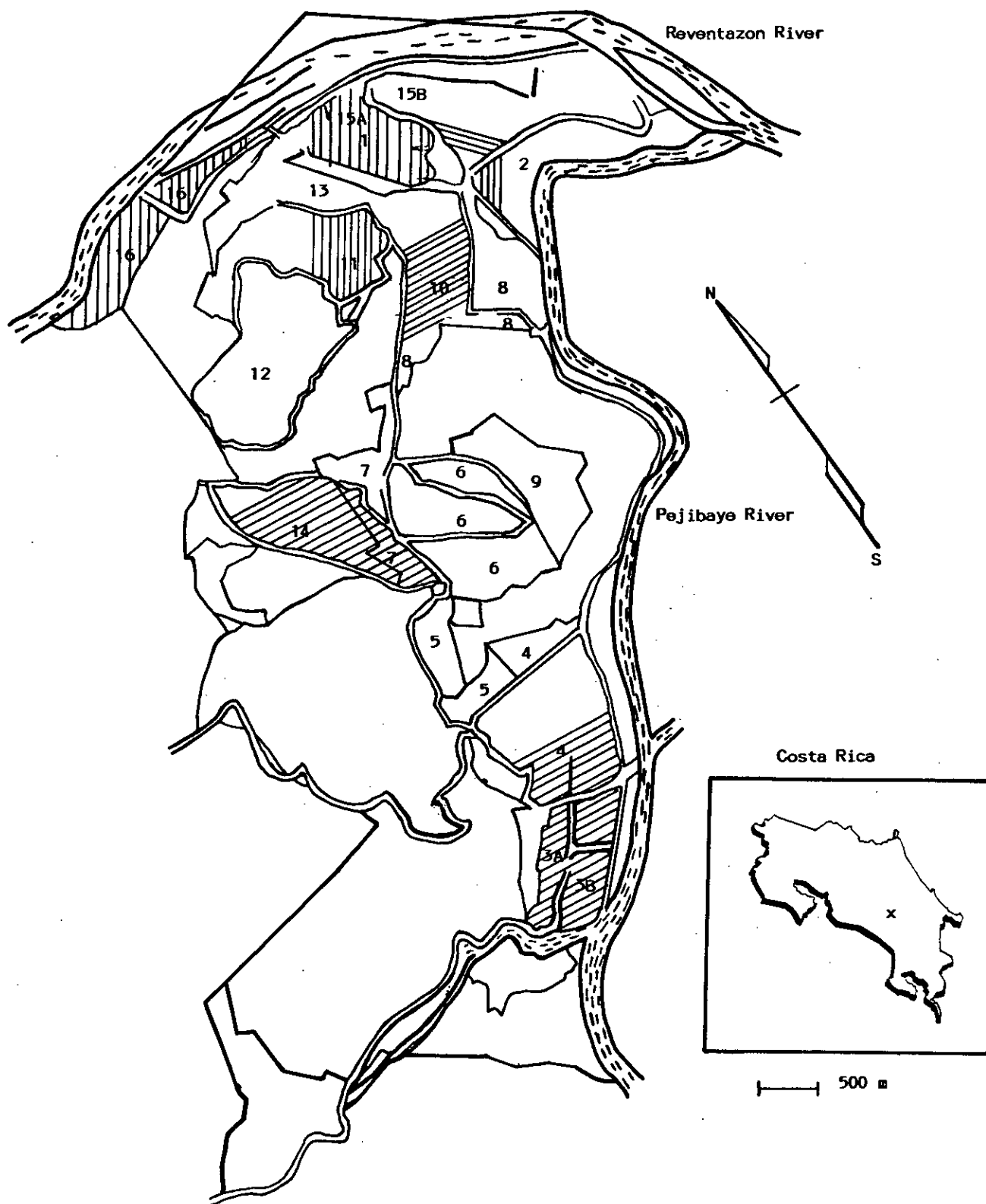
Plate 3.1. The distribution of the macadamia lots within Oriente Farm, Turrialba, Costa Rica. (Lot boundaries shown as single lines, roads as double lines).

sugarcane, pasture, and macadamia intercropped with coffee. Site 5 had a flat topography, and was isolated from the other lots. This site ran along the Reventazón River, and was surrounded by forest and a sugarcane plantation.

Harvested nuts were sorted into undamaged fully developed nuts, sick nuts (from pathogens or insects other than nutborers), immature nuts, and nuts damaged by the nutborer. Nuts damaged by the nutborer were opened to determine whether the husk alone was affected or whether the kernel was damaged also. Only the latter category of damage was considered of potential economic damage. The number of nutborer larvae inside each nut was recorded and, from October 1991 onwards, their instar. The numbers of nutborer and parasitoid pupae were likewise noted.

Percentage nut damage or infestation, was calculated by dividing the number of damaged nuts by the sum of undamaged, bored, sick and immature nuts.

$$\% \text{ nut damage} = \frac{\text{No. of damaged nuts}}{\text{(Total undamaged + immature + sick + bored)}} \times 100$$

The weight of the remaining nuts was transformed to the number of nuts by obtaining the mean nut weight from 100 nuts in each clone (clone 246, 13 g; clone 344, 17 g; clone 508, 15 g; clone 660, 14 g). The number of nuts with damaged husk or with damaged kernels were transformed by sqrt(x + 0.5) to homogenize error variance.

Analyses of variance were carried out separately for samples 1-24 and 25-62 on the total number of nuts with husk and kernel damage to assess the effect of clones and sites. Trees were nested within clones to test for differences in nut damage between trees. Differences in the means were calculated by the LSMeans, and Duncan's Multiple Range Test. Analyses of variance were conducted using the SAS program (SAS, 1985).

The daily maximum and minimum temperatures and rainfall were obtained from the weather recording station at CATIE.

The husk width for each clone was measured with a caliper during the parasitism study (Chapter 4) to see whether husk width was related to nut damage.

3.2 RESULTS

A total of 100,895 nuts were inspected for nutborer damage in 1991, 138,302 nuts in 1992, and 109,681 nuts in 1993, an overall total of 348,878 nuts. The number of nuts inspected depended directly upon the number of nuts falling naturally from the trees. This varied during the year, showing a peak in October 1991 when a mean of 275 nuts per tree were collected, and in August 1992 when a mean of 250 nuts per tree were collected (Fig. 3.1).

There was a significant difference in the percentage of nuts damaged between the different clones (Table 3.1). During sampling dates May 1991 - March 1992, nut damage was higher in clones 344 (8.07 % nuts damaged) and 246 (7.84 %), than in clones 660 (5.50 %) and 508 (4.77 %) (Table 3.2). During sampling dates April 1992 - September 1993, nut damage was also higher in clones 344 (6.30 % nuts damaged) and 246 (6.12 %), than clone 660 (4.60 %), and clone 508 (3.97 %). However, there was a significant difference for the interaction between clone and site for the latter sampling dates (Table 3.1).

The percentage of damaged nuts is presented in Figure 3.2. Three peaks of nut damage were observed: May 1991, June 1992, and April 1993. In 1991, nut damage peaked in May for clones 246 and 660, in July for clone 344, and in September for clone 508. During 1992, nut damage was highest in July for clones 246, 344 and 660, and in March for clone 508. Nut damage was highest in April for all clones in 1993 (Figs. 3.3 - 3.6).

Nut damage also differed between individual trees within clones to a highly significant degree (F = 3.54; df = 92; P < 0.001). Thus, although in general, nuts from clones 344 and 246 were damaged to the highest degree, some of the trees consistently suffered a low amount of damage. The opposite result was observed in trees from clones 508 and 660. Duncan's multiple range test did not detect differences between the means of damaged nuts of clones 344 and 246, or between clones 660 and 508.
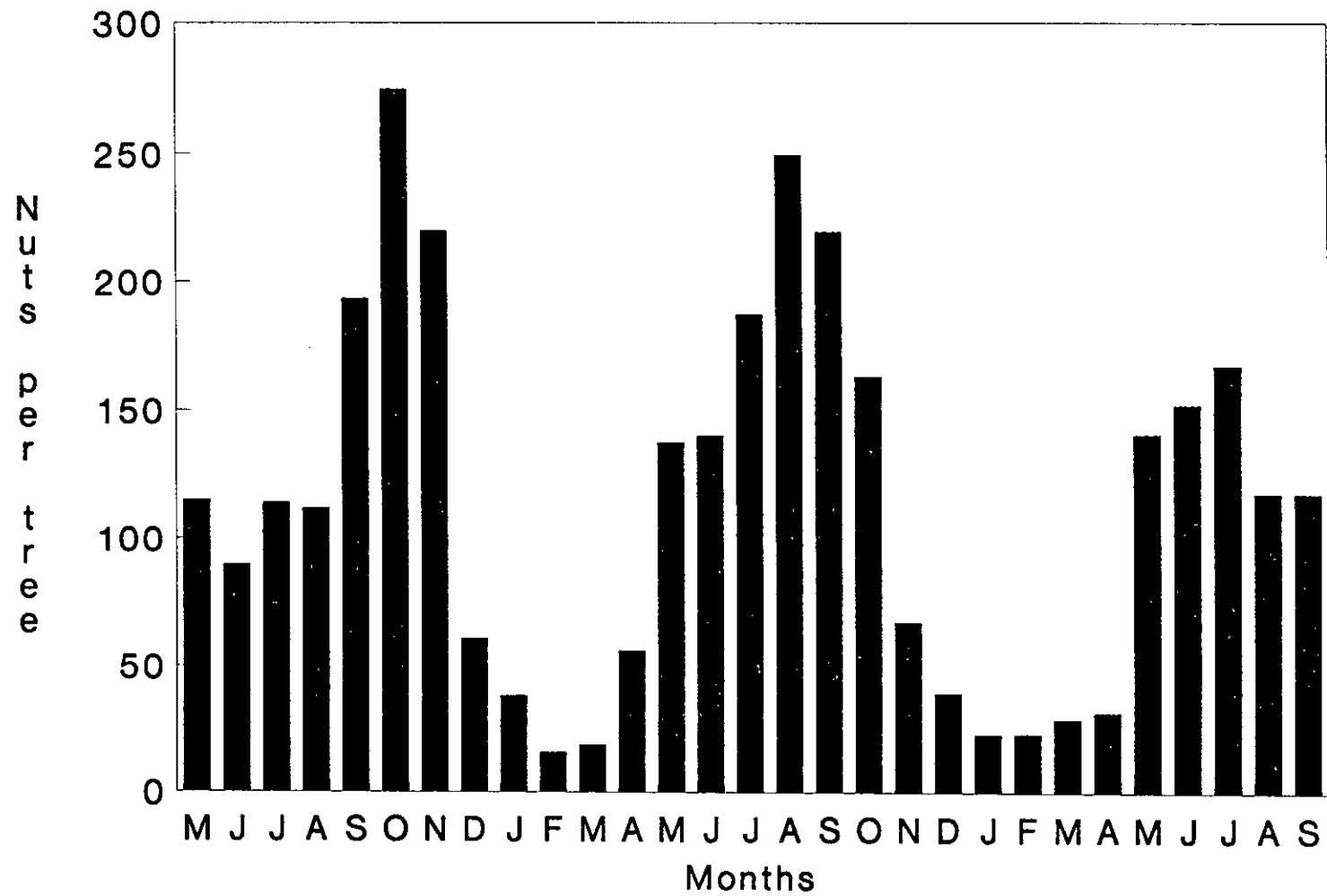
Fig. 3.1: The mean number of naturally fallen nuts per tree per sample at Oriente Farm, Turrialba, Costa Rica, from May 1991 to September 1993. Monthly averages from 1 to 3 (usually 2) sampling days are given.

Table 3.1: Statistical analysis of the percentage of nut damage by *E. torticornis* by clone and by site, Turrialba, Costa Rica.

Sample dates 1-24			Sample dates 25-62		
Source	DF	F	Source	DF	F
Clone	3	28.08***	Clone	3	12.41***
			Site	4	18.32***
			Clone*Site	12	4.71*

*P < 0.05;   *** P < 0.001

Table 3.2: Mean percentage of damaged nuts by *E. torticornis* by clone and site.

Sample dates 1-24		Sample dates 25-62			
Clone	Mean % damaged nuts	Clone	Mean % damaged nuts	Site	Mean % damaged nuts
344	8.07 a	344	6.30 a	1	6.73 a
246	7.84 a	246	6.12 a	4	6.10 ab
660	5.50 b	660	4.60 b	5	4.67 bc
508	4.77 b	508	3.97 b	2	4.65 bc
				3	4.08 c

Means followed by the same letter are not significantly different, LS Means test P = 0.05
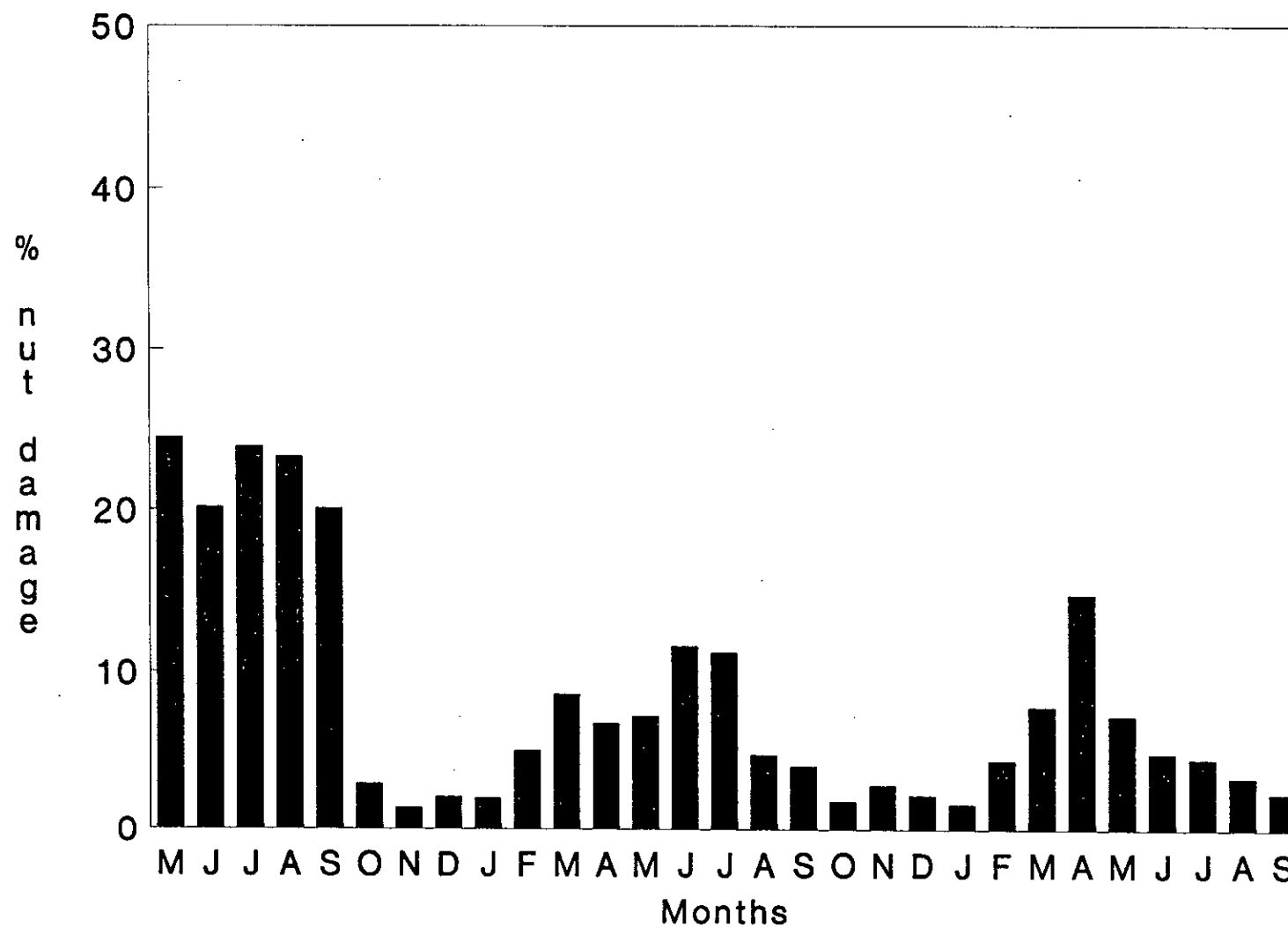
Fig. 3.2:   Percentage of macadamia nuts damaged by *E. torticornis* (all clones) in Oriente Farm, from May 1991 to September 1993.
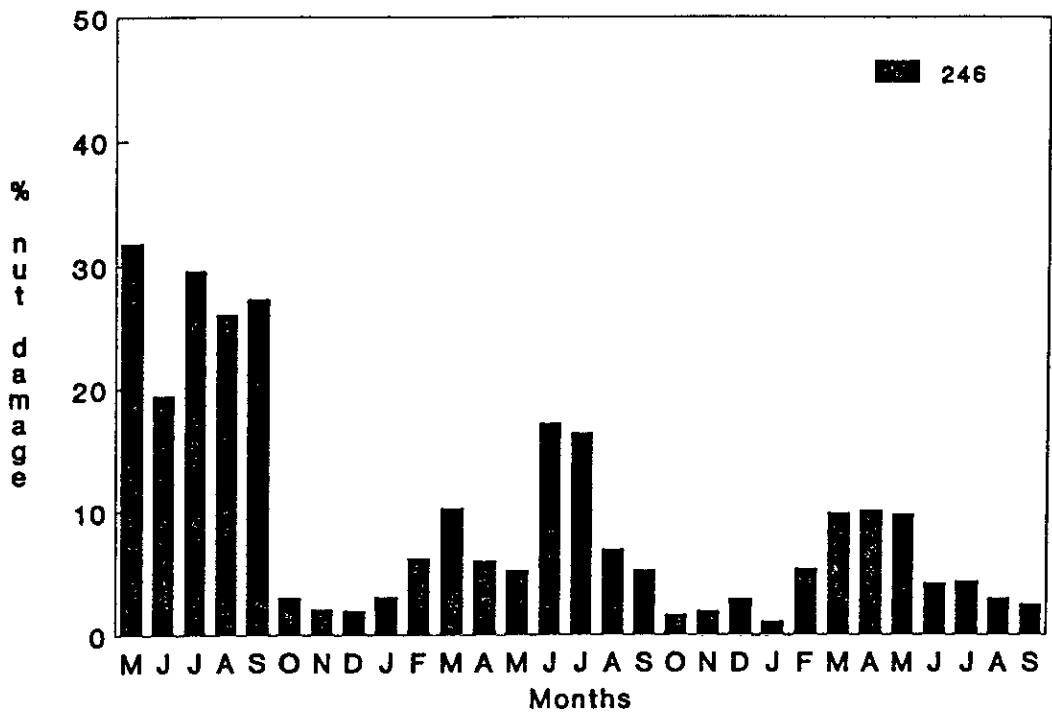
Fig. 3.3:   Percentage of macadamia nuts damaged by *E. torticornis*: clone 246, from May 1991 to September 1993.
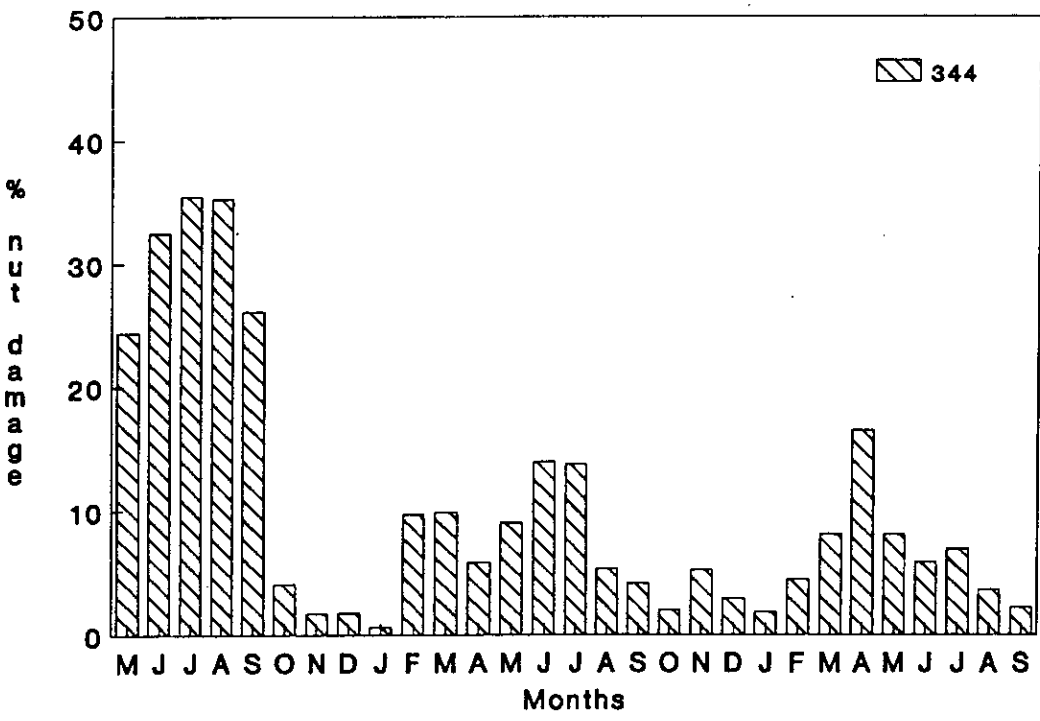
Fig. 3.4:   Percentage of macadamia nuts damaged by *E. torticornis*: clone 344, from May 1991 to September 1993.
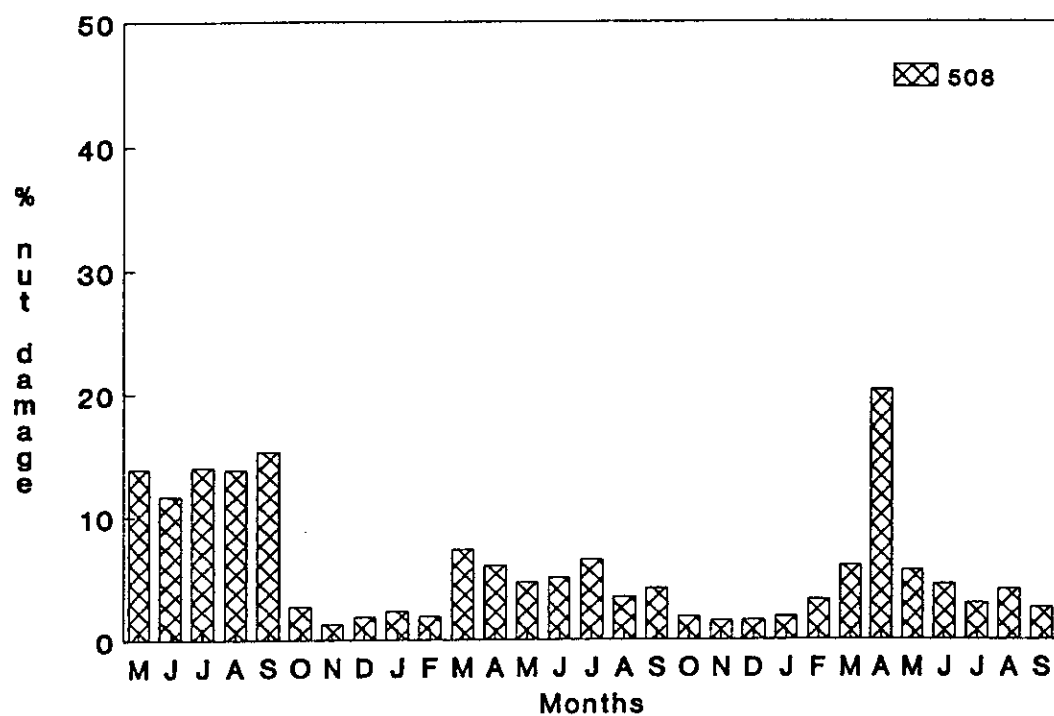
Fig. 3.5: Percentage of macadamia nuts damaged by *E. torticornis*: clone 508.
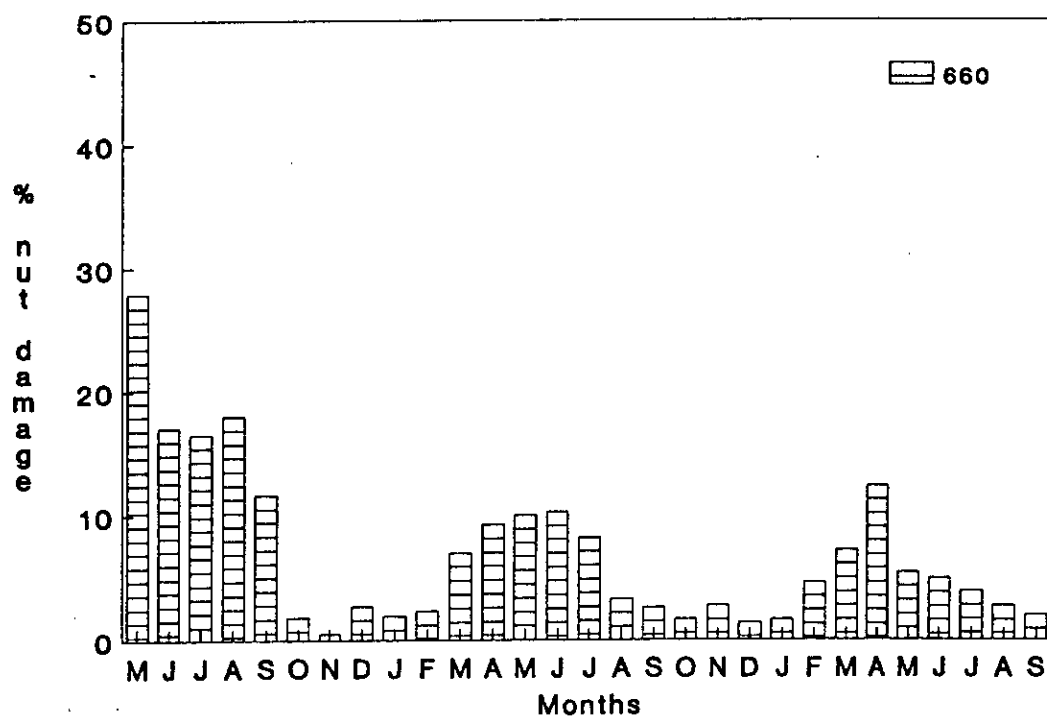
Fig. 3.6: Percentage of macadamia nuts damaged by *E. torticornis*: clone 660.

For all clones, nut damage peaked before nut production peaked (Figs. 3.7 - 3.10). There were three peaks where the mean number of nuts was highest: October 1991 for clones 246 and 344, November for clone 508 and September for clone 660. During 1992, the number of nuts was highest in September for clones 246 and 508, and in August for clones 344 and 660. In 1993, nut production was highest in June for clones 246, 344 and 508, and in July for clone 660.

Nut production decreased during the three years of sampling, being highest in 1991 followed by 1992 and 1993 (F = 258; df = 2; P < 0.0001) (Figs. 3.7 - 3.10). The same trend was observed for nut damage where a mean of 27.5 % damaged nuts was found in 1991, 5.8 % in 1992, and 4.6 % in 1993. The percentage of nut damage was highest in clone 344 (10.4), followed by clone 246 (10.1), clone 660 (6.96) and clone 508 (5.74). However, nut damage varied between clones each year (F = 10.12; df = 6; P < 0.0001). The between year pattern of nut damage per clone is consistent (Fig 3.11). However, nut damage was highest in clone 344 during 1991 to 1993.

Differences in nut damage for each site were recorded from April 1992 to September 1993. Nut damage was significantly different between sites (Table 3.1, Fig. 3.12). It was highest in sites 1 (6.73 %) and 4 (6.10 %), intermediate in sites 5 (4.67 %) and 2 (4.65 %), and lowest in site 3 where a mean of 4.08 % nuts were damaged. However, the interaction between clone and site was significant (F = 1.94; df = 12; P = 0.02). The percentage of damaged nuts per clone in each site is presented in Figure 3.13. Nut damage was similar for all sites for clones 508 and 660, and varied widely in clones 246 and 344.

Damage to the kernel, which represents direct commercial loss caused by the nutborer, was closely related to the percentage of immature nuts (Fig. 3.14). It was highest in May 1991, and decreased as immature nuts decreased. A similar trend was observed during 1992, where it peaked prior to the percentage of immature nuts which peaked in April 1992. In 1993, the percentage of kernel damage was highest after the percentage of immature nuts peaked, but was lower than that for 1991 - 1992.

Temperature and rainfall did not seem to have any influence on the percentage of nut damage (Fig. 3.15).
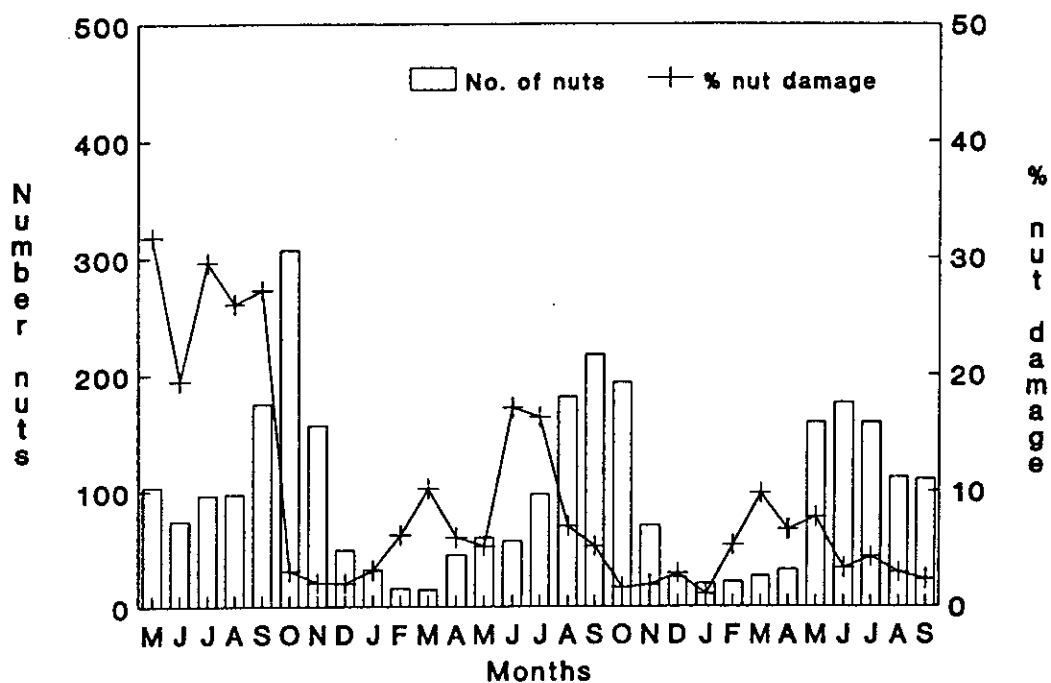
Fig. 3.7:   The mean number of nuts per sampling date and the
percentage of nut damage by *E. torticornis*:   clone 246,
from May 1991 to September 1993.
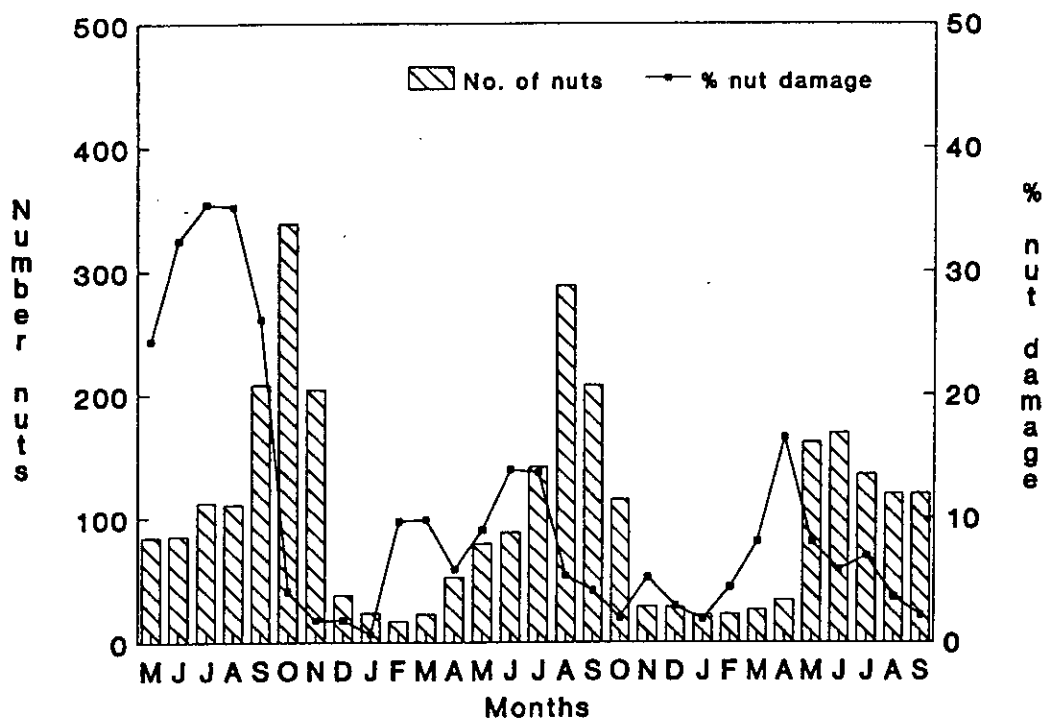
Fig. 3.8:   The mean number of nuts per sampling date and the
percentage of nut damage by *E. torticornis*:   clone 344,
from May 1991 to September 1993.
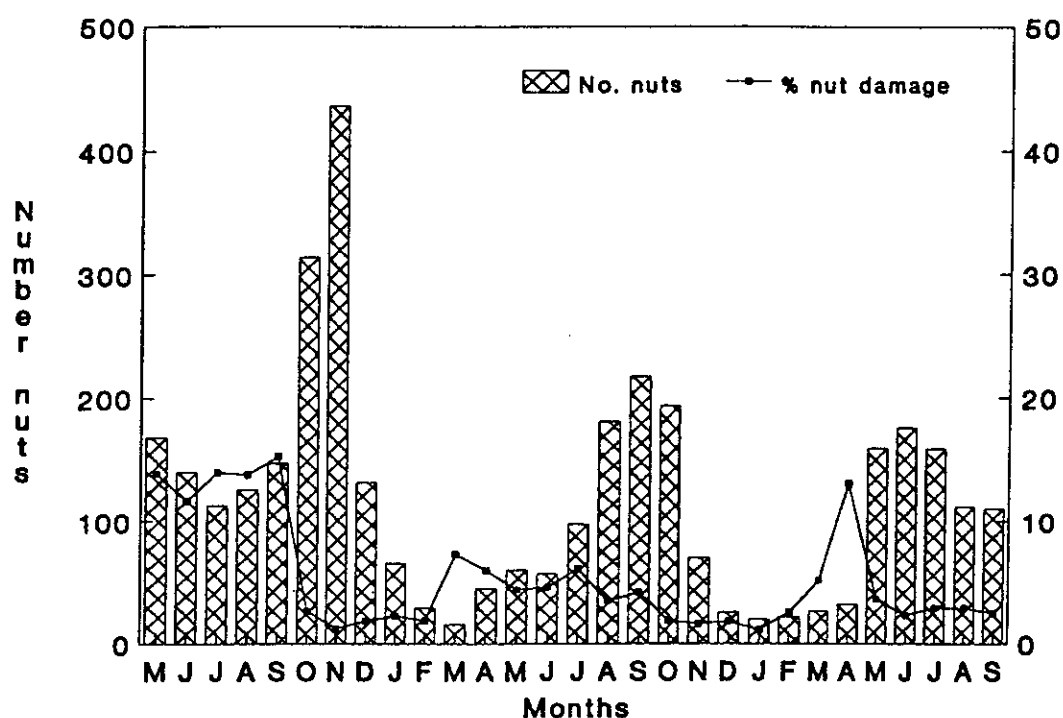
Fig. 3.9: The mean number of nuts per sampling date and the percentage of nut damage by *E. torticornis*: clone 508.
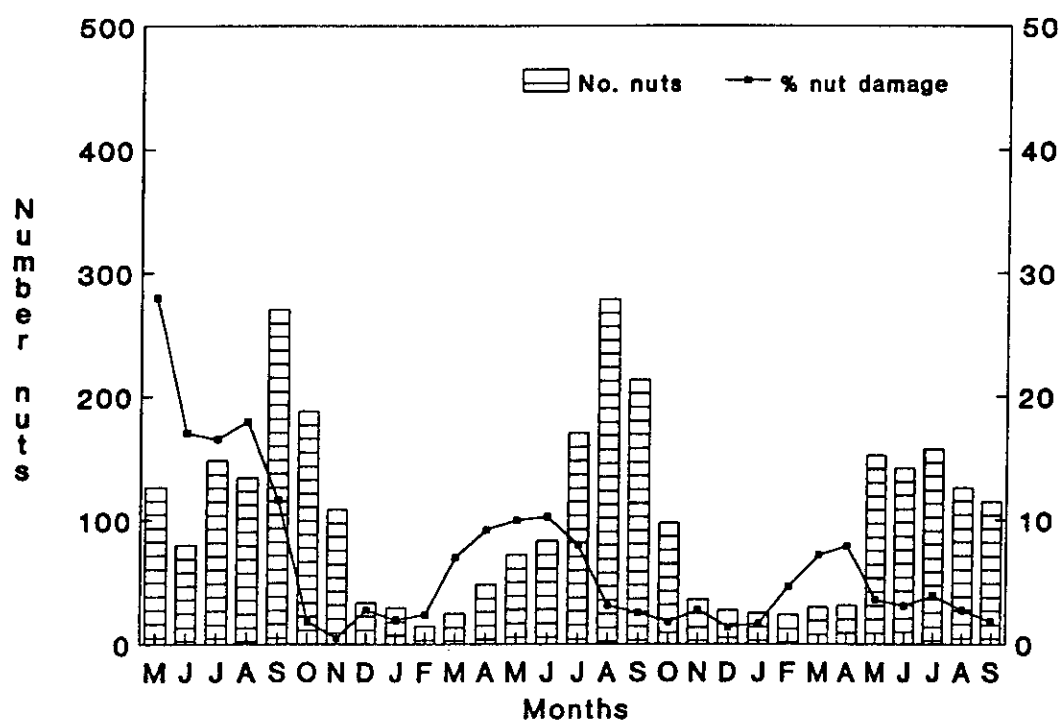
Fig. 3.10: The mean number of nuts per sampling date and the percentage of nut damage by *E. torticornis*: clone 660.
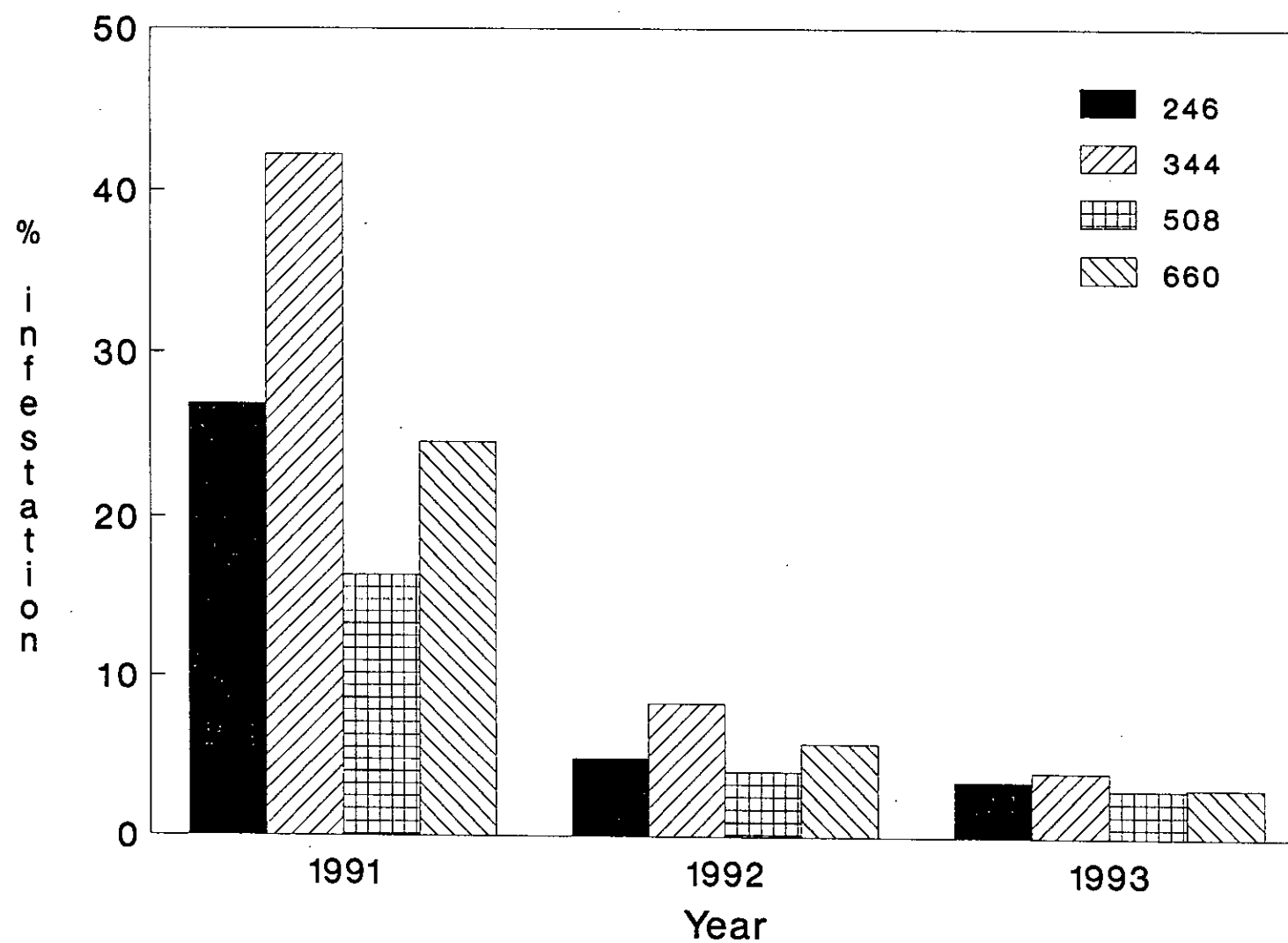
Fig. 3.11:   Mean percentage of nuts damaged by *E. torticornis* by clone, by year.
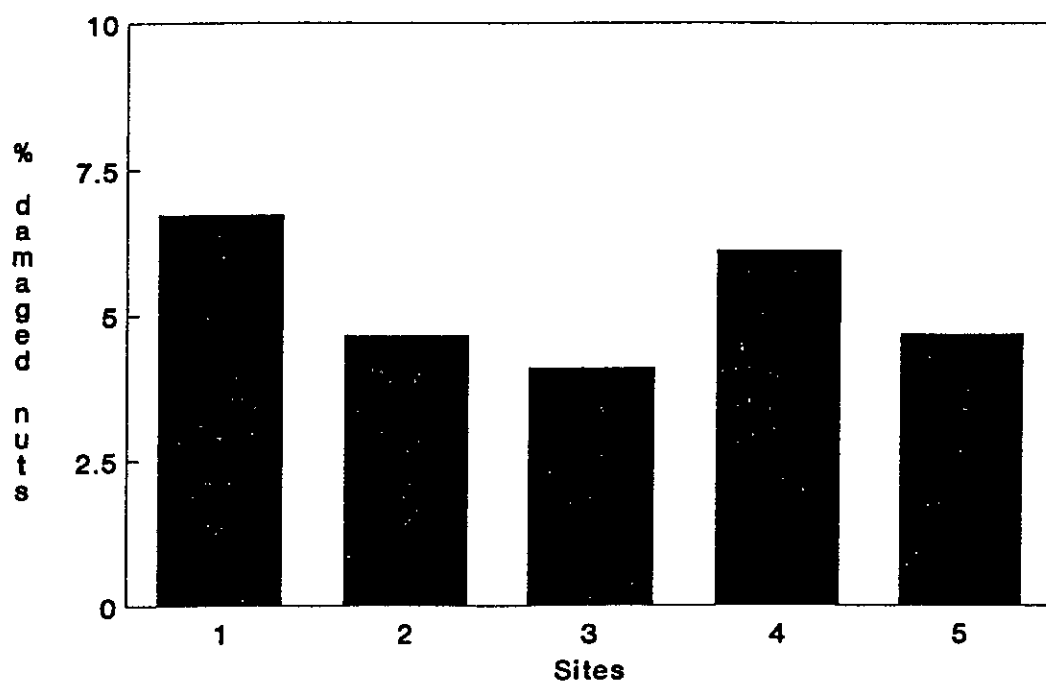
Fig. 3.12:   Mean percentage of macadamia nuts damaged by *E. torticornis* in five sites at Oriente Farm, Turrialba.
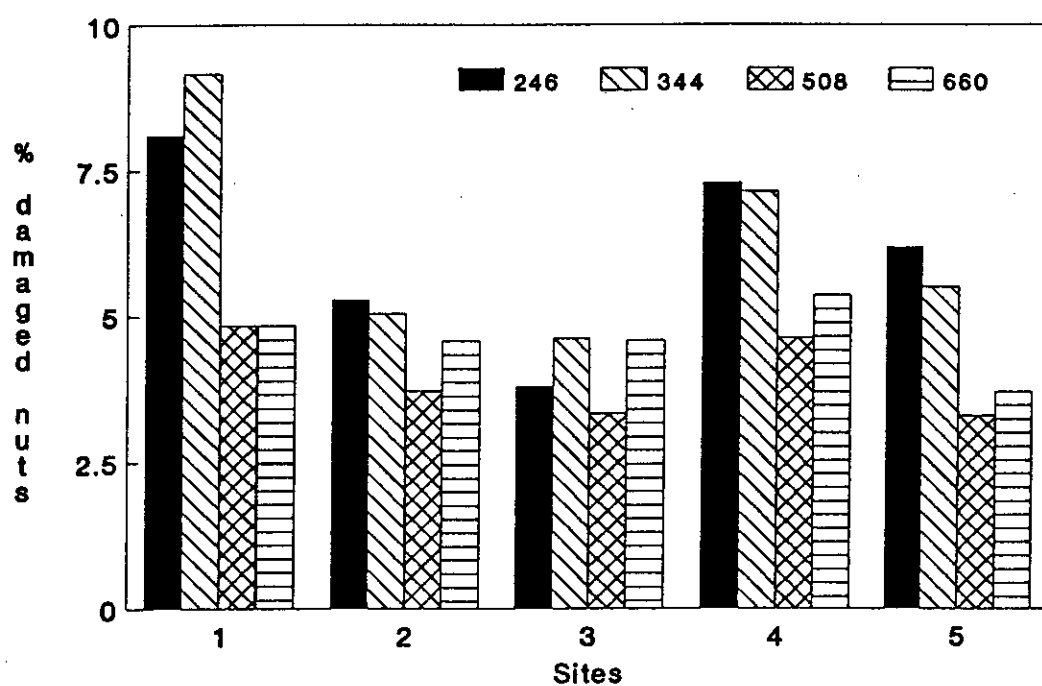
Fig. 3.13:   Mean percentage of macadamia nuts damaged by *E. torticornis* by clone in five sites at Oriente Farm, Turrialba.
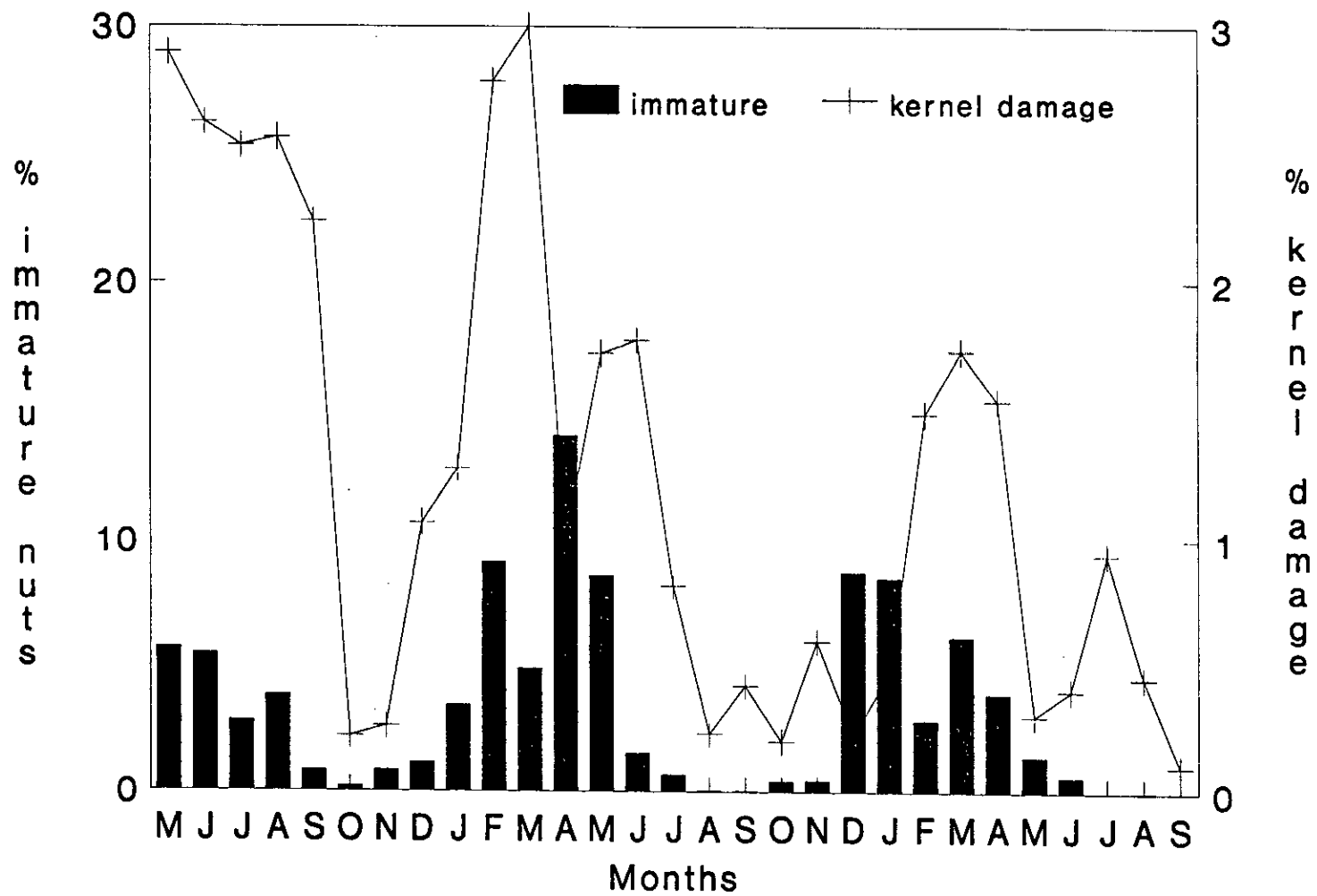
Fig. 3.14: Mean percentages of immature nuts, and nuts showing damage to the kernel, from May 1991 to September 1993.
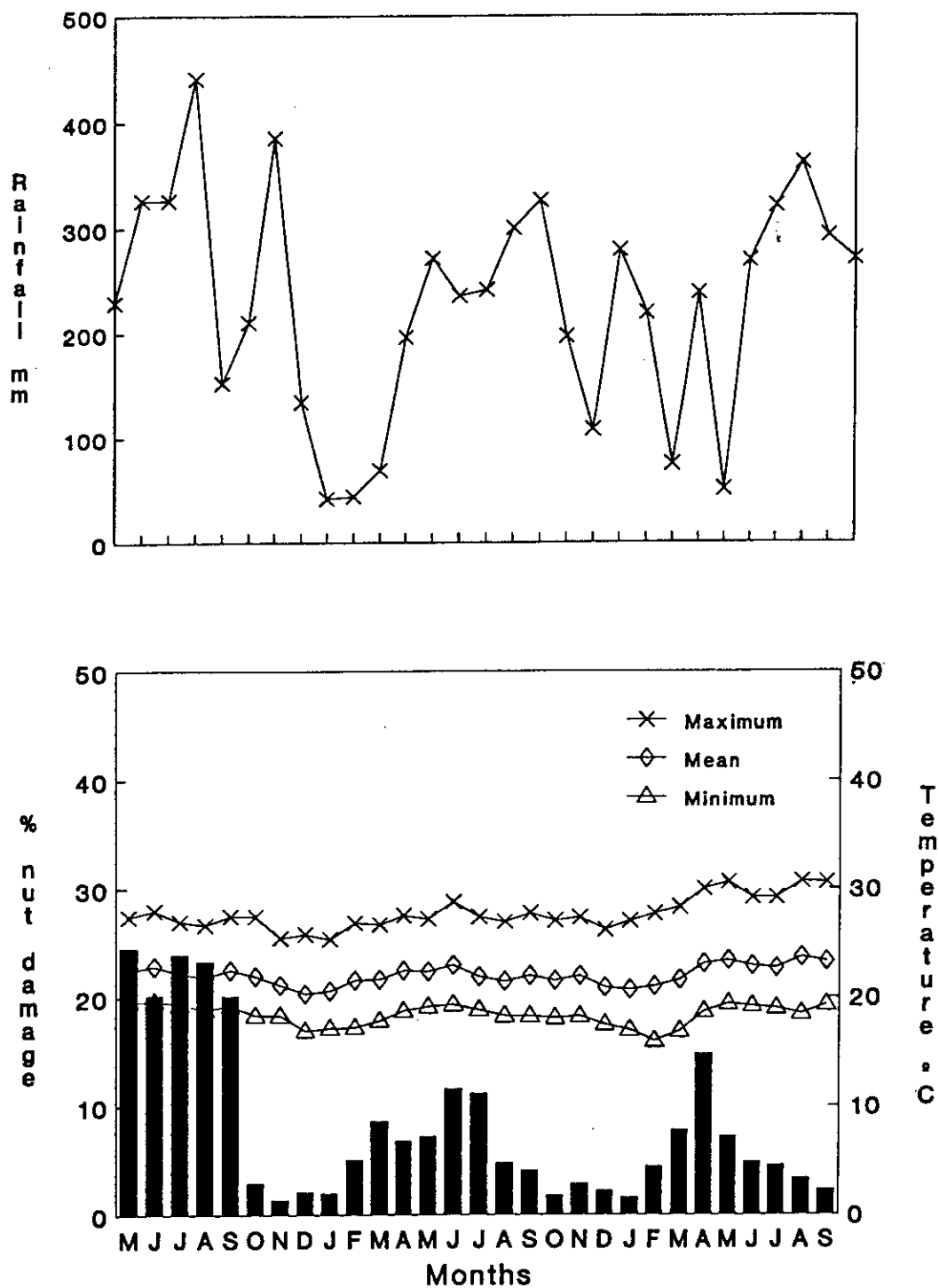
Fig. 3.15: Air temperature and rainfall during the period of nut damage by *E. torticornis* from May 1991 to September 1993.

As the nutborer is multivoltine, all larval instars were present on each sampling date. The mean number of larvae was highest in site 4, followed by site 1, site 5, site 2, and site 3 which registered the lowest number of larvae (Tables 3.3-3.4, Fig. 3.16). This result was consistent with nut damage per site (Fig. 3.12). The result observed for the number of larvae per clone per site is not clear, although generally it followed a similar trend to that of damaged nuts (Fig. 3.17).

No significant difference between clones was found in husk thickness, so it seems unlikely that ease of penetration of the husk by the larvae plays an important role in affecting the susceptibility of different clones to the nutborer (F=0.60; df=330; P=0.61).

3.3 DISCUSSION

Nut production varied within and between years. It was highest in 1991 and decreased progressively in 1992 and 1993. The pattern of nut damage within and between years closely followed that of nut production, suggesting that the abundance of *E. torticornis* was limited to some degree by its food supply. Dempster and Pollard (1981) concluded that variation in the carrying capacity is often the most important factor determining year to year fluctuations in the population size of insects. For example, studies on the cinnabar moth, *Tyria jacobaeae*, have shown that its abundance is determined largely by the biomass of food available to its larvae (Dempster, 1971, 1975). Similarly, Kidd (1985) concluded that the abundance of the large pine aphid, *Cinara pinea*, was primarily controlled by changes in the food quality, as measured by the number of actively growing shoots of *Pinus silvestris*. Atkinson and Carnegie (1989), who studied the mortality factors which regulated *Eldana saccharina* populations, found that because the sugarcane was the most abundant host plant of this insect in Natal, on every occasion that sugarcane was harvested, a sharp decline in the population of *E. saccharina* occurred. Although there are seasonal variations in flowering and nut production, macadamia trees flower all year round. The *E. torticornis* can remain active throughout the year and the abundance of the

Table 3.3: Statistical analysis of the number of larvae of *E. torticornis* by clone and by site, Turrialba, Costa Rica.

Sample dates 1-24			Sample dates 25-62		
Source	DF	F	Source	DF	F
Clone	3	20.23***	Clone	3	7.58***
			Site	4	6.04***
			Clone*Site	12	1.76*

*P < 0.05; *** P < 0.001

Table 3.4: Mean number of larvae of *E. torticornis* by clone and site, Turrialba, Costa Rica.

Sample dates 1-24		Sample dates 25-62			
Clone	Mean no. larvae	Clone	Mean no. larvae	Site	Mean no. larvae
344	1.10 a	344	0.50 a	4	0.48 a
246	0.91 a	660	0.40 ab	1	0.46 a
660	0.54 b	246	0.35 bc	5	0.37 ab
508	0.37 b	508	0.26 bcd	2	0.32 abc
				3	0.25 bcd

Means followed by the same letter are not significantly different, LS Means test P = 0.05.
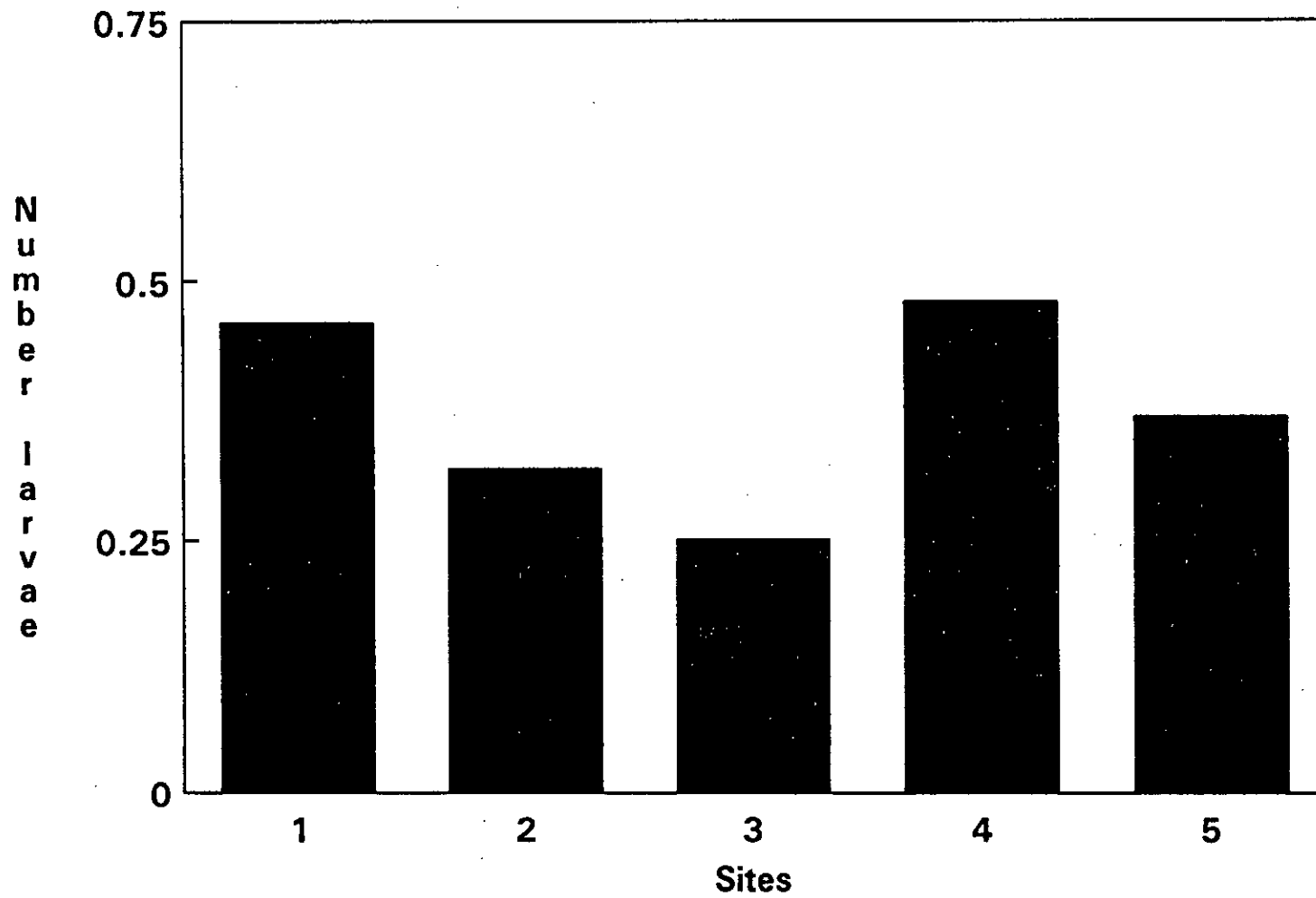
Fig. 3.16: The mean number of larvae of *E. torticornis* by site, Turrialba, Costa Rica.
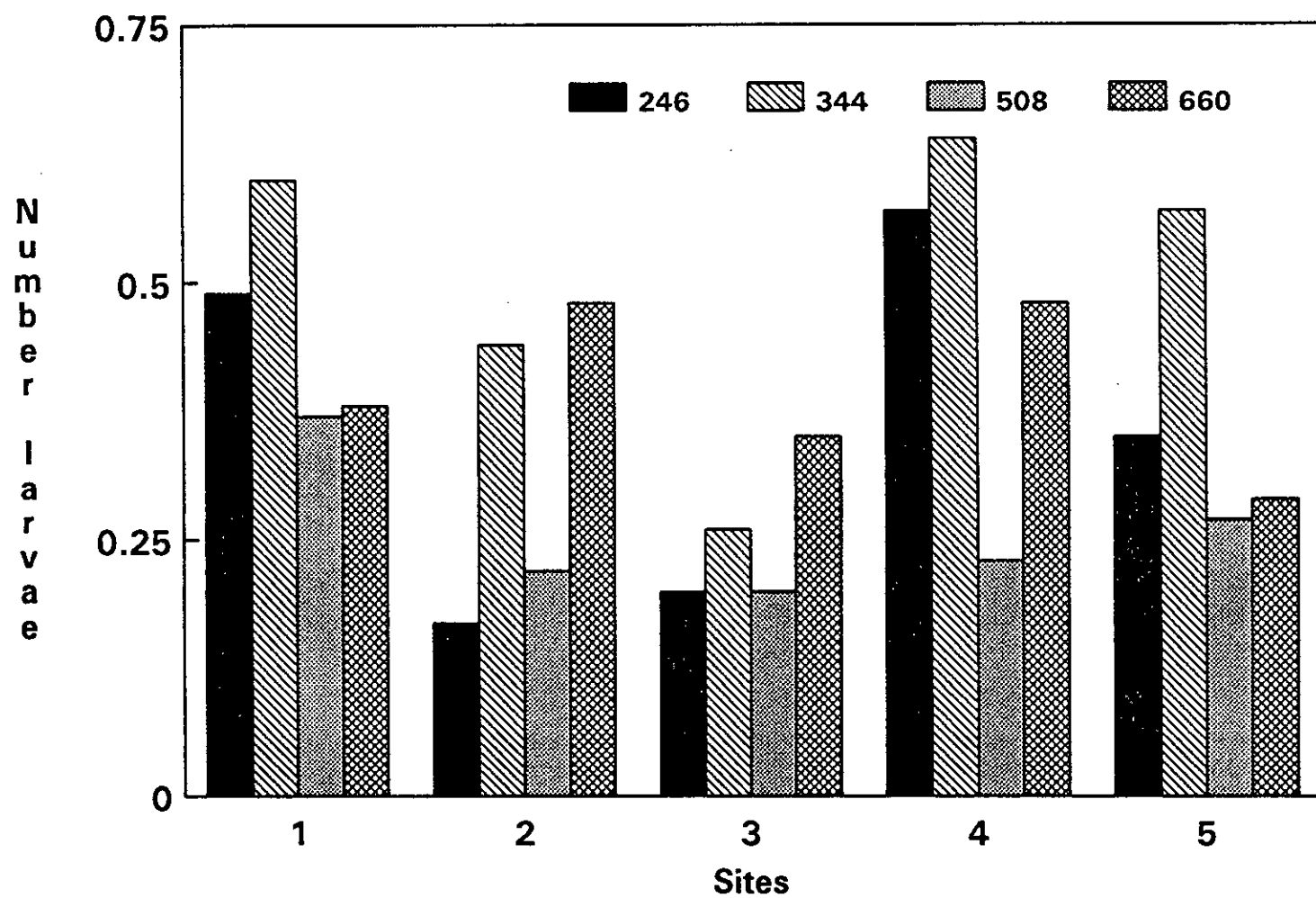
Fig. 3.17: The mean number of larvae of *E. torticornis* by site and clone, Turrialba, Costa Rica.

nutborer parallels the abundance of its food supply.

Different macadamia clones were found to vary in their susceptibility to nutborer attack. Clones 344 and 246 were the most susceptible. Similar results were obtained by Masís (1990), however, he found clone 246 to be the most susceptible of all. No conclusions can be made from his results for the differences between clones 246 and 344, since he performed no statistical analysis. Both this study and that of Masís indicate that clone 508 was the most tolerant to nutborer attack. Differences in clone damage may well be due to physical factors such as shape of the tree and nuts, colour of leaves and nuts, or chemical properties such as (N, water, and secondary compounds in the leaves or nuts). Prokopy and Bush (1973) found that *Rhagoletis pomonella* females oviposited on apples as a response to a combination of shape, colour, surface, texture and chemical compounds.

Nut damage peaked before nut production peaked. The probable reason for this is that prior to the production peak, the nuts are more digestible and nourishing food source, with softer husks and a higher water content.

Nut damage varied among sites, being highest in sites 1 and 4. It also differed between sites for clones 246 and 344, but was homogeneous among sites for clones 508 and 660. The difference in nut damage between sites is more likely to be due to a combination of factors such as the patchy distribution of the moth, the habitat surrounding each site, and the addition of pupae and adults brought in from the processing plant. A common practice in the farm, is the use of husk as a mulch for weed control. The husk is left to decompose primarily in sites 1 and less frequent in site 4 before it is applied under the tree canopy. Chamberlain (1989) considered that the nutborer is probably a poor flyer, and that this results in differences in nut damage between trees of the same clone causing a patchy distribution of the pest and of its damage. This might explain why nut damage in clones 344, and particularly in clone 246 varied so much between sites. A second possibility that could explain differences in damage between sites, especially the high level of damage in sites 1 and 4, is that there is an addition of nutborer adults and pupae due to husk deposition from the processing plant. Either the husk liberates chemical compounds which attract *E. torticornis*

moths, or pupae may be attached to the husks from the processing plant. A way of being sure that the population of this sites is local, and that it does not come from other farms, some of them very far from Turrialba, which have supplied nuts to the processing plant would be by studying the genetic variation of the moths from this sites. Pashley *et al.* (1985) analyzed the proteins of *Spodoptera frugiperda* electrophoretically, and concluded that populations in the southeastern United States were the offspring of moths overwintering in Mexico.

Kernel damage was restricted to the period when immature nuts were present. During this period the shell had not hardened, and the nutborer could bore through it. Since this damage has an effect on the commercial value of the nuts, measures must be considered to protect the crop during this period. Jones and Tome (1992) found a high correlation, r = 0.85, between the percentage of immature nuts harvested and the percentage of nuts with husk damage, but only when *Cryptophlebia* damage levels were high, (> 25 %).

The probable reason why no relationship was found between nut damage and abiotic factors is that temperature in Turrialba only varies slightly during the year, and although this is not the case for rainfall, after a larva has penetrated a nut, it occupies a protected habitat. The nut provides abundant fresh food, shields the larvae from abiotic factors and a high degree of protection against predators and falling from the tree. As the moths are poor flyers, and because they remain most of the time within the tree canopy (Chapter 1), and migration is not thought to affect the population size, it is also unlikely that rainfall affects the adult stage in a significant way. However, weather does interact with predation and parasitism and other biotic causes of mortality through its effect on the developmental rate of the larvae and nut production. Heavy rainfall can dramatically affect the number of nuts falling to the ground, and, therefore, considerably affect the patterns in nutborer damage. The data presented in the graphs represents the mean of rainfall in a month, and in Turrialba 300 mm of rain is possible in one day (unpublished CATIE weather recording station data).

The present study should be continued to see whether there is a cyclic pattern in the abundance of *E. torticornis* between years. If a

cyclic pattern is observed, this will provide useful information for focusing control measures before the period when nut damage is highest. However, Horn (1988) states that some insect populations are so variable as to be thoroughly unpredictable.

The laboratory data and field observations on *E. torticornis* damage pose the following questions: what makes clones 344 and 246 more susceptible to nutborer damage than clones 508 and 660, and what effect does the husk brought from the processing plant have on the nutborer population? These aspects are considered in Chapters 7 and 8.

CHAPTER 4

THE EFFECT OF PARASITISM ON THE POPULATION DYNAMICS OF *E. torticornis*

The aim of this study was to determine the presence of *E. torticornis* egg and larval parasitoids, to record population fluctuations in parasitoids, and to quantify the suppression of the nutborer population achieved.

4.1 MATERIALS AND METHODS

Parasitism was studied in forty damaged nuts per clone (246, 344, 508, 660), harvested at random from the trees each month, at Oriente Farm. Nuts were examined in the laboratory (23 ° C, 80 % RH) and the following variables were recorded: shell diameter, husk diameter, number of holes per nut, location of the larvae in the nut, number of larvae and their instar, and the number and species of parasitoids. From April 1992, sample size was increased to 15 damaged nuts per clone per site (five sites: 1, 2, 3, 4, 5, Plate 3.1) for a total of 300 nuts examined per month. The larvae found were incubated individually in split nuts in 165 cm^3 plastic cups until emergence of either the adult moth or a parasitoid. Large holes in the lids were lined with muslin to provide ventilation. Nuts were tied up with tape and moistened absorbent filter paper was added to the bottom of each cup in order to reduce dessication. Macadamia nuts clone 344, were used as the food source as this clone was found to be the most susceptible to *E. torticornis* (Blanco *et al.*, in press). Food was changed every two days.

Apparent percentage parasitism was estimated from the total number of parasitoids reared in relation to the total number of hosts either parasitized or succesfully reared to the adult stage. The following formula was used:

$$\% \text{ Parasitism} = \frac{\text{No. parasitoids emerged}}{\text{total host population}} * 100$$

4.2 RESULTS

Six species of hymenopteran parasitoids were recovered from the nutborer for the first time (Table 4.1). An egg parasitoid belonging to the family Trichogrammatidae was recovered in 1992 (Plate 4.1). Nuts containing fertile nutborer eggs collected from the field turned black in the laboratory, and a mean of 3.33 (SE = 0.68; n = 18) wasps per egg were observed (Plate 4.2). In view of its low occurrence, and the difficulties in finding unhatched nutborer eggs in the field, more emphasis was given to the study of larval parasitoids.

A total of three braconids, and one ichneumonid species were reared from the nutborer larvae between 1991 and 1993 (Plates 4.3 - 4.6). *Apanteles* sp. I occurred each year, while *Apanteles* sp. II and *Ascogaster* sp. occurred only during the latter years. The *Apanteles* species are named as I and II since specialists (see acknowledgements) were not able to identify them to the species level. The difference between these two species is based on the colour of the legs and their size: *Apanteles* I has brown legs and is larger, while *Apanteles* II has black legs. *Apanteles* I was the dominant parasitoid in terms of consistency. The larval parasitoid complex was dominated by *Apanteles* I during the first two years and by *Ascogaster* during the final year. *Apanteles* I was reared on 35 occasions in 1991, 63 in 1992 and 57 in 1993; *Apanteles* II was reared 13 times in 1992 and 22 in 1993; *Ascogaster* occurred once in 1992 and 193 times in 1993. The number of *Ascogaster* recorded was highest among all the parasitoid species, followed by *Apanteles* I and *Apanteles* II which occurred sporadically, and in small numbers (Fig. 4.1, Table 4.1A). There was a significant difference between the number of *Apanteles* I, and *Ascogaster* sp. parasitoids reared ($X^2 = 4.36$; df = 1; P < 0.05), (Chi square analysis was only calculated for these two parasitoids due to the very low abundance of the other species). *Pristomerus* sp. was reared only in two occasions during 1992. Although four parasitoids were reared from the nutborer larvae, multiple parasitism was not observed.

The percentage parasitism in each year of sampling is presented in Figure 4.1. The number of nutborer larvae parasitized by *Apanteles* I was 15 % in 1991, 16 % in 1992 and 4 % in 1993; parasitism by *Apanteles* II reached 4.3 % in 1992 and 3.7 % in 1993,

Table 4.1: The parasitoid complex and number of parasitoids reared from *Ecdytolopha torticornis* at Oriente Farm, Turrialba, Costa Rica, from 1991 - 1993.

	1991	1992	1993
Egg parasitoid			
Trichogrammatidae	-	18	-
Larval parasitoids			
Braconidae	35	77	272
Apanteles sp. I	35	63	57
Apanteles sp. II	0	13	22
Ascogaster sp.	0	1	193
Ichneumonidae	0	2	0
Pristomerus sp.	0	2	0
Larvae hyperparasitoid			
Perilampidae	0	0	1

Plate 4.1:   a) Tichogrammatidae adult, b) Egg of the
               macadamia nutborer, *Ecdytolopha torticornis*,
               parasitized by a species of Trichogrammatidae.
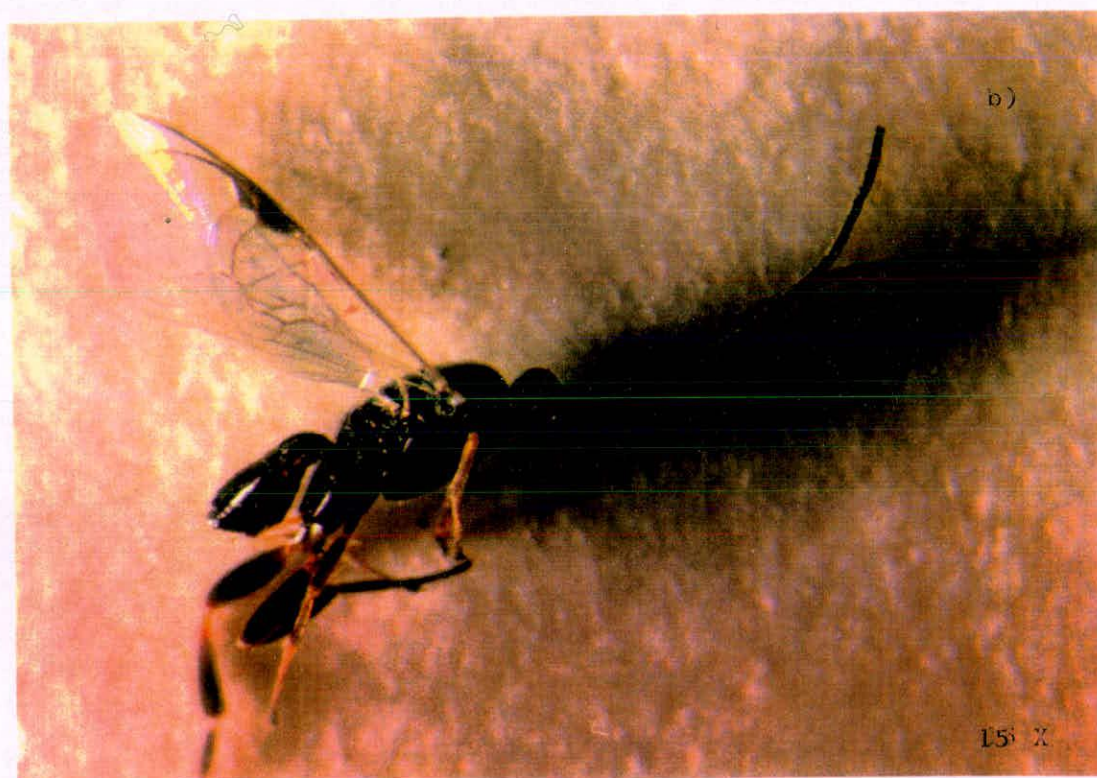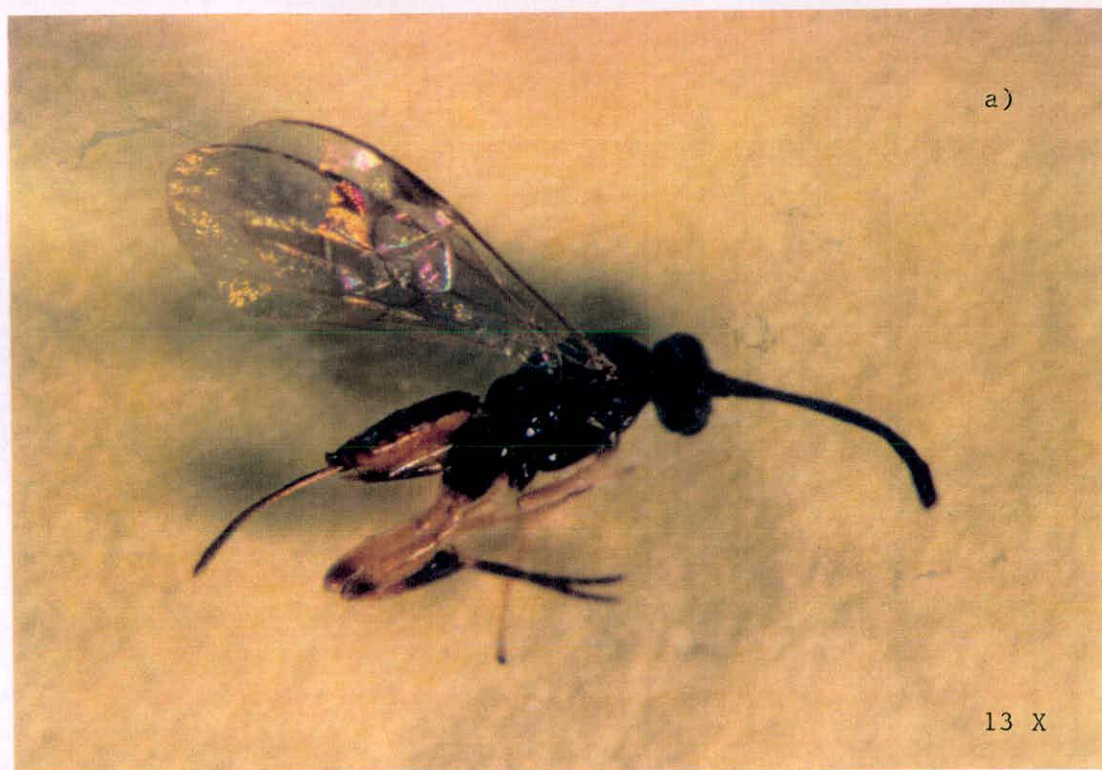
Plate 4.2:   a) *Apanteles* sp. I, b) *Apanteles* sp. II larval parasitoids of the macadamia nutborer, *Ecdytolopha torticornis*.
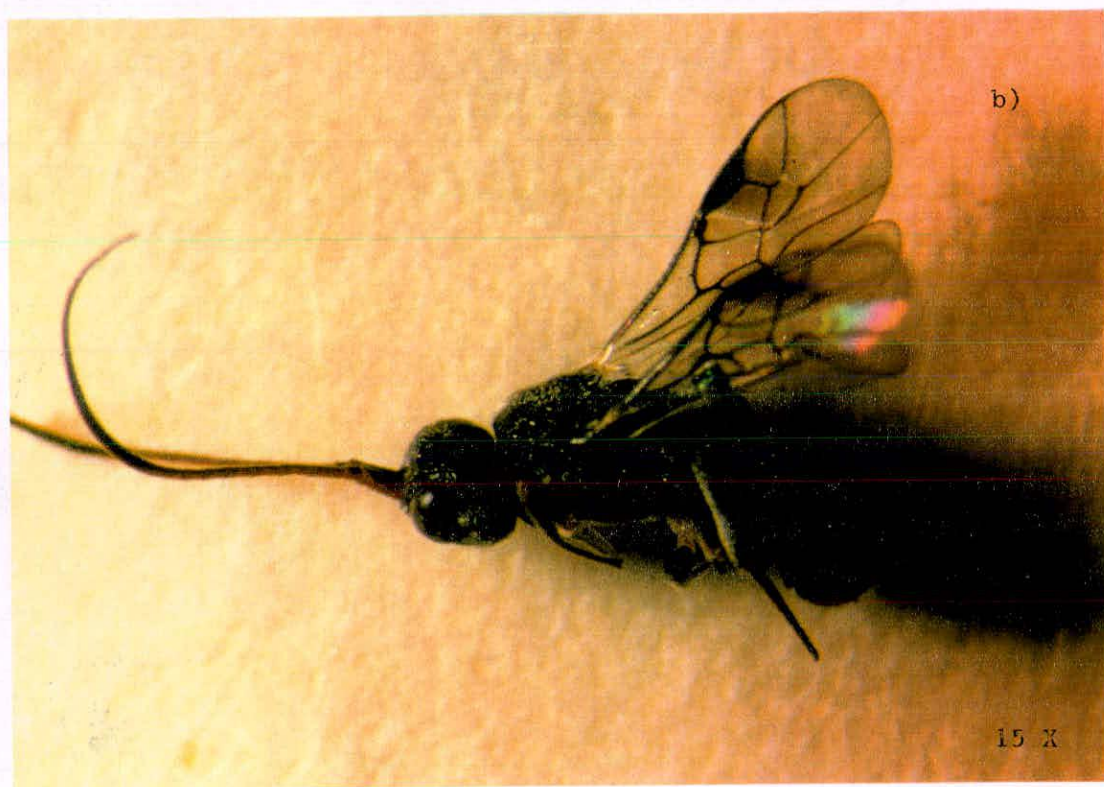
Plate 4.3:   a) *Pristomerus* sp., b) *Ascogaster* sp.,
              larval parasitoids of the macadamia
              nutborer, *Ecdytolopha torticornis*.
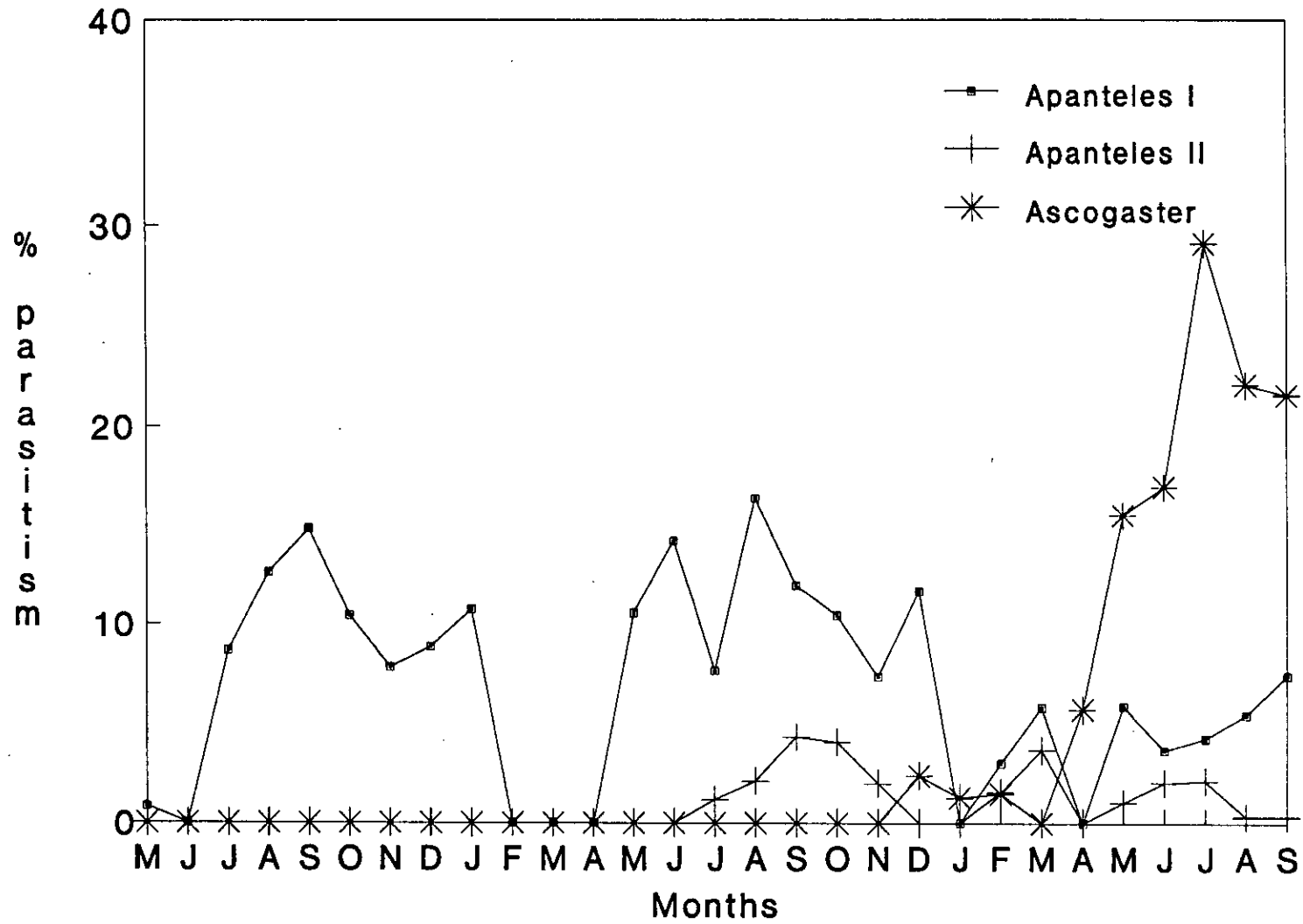
Fig. 4.1:   Percentage parasitism of *E. torticornis* by *Apanteles* sp. I, *Apanteles* sp. II, and *Ascogaster* sp. from May 1991 to September 1993.

while the level of parasitism by *Ascogaster* was 3 % parasitism in 1992 and 29 % in 1993.

A larva hyperparasitoid belonging to the family Perilampidae was found in 1993.

Total parasitism was related to the mean number of damaged nuts per month: there was an inverse relationship between the number of damaged nuts and percentage parasitism (Fig. 4.2). There were three peaks where parasitism was highest: September 1991, August 1992 and August 1993. These peaks followed the months when nut damage was highest, except in 1991 where it coincided with the peak number of damaged nuts. However, even in 1991 there was evidence of parasitism lagging slightly behind nutborer damage because parasitism remained at a high level while nutborer damage declined. The parasitoid population peaked after nut damage reached its highest value, indicating a delayed density-dependent response of the parasitoid population to that of *E. torticornis*. Percentage parasitism increased in 1992 and 1993, being highest at the end of the third year. However, parasitoids were not reared on every sampling date during the first two years, but were reared in every occasion during the third year of study, so for the early years percentage parasitism may be underestimated.

The percentage parasitism per clone is presented in Figures 4.3-4.7, Table 4.2A. The monthly estimates of percentage parasitism were highest among larvae from clone 660 reaching a maximum of 33 % in 1991, and 71 % for the same clone in 1992; percentage parasitism was highest in clone 246 in 1993 (80 %). Percentage parasitism for individual clones had a similar pattern to that of the mean number of damaged nuts and total parasitism (Fig. 4.2). There was a highly significant difference among the number of parasitoids reared per clone, being highest in clone 246 (129 parasitoids), followed by clone 660 (97 parasitoids), 344 (96 parasitoids), and 508 (64 parasitoids) (X^2 = 21.89; df = 3; P < 0.001). However, no significant difference was found for overall parasitism (X^2 = 2.76; df = 3; P = 0.53). The overall parasitism was highest in clone 246 (19.9 %, 649 larvae), followed by clone 660 (15.5 %, 624 larvae), clone 344 (13.1 %, 732 larvae), and clone 508 (11.3 %, 565 larvae). Parasitism might have been higher than estimated since some of the small larvae died during rearing. Parasitism fluctuated widely between sites (X^2 = 30.14; df = 4;
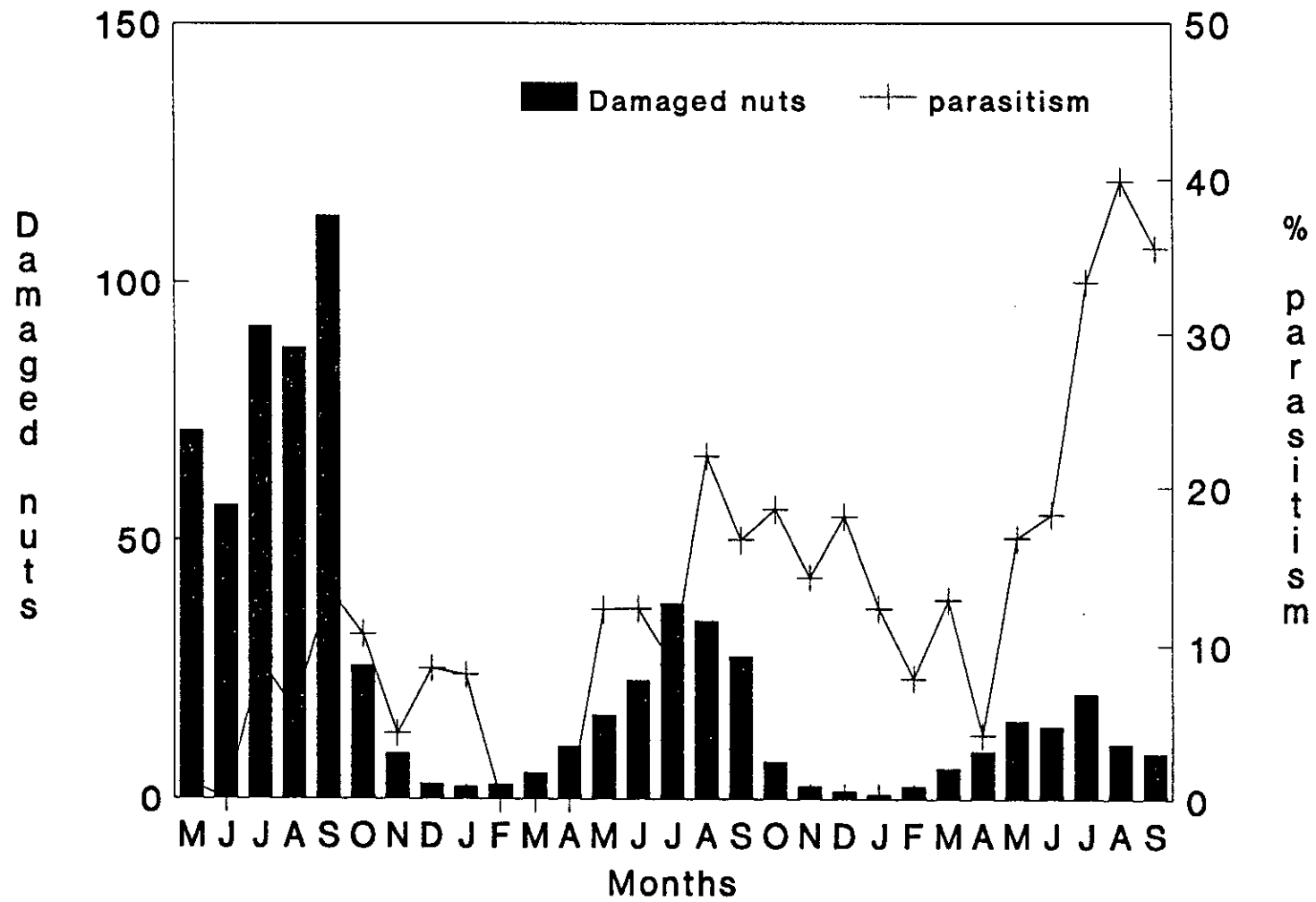
Fig. 4.2:   The mean number of damaged nuts per month and the percentage parasitism of *E. torticornis*, from May 1991 to September 1993.
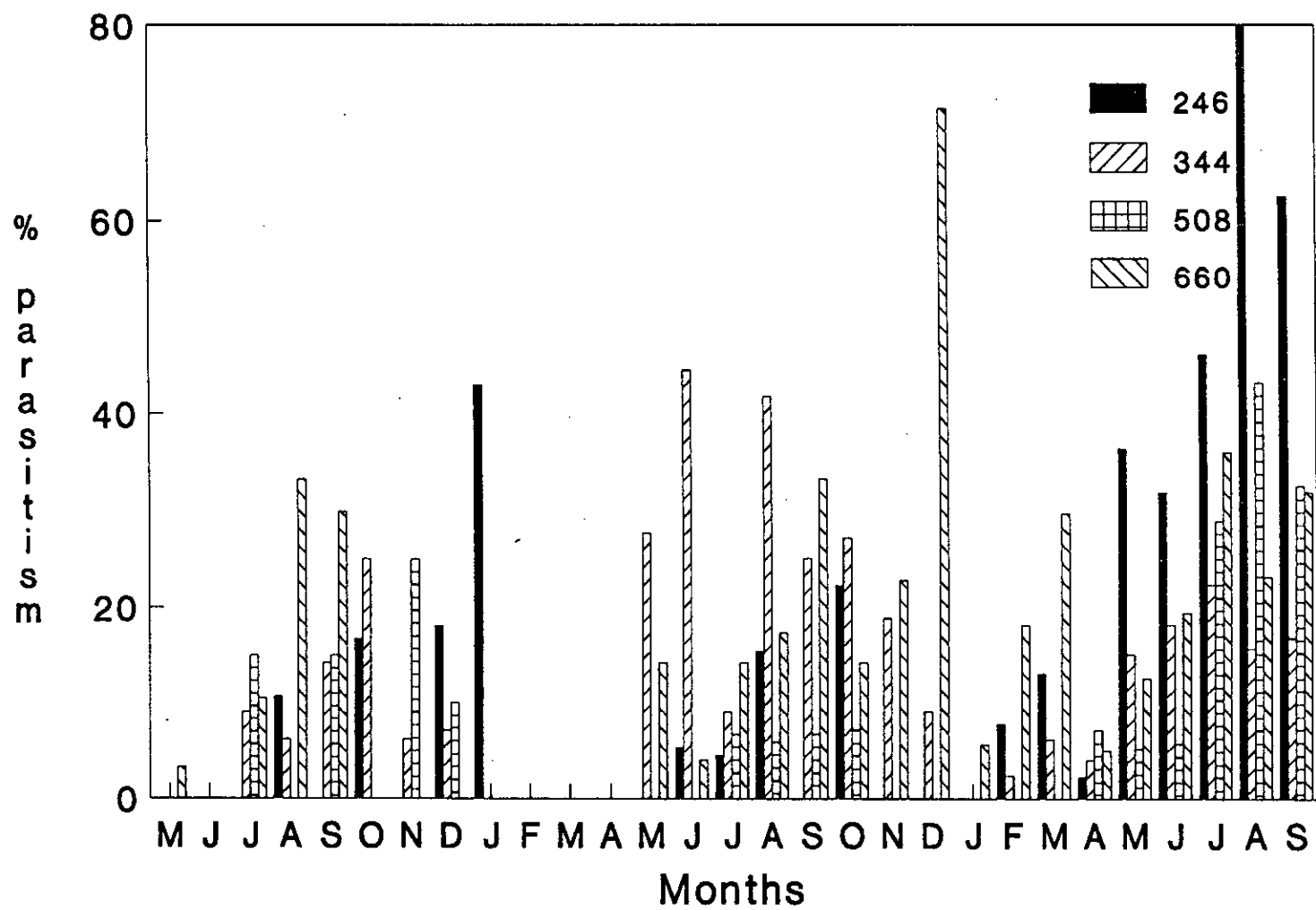
Fig. 4.3:   Percentage parasitism of the macadamia nutborer *E. torticornis* in different macadamia clones, from May 1991 to September 1993.
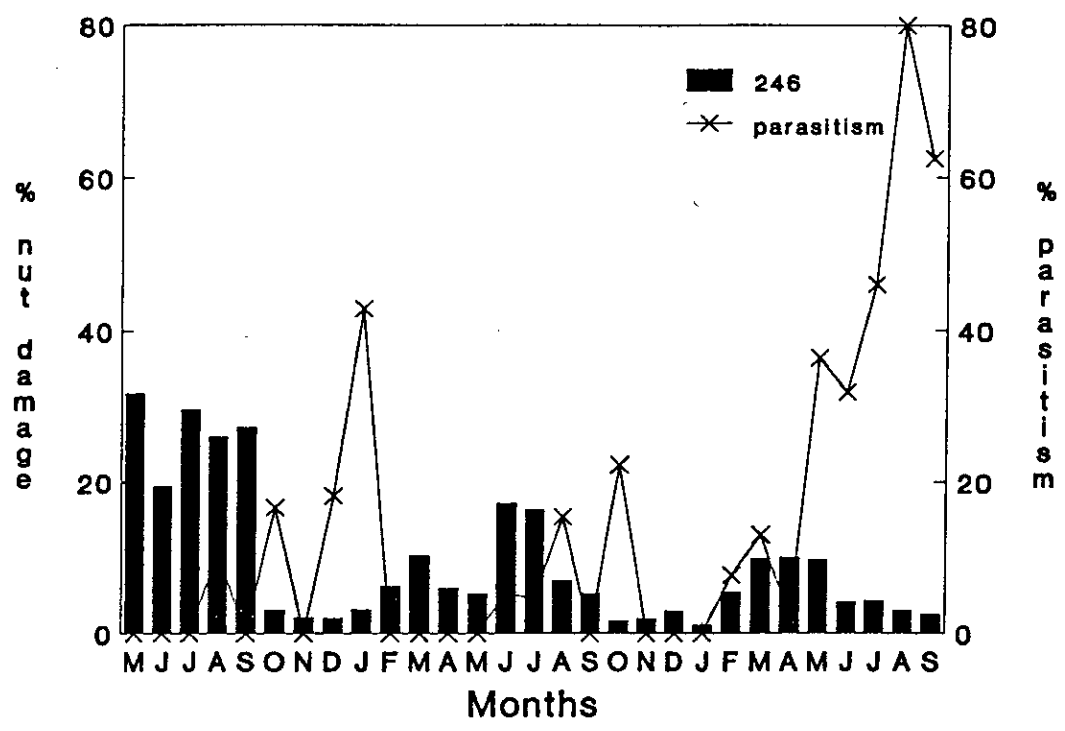
Fig. 4.4: Percentage parasitism of *E. torticornus*, and percentage nut damage: clone 246, from May 1991 to September 1993.
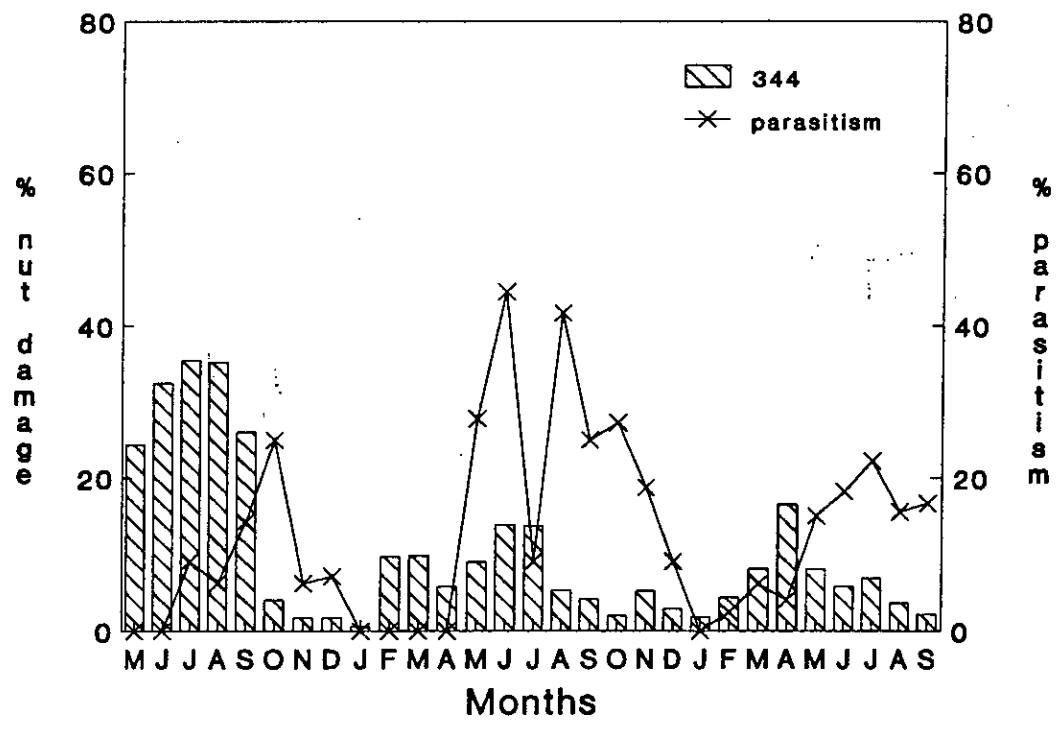
Fig. 4.5: Percentage parasitism of *E. torticornus*, and percentage nut damage: clone 344, from May 1991 to September 1993.
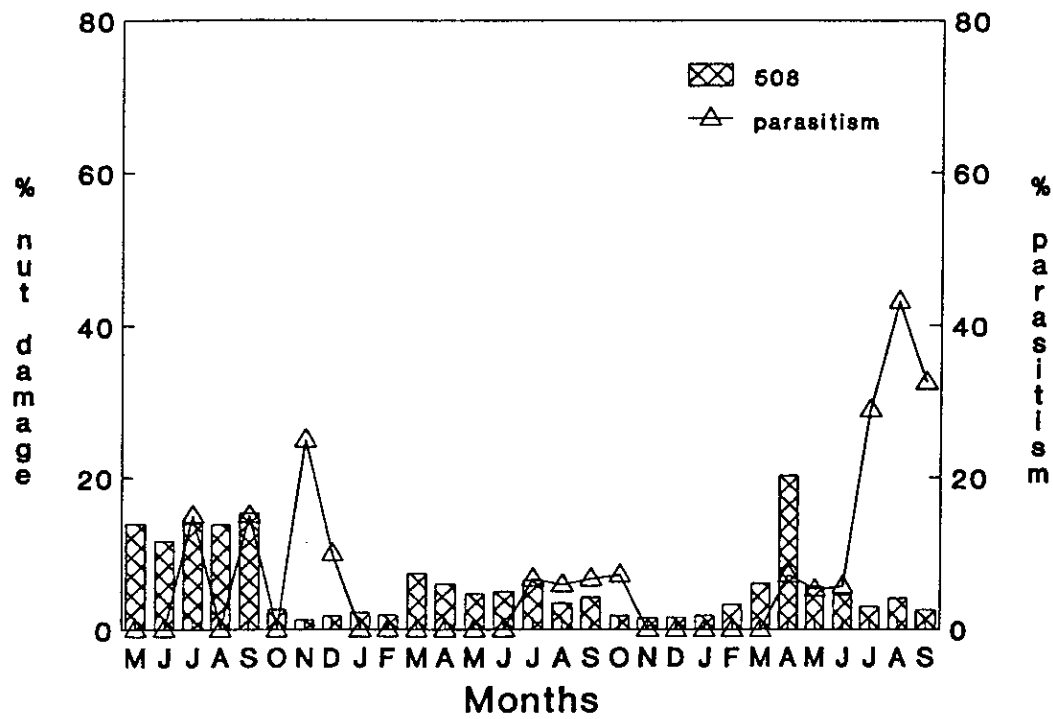
Fig. 4.6: Percentage parasitism of *E. torticornus*, and percentage nut damage: clone 508, from May 1991 to September 1993.
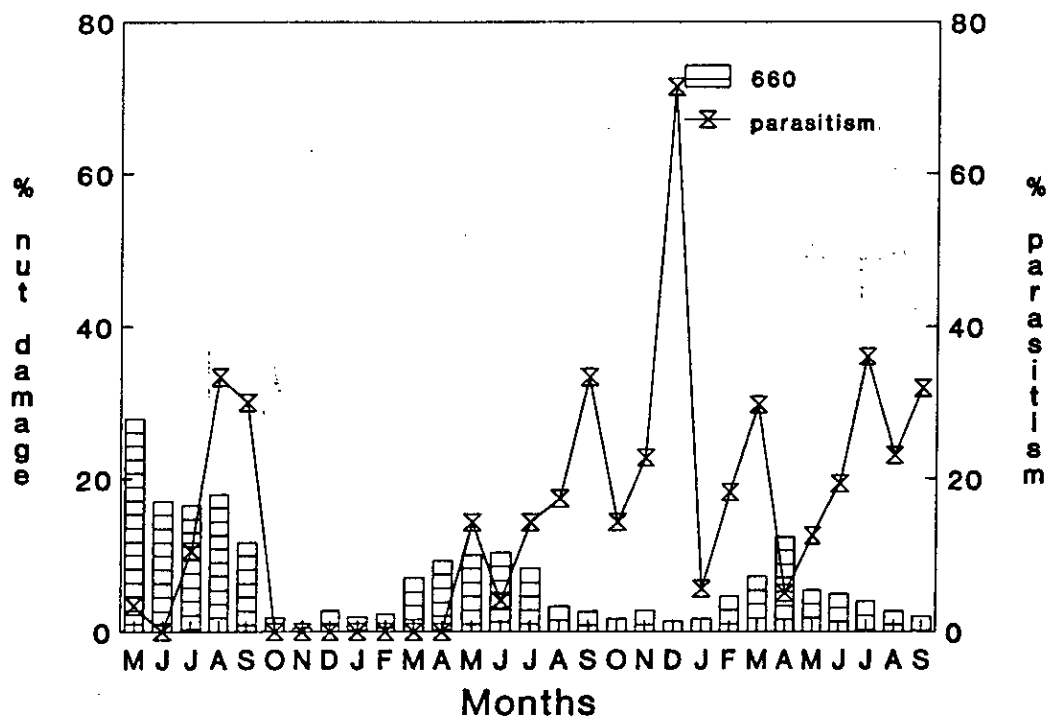
Fig. 4.7: Percentage of *E. torticornus*, and percentage nut damage: clone 660, from May 1991 to September 1993.

P < 0.001) (Fig 4.8, Table 4.3A). Parasitoids did not occur in every site throughout the year. Parasitism was highest in site 3 from May to September, reaching its peak in July where 72 % parasitism was achieved. Site 5 followed in high levels of parasitism, reaching 56 % in August. However, parasitoids from this site were reared only from April onwards.

4.3 DISCUSSION

The fact that six hymenopteran parasitoids were reared from the nutborer in the macadamia orchard, although only two reached high levels of parasitism, supports the view that E. torticornis is likely to be an indigenous species which switched to a more abundant food source (Chapter 1). However, it is not known whether the parasitoids are generalist or specific to the nutborer, since they could not be identified to the species level. If the nutborer was an exotic species, there would not have been enough time for the host-parasitoid relationship to develop since Macadamia is a relatively new introduction into Costa Rica, unless both the nutborer and its parasitoids were simultaneously introduced. Furthermore, the parasitoids genera collected in this study have also been reported in *Cryptophlebia* studies (La Croix and Thindwa, 1988; van der Geest *et al.*, 1992).

A similarity in the population trends between the nutborer and its parasitoids is evident: as the nutborer population increased the parasitoid population also increased, but with a time lag strongly suggesting a delayed density-dependent response. This also indicates that the nutborer population may be regulated to some degree by natural enemies. Further evidence for this comes from the inverse relationship between nut damage and parasitism between years: parasitism increased during the second and third year, while nut damage decreased (Fig. 4.2). However, a longer study of nutborer parasitism is needed as the situation described here could change with time due to external factors affecting either population. For example, Münster-Swendsen (1980) found strong spatially density-dependent parasitism of lepidopteran larvae by the braconid
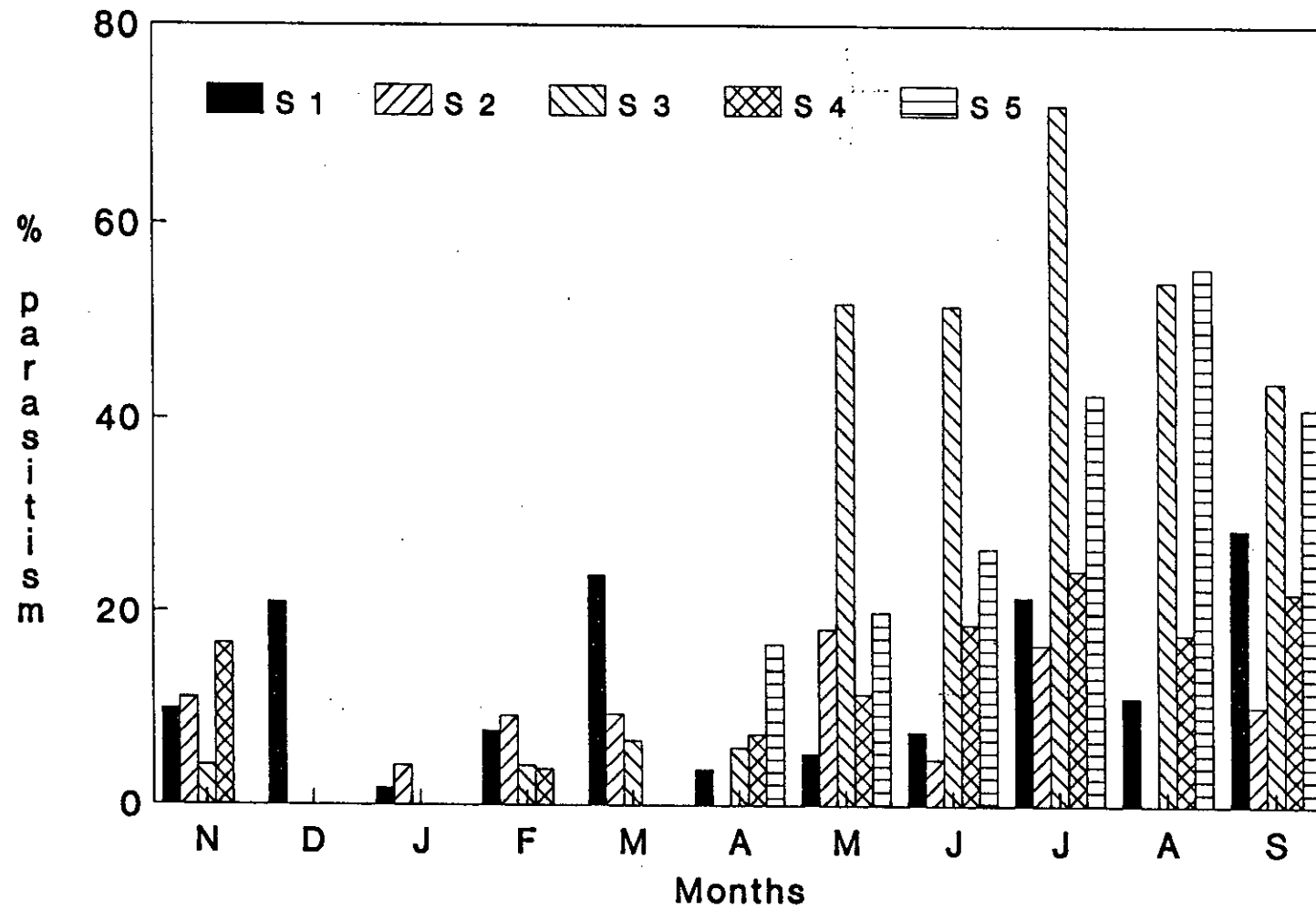
Fig. 4.8:   Percentage parasitism of *E. torticornis* at different sites within Oriente Farm, Turrialba, November 1992 to September 1993.

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Apanteles tedellae, but over a period of nine years, the abundance of adult parasitoids was unrelated to that of their hosts in the same year.

Although parasitoids are widely thought to cause spatially density-dependent mortality, Hassell (1978) reports that this pattern is clearly manifested in only a minority of instances. Strong *et al.* (1984) concluded that for herbivorous insects, natural enemies are of overriding importance as agents of density-dependent control and that intra-specific competition for food is, in contrast, quite rare. The opposite conclusion was reached by Dempster (1983) in reviewing natural control of lepidopteran populations because he found more evidence of density-dependence due to intra-specific competition than to natural enemies. In addition, Stiling (1988) found that out of 32 cases in which density-dependence had been demonstrated, in 19 cases (59.4 %) it was due to factors acting from the trophic level below (the plant), whereas in only 13 (40.6 %) was density-dependence found to be acting from the trophic level above (predators and parasites).

Apanteles I can be considered to be an effective nutborer parasitoid because it was present throughout each of the three years of study, and also because the level of parasitism it achieved was relatively high. The reason why *Ascogaster* was found only at the end of the second year, and why it became the dominant parasitoid, thus suppressing *Apanteles* I, is not clear. However, the aggressiveness of this parasitoid makes it an important biological control agent. Therefore, this should be taken into consideration when designing a pest management programme.

Due to the infrequent occurrence of *Pristomerus* and the hyperparasitoid, it is likely that they were transients rather than permanent inhabitants of the crop, and that the original hosts of these two parasites were probably other lepidopteran larvae from the surrounding forest. Since the Perilampidae is a hyperparasitoid its contribution to natural control must be considered negative.

There are various reasons which can explain the variability observed in the levels of parasitism: the death of small larvae during rearing which might have been parasitized, thus underestimating the percentage parasitism; the distribution of the nutborer and its parasitoids across the orchard and within the tree, relative to the

sampling procedure used; and, finally, the frequency of sampling. A more regular sampling programme, for example at fortnight intervals, could have avoided or reduced some of the variability observed.

Although no differences were found between clones for the overall parasitism, the data suggest some pattern in parasitism of nutborer. It was particularly high in the middle part of the study in clone 344 and towards the end of the study in clone 246. Apart from one sampling date, parasitism of larvae in clone 660 were relatively consistent and parasitism in clone 508 was lower than that found in other clones. It must be stressed that these are tentative interpretations and that further studies of parasitism are required. There is no clear explanation why clone 660 had the highest parasitism in two of the three years of study. It could have been an artifact due to the relatively high number of parasitoids reared from a small number of nutborer larvae, (71 % parasitism in 1992 from 7 larvae). Van Driesche (1983) critisizes the use of peak percent parasitism such as this, as a statistic for comparing or assessing parasitoid impact on pest regulation. He considers that percentage parasitism is often of little or no biological significance, since depending on the relative phenological processes of the host stage and the parasitoid, peak percentage parasitism can be higher, lower, or the same as the generational percentage parasitism value. Nevertheless, it is more important to study the way that parasitism varies, than simply to record overall levels of parasitism, because it is the way that parasitism responds to host abundance that determines its ability to play a role in regulating its abundance.

Differences in the architecture of different tree species has been shown to influence the rate of parasitism of insects feeding on them (Aegerter, in preparation). Clones 246 and 508 which tended to have the greatest and lowest number of parasitoids respectively, both have a spreading and semiupright (plagiotropic) tree habit, while clones 660 and 344 present an upright tree habit (ortotropic) (Queensland Department, 1984). The tendency for clone 508 to have low levels of parasitism may relate to the relatively low number of larvae found on trees of this clone in comparison to the other clones. The opposite result was expected for the number of parasitoids reared from clone

344. As this clone presented the highest number of *E. torticornis* larvae, it was also expected to rear the highest number of parasitoids, yet it was the least affected by parasitoids. Parasitism levels in clones 344 and 660 remains an open question.

The reason why percentage parasitism was higher in site 3 is not clear. Parasitism in site 1 was expected to be higher since nut damage was higher in this site. Perhaps, as stated earlier, parasitism was overestimated. Although a high level of nut damage was found in site 5, parasitism in this site was high during the last 6 months. Because this site has a mountain, sugarcane crop, and river as boundaries, it is likely that parasitoids could have come from host living in the surrounding area. An increase in the natural population of parasitoids in diverse plant habitats has been reported by Altieri *et al.* (1977).

The existence of nutborer parasitoids is important in planning pest management strategies. The presence of high larval nutborer populations is an indicator that egg parasitoids are inadequate in suppressing borer populations. Because of the importance of Trichogrammatidae in reducing the nutborer population from the egg stage, efforts should be made to increase the population of this parasitoid. A similar conclusion was reached by Ironside (1992) who strongly recommended the introduction of *Trichogrammatoidea* sp. to other macadamia growing areas, because of its strong affinity for macadamia in Malawi, and for their distribution at all heights within the tree. The benefits of mass releasing *Trichogramma* for the control of the codling moth *Cydia pomonella* and the summer fruit tortrix moth, *Adoxophyes orana* on apple orchards was reported by Hassan *et al.* (1988). They found that *T. dendrolini* reduced the damage of *C. pomonella* by 61 % and of *A. orana* by 73 %. A reduction of 67 % in the number of damaged fruits was considered economic.

CHAPTER 5

THE EFFECT OF PREDATORS ON THE POPULATION DYNAMICS *OF E. torticornis*

The purpose of this study was to quantify the mortality of nutborer larvae and pupae caused by predators during the period of nut drop and harvest. It was conducted as a result of observations in the field which showed differences between the number of larvae found in nuts collected from trees and nuts collected from the ground.

5.1 MATERIALS AND METHODS

The field study was conducted in site 1, at Oriente Farm, during July 1992 and July 1993. This site was chosen because it showed the highest amount of nutborer damage. Although the site is a mixture of clones 246 (Keahou), 344 (Kau), 508 (Kakea), and 660 (Keaau), the study was carried out only with nuts of clone 344 since it was reported to be the most susceptible clone to *E. torticornis* (Blanco *et al.*, in press).

Six trees were randomly selected for the first experiment in 1992, and ten trees were selected for the second experiment in 1993. Fourteen wooden frames constructed from wooden battens to form a 0.5 m quadrats each with a side height of 0.2 m were placed under the canopy of the trees (Plate 5.1). The fourteen frames represent the standard harvest interval of 2 weeks, each representing one day.

All the nuts from 50 trees (clone 344) were removed from the ground for both experiments. On the following day, the new nuts that had naturally fallen were harvested and sorted into damaged by the nutborer and undamaged nuts. The size of the nuts was restricted to fully developed nuts so that differences in nut size would not affect the ants' searching behaviour. Ten damaged and ten undamaged nuts were placed at random in each frame, giving a total of 1680 nuts for experiment 1, and 2800 nuts for experiment 2. Damaged nuts were marked with nail polish in order to distinguish them from other nuts that would drop from the tree during the course of the experiments.

Plate 5.1:   Distribution of the frames under the tree canopy
               used in the experiments on the effect of predation
               on the population dynamics of *E. torticornis* in
               Turrialba, Costa Rica.

Each day, for 14 days, damaged nuts from one frame (chosen at random) per tree were collected and taken to the laboratory for examination. Undamaged nuts were left in the field to limit the amount of interference to the environment of potential predators. Damaged nuts were opened in the laboratory, and the number of larvae and their instar, and the number of nutborer and parasitoid pupae recorded.

Data were analyzed by the Sigma Plot Program (1993).

5.2 RESULTS

Three insect species were found to be preying on nutborer larvae or eggs during the time between nut fall and harvest. These species were the fire ant *Solenopsis geminata* (F.) (Hymenoptera: Formicidae), the earwigs *Doru* spp. Dorhn (Dermaptera: Forficulidae), and the wasp *Polybia* sp. (Hymenoptera: Vespidae). Fire ants were the most common predators, whereas the other species were only occasionally observed.

Ant foraging activity was observed on the second day of the study. In some cases, small mounds of soil were seen around the base of damaged nuts, which (although queens were never observed), could indicate the beginning of the construction of a nest. Ants were frequently observed wandering over the nuts, and, on two occasions, a group of four to five ants were seen pulling second instar larvae from the entry/exit hole of a nut.

The number of larvae in 1992 decreased from 23 to zero during the fourteen days that nuts were on the ground, and from 57 larvae to one during 1993 (Fig. 5.1). In both years, but particularly in 1993, the number of larvae decreased steadily from the first day, suggesting that there was a mortality factor that acted rapidly. Due to the high number of ants observed on the ground, it is likely that ant predation was responsible for this decrease in the numbers of nutborer larvae.

From the fifth day of sampling onwards, it was observed that the nuts which received direct sunlight tended to dry faster than the nuts in the shade, and their husks split. An increase in the number of ants near these nuts was observed.
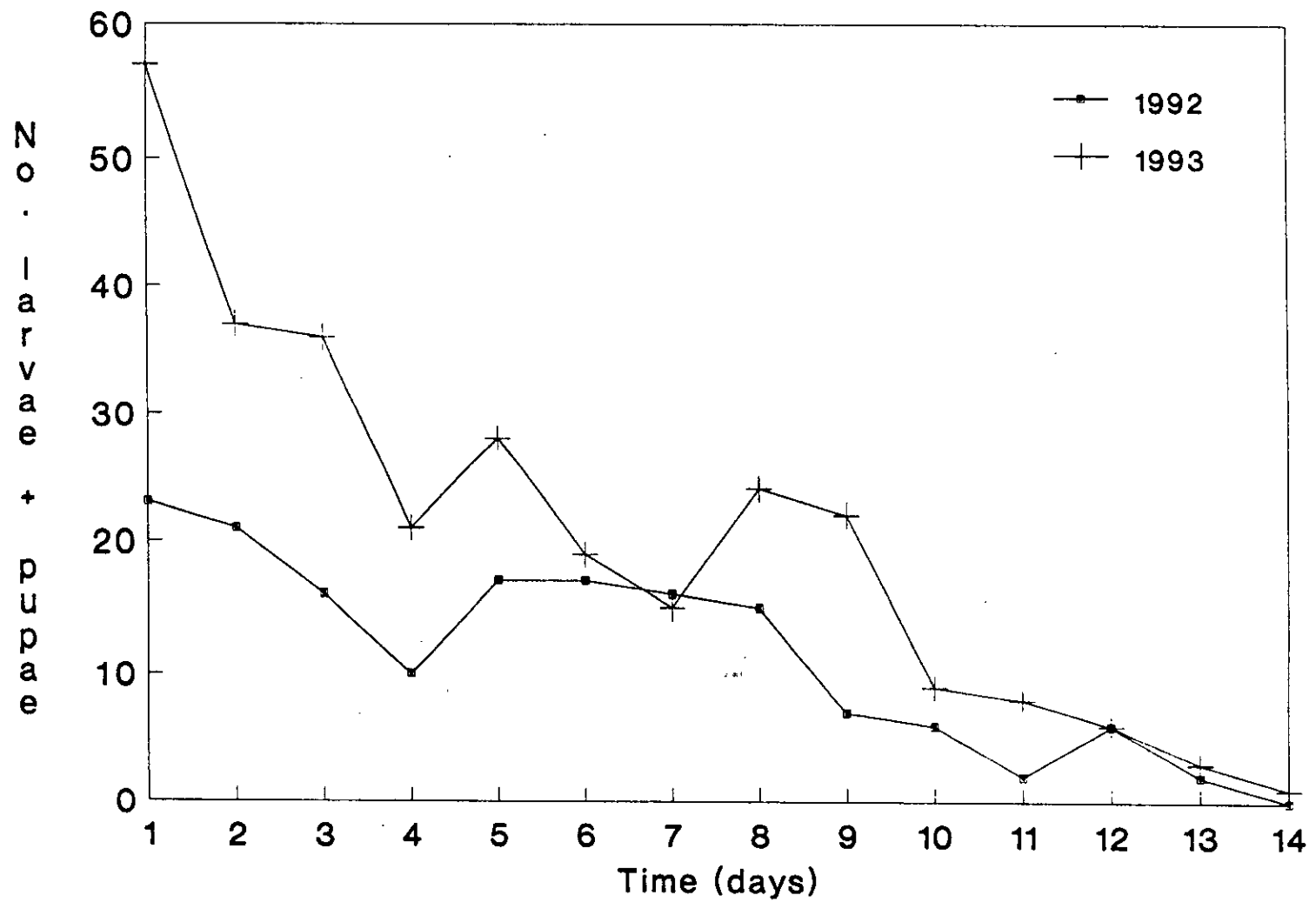
Fig. 5.1: The total number of macadamia nutborer larvae and pupae of *Ecdytolopha torticornis,* found in nuts on the ground between nut fall and nut harvest, Turrialba, Costa Rica.

The daily variation in the number of nutborer larvae in each developmental stage is presented in Figure 5.2, Table 5.1, data from both experiments were pooled together. It can be observed that the number of larvae and pupae steadily decline through the 14 days of each experiment. The mean number of larvae and pupae is presented in Figure 5.3. Figure 5.4 shows the same data with standard errors; although there seemed to be a difference between the number of larvae in the different experiments, a similar decline was observed. It can be assumed from the data shown in Chapter 1 on the length of different instars, that part of the population passed to the next instar as there was some evidence of recruitment to the second and third instars during the course of the experiment, peaks at days 5 - 9 (Fig. 5.2).

The developmental stage of the nutborer which was found in highest number was the second instar (149 larvae), followed by the third instar (123 larvae), the fourth instar (92 larvae) and the first instar (67 larvae) (Table 5.1). The smaller number of first instar larvae suggests that a higher mortality factor is acting on this developmental stage. A steady decrease in the number of insects from successive developmental stages has been reported in life table studies (Mason, 1976; Southwood, 1978; Horn, 1988). The number of the nutborer pupae and parasitoid pupae recorded were 13 and 6 respectively.

The number of larvae and pupae for 1992 and 1993 were inversely correlated (r = -0.90 for 1992; r = -0.91 for 1993) to the number of days between nut drop and harvest (Fig. 5.5). These results demonstrate that the nutborer larvae are actively preyed upon and that the longer the nuts are on the ground, the more likely the larvae are to be predated. Field observations indicate that fire ants are the major predator responsible.

Various spiders, which were not identified, were abundant but were not seen to eat the larvae. However, Kaczmarek (1955) includes spiders among the predators on potato beetles, so they also might be considered as potential *Ecdytolopha* predators. Nyffeeler *et al.* (1987) reported the green lynx *Pencetia viridans* feeding on pest insects of the orders Diptera, Heteroptera, Coleoptera, Lepidoptera, and Homoptera in cotton fields. However, this spider also fed on beneficial insects and other spiders.
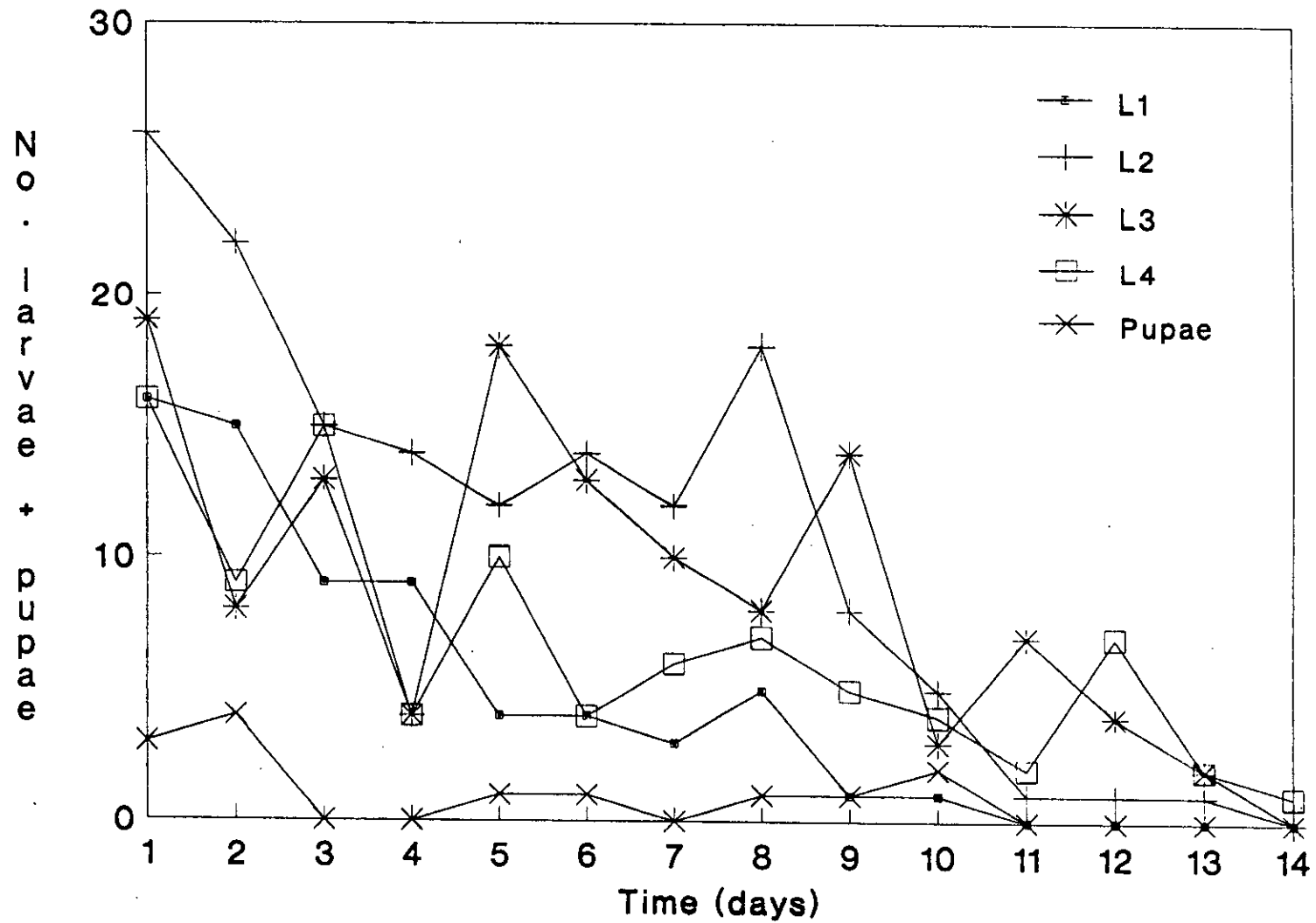
Fig. 5.2: The number of larvae and pupae, of *Ecdytolopha torticornis*, found in macadamia nuts on the ground between nut fall and nut harvest, Turrialba, Costa Rica.

Table 5.1: Number of *Ecdytolopha torticornis* larvae and pupae found in macadamia nuts on the ground from nut fall to nut harvest, during July 1992 and 1993, Turrialba, Costa Rica.

Sampling day	Life-cycle stage: Larval instar; Pupa;						
	L1	L2	L3	L4	P	ΣEt	Pp
1	16	26	19	16	3	80	4
2	15	22	8	9	4	58	0
3	9	15	13	15	0	52	1
4	9	14	4	4	0	31	0
5	4	12	18	10	1	45	0
6	4	14	13	4	1	36	0
7	3	12	10	6	0	31	0
8	5	18	8	7	1	39	1
9	1	8	14	5	1	29	0
10	1	5	3	4	2	15	0
11	0	1	7	2	0	10	0
12	0	1	4	7	0	12	0
13	0	1	2	2	0	5	0
14	0	0	0	1	0	1	0
Σ	67	149	123	92	13	444	6
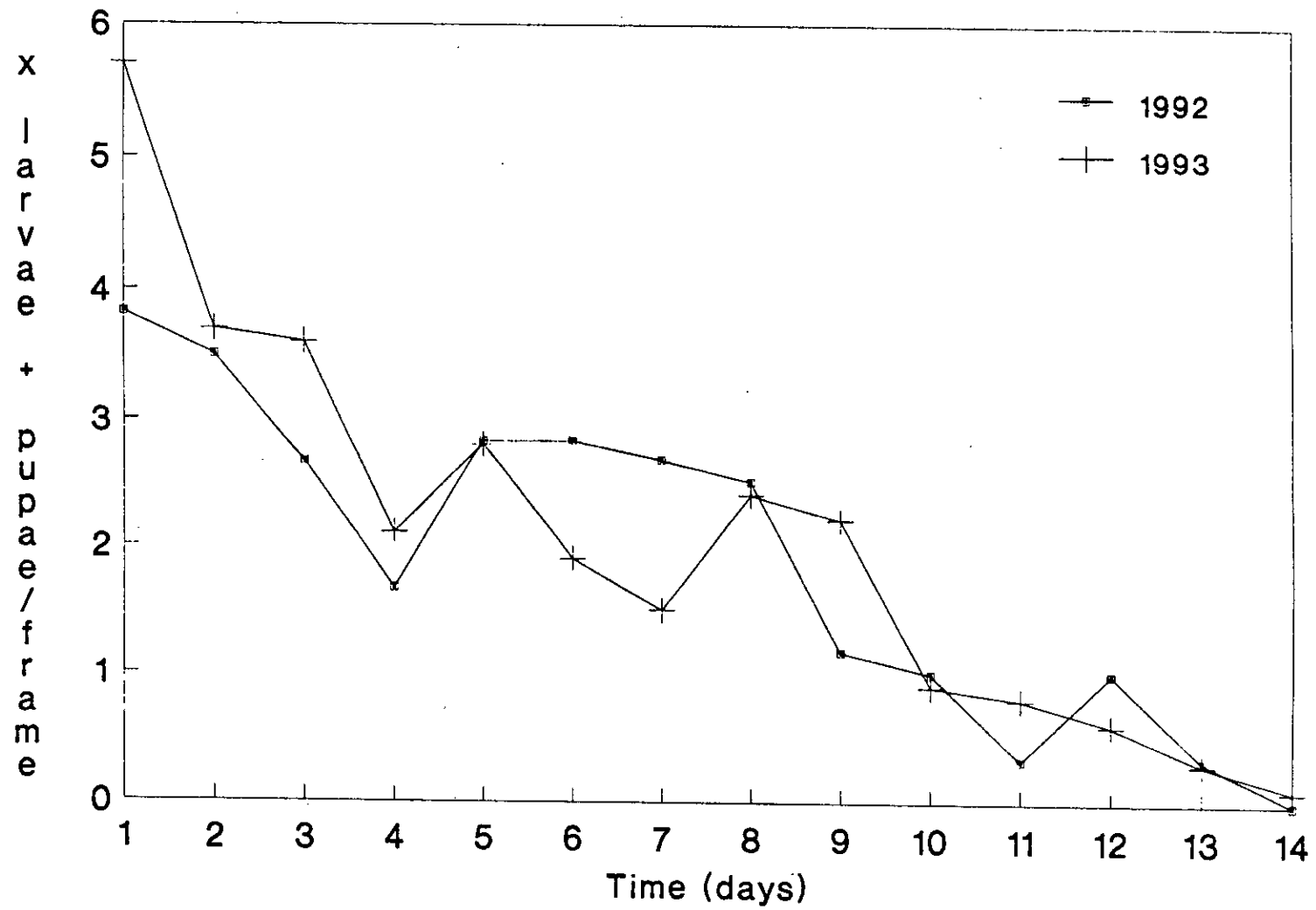
Fig. 5.3: The mean number of larvae and pupae of the macadamia nutborer, *Ecdytolopha torticornis*, found in nuts on the ground between nut fall and nut harvest, Turrialba, Costa Rica.
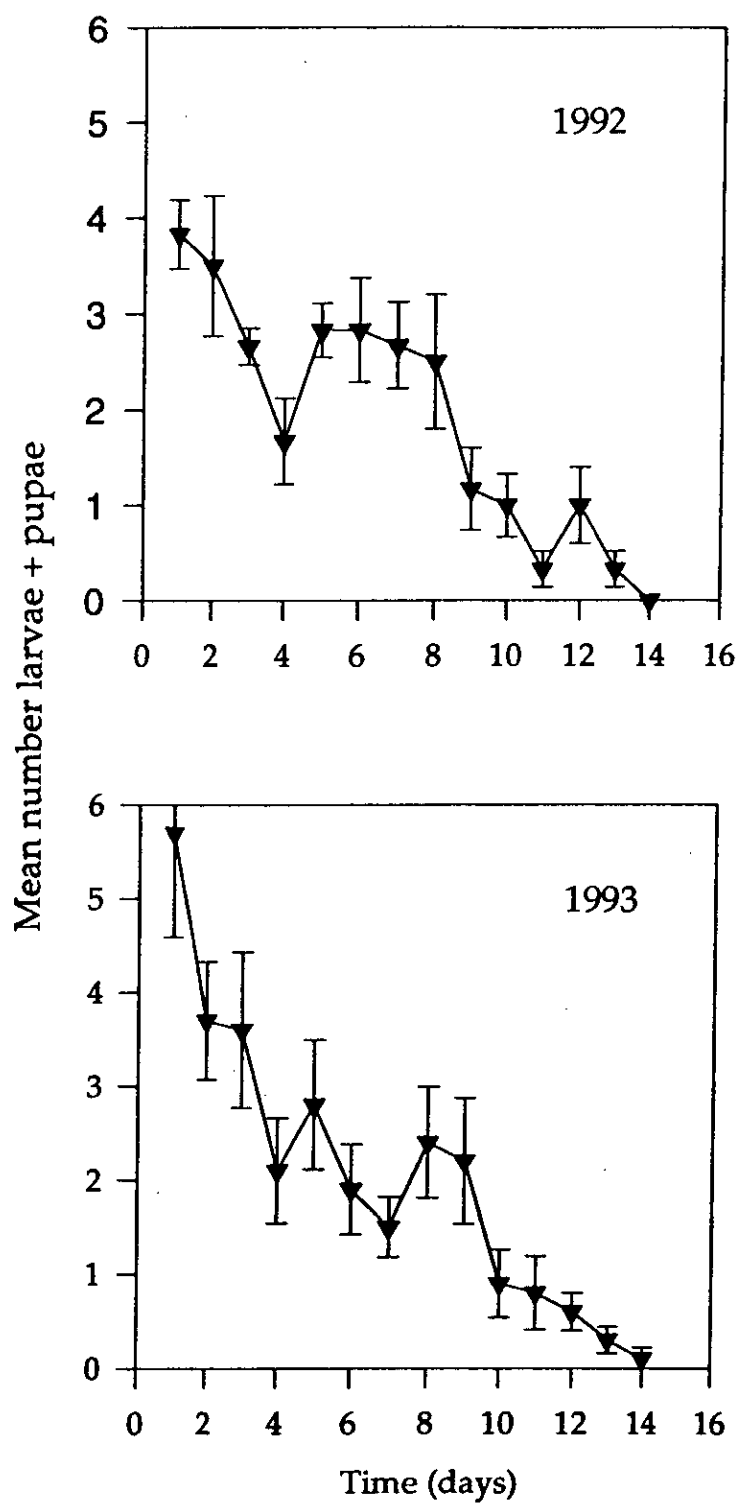
Fig. 5.4:   The mean number of larvae and pupae (+SE) of the macadamia nutborer *Ecdytolopha torticornis*, found in nuts on the ground between nut fall and nut harvest, Turrialba, Costa Rica.
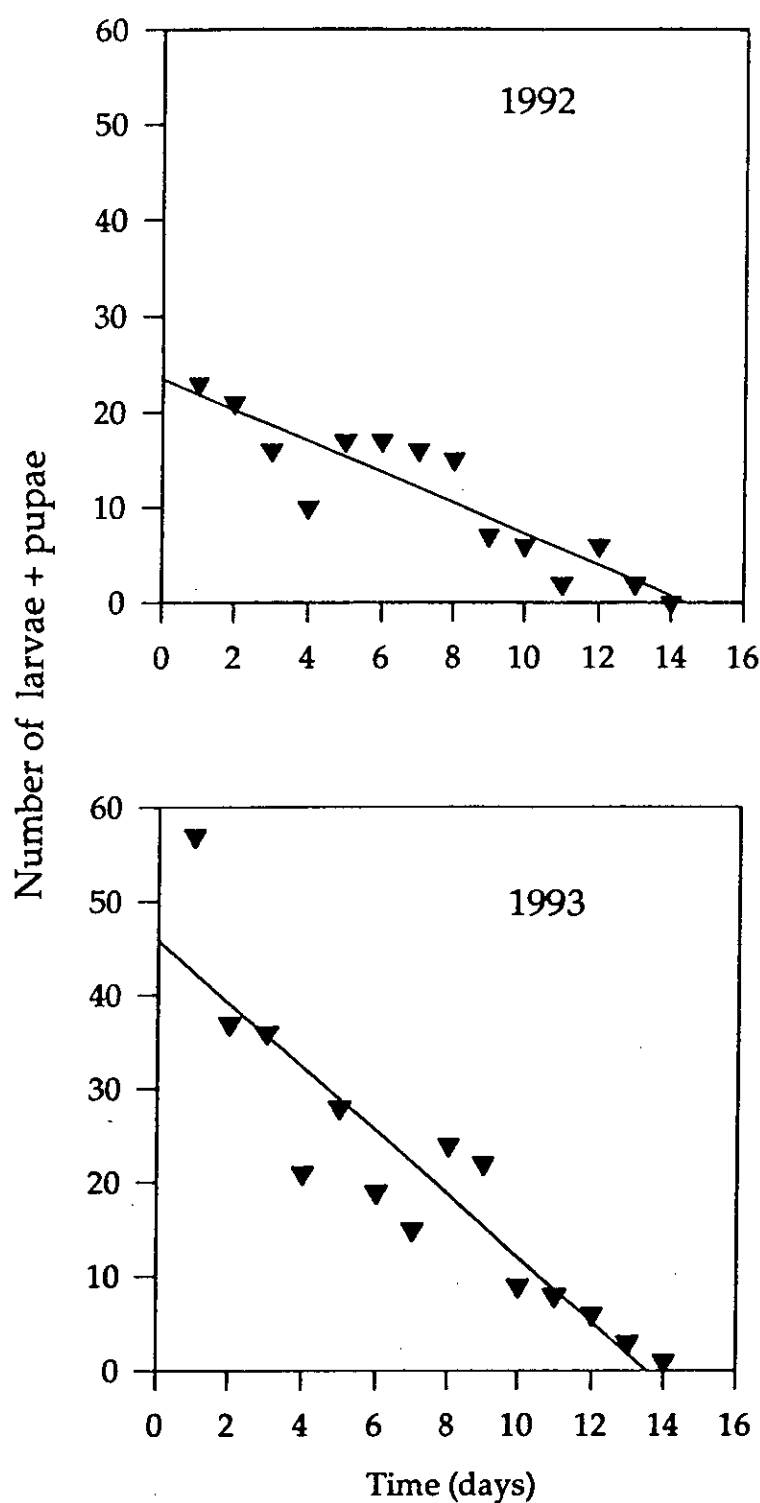
Fig. 5.5:   The relationship between the number of macadamia nutborer larvae + pupae, *Ecdytolopha torticornis*, and the number of days the nuts were on the ground (a) 1992 ($y = 23.48 - 1.62\,x$; $r^2 = 0.82$; $P < 0.001$; $n = 6$),   (b) 1993 ($y = 45.81 - 3.38\,x$; $r^2 = 0.83$; $P < 0.001$; $n = 10$).

Some vertebrates such as toads, birds, carabids, lizards and small mammals in the study field might occasionally consume larvae, although there was no direct evidence of this.

It should be stressed that all the predators observed to predate *Ecdytolopha* in the field were generalist predators.

5.3 DISCUSSION

Many insect species are known to be good pest control agents. Ants, in particular, are regarded as one of the most important insect predators (Perfecto, 1990). Whitcomb (1971) considers them to be the most important predators in the world. Ants have an advantage over other predators due to the large number of individuals which comprise each colony.

The fire ant *Solenopsis geminata* has a neotropical distribution ranging from the southern part of United States to South America and the Carribean. As well as being predators, fire ants are also known to damage germinating seeds and young seedlings of several crop plants (King and Saunders, 1984). The typical foraging pattern of this species is an overdispersion of nest sites, which gives them the advantage of a more uniform coverage of the ground and thus a better chance of finding a food source (Holldobler and Wilson, 1990).

Ants are also known to contribute to crop yields by their impact on crop structure, nutrient cycling, pollination, and reduction of insect and weed pests (Way and Khoo, 1992; Carroll and Risch, 1993). While regarded as important control agents, ant populations present potential disadvantages. Among these are: they may act as vectors of plant diseases, affect the architecture of trees by foraging meristems and deforming the branches, attack or irritate people, affect harvesting equipment by the construction of mounds in the fields, and they often frustrate attempts to introduce control parasitoids by predating these insects before they have become established (Carroll and Risch, 1983; Horn, 1988; Way and Khoo, 1992).

The earwig *Doru* spp. is distributed throughout the southern United States, Central America and Northern South America (van Huis, 1981; Andrews, 1988). It is more frequently reported as an

insect egg predator, but it is also known as a predator of larvae of many insect species. The wasp *Polybia* spp. is known as a generalist predator throughout the tropical countries (King and Saunders, 1984).

The decrease in number of the nutborer larvae and pupae between nut fall and harvest is unlikely to be only due to predation by ants, earwigs, and wasps alone; other factors could have affected the nutborer's abundance. Among these factors are food quality, water logging, predation by birds or rats, and infertile eggs (see Table 2.1). The fact that nuts which received more sunlight tended to dry out and split, may have affected larval survivorship in various ways also. First, as the husk gets dryer, its food quality inevitably declines, and the larvae may also dry out (although no evidence of this was observed) or search for other more suitable nuts in which to complete their development. La Croix and Thindwa (1986) reported a movement of small *Cryptophlebia* spp. caterpillars from one fruit to another when more food was needed. This latter behaviour if true also for *E. torticornis* might expose the nutborer larvae to being predated more freely. Also, as mentioned in Chapter 1, larvae are less commonly found in mature nuts due to the husk being dry and hard. An increase in food toughness can cause a reduction in larval growth development and, thus a decrease in the abundance of adults. Second, as nuts split, larvae are more exposed to predators (ants, birds, toads, carabids, etc.), and to the effect of environmental factors such as rain. In this study, abiotic factors *per se* probably accounted for low mortality of first larval instar prior to their boring into the nut, and probably exerted even less influence on older larvae. An increase on mortality of *Plutella* first instar larvae due to rainfall was reported by Hardy (1937). A similar finding was reported by Harcourt (1966) in *Pieris rapae* caterpillars.

The fire ant is primarily a terrestrial forager and will encounter fallen nuts (Risch, 1980). Whilst nutborer larvae and pupae are an easy source of food since they are immobile, they are concealed and require to be found. In this, the ants may be helped by odors produced directly by the prey or by damaged nuts. Horn (1988) reported that the interactions between phytophagous insects and their host plants might influence the activity and effectiveness of parasitoids and predators. He suggests that natural enemies may use

chemical cues from plants to locate potential meals.

Many studies report that ants are density-responsive predators which can therefore concentrate on localized pest populations (Carroll and Risch, 1983; Eickwort, 1977). The pheromone recruitment behaviour of many ants makes the density-responsive component of foraging very efficient relative to that of other foragers (Carroll and Risch, 1983). Although ants are commonly reported as density-dependent predators, due to the habit of *E. torticornis* living inside the nut, it is probable that in this case, ants have a density-independent mortality effect. As ants are numerous, with well distributed nests, and since nutborer larvae are not their only food source, they are unlikely to concentrate their feeding activity on dense patches of nutborer larvae. This inference is consistent with Stiling's (1987) difference in opinion that polyphagous enemies are unlikely to impose density-dependent mortality since they do not rely on only one prey species. A similar argument is presented by Münster-Swendsen (1991) who found that spiders caused the same level of mortality irrespective of prey density. Freeman and Smith, (1990) reported predation of the leafmining fly *Liriomyza commelinae* by *Crematogaster brevispinosa* Mayr to be 21.2 % and that it was independent of population density at all spatial levels. In the case of exposed prey, although depending upon type predator is more likely to employ a density-dependent strategy.

Sequeira (1987) and Andrews (1988), reported that the fire ant, *S. geminata* and the yellow stripped earwig *Doru taeniatum* are good candidates for controlling *Spodoptera frugiperda* in Central America. Studying a maize-squash ecosystem, Risch and Carroll (1982) found that the fire ant significantly reduced the total numbers of arthropods and their diversity. They also found that the corn weevil, *Sitophilus* sp. was nearly 50 times more abundant in the absence of *S. geminata*, while the frequency of corn plants with aphids was nearly twice as high in the presence of this ant since by the mutualism involved with honeydew gathering afford protection to the aphids. Other studies where ants have been shown to achieve successful control of pests, include that of Way and Cammell (1989) who found that under artificial infestation, egg removal by *Moromorium floricola* almost completely removed the caterpillar, *Opisina arenosella* from coconut

palms; Clinton *et al.* (1984) reported that ants and birds reduced injury of small conifer trees caused by the spruce budworm (*Choristoneura occidentalis*) larvae by up to 50 %; Escalante and Benado (1990) reported a reduction of 90 % in the survivorship of drosophilid larvae when predated by *Pilosocercus lanuginosus*.

CHAPTER 6

VERTICAL DISTRIBUTION OF *E. torticornis* ON MACADAMIA TREES

The aim of this study was to investigate the within-tree distribution of the nutborer by recording its oviposition sites.

6.1 MATERIALS AND METHODS

The vertical distribution of *E. torticornis* eggs in clones 246, 344, 508 and 660 was examined each month from July to December 1991, at Oriente Farm. The nuts were examined in the laboratory (23 ° C, 80 % RH), and the following variables were evaluated: the number of eggs per nut, the number of fertile and infertile eggs and empty chorions, and the number of nutborer holes per nut. The number of holes was included as some nuts were found to have holes but no chorions present, perhaps because they had been disloged by the rain, been blown away by the wind, or eaten by predators. Trees were divided into three crown levels (Plate 6.1):

I) crown top, 3.2 m from the ground to the highest point of the tree crown (position 1);

II) mid-crown, 1.6 - 3.2 m from the ground (positions 2 and 3);

III) lower-crown, 0 - 1.6 m from the ground (positions 4 and 5).

Levels II and III were each divided into two positions: positions 3 and 5 = nuts sampled in an area up to 1 m from the tree trunk; positions 2 and 4 = nuts sampled in an area up to 1 m from the end of the branches. Twenty nuts (over 0.8 cm in diameter) per crown level were collected at random; ten nuts per position for crown levels II and III.

The experimental design used was a split split plot where the tree was the big plot, the combination of levels and positions was the split plot and the time (6 months, July to December) was the split split plot. Data were transformed by sqrt (x + 0.5) as many nuts

Positions   **Crown Levels**

I

\> 3.2m

1.6-3.2m   II

\<1.6m   III
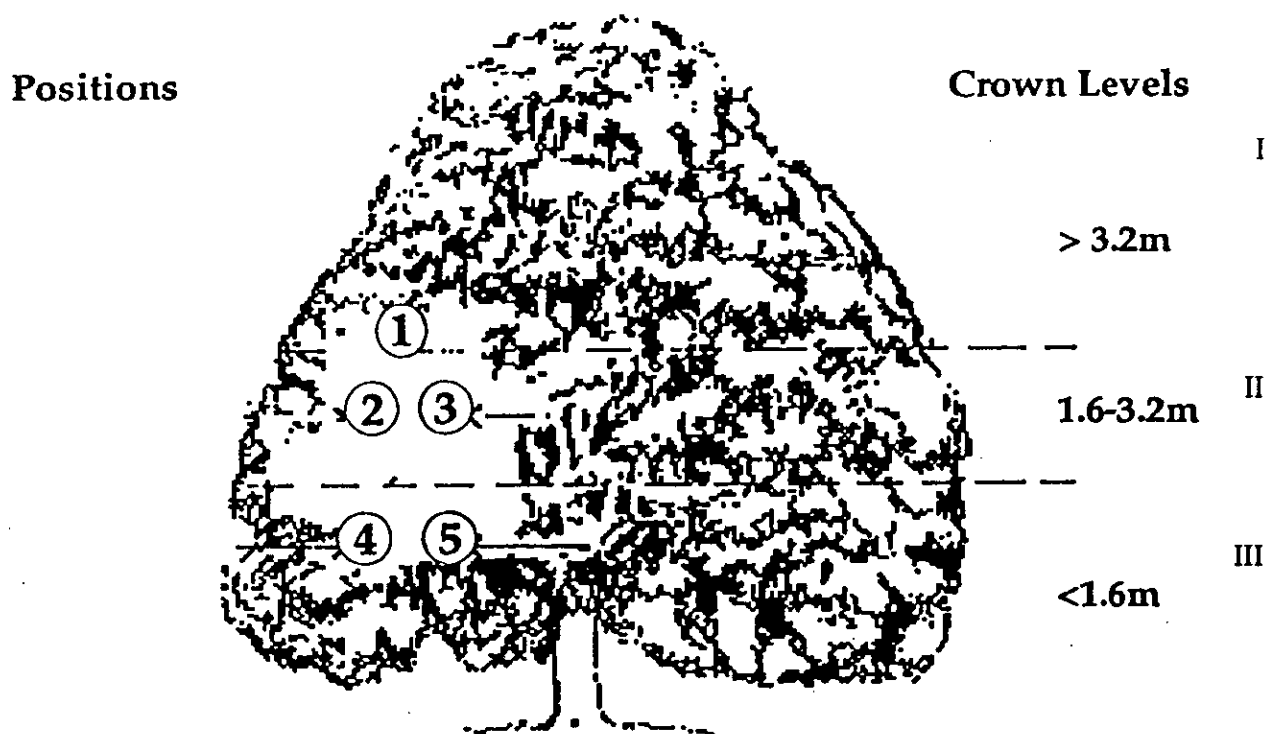
Plate 6.1:   A diagrammatic representation of the sampling positions used in the determination of the vertical distribution of the nut borer's eggs on macadamia.

were free of eggs. Nuts were collected from five trees per clone, 20 trees were sampled in total.

In the statistical analysis, crown level I was compared with levels II and III together (D); level II versus level III (Est (D)); and the inner sampling positions (3 and 5) were compared with the outer sampling positions (2 and 4) (Pos (D)).

6.2 RESULTS

A total of 6939 nuts was inspected during the six month study. The number of eggs laid per nut varied from 0 to 8 eggs with a mean of 0.8 eggs (n = 201 nuts) (Chapter 1). Newly oviposited eggs were observed on nuts already containing eggs or holes, which could imply that moths are attracted to lay their eggs in part by some chemical stimuli, perhaps from the eggs.

No significant differences were found for the number of eggs per clone (Table 6.1). Eggs were found on macadamia trees at all heights; however, they were significantly more numerous in crown levels II and III than in level I (P < 0.001). The mean number of eggs per nut in level II was 0.29, and in level III, 0.30, but in level I only 0.14 eggs per nut were found (Table 6.2).

There were no significant differences between the number of eggs found on nuts from the bottom two levels (Est (D)), nor between the mean of eggs found on nuts on the inner and outer parts of the branches (Pos D) (Table 6.1).

When positions were analyzed separately (n = 5), there was a significant difference (P < 0.0001) between the number of eggs in position 1 and in the other four positions (Table 6.3). The inner sampling positions (3 and 5) presented a smaller number of eggs than the other sampling positions (2 and 4). However, no statistical difference was found between the number of eggs in either positions for levels II and III.

There was a significant difference (P < 0.0001) in the number of eggs per nut (0.14 - 0.32) over the six months sampling period (Table 6.4). The number of eggs per nut was highest from July to October (0.28 - 0.34 eggs per nut), decreased in November (0.20 eggs per nut), and dropped steeply to 0.06 eggs per nut in December (Fig. 6.1). The

Table 6.1: Statistical analysis of the vertical distribution of *E. torticornis* eggs within the macadamia trees (n = 20), Turrialba, Costa Rica, 1991.

Source	DF	F
Clone	3	0.69 ns
D	1	50.41 ***
Est (D)	1	0.22 ns
Pos (D)	1	2.00 ns

Data transformed by $\sqrt{}$ (x + 0.5); ns not significant ***, P <0.001; See text for definition of D, Est (D) and Pos (D), different areas within the tree crown.

Table 6.2: Mean number of *E. torticornis* eggs per nut per level within the macadamia trees, Turrialba, Costa Rica, 1991.

Crown level	n	Mean eggs per nut
1 (Top)	2233	0.14 b
2 (Middle)	2377	0.29 a
3 (Bottom)	2329	0.30 a

Means followed by the same letter are not significantly different (P = 0.05) (Duncan's Multiple Range Test).

Table 6.3:   Statistical analysis of the vertical distribution of *E. torticornis* eggs by position and over time within the macadamia trees (n = 20), Turrialba, Costa Rica, 1991.

Source	DF	F
Clone	3	0.69 ns
Position	4	33.00 ***
Time	5	48.83***

Data transformed by $\sqrt{}$ (x + 0.5); ns not significant; ***, P <0.001.

Table 6.4:   Mean number of *E. torticornis* eggs per nut, by position and over time, Turrialba, Costa Rica, 1991.

Position	n	Mean eggs per nut	Monthly sample	n	Mean eggs per nut
4	1157	0.32 a	Oct	1200	0.34 a
2	1198	0.30 a	Jul	1149	0.34 a
5	1172	0.28 a	Sep	1190	0.29 a
3	1179	0.28 a	Aug	1000	0.28 a
1	2233	0.14 b	Nov	1200	0.20 b
			Dec	1200	0.06 c

Means followed by the same letter are not significantly different (P = 0.05) (Duncan's Multiple Range Test).
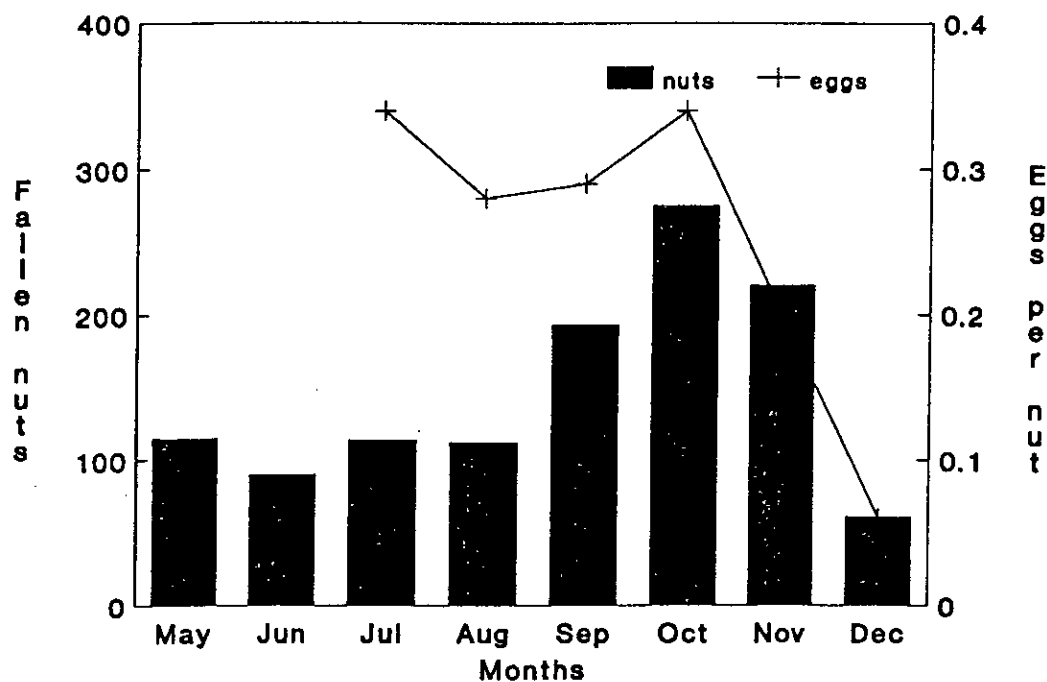
Fig 6.1:   The mean number of fallen nuts and the mean number of eggs per nut per month.
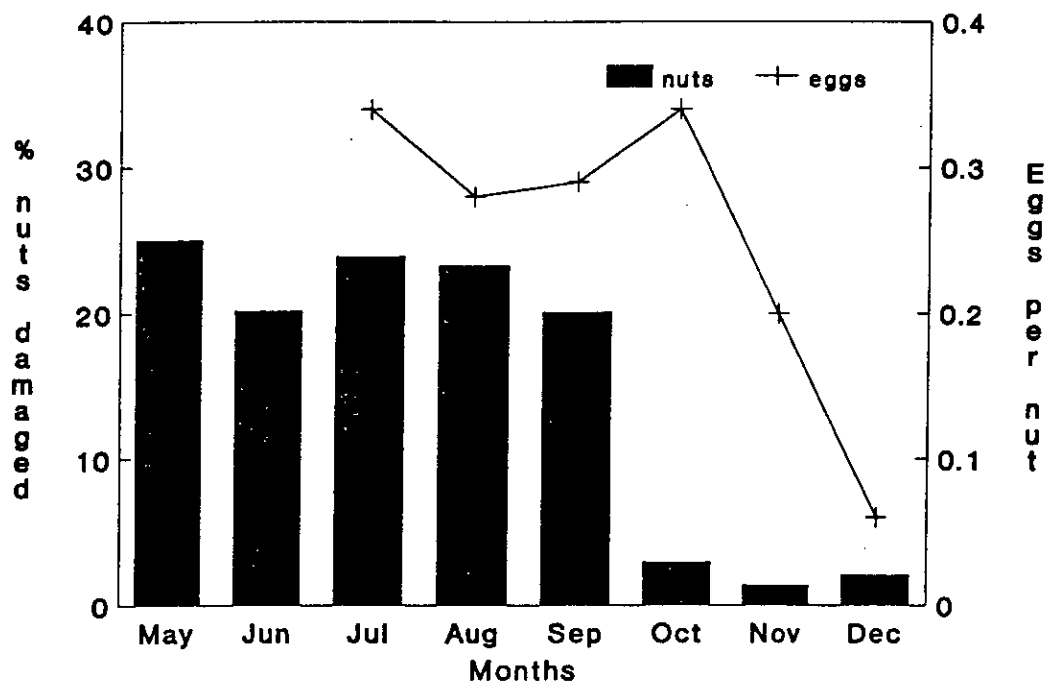
Fig 6.2:   The mean percentage of nuts damaged and the mean number of eggs per nut per month.

decline in the number of eggs per nut was closely related to the decline in nut production, but was not related to the decline in the number of damaged nuts which occurred approximately one month earlier (Fig. 6.2).

6.3 DISCUSSION

Oviposition site selection is one of the most important aspects of habitat selection in insects (Higashiura, 1989). It varies with insect species and is closely related to offspring survival. The observed habit of laying eggs on nuts already containing eggs or on damaged nuts might give the larvae the advantage of escaping from parasitoids and predators, or prevent them from being dislodged by the rain. It was reported in Chapter 1 that it took a larva approximately fifty minutes from emerging from the egg to completely boring through the husk. Therefore, if an entrance to the nut has already been made, the first instar larvae are more likely to evade some of the factors affecting their survival. At the same time, the custom of the moths of laying eggs on damaged nuts can give the larvae the disadvantage of intra-specific competition for food or space, and may diminish the probability of larval survival due to early nut-drop (see Chapter 1). Sinclair (1979) observed that *Cryptophlebia ombrodelta*, also tended to lay its eggs preferentially on damaged macadamia nuts. He concluded that this behaviour lowered the chances of survival of the larvae in dense populations due to cannibalism and early nut-fall.

The fact that no differences were found for the number of eggs between clones eliminates the possibility that during oviposition moths were influenced by the factors of shape, size, and colour of the nuts. Thus, the differences observed in nut damage for clones 246, 344, 508 and 660, reported in Chapter 3, might reflect differences in larval survival due to the quality of their food: secondary plant compounds and husk toughness.

The tendency of finding a major number of eggs in the outer bottom level, followed by the outer middle level, could be that, because nut production is highest in this part of the tree (Diego Pérez, personal communication), the moths lay their eggs where food

abundance is highest to ensure optimum conditions an ideal place for their offspring. Also since *E. torticornis* has been reported as probably being a poor flyer (Chamberlain, 1989), the adults reach this part of the tree more easily from the weed canopy where they are believed to feed. Thus during the period of oviposition, they do not have to fly far to find their host and lay their eggs. In Oriente Farm, weed control is limited as they have found that weeding increases root fungi problems and soil erosion (Diego Pérez, personal communication).

There are three probable reasons which could explain the differences in the number of eggs per nut over time. First, during the period September to November, nut production was high, and females found plenty of oviposition sites. As time passed and fewer nuts were available, the moths did not find enough sites for laying their eggs. Second, a reduction in the number of nuts implies a reduction in the larval food source, and therefore, a reduction in the number of adults that will eventually emerge. Third, as moths discriminate the age of nuts for egg laying (Chapter 1), the presence of higher number of mature nuts will have an effect on the abundance of parasitoids related to the nutborer population. However, damage also decreased with nut maturation because as the husk dries it provides food of a poorer quality and quantity.

It is concluded that *E. torticornis* prefers to oviposit upon nuts within the first three metres of the ground (Table 6.2). However, Jones and Tome (1992) reported that there appeared not to be a preference by *Cryptophlebia* moths for laying their eggs at different heights of the trees. The identification of host characteristics relevant to oviposition behaviour and insect distribution (both inter and intra-plant) is important as this may help in the design of sampling programmes, the forecasting of insect damage, and more effective assessment of control programs (Southwood, 1978; Horn, 1988). For example, annual surveys of spruce budworm, *Choristoneura fumiferana* (Clemens, 1989?; Lysyk, 1990), are conducted during summer to determine populations levels, monitor damage, and forecast the intensity of infestation during the following years. The egg mass population is surveyed because these are retained on the foliage for about a month (Morris, 1955), and are a stable indicator of density.

Watt *et al.* (1992) studied the egg distribution of winter moth, *Operophtera brumata*, on sitka spruce trees. They found that egg distribution on Sitka spruce trees where 27 % were found on the main stem and 39 % along branches within 20 cm, differed from that on broadleaved host plants. Because larvae feed on buds, this is an example of a poor strategy of a native pest on an introduced host plant.

CHAPTER 7

EFFECT OF QUALITY OF FOOD SOURCE
ON THE ABUNDANCE OF *E. torticornis*

This study examined the effect on the abundance of *E. torticornis* of (i) the nitrogen content; (ii) the secondary compounds tannin and proanthocyanidin content; and (iii) the dry matter content of four clones and the different developmental stages of macadamia nuts.

7.1 MATERIALS AND METHODS

i) Nitrogen content. The present study was carried out during November 1991 to July 1992 at the physiology laboratory at CATIE. Nuts of four developmental stages: < 60 days; 60 - 75 days; 75 - 90 days; and 90 - 100 days, were harvested from trees of each clone, 246, 344, 508 and 660 every month. Each nut was split and the husk was dried for 8 hours at 105 °C. Dried husks were ground to pass through a 40 mesh screen. Nitrogen content was analyzed by the modified micro-Kjeldhal methodology (Müller, 1961), and was calculated by the formula:

$$\% N = \frac{A * B * C}{D} * 100$$

$A = cm^3\ H_2SO_4$
$B = $ acid normality
$C = meq\ N$
$D = $ sample weight (g)

The experimental design used was a randomized design. The significance of treatment effects was determined by analysis of variance (GLM), using the SAS program (SAS, 1985). The differences between means were calculated by the LSMeans test.

ii) Secondary compounds

Analyzes were carried out during August-September 1993 in the animal nutrition laboratory at CATIE. This study used the same developmental stages of nuts described for the nitrogen analyzes, but included a fifth stage: > 100 days. Nuts were split and separated into three layers: 1) the exo- and mesocarp; 2) the endocarp, and 3) the seminal coat, and placed in the freezer until analyzes were carried out. Each layer was broken into small pieces, and liofilyzed (freeze dried) for 12 hours. The layers were then ground to pass through a 40 mesh screen.

Tannin content. Soluble tannins were determined gravimetrically after precipitation with trivalent ytterbium (Reed et al., 1985). Tannin content was calculated by the following formula:

$$\% \text{ Tannin} = \frac{[(E - (C * D))] - (F + G - I)]}{A * B} * 100$$

A = sample weight (g)
B = dry matter sample (g)
C = filter weight (g)
D = dry matter filter (g)
E = crisol + filter weight (g) at 105 °C
F = blank (x of 4 crisol) weight (g) at 550 °C
G = crisol weight (g)
I = ash weight (g) at 550 °C

Proanthocyanidin content. Soluble proanthocyanidins were determined by the Rittner and Reed (1992) methodology. Proanthocyanidins were not determined for layer 3 since the nut sample from the early developmental stages, < 60 days and 60 - 75 days, finished.

iii) Dry matter content. This study used the same developmental stages of nuts described in the secondary compound study. Dry matter content was determined from the difference between the initial and final weight of the sample after 8 hours in an oven at 105 °C.

Data were analyzed using analysis of variance (SAS Institute, 1985) for a replicated split-plot design with two replicates, with

clones as the main effect and stages of development as subplot. Layers were nested within the developmental stages. Differences between means were calculated by Tukey's Test. Tannin and dry matter data were transformed by arcsin (tannin/100), and arcsin (dry matter/100).

7.2 RESULTS

Nitrogen content varied significantly among clones, developmental stages and between clones and stages of development of the nut (Table 7.1). It was higher in clones 508 (1.66 %) than the other three clones: 660 (1.52 %), 246 (1.50 %) 344 (1.46 %) (Table 7.2, Fig. 7.1). Nitrogen content decreased with nut maturation (Table 7.2, Fig. 7.2). It was highest in the first stage of development (1.93 %) followed by the stages of development 2 (1.59 %), 3 (1.40 %) and 4 (1.21 %). Differences in nitrogen content between clones and developmental stages are shown in Table 7.2, Figure 7.3. A similar pattern was observed for nitrogen content between the stages of development of the nuts within clones. No relationship was found between the percentage of nuts damaged and the percentage of nitrogen content of the nuts (Fig. 7.4).

Tannin content ranged from 19 to 85 %. Highly significant differences in tannin content were found among clones (F= 11.81; df = 3; P < 0.001) and layers (F = 13; df = 2; P < 0.001), and significant differences were found between the stages of development (F = 3.77; df = 4; P = 0.02). However, the interaction between clones, layers and stages of development was also significant (F = 2.58; df = 18; P < 0.01). Therefore differences among variables cannot be explained.

No significant differences were found for proanthocyanidin content for the stages of development of the nuts (P = 0.07) (Table 7.3). Proanthocyanidin content varied significantly between clones, being higher in clones 660 (5.73 abs), and 508 (3.66 abs) followed by 344 (2.25 abs) and 246 (1.90 abs) (Table 7.4, Fig. 7.5). Tukey's test did not detect differences between the means for proanthocyanidin content of clones 660 and 508, or between the means of clones 508, 344 and 246. There was a significant difference between proanthocyanidin content for layers 1 and 2, being higher in layer 2

Table 7.1: Nitrogen content (%) in four clones and four developmental stages of the nut Turrialba, Costa Rica, during November 1991 - July 1992.

Source	DF	F
Clone	3	5.37 **
Dev. stages	3	65.47 ***
Clone* Dev. stages	9	2.20 *

* P < 0.05; ** P < 0.005; *** P < 0.001

Table 7.2: Means for nitrogen content (%) in four clones, four developmental stages of the nut and between clones and developmental stages, Turrialba, Costa Rica, during November 1991 - July 1992.

Clone	Mean	Dev. stages	Mean	Clone* Dev. stages	Mean
508	1.66 a	1	1.93 a	508 -1	2.14
660	1.52 ab	2	1.59 b	660-1	1.98
246	1.50 bc	3	1.40 c	344-1	1.91
344	1.46 bcd	4	1.21 d	508-2	1.76
				246-1	1.69
				660-2	1.60
				246-2	1.57
				508-3	1.50
				344-2	1.42
				246-3	1.48
				344-3	1.33
				660-3	1.30
				246-4	1.28
				504-4	1.23
				660-4	1.18
				344-4	1.16

Means followed by the same letter are not significantly different P = 0.05 Tukey's Test.
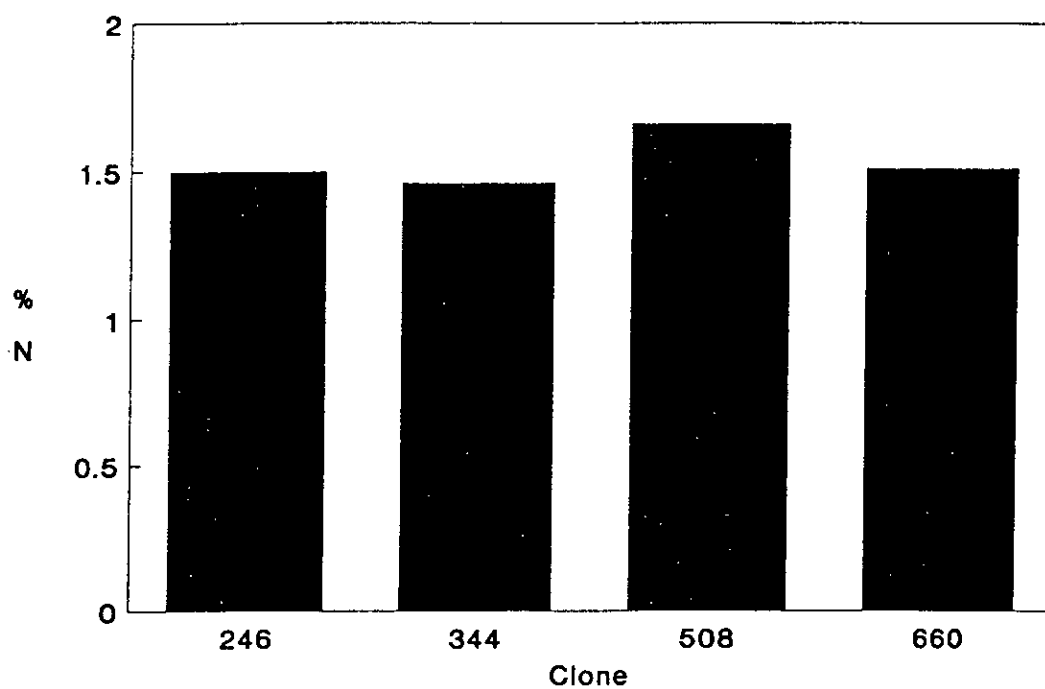
Fig. 7.1:   Percentage of nitrogen content in four clones of
               macadamia nuts in Turrialba, Costa Rica, during
               November 1991 to July 1992.
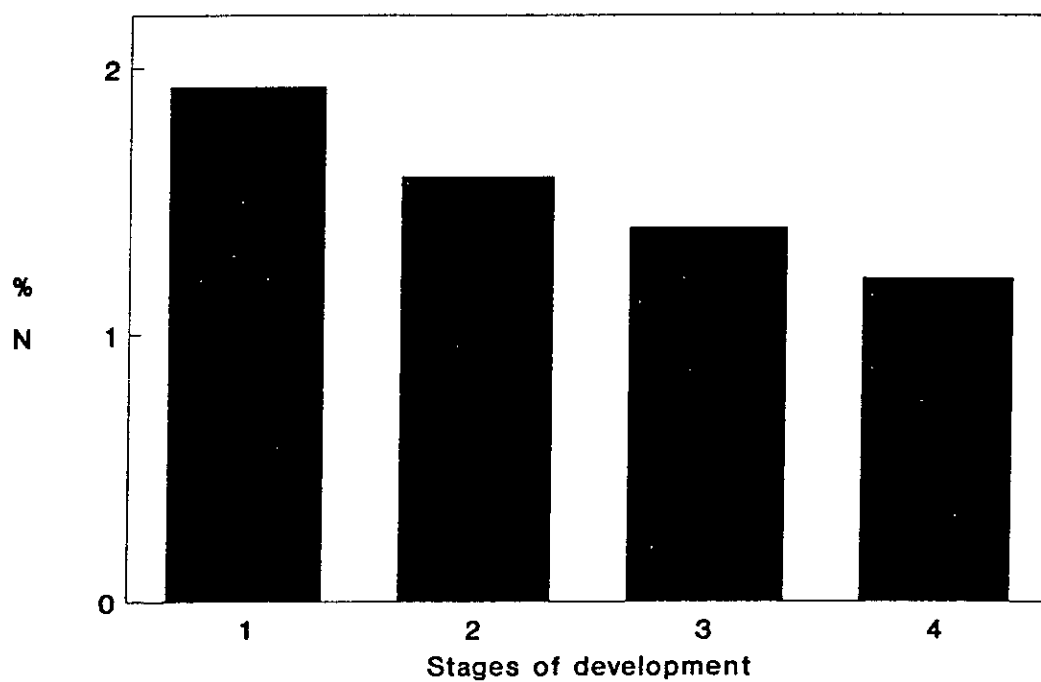
Fig. 7.2:   Percentage of nitrogen content in four stages of
               development of macadamia nuts in Turrialba, Costa
               Rica, during November 1991 to July 1992.
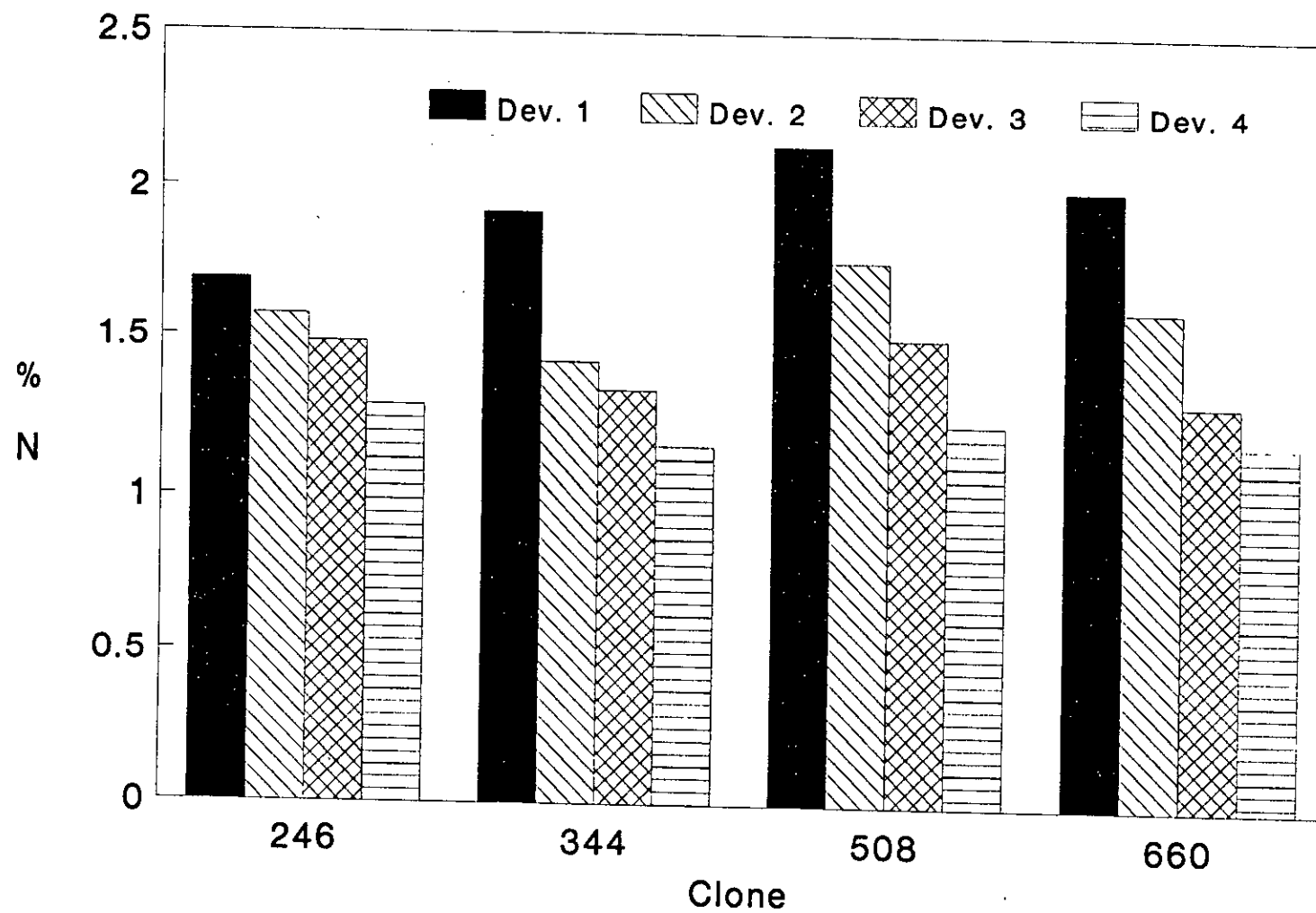
Fig. 7.3:   Percentage of nitrogen in four clones and four stages of development of macadamia nuts in Turrialba, Costa Rica, during November 1991 to July 1992.
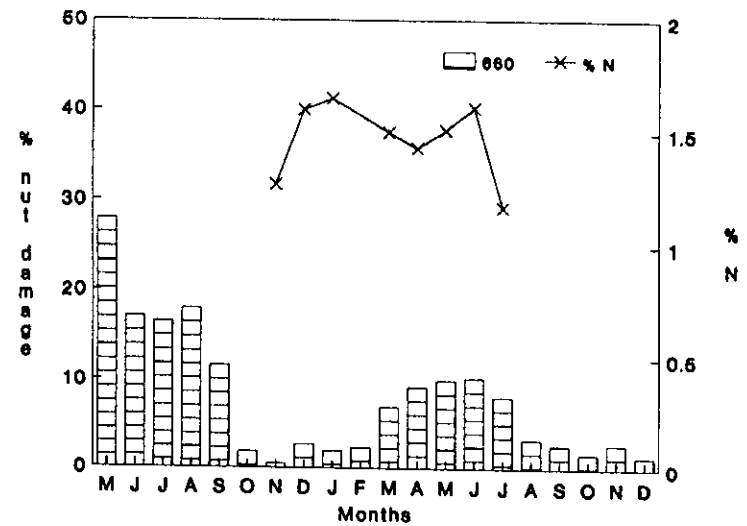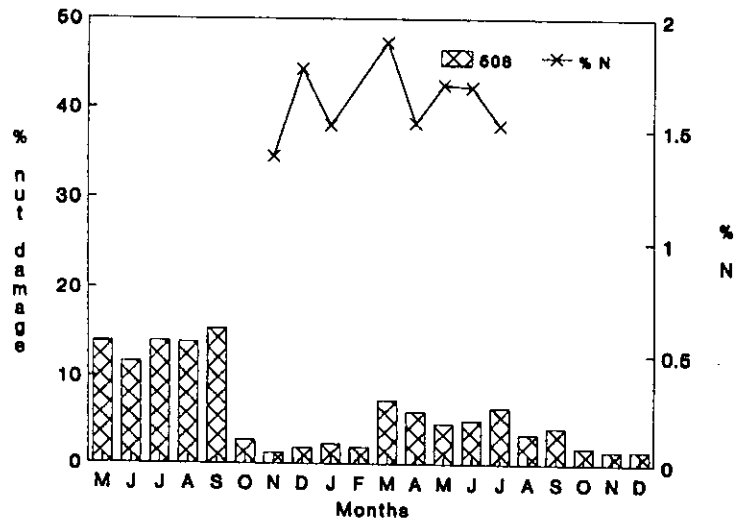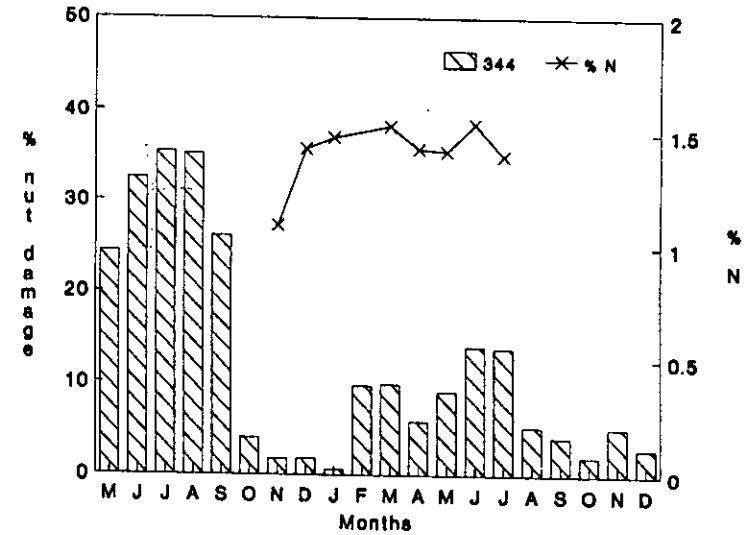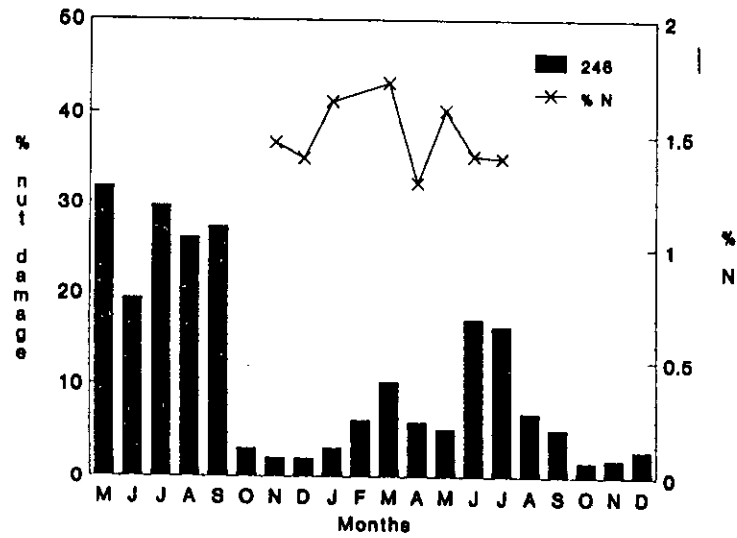
Fig. 7.4: Percentage of nut damage and nitrogen content of four clones of macadamia nuts per month in Turrialba, Costa Rica.

Table 7.3: Proanthocyanidin content (abs) in four macadamia clones, five developmental stages of the nut and two layers, Turrialba, Costa Rica, 1993.

Source	DF	F
Clone	3	6.55 *
Dev. stages	4	2.55 ns
Clone * Dev. stages	12	1.16 ns
Layer	1	32.94 ***
Clone * Layer	3	5.22 *
Dev. stages * Layer	4	2.09 ns

ns = not significant; * P < 0.05; *** P < 0.001

Table 7.4: Means for proanthocyanidin content (abs) in four clones, two layers and between clones and layers, Turrialba, Costa Rica, 1993.

Clone	Mean	Layer	Mean	Clone * Layer	Mean
660	5.73 a	2	5.20 a	660-2	9.30 a
508	3.66 ab	1	1.57 b	508-2	6.03 b
344	2.25 b			246-2	2.83 c
246	1.90 b			344-2	2.62 c
				660-1	2.16 c
				508-1	1.88 c
				246-1	1.28 c
				344-1	0.97 c

Means followed by the same letter are not significantly different P = 0.05, Tukey's Test.
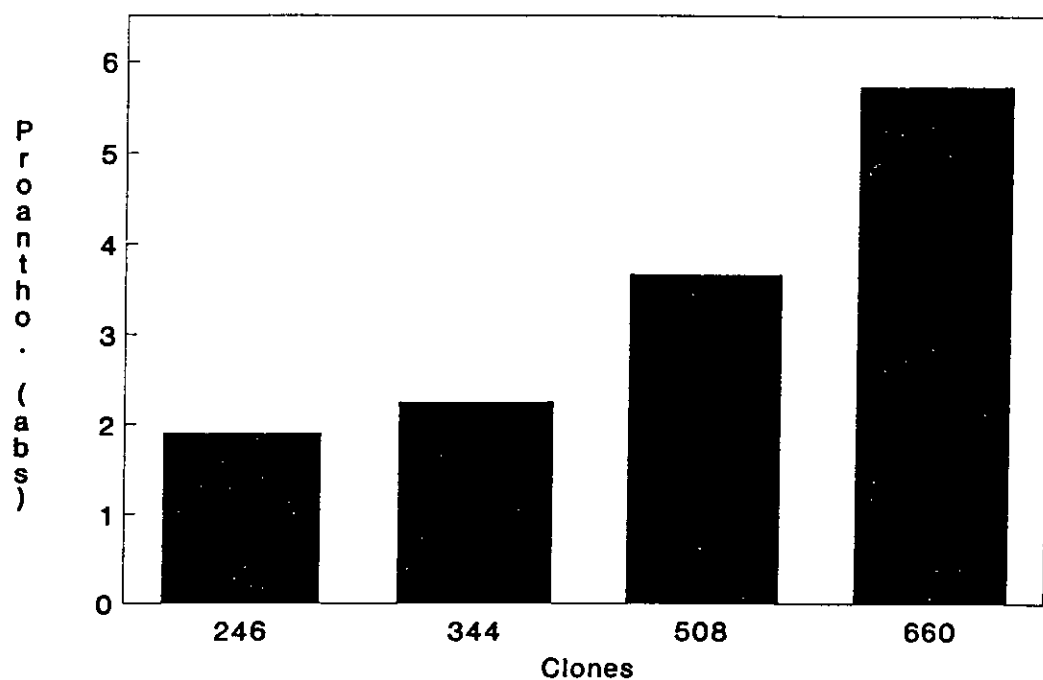
Fig. 7.5:   Proanthocyanidin   content   (abs)   in   four
macadamia clones, Turrialba, Costa Rica, 1993.
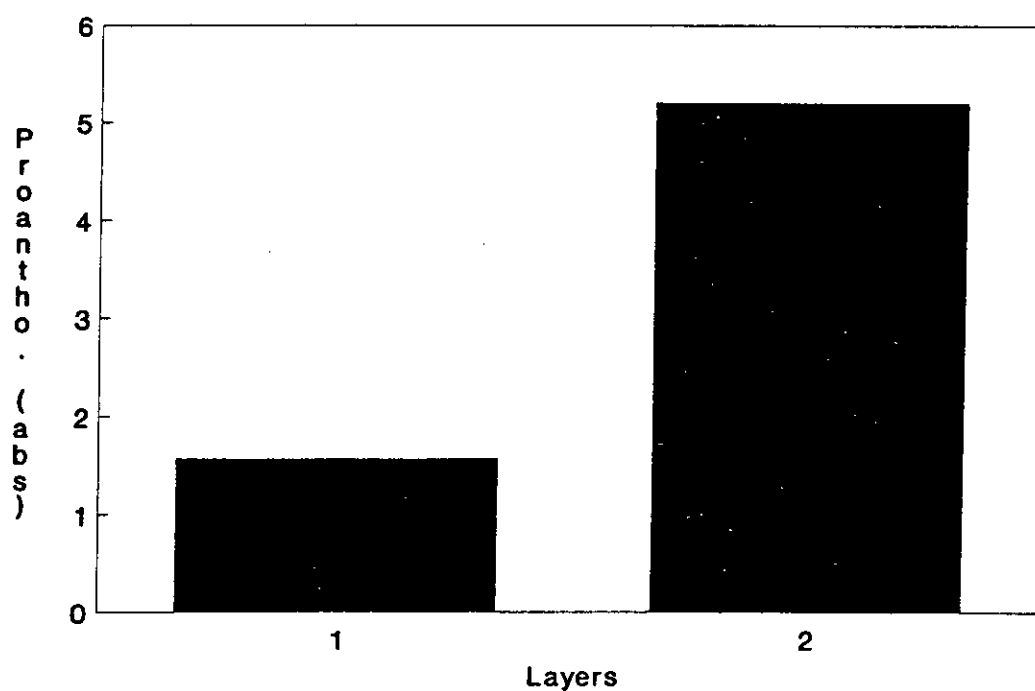
Fig. 7.6:   Proanthocyanidin content (abs) in two layer
macadamia nut, Turrialnba, Costa Rica, 1993.

(5.20 abs) than in layer 1 (1.57 abs). A similar trend in proanthocyanidin content was observed for layers within clones (Table 7.3-7.4, Fig. 7.6). However, there was a significant difference in proanthocyanidin content between clones and layers, interclonal differences were more marked in layer 2 than in layer 1 (Fig. 7.7).

Percentage dry matter varied between clones at a highly significant level (Table 7.5). It was highest in clones 660 (90.4 %) and 508 (89.9 %), followed by clones 344 (87.5 %) and 246 (87.2 %). No significant differences were found between the stages of development for dry matter content (Table 7.5). Dry matter content between layers varied significantly, being highest in layer 1 (96 %) than in layers 3 (91.5 %) and 2 (90.2 %) (Table 7.6). Tukey's test did not detect differences between the means of layers 2 and 3.

7.3 DISCUSSION

The development of phytophagous insects often depends on the physiological condition of the plant. Nitrogen content is regarded as a critical aspect of plant quality because it is often a limiting nutrient for both plants and herbivorous insects (Mattson, 1980). A high nitrogen supply may increase protein production and decrease the carbohydrate content resulting in the formation of thin cell walls and softer and succulent tissue, which make the plant more susceptible to insect grazing (Singh and Singh, 1969). A high nutritious quality of the plant has been found to increase larval survivorship and hence overall abundance of an insect (White, 1978).

Nitrogen content differed between clones and the stages of development of the nuts. Since nitrogen content is associated with more nutritious food and differed between clones and developmental stages of the nuts, higher levels of nitrogen were expected in the susceptible clones 246 and 344 than in the tolerant clones 508 and 660. Therefore, this result suggests that moths are not attracted to lay eggs on a more nutritious food source, thus supporting the hypothesis that *E. torticornis* is a native species which recently switched to macadamia nuts. Nitrogen concentration influences host plant choice (Feeny, 1970; Athey and Connor, 1989) and oviposition (Ohmart *et al.*, 1985). Higher herbivory has been found among closely-related plants
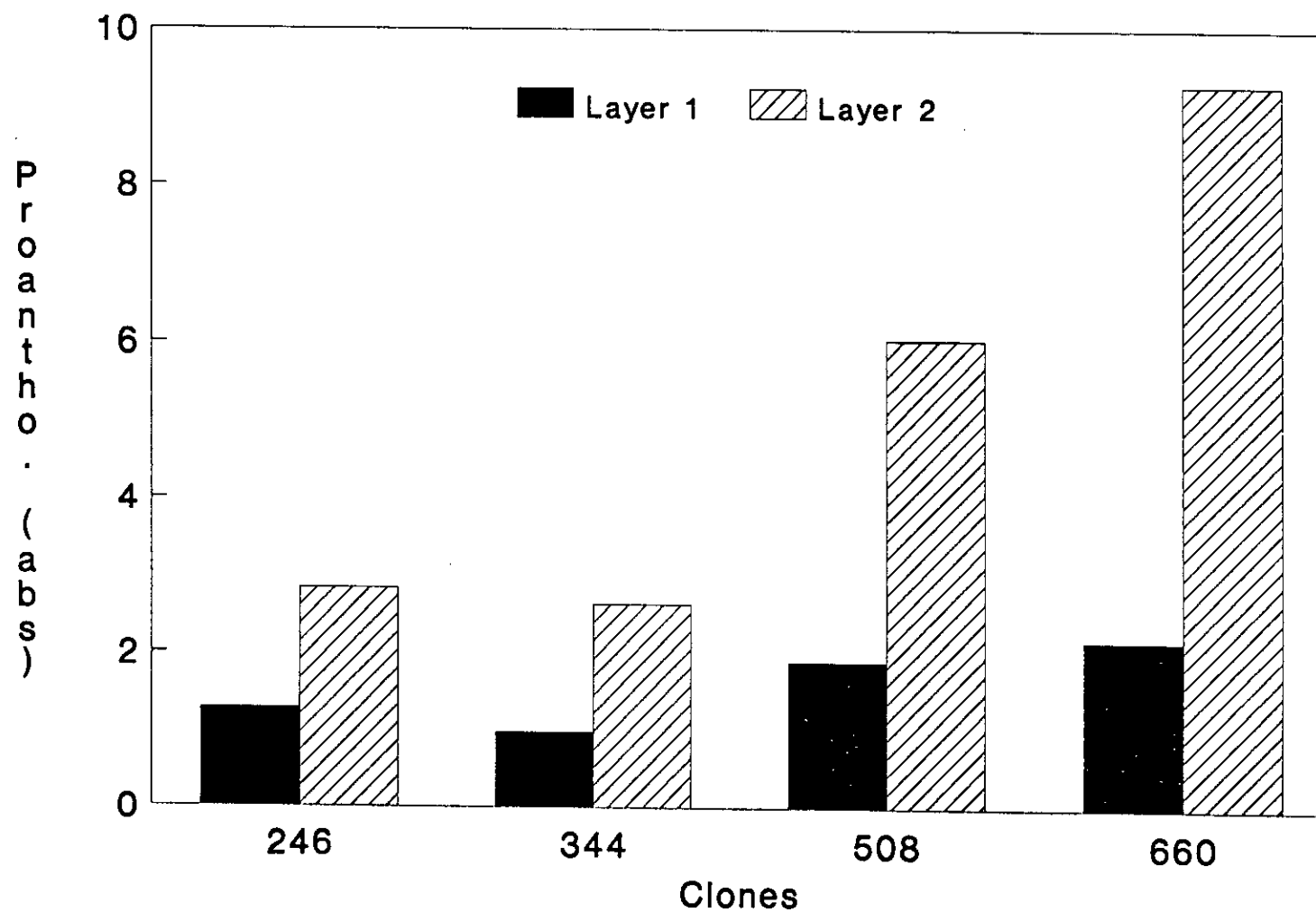
Fig. 7.7:   Proanthocyanidin content (abs) in four clones and two layers of macadamia nut, Turrialba, Costa Rica, 1993.

Table 7.5: Dry matter content in four macadamia clones, five developmental stages of the nut and three layers, Turrialba, Costa Rica, 1993.

Clone	DF	F
Clone	3	12.31 ***
Dev. stages	4	1.01 ns
Clone * Dev. stages	12	1.54 ns
Layer	2	97.30 ***
Clone * Layer	6	0.36 ns
Dev. stages * Layer	6	2.55 ns

ns = not significant; *** P < 0.001

Table 7.6: Means for the dry matter content in four clones and three layers, Turrialba, Costa Rica, 1993.

Clone	Mean	Layer	Mean
660	90.4 a	1	96.95 a
508	89.9 a	3	91.50 b
344	87.5 b	2	90.22 b
246	87.26 b		

Means followed by the same letter are not significantly different P = 0.05, Tukey's Test.

with higher foliar nitrogen concentrations (Tabishnik, 1982). Variability in the growth and survival of the pine beauty moth, *Panolis flammea*, was found to be positively correlated with foliar nitrogen of lodgepole pine and Scots pine (Watt, 1990). Stiling *et al.* (1982) examined the effect of total nitrogen content as the possible cause of the shoreline concentration of *Hydrellia valida* on *Spartina alternifolia*. Greater concentrations of *H. valida* were found along the shoreline plants which contained up to twice as much total nitrogen as the inland plants. Ohmart *et al.* (1985) reported an increase of 500 % in the total number of eggs laid and 400 % in the production of eggs laid by *Paropsis atomaria* when nitrogen in the foliage of *Eucalyptus blakely* was increased from 1.5 % to 4 %.

The fact that nitrogen content decreased with nut maturation is consistent with what has been reported in the literature. Higher concentrations of nitrogen occur in actively growing tissues or storage tissues, such as seeds. Such tissues require high nitrogen levels to support rapid protein synthesis during bursts of growth. As tissue growth begins to wane, so does nitrogen content (Mattson, 1980; Rockwood, 1974). Since *E. torticornis* discriminate against small nuts (< 8 mm in diameter) for egg laying (Chapter 1), it may be that on their previous host(s), they lay eggs on fruits larger than 8 mm in diameter.

Higher dry matter contents were found in the tolerant clones, 508 and 660, and in the outer layer than in the susceptible clones 246 and 344 and the inner layers (2 and 3). This observation suggests that larval survival is primarily affected by a physical barrier; as the husk matures, it gets drier and is more difficult to chew. Coley (1983) studied the rates of herbivory and defensive characteristics of young and mature leaves of 46 tree species in a lowland tropical forest. He found that leaf toughness and fiber content were the most important characteristics which determined grazing levels and suggested that the importance of phenolic content as a defense may have been over emphasized. At the same time, the hardness of plant tissues may affect fecundity of insects by affecting feeding or oviposition. Iheagwam (1981) found an inverse relationship between fecundity of the cabbage whitefly, *Aleyrodes brassicae*, and leaf hardness. Tougher surfaces will imply that larvae need more time to bore through the

husk which will expose them for longer periods to predators and parasitoids.

Proanthocyanidin content was highest in layer 2 of clones 508 and 660 than in clones 246 and 344, representing another potentially detrimental on larval survival. Larvae have to overcome this defensive characteristic to feed on the husk or to be able to bore through the kernel. Proanthocyanidins may lower the nutritive value of plant tissue (Klocke and Chan, 1982). However, they can inhibit herbivore feeding in various ways including direct enzyme inhibition or by forming indigestible complexes with leaf proteins; however, their effects vary depending on various factors including chemical composition and concentration (Bernays *et al.*, 1989).

It cannot be concluded that nitrogen and tannin content affect the abundance of the nutborer. However, *E. torticornis* is affected by dry matter and proanthocyanidin content which act as physical and chemical barriers respectively.

CHAPTER 8

THE EFFECT OF WEED MANAGEMENT ON
E. torticornis POPULATION

This study was conducted to determine the effect of weed management on the abundance of the nutborer. The different types of management used were: macadamia husk as a mulch, bare ground, and weeds allowed to grow freely.

8.1 MATERIALS AND METHODS

This experiment was carried out from June to September 1992 at Oriente Farm. Three weed management systems, use of macadamia husk as a mulch, bare ground, and weeds growing freely, were studied at three different sites: site 1 = lot 4, site 2 = lot 15, site 3 = lots 7 and 14 (Plate 3.1). Treatments were replicated five times in each site (5 replicates x 3 treatments) for a total of 45 trees. Forty five nuts from each tree were harvested on five occasions at intervals of 22 days. The nuts were examined in the laboratory (23 °C, 80 % RH), and the number of eggs per nut were recorded. Differences in the number of eggs between clones were not investigated since no differences were found for the number of eggs layed among clones (see Chapter 6).

Treatments were established one month prior to the first date of sampling. Each treatment comprised the tree from which nuts were subsequently collected and the eight trees surrounding it. Macadamia trees are planted at a distance of 6 - 7 metres from each other, giving an area of 168 m ^{2} per group of trees. The husk applied was taken from piles of husk usually left to decompose in lots 3 and 4 (Plate 3.1). Macadamia husk cannot be applied as a mulch directly from the processing plant, as it liberates considerable heat during decomposition. Since the roots of macadamia trees are localized within the first 30 cm of the soil (Montero, 1991), the addition of fresh husk could cause root burn and negatively influence the growth of the trees. The bare ground treatment was achieved by cutting the weeds with a machete every three weeks.

Weeds present in each site were classified as gramineous or broadleaf. Among the gramineous weeds were: *Panicum maximum*, *Eleusine indica*, *Rottboellia exaltata*, and *Digitaria decumbens*. Broad leaf weeds included *Impatiens balsamina*, *Bidens pilosa*, *Emilia sonchifolia*, and *Sida rombifolia*. For all three sites, gramineous weeds were dominant over broadleaf weeds, the highest density of *P. maximum*. There were differences in broadleaf weed composition between sites. At site 1 there was a small number of broadleaf weeds, any of them dominant over the others. Site 2 was dominated by *I. balsamina*, and site 3 had very few broad-leaf weeds.

The experimental design used was a factorial of 3 sites x 3 treatments, replicated five times. The significance of treatment effects was determined by analysis of variance (GLM), using the SAS program (SAS, 1985). The differences between the means were calculated by the LSMeans Test. Data were transformed by the sqrt(x + 0.5) because many nuts were free of damage.

8.2 RESULTS

A total of 9926 nuts were inspected. The number of eggs per nut differed significantly among sites and treatments (Table 8.1). However, the interaction between site and treatment was also highly significant. The number of eggs was highest in site 3 (0.48 eggs per nut), followed by site 1 (0.40) and site 2 (0.21) (Table 8.2).

The highest number of eggs was recorded when the husk was added (0.40 eggs per nut), followed by the unweeded treatment (0.35), and the bare ground treatment (0.32) (Tables 8.1-8.2). The LSMeans Test could not detect differences between the means of the number of eggs for the weed and bare ground treatment.

The mean number of eggs per treatment in each site is presented in Table 8.2, Figure 8.1. In sites 1 and 2 the number of eggs was lowest in the weed treatment, followed by the bare ground and husk treatment. In site 3, however, while this trend was seen for the bare ground and husk treatments, there were by contrast more eggs in the weed treatment.

Table 8.1: Analysis of variance of mean number of eggs per nut of *E. torticornis* in three sites and three weed management systems at Oriente Farm, Turrialba, 1992.

Source	DF	F
Site	2	125.10***
Treat	2	9.71***
Site*Treat	4	7.70***

Data transformed by $\sqrt{(x + 0.5)}$; ***, $p < 0.001$.

Table 8.2: Means of eggs of *E. torticornis* per nut in (1) three sites; (2) three weed management; and (3) the interaction of site and weed management at Oriente Farm, Turrialba, 1992.

(1)Site	Mean	(2)Treat	Mean	(3)Site*Treat	Mean
3	0.48 a	Husk	0.40 a	3-Weed	0.55 a
1	0.40 b	Weed	0.35 b	3-Husk	0.50 ab
2	0.21 c	Bare ground	0.32 bc	1-Husk	0.47 abc
				3-Bare ground	0.39 cd
				1-Bare ground	0.37 de
				1-Weed	0.36 def
				2-Husk	0.24 g
				2-Bare ground	0.23 gh
				2-Weed	0.17 hi

Means followed by the same letter are not significantly different (P=0.05), LS Means Test.

n = 15 in each case.
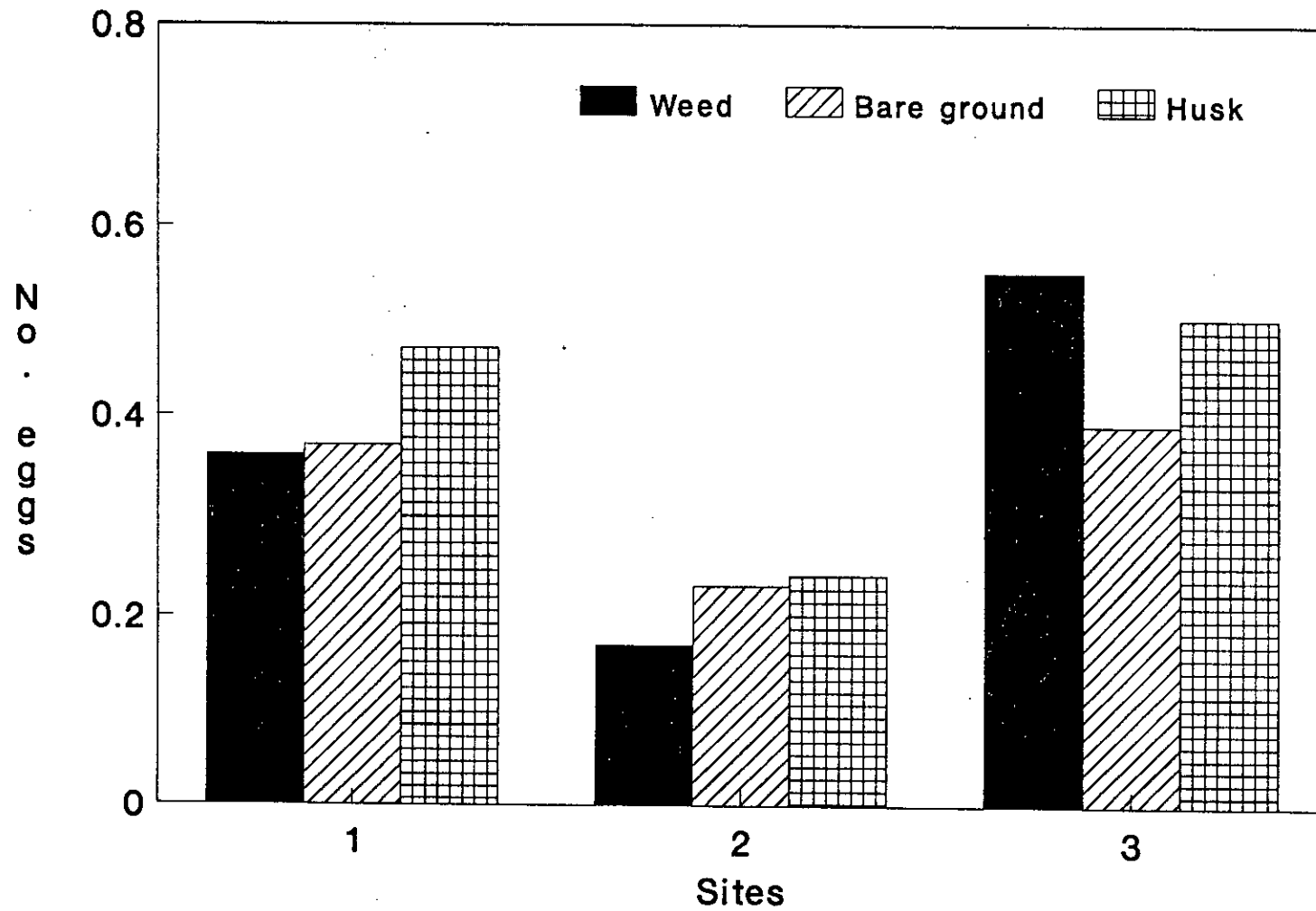
Fig. 8.1:   The mean number of eggs of *E. torticornis* per nut in three sites and three weed management treatments, at Oriente Farm, Turrialba, 1992.

8.3 DISCUSSION

Weeds are major components of agro-ecosystems and play an important role in determining the diversity and stability of insect populations. Studies on weeds have concentrated on controlling them by either cultural or chemical means, but not many studies have focussed on the benefits they provide (Altieri et al., 1977). Among the cultural practices for managing weeds are the use of cover crops, the use of mulches such as plastics, plant residues, sawdust, rice husk, and variations on tillage (Ramiro de la Cruz, personal communication).

The number of eggs of E. torticornis differed between the weed management system used. When husk was applied, a higher number of eggs was found than in the weed and bare ground systems. The addition of husk might affect the nutborer population by concentrating odours which could attract the adults, or by disrupting the parasitoid and predator population. Shelton and Edwards (1983) found that Epilachna varivestis, the primary soybean pest species in Indiana, was significantly more abundant in weed-free soybeans than in weedy soybean habitats. Altieri et al. (1977) reported a decrease in the colonisation and reproduction of Empoasca kraemeri in grass weed-bean habitats and suggested that it was caused by a repellent or masking stimuli from Eleusine indica and Leptochloa filiformis, two common grass weeds in Colombia.

Because a higher number of eggs were found in site 3 than in site 1, where most of the husk material is left in the farm to decompose, it is unlikely that this practice had a pronounced effect on nutborer abundance (Chapter 3). The higher population of broad-leaf weeds in site 2 could be the reason for the lower number of eggs of the nutborer at that site, as more predators and parasitoids have been reported from vegetationally diverse habitats (Root, 1973; Andow, 1990). Root (1973) pointed out that the two major explanations for decreases in the abundance of herbivorous insects in diversified habitats are the resource concentration hypothesis and the natural enemies hypothesis.

The addition of husk as the only weed control method appears to increase the abundance of E. torticornis in some way. Weeds under the macadamia tree canopy must be controlled as they interfere with

the harvest since the nuts are gathered from the ground every fourteen days, and because the trees have superficial roots, alternatives to chemical control must be found. The use of cover crops in the mid-rows might be an alternative for controlling weeds and increasing beneficial enemies. Other benefits that could be achieved with leguminous cover crops are that they help increase soil N levels, promote better soil structure, and decrease erosion. On the other hand, cover crops may compete with trees for water and nutrients, interfere with harvesting if not managed adequately and provide refuges for insects which might eventually damage macadamia production (Bugg *et al.*, 1991).

There is a need for testing these weed management systems for longer periods, and perhaps, to enlarge the area of each treatment. For example, Altieri and Schmidt (1986) studied the effect of cover crops on the population of the codling moth in apple orchards. On the first year of study, they found a slight decrease in the number of fruit with codling moth damage, but a significant decrease, from 88 to 4 %, in the number of damaged fruits was observed during the second year of having cover crops in the apple orchard. Their result suggest that a longer period is needed to observe the effect of weed management on the abundance of a pest.

CHAPTER 9

GENERAL DISCUSSION

THE LIFE CYCLE AND FECUNDITY OF *Ecdytolopha torticornis*

The macadamia nut is a recent crop in Costa Rica. One of its main insect pests, *E. torticornis*, has only been reported as a macadamia pest in Costa Rica. The biology of this insect resembles that of other macadamia nutborers, which are *Cryptophlebia ombrodelta, C. batrachopa, C. leucotreta,* and *C. illepida* present in macadamia orchards in Australia, Malawi and Hawaii (Namba, 1957; Ironside, 1974; La Croix and Twinda, 1986; Jones and Tome, 1992).

Four larval instars were identified. The egg stage was completed in 5-6 days, the first three larval instars each had a duration of 3-4 days, while the fourth instar plus prepupa had a duration of 3-9 days. The life cycle from egg to adult lasted 36 days, and thus approximately ten generations per year may be completed in Turrialba. Since the macadamia trees flower and bear fruits throughout the year, food availability allows the insect to be active all year although varying in quantity. Alternative hosts in the forest may play an important role in maintaining nutborer populations during the time when nut production is low. Therefore, efforts must be made to identify these potential alternative hosts.

The fecundity of *E. torticornis* was found to be 37 eggs per female, which is similar to that reported for other tortricids (Geier 1963; Ironside 1974; Powell 1976; Daiber 1980). The number of eggs laid per female varied from 2 to 74, with 35 % of them being infertile. Due to the importance of fecundity in the growth of insect populations, further studies are required to explain the high percentage of infertile eggs.

Devising management strategies for any pest requires an intimate knowledge of their biology and particularly their phenology at every location where management decisions are required.

FACTORS AFFECTING THE ABUNDANCE OF *Ecdytolopha torticornis*

It is apparent that annual infestations of macadamia nuts by *E. torticornis* in Oriente Farm may be attributed to nutborer larvae which feed in the few nuts remaining in the trees during low nut production. It is unlikely that migration is an important factor affecting nutborer abundance since the insect has been reported as being a poor flyer by Chamberlain (1989), and also, as observed in Macaloha Farms, Siquirres (personal observation) the dispersal of the moth within a macadamia orchard was due to nut transportation to a storage room prior to transportation to the processing plant. Due to the poor dispersal of moths and larvae observed in the field, it is likely that dispersal of this insect primarily happens due to transportation of nuts. Since macadamia growers store the nuts in their farms until there is enough product to be taken to the processing plants, and dispersal of the insect is mainly due to nut transportation, the nutborer population may be reduced by putting a wire screen on top of the nut piles stored in open galleries. This practice will allow parasitoids to disperse to the field and would prevent the emerging nutborer adults from colonizing new areas. A similar practice was used by Quezada and Rodríguez (1989) during a severe outbreak of *Rothschildia orizaba* in a coffee plantation near Turrialba. Their results showed that by confining the moth cocoons in screen cages, the emerging moths were trapped, while allowing egg and pupal parasitoids to disperse.

Macadamia clones differed in their susceptibility to *E. torticornis*. Clones 246 and 344 were more susceptible than clones 508 and 660 to nutborer attack. Most macadamia clones are self-incompatible; a mixture of clones in an orchard is recommended to increase cross pollination between clones and to improve tree distribution within the orchard (Queensland Department, 1984; Montero, 1991). Therefore, the practice of planting single tolerant clones of macadamia cannot be recommended.

The abundance of the nutborer was strongly related to food availability. Nut damage varied between years. It was highest in 1991 and decreased in 1992 and 1993. A probable explanation is that due to a decrease in the price of the macadamia nut in the world

market in 1991, certain costly management practices were abandoned. This resulted in a decrease in nut production with less food available for the nutborer. Other possibilities that could explain the decrease in nutborer population are that this insect may have a cyclic pattern of abundance or that the population was regulated in some extent by natural enemies.

Differences in nutborer damage between sites may be due to the patchy distribution of the moth, to the habitat surrounding each site, and to husk transportation from the processing plant. To reduce damage, the husk should be left to decompose in other plots than the macadamia orchards, with the use of wire screens as specified earlier. At the same time, the processors could offer incentives to the growers to hand in dehusked nuts.

Kernel damage was highest when immature nuts were present. This damage was expected since there were proportionally more fruits suitable for infestation with penetrable shells at that time than at any other time of the year.

Six species of hymenopteran parasitoids, not reported previously, were recovered from the nutborer. There were four larval parasitoids: *Apanteles* sp. I, *Apanteles* sp. II, *Pristomerus* sp. and *Ascogaster* sp., and an egg parasitoid belonging to the family Trichogrammatidae. One hyperparasitoid was found belonging to the family Perilampidae. *Apanteles* I and *Ascogaster* sp. were the dominant parasitoids, which accounting for 40 and 50 % of the parasitoids reared. The ability of these two parasitoids to reduce the damage inflicted by *E. torticornis* makes them desirable as biotic control agents. However, it is not clear why *Ascogaster* sp. appeared during the third year of study, and the reason why it became the dominant parasitoid. Parasitism trends were related to nut damage trends, but with a time lag suggesting a delayed-density dependent response to nutborer abundance. Extensive biological studies of the parasitoids are required to determine if their levels of parasitism could be improved by modifications of the orchard environment. Such studies should be preceeded by the determination of economic damage thresholds for the crop, and potential savings on the cost of chemical crop protection should be balanced against the cost of those biological studies.

Predation was found to negatively affect nutborer abundance. The fire ant, *Solenopsis geminata*, was considered the most important predator. An increase in the harvest interval could decrease the nutborer population even more. This is not a practical recommendation to be considered in Turrialba, where the high temperature and rainfall would cause a rapid decrease in nut marketable qualities if they remain on the ground for a long period. An opposite recommendation was suggested by Jones *et al.* (1992) for the management of the macadamia shotborer, *Hypothenemus obscurus*. As macadamia nuts are harvested once a month in Hawaii, a more regular harvest interval was suggested as a solution to minimize beetle reproduction and damage.

E. *torticornis* moths preferred to oviposit upon nuts on branches within the first three metres from the ground. The knowledge of the ovipositional preference of the moths will help significantly in reducing time of sampling, and hence money, when sampling the nutborer and its parasitoid population. It is clear that nuts of 8 to 20 mm in diameter are the most important to protect. The spread of fruitset prolongs this period somewhat, but clones with a more concentrated flowering period should be adopted in the future to simplify management.

Female moths did not discriminate between clones during oviposition. However, clone susceptibility to E. *torticornis* varied, suggesting that food quality was one of the factors limiting the insects' survival or growth, or both. Nitrogen is the plant nutrient which has been more clearly associated with a better insect performance; high nitrogen concentrations results in higher feeding (Horn, 1988) and higher fecundity (van Emden *et al.*, 1969), while low nitrogen concentrations result in lower growth rates of insects (White, 1978). Quantitative defenses such as tannins, resins and lignins reduce the digestibility of plant tissues to herbivores (Rhodes, 1983). In this study, nitrogen and tannin content did not affect the abundance of the nutborer, while higher proanthocyanidin and dry matter contents were found in the tolerant clones. Since dry matter was highest in the exocarp and mesocarp of the nuts from the tolerant clones and proanthocyanidin was highest in the endocarp, the nutborer larvae have to overcome first a physical barrier followed by a chemical barrier to feed on macadamia nuts. The importance of leaf

toughness on insect feeding was demonstrated by Coley (1983). She studied the effect of physical and chemical properties on the levels of insect herbivory of forty six species of plants in Barra del Colorado, Panama. Her results showed that leaf toughness was the main characteristic which affected the levels of herbivory.

Weed management affects the abundance of the nutborer. The practice of spreading the husk under the tree canopy as a mulch was found to increase the number of *E. torticornis* eggs. Alternative mulch substrates or the use of cover crops must be studied for weed control. Mulches and cover crops produce a beneficial effect on the trees in many ways: the humus content of the soil increases the moisture-holding capacity and aeration is improved, nutrient elements are added to the soil, erosion and water run-off are eliminated and there is less fluctuation in soil temperature.

The judicious use of insecticides, combined with proper orchard management practices, will not only save the growers' time and money, but would also reduce environmental contamination, would help in maintaining populations of beneficial insects, and would lessen the likelihood of nutborer populations becoming resistant to insecticides.

Various results from this study lead to the conclusion that *E. torticornis* is an indigenous species to Costa Rica, which switched to macadamia due to it being a more abundant food source. These results were: the presence of five parasitoids, although only two reached high levels of parasitism and the lack of preference of ovipositing moths for nuts of the highest quality, as measured by nitrogen content.

E. torticornis has a short life cycle, and it is possible to obtain up to ten generations per year. Its abundance is affected by four factors: food quantity and quality, parasitism and predators.

This is the first study which describes the biology and the factors that affect the abundance of *E. torticornis* population. Future studies are needed which would implement integrated pest management strategies to maintain fluctuating pest populations below economic injury levels.

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Table 4.1A: Number of larval parasitoids obtained from exposed hosts of *E. torticornis* at Oriente Farm, Turrialba, Costa Rica, from 1991 - 1993.

Sample	ApI	ApII	Asco	Pris	Sample	ApI	ApII	Asco	Pris
1	1	0	0	0	16	15	2	0	0
2	0	0	0	0	17	6	4	0	0
3	6	0	0	0	18	7	3	0	1
4	8	0	0	0	19	4	3	0	1
5	8	0	0	0	20	5	0	1	0
6	6	0	0	0	21	0	0	2	0
7	2	0	0	0	22	3	4	2	0
8	4	0	0	0	23	8	9	0	0
9	3	0	0	0	24	0	0	6	0
10	0	0	0	0	25	7	1	16	0
11	0	0	0	0	26	6	3	23	0
12	0	0	0	0	27	8	3	44	0
13	7	0	0	0	28	12	1	54	0
14	10	0	0	0	29	13	1	46	0
15	6	1	0	0	Total	155	35	194	2

* Sample days 1-8 = 1991; 9-20 - 1992; 21-29 = 1993

Table 4.2A: The number of the macadamia nutborer *Ecdytolpha torticornis* larvae and pupae, the number of parasitoids and the percentage parasitism per clone: 246, 344, 508, 660 in Turrialba, Costa Rica.

Date	Sample	L+P	246 Par	%P	L+P	344 Par	%P	L+P	508 Par	%P	L+P	660 Par	%P
1991	1	36	0	0.0	14	0	0.0	15	0	0.0	30	1	3.3
	2	47	0	0.0	9	0	0.0	5	0	0.0	21	0	0.0
	3	16	0	0.0	11	1	9.0	20	3	15.0	19	2	10.5
	4	28	3	10.7	16	1	6.2	13	0	0.0	12	4	33.3
	5	15	0	0.0	14	2	14.2	20	3	15.0	10	3	30.0
	6	12	2	16.7	16	4	25.0	14	0	0.0	14	0	0.0
	7	12	0	0.0	16	1	6.2	4	1	25.0	14	0	0.0
	8	11	2	18.1	14	1	7.1	10	1	10.0	12	0	0.0
1992	9	7	3	42.9	9	0	0.0	12	0	0.0	9	0	0.0
	10	13	0	0.0	26	0	0.0	8	0	0.0	19	0	0.0
	11	16	0	0.0	27	0	0.0	15	0	0.0	20	0	0.0
	12	9	0	0.0	18	0	0.0	21	0	0.0	12	0	0.0
	13	12	0	0.0	18	5	27.8	16	0	0.0	14	2	14.2
	14	19	1	5.3	18	8	44.4	19	0	0.0	25	1	4.0
	15	22	1	4.5	22	2	9.0	15	1	6.7	21	3	14.2
	16	13	2	15.4	24	10	41.7	17	1	5.9	23	4	17.3
	17	11	0	0.0	28	7	25.0	15	1	6.7	6	2	33.3
	18	9	2	22.2	22	6	27.2	14	1	7.1	14	2	14.2
	19	5	0	0.0	16	3	18.8	9	0	0.0	22	5	22.7
	20	10	0	0.0	11	1	9.0	10	0	0.0	7	5	71.4
1993	21	23	0	0.0	27	0	0.0	8	0	0.0	36	2	5.6
	22	26	2	7.7	41	1	2.4	14	0	0.0	33	6	18.1
	23	23	3	13.0	49	3	6.1	23	0	0.0	37	11	29.7
	24	44	1	2.3	50	2	4.0	28	2	7.1	20	1	5.0
	25	33	12	36.4	40	6	15.0	38	2	5.2	32	4	12.5
	26	47	15	31.9	44	8	18.1	53	3	5.7	31	6	19.3
	27	50	23	46.0	45	10	22.2	45	13	28.9	25	9	36.0
	28	40	32	80.0	45	7	15.6	44	19	43.1	39	9	23.0
	29	40	25	62.5	42	7	16.7	40	13	32.5	47	15	31.9
	Total	649	129	34.8	732	96	13.1	565	64	11.3	624	97	15.5

* Sample days 1-8 = 1991; 9-20 = 1992; 21-29 = 1993
L+P = number of nutborer larvae + pupae
%P = number of parasitoids reared
%Par = percentage parasitism

Table 4.3A: The number of *E. torticornis* larvae and the number of parasitoids reared from each site, Turrialba, Costa Rica, November 1992 - September 1993.

Sample	Site 1		Site 2		Site 3		Site 4		Site 5	
	Larvae	Par	Larvae	Par	Larvae	Par	Larvae	Par	Larvae	Par
N	23	5	9	1	13	1	11	1	1	0
D	25	6	3	0	5	0	0	0	0	0
J	28	1	15	1	17	0	15	0	1	0
F	39	5	24	2	25	1	21	1	2	0
M	41	12	25	3	39	2	28	0	2	0
A	24	1	32	0	33	2	21	2	6	1
M	60	2	37	5	33	11	32	5	5	1
J	45	3	31	1	32	15	31	9	21	4
J	31	5	35	8	37	16	40	12	34	15
A	25	3	32	0	39	31	41	10	40	23
S	26	5	29	4	27	23	46	12	40	15
Σ	367	48	272	25	300	102	286	52	152	59
%P	13.07		9.19		34		18.18		38.81	

Annex: Publications produced during period of postgraduate training

Contents

Blanco, H. (1991). Macadamia: un parasitoide del barrenador de la nuez. *Boletín Informativo MIP* No. 19/20:3.

Blanco, H. (1993). Nueva plaga en macadamia almacenada. *Boletín Informativo MIP* No. 26:1.

Blanco, H.; Watt, A.; Cosens, D. (1993). Ciclo de vida y comportamiento de oviposición de *Ecdytolopha torticornis* (Lep: Tortricidae) barrenador de la nuez de macadamia. *Revista Manejo Integrado de Plagas* No. 29:36-39.

Blanco, H.; Watt, A.; Shannon, P. (In press). Dynamics of macadamia nut damage by *Ecdytolopha torticornis* (Lep: Tortricidae) and parasitism by *Apanteles* sp. Individuals, Patterns, and Populations (Norwich, England, 7-10 September, 1992). Proceedings.

Blanco, H. (In press). Opciones al uso unilateral de plaguicidas en el combate de insectos en macadamia: pasado, presente y futuro. *In* García, J.; Fuentes, G. (Eds.). Opciones al uso unilateral de palguicidas en Costa Rica: pasado, presente y futuro.

MACADAMIA

Un parasitoide del barrenador de la nuez

La nuez de macadamia fue introducida en Costa Rica en 1952, pero sólo en 1965 se comenzó a cultivar comercialmente como una alternativa a la caficultura. Costa Rica ofrece para su producción excelentes condiciones ecológicas, además su precio internacional, ha sido un estímulo para que el número de plantaciones de macadamia se incrementara de 2 000 a 5 700 ha en el período de 1982 a 1989. Paralelamente al incremento en el área de cultivo, han aparecido las plagas insectiles. Ecdytolopha torticornis (Meyrich) (Lepidoptera: Tortricidae) es uno de los organismos que causa daño a la nuez, que barrena el fruto, alimentándose de la nuez y de la cáscara. El combate químico aún no se ha considerado necesario, a pesar de que la presencia de este insecto en las nueces es de un 30%.

Como parte de su tesis de doctorado, la autora de esta nota está estudiando la biología y construyendo una tabla de vida para E. torticornis. Durante este estudio se encontró a Apanteles spp. (Hymenoptera: Braconidae) parasitando larvas del primer y segundo estadío de dicha plaga. El nivel de parasitismo detectado varía, alcanzando hasta un 29%. Está en estudio la dinámica poblacional del parasitoide, así como el impacto que pueda tener en la regulación de la población de E. torticornis. □

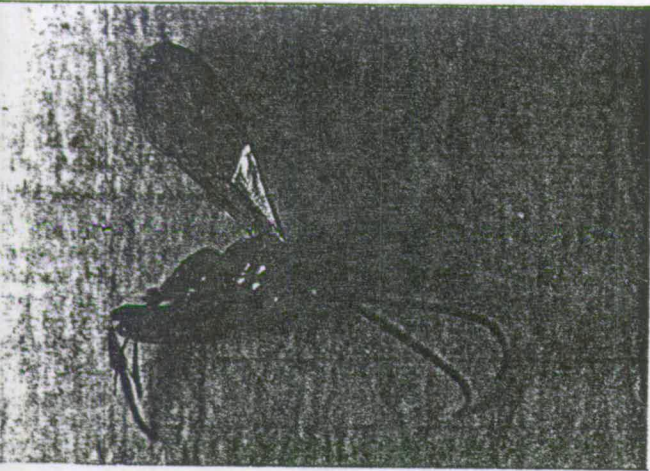(MSc. Helga Blanco, HIP/CATIE, 7170 Turrialba, Costa Rica).

Foto 1.

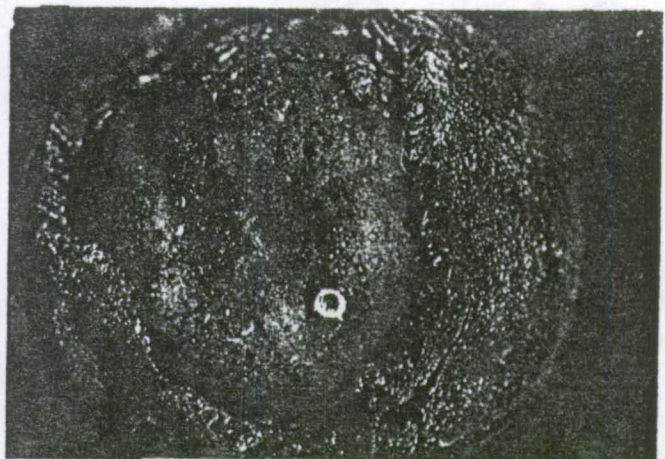Adulto de Apanteles spp., parasitoide de larvas del barrenador de la nuez de macadamia.

Foto 2.

Pupa de Apanteles spp., parasitoide de larvas del barrenador de la nuez de macadamia.

PLAGAS NUEVAS O EN EXPANSION

Oryzaephilus surinamensis ataca nueces de macadamia (*)

Costa Rica. A partir de 1968 cuando se incrementa en el país la siembra de la nuez de macadamia, cada año aparecen organismos que atacan este cultivo. En 1992, la empresa Macadamia de Costa Rica solicitó ayuda al CATIE para identificar unos "gorgojos" presentes en nueces procesadas. El Dr. J. Pakaluk del Beltsville Plant Institute, Maryland, identificó el insecto como *Oryzaephilus surinamensis* (L) (Col: Silvanidae).

O. *surinamensis* es conocido por el daño que ocasiona al arroz poco pulido, o sea, aquel que aún conserva una porción de salvado oleoso. Tanto los adultos como las larvas se alimentan de la parte exterior de los granos de arroz. En macadamia, se alimentan principalmente del interior de la almendra llegando a desintegrarla totalmente (Fig. 1).

El adulto mide cerca de 3 mm, es bastante plano y ovalado; posee 6 dientes grandes en cada lado del protórax (Fig 2). En arroz, la hembra pone hasta 300 huevos en un período de 10 semanas; el ciclo de vida se completa en 4 - 5 semanas. En macadamia se presentan las cuatro fases del insecto: huevo, larva, pupa y adulto.

Debido a que es un insecto de granos almacenados y cuya procedencia como fuente de infestación en macadamia es desconocida, se recomienda evitar el almacenamiento de la nuez cerca de arroz, maíz o granza de arroz con el fin de evitar posibles contaminaciones.

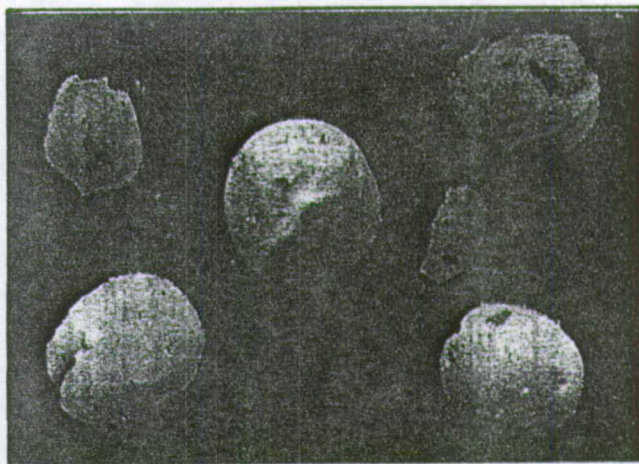(*) (M.Sc. **Helga Blanco**, MIP/CATIE, 7170 Turrialba, Costa Rica)

Fig. 1: Daño de O. *surinamensis* en nueces de macadamia procesadas.
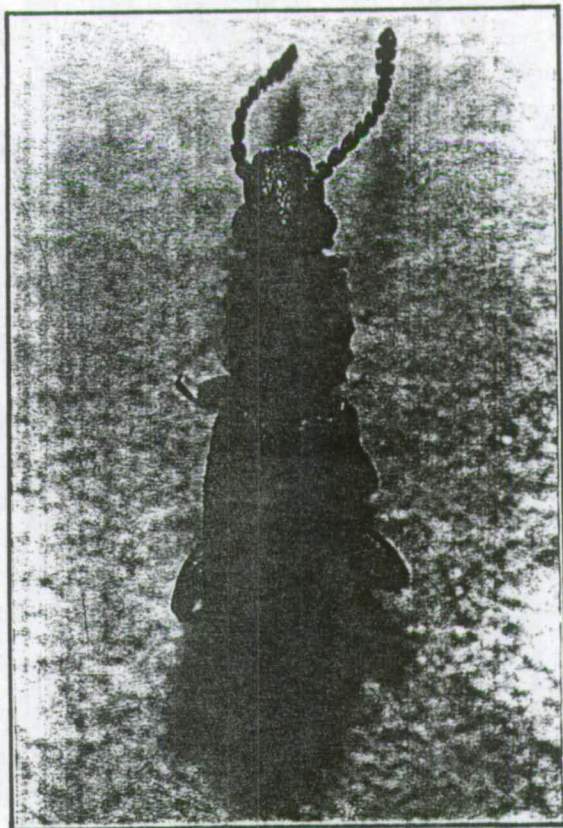

Fig. 2: Adulto de O. *surinamensis*

CICLO DE VIDA Y COMPORTAMIENTO DE OVIPOSICION DE *Ecdytolopha torticornis* (LEP:TORTRICIDAE) BARRENADOR DE LA NUEZ DE MACADAMIA*

Helga Blanco**
Allan Watt***
Derek Cosens****

ABSTRACT

Advances on the biology and life cycle of the macadamia nutborer (*Ecdytolopha torticornis*) are presented. Studies were carried out, under field and laboratory conditions (23°C, 80% RH). Observation of ecdysis and measurements of head capsule width identified four larval instars. Life cycle was completed in 36 days (egg-adult) with 5-6 days for eggs to hatch, 3-4 days for each of the three instars, and 3-9 days for the final instar + prepupa. Pupation lasted 7-15 days. Insects laid from 2-74 eggs, with a mean of 33 eggs n = 38. The number of eggs per nut laid in the field varied from 1-8. Oviposition took place upon nuts within the first three meters from the ground. Pupation took place in the nuts, on branches, and within moss on the trunk and branches.

RESUMEN

El propósito de este estudio fue conocer aspectos biológicos del barrenador de la nuez de macadamia, *Ecdytolopha torticornis* bajo condiciones de campo y laboratorio. La duración del ciclo de vida (huevo-adulto) bajo condiciones de laboratorio (23°C, 80%HR), fue de 36 días, encontrándose cuatro estadios larvales. La incubación de los huevos varió de 5-6 días, la duración de los tres primeros estadios fue de 3-4 días, mientras que la del cuarto varió de 3-9 días. El estado de pupa tuvo una duración de 7-15 días. El número de huevos depositados por hembra varió entre 2-74, con un promedio de 33 huevos n = 38. En el campo, el número de huevos en las nueces varió entre 1-8 y su distribución se concentró en las nueces presentes en los tres metros del suelo hacia la copa. Empupa principalmente en las nueces, aunque se observó en el musgo del tronco principal, ramas laterales y en el peciolo junto al racimo.

INTRODUCCION

La nuez de macadamia es originaria de los bosques lluviosos de Australia (Ironside 1987) y se ha extendido a regiones tropicales de América y Africa. En Costa Rica se cultiva en las zonas de Turrialba, Siquirres, Limón, San Vito de Java, San Carlos, Upala y Tilarán. Fue introducida a Costa Rica en 1952, pero no fue sino hasta 1965 cuando se estableció comercialmente como una alternativa al cultivo del café. La producción de nueces sobrepasó las expectativas y pronto se convirtió en un cultivo no tradicional de exportación (González 1981). En poco tiempo la siembra de este cultivo cobró gran interés, incrementándose el área de siembra de 2000 a 8000 ha entre 1982 y 1993.

Con el incremento en el área de siembra y en áreas en monocultivo, los agricultores han presentado numerosos informes sobre plagas en diversas localidades del país. Entre los principales daños se menciona el aborto prematuro de las nueces debido a 5 especies de chinches (*Loxa* sp., *Antiteuchus* sp., *Nezara viridula*, *Hyalimenus* sp., *Leptoglossus* sp.) los cuales varían en importancia según las zonas y según fincas dentro de las zonas; la transmisión de levaduras en el fruto ocasionada por los chinches; la presencia de altas poblaciones de áfidos durante la floración; el

arragre (*Trigona* sp.), el cual al alimentarse de las hojas y brotes tiernos de plantas en el vivero y establecimiento del cultivo, provocan la deformación de los árboles y retrasan su crecimiento; y el barrenador de la nuez de macadamia *Ecdytolopha torticornis*.

A partir de 1986, *E. torticornis* se menciona como un insecto de importancia económica en ciertas fincas de Siquirres. Lara (1987) informó de un 16% de infestación. Tres años más tarde, Masís y Campos (1990) observaron un incremento del 12% en la infestación. Blanco *et al.* 1992a identificaron una variación del daño entre 12-39% en la cáscara, y de un 1-7% en la almendra. El incremento en la población de este insecto hace necesario el conocimiento de aspectos básicos de su biología y ecología, elementos esenciales en la formulación de programas de manejo de plagas. Este trabajo contempla los avances de los estudios realizados sobre la cría y biología de *E. torticornis*.

MATERIALES Y METODOS

Ciclo de vida. El estudio de campo se realizó en la Finca Macadamia de Costa Rica, en el cantón de Turrialba, Provincia de Cartago, Costa Rica, a 9°58'N y 83°9'O con una altura de 700 msnm, una precipitación promedio anual de 2605 mm y una temperatura promedio anual de 27°C(1).

(1)CATIE. 1992. Datos agrometereológicos.

El ciclo de vida se obtuvo mediante el proceso de producción de los huevos en el laboratorio y de la recolección en el campo de nueces con huevos fértiles. Los huevos y larvas fueron criados individualmente en recipientes plásticos (160 ml) sobre mitades de nueces que se cambiaban a diario. Los estadíos se asignaron cada vez que se encontró la cápsula cefálica y/o muda de las larvas.

El estudio de laboratorio se realizó en la unidad de entomología del CATIE bajo condiciones controladas de 23ºC y 80% HR. Las observaciones referentes al comportamiento del barrenador se realizaron principalmente en el campo.

Fecundidad: Se probaron tres tamaños de jaulas de madera con cedazo (35 x 35 x 35 cm; 40 x 40 x 50 cm; 80 x 40 x 50 cm). En cada jaula se incluyó un racimo de nueces de macadamia, una inflorescencia de macadamia y de la maleza *Emilia sonchifolia*, donde trabajadores de campo informaron haber visto al adulto. El acceso al interior de las jaulas fue a través de una manga de manta o de una puerta con visagras. La proporción de hembras y machos por caja varió según su disponibilidad. Los adultos se alimentaron con una solución de miel de abeja al 10%. La ubicación de las cajas fueron alternadas entre el laboratorio y el jardín con el propósito de proveer diferentes grados de luz y aireación con lo cual se quería observar el comportamiento durante la copulación.

Se probaron cinco frascos de forma y tamaño variable (Fig. 1). En cada frasco se incluyó un papel de filtro en la base, el cual se humedecía según fuera requerido para mantener una humedad relativa alta. En los frascos se introdujeron dos nueces (aprox. 1.5 cm de diámetro), una tapa pequeña con un algodón con miel y agua y una tira de papel encerado. Todos los frascos se cubrieron con malin y se amarraron con una liga.
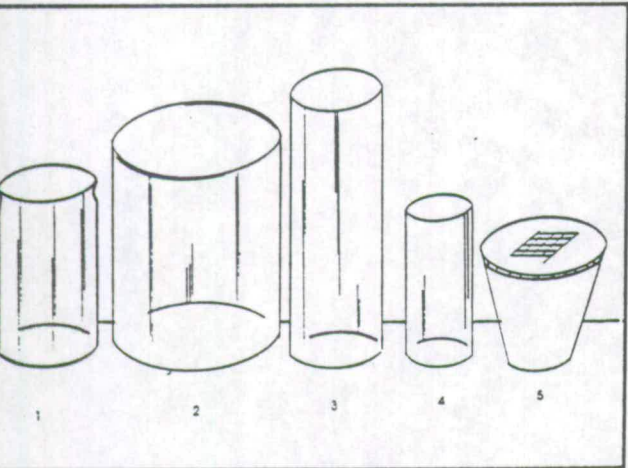
Fig. 1. Envases utilizados en el estudio de fecundidad de *Ecdytolopha torticornis*.

CUADRO 1. Duración del ciclo de vida de E. torticorni criados en el laboratorio, CATIE, 1991-92.

Estado	n	Tiempo (días) Promedio $\pm$ S^2		Rango
Huevo	33			5- 6
Larva				
L1	8	3.33	0.51	3- 4
L2	8	3.75	0.46	3- 4
L3	8	3.41	0.90	3- 4
L4 + prepupa	23	6.34	1.30	3- 4
Pupa	37	13.24	1.59	7-15
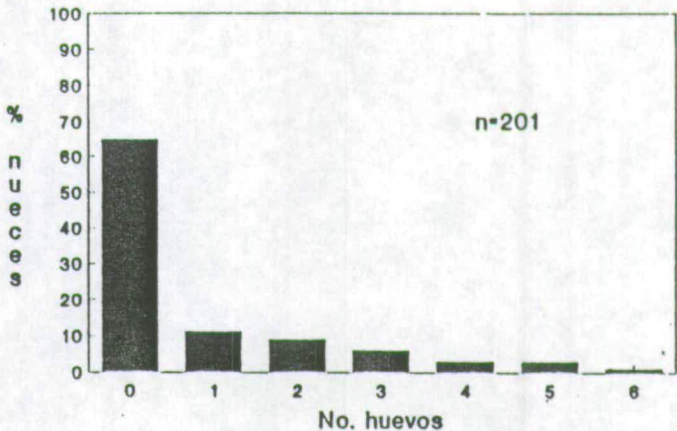
Fig. 2. Número de huevos de *E. torticornis* por nuez de macadamia.

RESULTADOS Y DISCUSION

Ciclo de vida. El período de incubación de los huevos fue de 5-6 días. Se encontraron cuatro estadíos larvales, donde la duración del primero, segundo y tercer estadío varió entre 3-4 días, mientras que la duración del cuarto estadío (+ prepupa) varió entre 3 y 9 días (Cuadro 1).

En los casos donde no se encontró la cápsula cefálica ni la muda, la duración de los estadíos se obtuvo al promediar la duración de los estadíos de tiempo conocido.

Los huevos son depositados en la parte media de las nueces con diámetros mayores de 0.8 cm; las nueces maduras (cáscara dura) parecieran no ser atractivas para la oviposición. El número de huevos por nuez varió entre 1-8, con un promedio de 0.8 huevos por nuez (Fig. 2). La larva recién emergida deambula por la nuez hasta encontrar el sitio

CUADRO 2. Número de huevos de *Ecdytolopha torticornis* ovipositados en los frascos 3 y 5 en el laboratorio, CATIE, Turrialba, 1992.

Rep	Hembra	Macho	Fértil	Infértil	Total	Prom
1	2	5	47	NR	47	23.5
2	2	4	68	NR	68	34.0
3	2	2	7	14	21	10.5
4	3	8	91	20	111	37.0
5	1	2	35	21	56	56.0
6	2	6	31	1	32	16.0
7	1	3	24	NR	24	24.0
8	1	5	27	22	49	49.0
9	3	1	18	47	65	21.6
10	1	2	19	23	42	42.0
11	1	1	43	21	54	54.0
12	1	2	38	28	66	66.0
13	1	1	26	47	73	73.0
14	1	2	58	16	74	74.0
15	3	2	112	65	177	59.0
16	1	2	62	8	70	70.0
17	1	2	43	19	62	62.0
18	1	2	4	3	7	7.0
19	1	2	5	1	6	6.0
20	1	2	48	15	63	63.0
21	1	2	0	3	3	3.0
22	1	2	2	0	2	2.0
23	2	2	12	4	16	8.0
24	2	3	8	3	11	5.5
25	2	3	35	12	47	23.5
	38				1256	33.0

NR= No registrado

adecuado para iniciar la perforación. Una vez que ha penetrado la cáscara, tiende a barrenar hacia los extremos de la nuez ya que el grosor de la misma es mayor. Es difícil detectar nueces que contengan larvas del primer estadío, por la pequeñez del orificio (punteadura de un alfiler). Conforme la larva crece, el orificio de entrada/salida se amplía y se hace más visible, permitiendo detectar las nueces dañadas con suma facilidad por la acumulación de desechos en el orificio.

La mayoría de las larvas se alimenta del meso y endocarpo de las nueces, pero si la cubierta seminal (concha) no ha endurecido, pueden continuar barrenando hasta la almendra. Con frecuencia se observan daños a la concha debido a los intentos de la larva por alcanzar la almendra. Por lo general se encuentra una larva por nuez dañada, aunque en
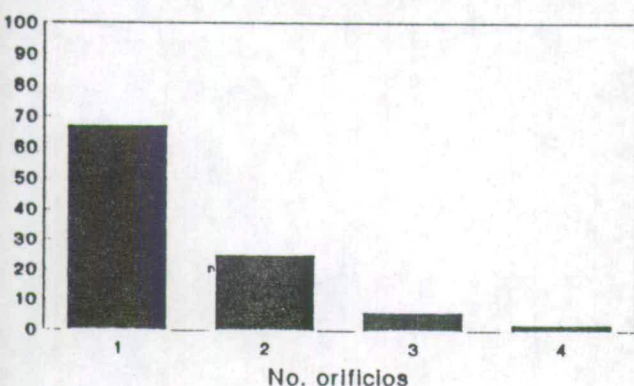

Fig. 3. Números de orificios causados por *E. torticornis* por nuez de macadamia.

poblaciones altas de *E. torticornis* es posible encontrar hasta 4 larvas por nuez. Cuando se encuentra más de una larva por nuez, en su mayoría corresponden a diferentes estadíos, lo que podría implicar que las hembras son atraídas a ovipositar en nueces que ya contienen huevos o larvas. Este comportamiento podría dar la ventaja a las larvas de primer estadío de evadir parasitoides y depredadores al penetrar más rápidamente la nuez, y la desventaja de aumentar la competencia intraespecífica entre larvas por espacio y comida. Durante los dos años de estudio, no se observó canibalismo entre larvas. El número de orificios por nuez varió de 1 a 4 (n=882) (Fig. 3).

Las larvas presentan un fototropismo negativo y se refugian en cualquier sustrato. Conforme se acercan a la pupación cesan de alimentarse y elaboran un capullo con desechos y una tela de seda que ellas producen. Seis días después se observa una pupa amarillo claro y conforme se endurece la quitina, se torna café oscuro. La duración del estado de pupa fue de 7-15 días (Cuadro 1). Las pupas de las hembras son más grandes (7.40 a 12.70 mm, promedio 9.87 mm n=34) que la de los machos (6.00 a 10.30 mm, promedio 8.53 mm n=38). Tortós (1991) encontró la factibilidad de sexar las pupas por medio de diferencias morfológicas entre los sexos, presentes en los segmentos 8 y 9.

Se determinó la proporción de sexos por medio de 72 pupas tomadas al azar de una colonia del laboratorio. Se encontró que había 38 machos y 34 hembras, por lo que se puede decir que existe una proporción próxima a 1:1 ($x^2 = 0.22$).

La pupación se lleva a cabo principalmente en las nueces, aunque fue factible observarla en el musgo del tronco principal, ramas laterales, en el pecíolo del racimo y entre las nueces del racimo. En el laboratorio, la pupación se realizó prácticamente en cualquier sustrato (cerca a las nueces, en el suelo, en los borradores, en papeles, en cortinas, etc.), con los cuales, al doblarlos forman el capullo.

Los adultos emergieron generalmente durante el día, aunque algunos lo hicieron durante la noche o a tempranas horas de la mañana. No se registró diferencia en la hora de emergencia entre los machos y las hembras. El período de mayor emergencia fue entre las 13:00-14:30 horas.

Blanco et al. (1992) estudiaron la distribución vertical del barrenador en los árboles (clones 246, 344, 508, 660) por medio del conteo de perforaciones y huevos (fértiles, eclosionados y parasitados) a tres niveles o alturas del árbol y cinco posiciones de muestreo. Encontraron una diferencia altamente significativa entre el número de posturas (0.14 huevos por nuez) presente en las nueces en el nivel más alto (> 3.2 m) que en los niveles medio (0.29 huevos por nuez) (1.6-3.2 m) y bajo 0.30 huevos por nuez (0-1.6 m), sitios donde se encontró el mayor número de huevos, lo que implica que la hembra del barrenador no distingue entre nueces de clones para la oviposición. No se detectaron diferencias estadísticas entre clones para el número de huevos. Este resultado podría implicar que existe un efecto en la calidad de la comida (toxinas o dureza de la cáscara) que afecta la sobrevivencia de las larvas.

Fecundidad. No se observó el apareamiento, sin embargo se estima que ocurre cerca del anochecer debido a que se notó un aumento en la actividad de los insectos alrededor de las 17:30 horas, cuando las hembras movían insistentemente las alas, levantando el abdomen y los machos realizaban una serie de vuelos cortos. Además, los huevos en su mayoría fueron descubiertos por la mañana. Se obtuvieron pocos huevos en los frascos 1, 2 y 4, siendo los más efectivos los números 3 y 5. Los huevos fueron depositados principalmente en las paredes de los frascos de vidrio, aunque también en el papel filtro, en el papel encerado y en las nueces. En el frasco 5 los huevos fueron depositados en su mayoría sobre las nueces.

E. torticornis prefirió ovipositar en el frasco 3 quizá debido al tipo y grosor del vidrio y a la forma de los frascos. El éxito en la oviposición en el frasco 5,

podría deberse al tipo de material de que está hecho, el cual disminuye el paso de luz. El número de huevos por hembra varió desde 2-74 huevos, con un promedio de 33 huevos (Cuadro 2).

Dentro de los parasitoides se encontró a un microhimenoptera perteneciente a la familia Trichogrammatidae parasitando los huevos del barrenador. Blanco (1991) reportó a *Apanteles* sp. (Hym: Braconidae) parasitando larvas del primer estadío, con un parasitismo del 47%. En el transcurso de 1992, se observó a los parasitoides de larva: *Apanteles* II sp. y *Ascogaster* sp., ambos pertenecientes a la familia Braconidae, y a *Pristomerus* sp. de la familia Ichneumonidae.

En los árboles de macadamia coexisten 5 especies de hormigas, pero no se conoce su interacción con *E. torticornis*. Se ha observado que *Solenopsis* sp. depreda larvas de las nueces del suelo y en ocasiones se observó su presencia dentro de las nueces. Esto ocurre en nueces maduras cuyo orificio está ampliado. También es frecuente observar avispas del género *Polibia* y tijerillas *Doru* sp. recorriendo las nueces.

Se ha encontrado un hongo, posiblemente *Beauveria bassiana* afectando larvas y pupas del barrenador.

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DYNAMICS OF MACADAMIA NUT DAMAGE BY
Ecdytolopha torticornis (Lep: Tortricidae) AND
PARASITISM BY *Apanteles* sp.

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Introduction

Macadamia nuts are an important export crop in Costa Rica. Since the crop's introduction in 1952, orchards have increased in size and number to a total of nearly 8000 ha in 1992. One of the most serious pests of Macadamia is the nutborer, *Ecdytolopha torticornis* (Meyrick) (Lepidoptera: Tortricidae), which, as well as directly damaging fully formed but immature nuts, also causes premature nut fall when it feeds on the husk of older nuts.

This study is investigating the biology and ecology of this pest as a basis for developing an integrated pest management programme. One aim of this study is to characterise the seasonal changes in a) nut damage by *Ecdytolopha torticornis* in relation to nut production and b) parasitism by the main parasitoid, *Apanteles* sp. Preliminary results are presented in this paper.

Methods

Field work was carried out in a 222 ha Macadamia estate located at Turrialba, Costa Rica, at 620 to 700 m above sea level. Mean annual rainfall is 2600 mm, mean temperature is 21.4 ° C, and relative humidity is around 80%.

a) Damage was evaluated every two weeks in the nuts which had fallen naturally from 10 trees of each of 4 Macadamia nut clones. From April 1992, sample size was increased to 25 trees (5 trees at 5 sites), and a maximum of 100 nuts per tree were evaluated. The total number of nuts falling from each tree was estimated by weighing the total number of fallen nuts.

b) Parasitism was studied in forty damaged nuts per clone, harvested at random from the trees each month. Nuts were examined in the laboratory and the number of larvae and their instar recorded. The larvae were incubated individually in split nuts in 165 ml plastic cups until emergence of either the adult moth or a parasitoid.
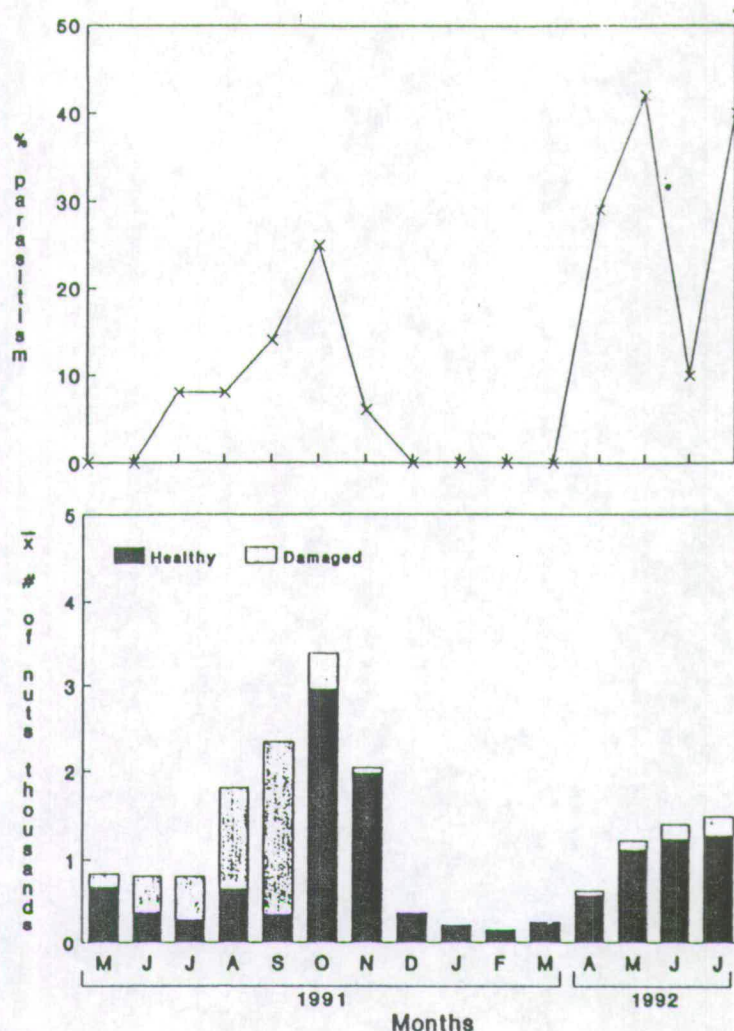
Figure 1.   Mean number of nuts damaged by *E. torticornis* and percentage of parasitism by *Apanteles sp.*: clone 344.

Results and Discussion

Differences in susceptibility to damage were found between clones: clone 344 was most damaged, followed by clones 246 and 660, and clone 508 was least susceptible to damage.

In clone 344 damage was highest during the early part of the peak production period (August-September) when a large number of suitably mature nuts are available (Table 1, Fig. 1). Damage declined in October, perhaps due to there being fewer suitable nuts for oviposition (husk too mature), but it also corresponded to the period of highest levels of parasitism by *Apanteles* recorded during 1991. However the association of parasitism with reduction of damage is less obvious during the first half of 1992 in both clones 344 and 508 (Fig. 2). In both cases, high levels of parasitism occurred during periods of low pest attack. The possible role of *Apanteles* in regulating *Ecdytolopha* populations requires further study.

Differences in susceptibility to nut damage between clones may be due to physical factors. Current work centres on studies of nitrogen, water and tannin content of the nuts to determine if these relate to susceptibility. As no significant difference between

Table 1. Mean number of nuts damaged by *E. torticornis* by tree per clone.

Clone	# of trees	Mean damaged nuts
344	24	8.9 a
246	25	8.2 ab
660	25	8.0 b
508	21	7.6 b

Means followed by the sample letter are not significantly different (P=0.05) (Duncan's multiple range test). F=3.44, d.f.=3 P=0.021
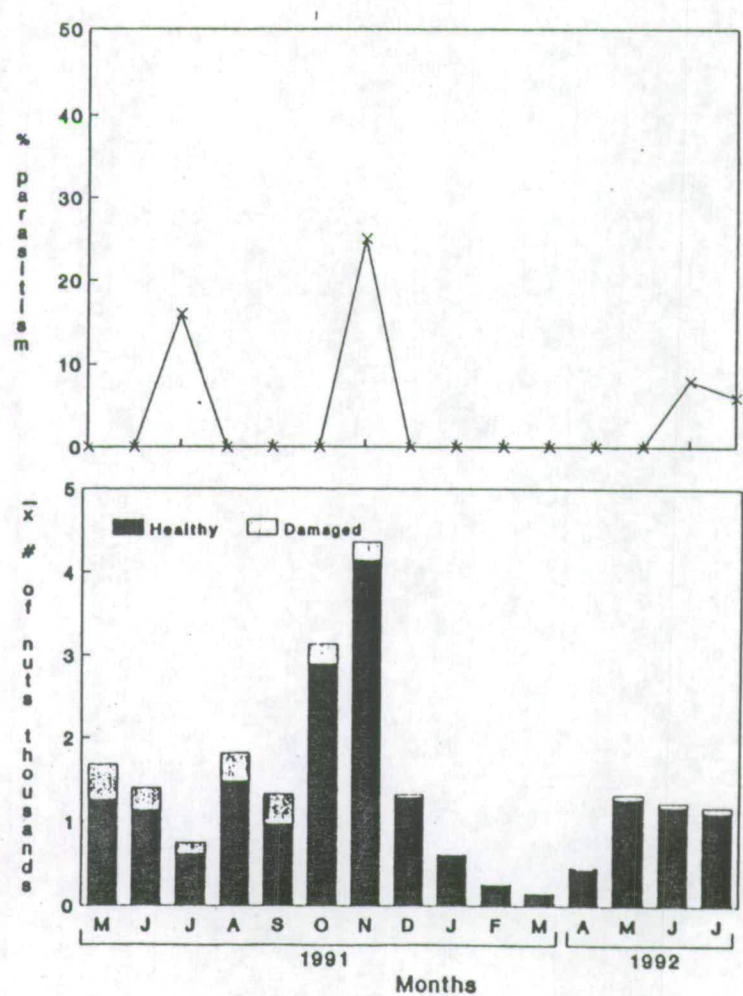

Figure 2. Mean number of nuts damaged by *E. torticornis* and percentage parasitism by *Apanteles* sp.: clone 508.

clones has been found in husk thickness, it is unlikely that ease of penetration of the husk by the larva plays an important role.

Acknowledgements

OPCIONES AL USO UNILATERAL DE PLAGUICIDAS EN EL COMBATE DE INSECTOS EN MACADAMIA: PASADO - PRESENTE - FUTURO

Helga Blanco

La nuez de macadamia (*Macadamia integrifolia*), es originaria de los bosques lluviosos de Australia (Ironside, 1987). Su introducción en Costa Rica data desde 1952, cuando el Dr. Ernest P. Imle introdujo las primeras semillas a la Estación Experimental de Hule del IICA, Turrialba (Lizano, 1969). Con la baja en el precio internacional del café, los bancos e instituciones gubernamentales buscaron cultivos alternos que disminuyeran la excesiva dependencia económica en este cultivo, pero que a la vez, fueran altamente remunerativos. En 1965 se establecieron las primeras plantaciones comerciales de macadamia, y se proveyó de incentivos para su expansión. Debido a su excelente adaptación a las condiciones agroclimáticas de Costa Rica, en poco tiempo surgió un boom por la siembra de macadamia, extendiéndose a 8350 hectáreas sembradas en 1992, principalmente en Turrialba, Siquirres, Tilarán, San Carlos, Upala, San Vito de Java y Coto Brus.

Con el incremento en el área de siembra, y en la diversidad de los sitios de siembra, los agricultores han presentado reportes sobre los diferentes insectos encontrados; algunos de estos no habían sido reportados en el país, y otros eran insectos generalistas que no alcanzaban el nivel de plaga, pero que de una u otra forma afectaban la producción.

El primer insecto de importancia económica que se reportó fue el barrenador de la nuez de macadamia, *Ecdytolopha torticornis* (Lep: Tortricidae) (Meyrick) (Lara, 1987), (inicialmente identificado como *Cryptophlebia leucotreta*; pero rectificada por Tortós 1991 *Ecdytolopha torticornis*). Posteriormente se dan informes sobre un complejo de chinches,

Nezara viridula, *Hyalimenus tarsatus*, *Loxa*, *Antiteuchus costarricensis*, y *Leptoglossus zonatus*, los cuales presentan importancia local, tanto a nivel de finca como a nivel de zona. Existen otros insectos asociados al cultivo de la macadamia aunque su daño económico no ha sido cuantificado (Blanco, 1993; Masís y Soto-Manitu, 1992).

Debido a que este cultivo es relativamente nuevo para el país y que existe un incipiente conocimiento sobre el manejo de sus plagas (insectos, patógenos y malezas) se ha incurrido en errores sobre su manejo, lo cual ha traído penosas consecuencias. Un ejemplo de esto es la defoliación severa que sufrió la finca Kailúa en Siquirres en 1986, al realizar una aplicación generalizada de la mezcla de los fungicidas captafol + benomyl para contrarrestar el daño causado por *Botritis cinerea*. El escaso conocimiento sobre el manejo de los insectos presentes en esta finca, hizo que al aplicar fungicida se controlara a un entomopatógeno el cual mantenía la población de *Microrape hippopotama* Hopp (Lepidoptera: Megalopygidae) a niveles casi imperceptiles (Pérez, D. 1993. Macadamia de Costa Rica. Comunicación personal. Turrialba) . Este es un claro ejemplo de los daños que pueden resultar del rompimiento del balance ecológico.

En atención al incremento en el número de especies de insectos que causan daño al cultivo, y a la severidad de algunas de ellas, varias instituciones (CATIE, UCR, MAG, ICAFE, CINDE) se han unido a la lucha por conocer aspectos relacionados con la biología y ecología de estas plagas, su distribución a nivel nacional, y su interacción con el cultivo.

Los estudios formales de *E. torticornis* tuvieron sus inicios en la Universidad de Costa Rica, donde se estudió la dinámica poblacional de este insecto en la finca Oriente, Turrialba, durante 1989 y 1990 (Masís y Campos 1990 a). Otros estudios comprendieron la utilización de

agroquímicos para el combate de este insecto (Masís y Campos 1990 b). Posteriormente se condujeron estudios sobre la biología y ecología de E. *torticornis* (Blanco 1992 a) y se determinó el ciclo de vida, recipientes óptimos para la reproducción y fecundidad del barrenador (Blanco 1993). Los estudios ecológicos que se llevan a cabo se relacionan con la variación estacional del daño a las nueces y su relación con los parasitoides, la distribución del insecto en el árbol (1992 b, c), el efecto en el rendimiento (bajos contenidos de aceite) debido al aborto prematuro de la nuez desarrollada, cómo afectan (positiva y negativamente) las condiciones físico-químicas de la comida a la población del barrenador, así como el uso de coberturas y del hongo *Beauveria bassiana* para el manejo de este insecto.

El problema de los chinches como plaga se inició en 1990, cuando los productores observaron un aumento desproporcionado en el aborto de los frutos jóvenes (mayores de 6 mm de diámetro). Al examinar los frutos del suelo, se encontró que la mayoría de los frutos caídos presentaban una serie de lesiones similares a las causadas por el estilete de los chinches (Campos, L.F. 1992. Universidad de Costa Rica. San José. Comunicación personal). Posteriormente se encontró que una de las causas de las pudriciones del fruto era principalmente la levadura *Nematospora coryli*, transmitida por el chinche *Nezara viridula* (chinche verde hediondo) (Umaña, et al 1991). También se estudiaron diversas alternativas para el manejo de los mismos: alternativa etológica la cual incluyó el uso de cultivos trampa como la *Crotalaria*, y el uso de coberturas de malezas, así como de agentes químicos y biológicos (Umaña et al 1992).

Paralelo al aumento en la extensión del cultivo, como en el número de plantaciones que entran en producción, cada año se reciben informes sobre nuevas especies insectiles que afectan al cultivo, o sobre la presencia de una plaga en una zona la cual estaba libre de ella (Blanco, 1993). Debido

a que el cultivo de la macadamia es una actividad perenne, se deberán hacer mayores esfuerzos en el entendimiento de la interacción insecto - plaga - ambiente, y en los controles cultural y biológico.

Tanto el barrenador como varias especies de chinches presentan potencial para que sus poblaciones bajen a niveles económicos. El barrenador, por ejemplo, tiene una especie de la familia Trichogrammatidae que parasita los huevos, y cinco especies de parasitoides de larva: dos especies de *Apanteles* y *Ascogaster* (Braconidae), *Pristomerus* sp. (Ichneumonidae) y un Chalcidae? Por su lado el chinche *Antiteuchus* cuenta con el parasitoide de huevo *Trissolcus* sp., el cual presenta un 70 % de parasitismo.

Nunca deberán de aplicarse por medio de avioneta, agentes químicos para el combate de cualquiera de estas plagas, debido a que se exterminarán muchos parasitoides y depredadores. En el caso de los chinches, debe hacerse tomando en cuenta los umbrales de acción para las diferentes especies. La selección del insecticida deberá estar basada en un insecticida noble para los polinizadores ya que es bien conocido los beneficios para el cuaje que proporcionan las abejas comunes y el arragre. Con respecto al barrenador, no es aconsejable el uso de agroquímicos en forma generalizada, ya que debido al hábito de vida del mismo, el insecticida no llega al interior del fruto. Además, como el barrenador afecta nueces desde pequeñas hasta bien desarrolladas, el uso de insecticidas en las últimas etapas de desarrollo de las nueces pueden presentar problemas de residuos en los frutos, los cuales pueden afectar su venta en los mercados internacionales.

En el futuro, los insectos plaga deberán de ser manejados integrando las prácticas de manejo cultural, biológico y químico. El uso de insecticidas

deberá de restringirse a las primeras etapas de desarrollo de los frutos, y su aplicación concentrarse en áreas de la finca, ya que por lo general la distribución de los insectos es en parches.

RECOMENDACIONES

- Intensificar los estudios sobre la biología y la ecología de las plagas con el fin de entender la interacción plaga - hospedero - ambiente.

- Ser precavidos con la aplicación de tecnología generada en otras partes del mundo.

- Disminuir el uso de plaguicidas, y de ser necesaria su aplicación, realizarla bajo los principios del manejo integrado de plagas (combinación de prácticas de control cultural biológico y químico).

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