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Within-tree distribution of *Ecdytolopha torticornis* (Lepidoptera: Tortricidae) oviposition on macadamia nuts

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Abstract: Vertical distribution of eggs of the macadamia nutborer *Ecdytolopha torticornis* Meyrick (Lepidoptera: Tortricidae) and its preference of oviposition sites within and between macadamia cultivars were studied in Turrialba, Cartago, Costa Rica, in 1992 (N = 6 939). *E. torticornis* eggs were found throughout the foliar parts of the tree, but fewer eggs were laid in the crown top than in the mid or lower crown. Differences in the horizontal distribution of the eggs were not significant, albeit more eggs were found in the outer positions. The numbers of eggs found within the crowns of different clones were similar, implying that the nutborer has no preference for a particular cultivar.

Key words: *Ecdytolopha torticornis*, oviposition, sampling, macadamia, Costa Rica.

Since it was first recorded in Costa Rica (F. Lara 1987 unpublished) the nutborer *Ecdytolopha torticornis* Meyrick (Lepidoptera: Tortricidae), has been responsible for an increase in damage to the nuts of *Macadamia integrifolia* Maiden and Betche (Proteaceae) from a loss in yield of 16% in 1987 (Lara 1987), to 28% in 1990 (C.E Masís and L.F. Campos 1990 unpublished), and 39 % in 1992 (Blanco-Metzler *et al*. 1994).

The *E. torticornis* female lays its eggs singly on the middle zone of macadamia nuts and, usually, in the narrow space between adjacent nuts within a cluster. Upon emergence the larva bores into the nut and feeds on the husk, if the nut shell has not hardened the larva will bore through, and feed on the kernel (Blanco *et al*. 1993). The biology of *E. torticornis* closely resembles that of the koa seedworm *Cryptophlebia illepida* (Butler) (Lepidoptera: Tortricidae), and the litchi fruit moth, *C. ombrodelta* (Lower) (Jones and Caprio 1992). *E. torticornis* moths have been reported to be poor fliers (Chamberlain 1989) living in the tree canopy (Blanco-Metzler 1994), and since the larvae feed inside the nut, they are limited in their ability to disperse. Thus, the distribution of larvae and hence nut damage are largely determined by egg distribution.

The oviposition behaviour of the nutborer within the host plant has provided useful and necessary information for the development of sampling methods. A survey of total egg mass is one of the methods used in determining pest abundance in many horticultural crops as *Diaphania nitidalis* (Stoll) (Lepidoptera: Pyralidae) in cucumber (Blanco-Metzler 1983); *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae) in maize (Hoffmann *et al*. 1991), and in forest pests such as the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) in birch trees (Higashiura 1989, Thorpe and Ridgway 1992) or the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae) in spruce trees (Lysyk 1990). The aim of this study was to investigate the within-tree distribution of the nutborer by recording its oviposition sites, and to determine whether moths showed ovipositional preferences between cultivars.

MATERIALS AND METHODS

The study site was located at Oriente Farm, Turrialba, Costa Rica, at elevations ranging from 620 to 700 m above sea level. The vertical distribution of *E. torticornis* eggs was studied in a mixed stand planted in 1978 of four of the most commonly planted cultivars in Costa Rica: Keahou (HAES 246), Kau (HAES 344), Kakea (HAES 508) and Keaau (HAES 660) with a height ranging from 4.5 m to 6 m. The study period was from July to December 1992. The nuts were examined in the laboratory (23 ºC, 80 % RH) at CATIE (Tropical Agronomical Research and Higher Education Centre, Turrialba), 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 an indication of multiple, successful ovipositions. Some nuts were found to have holes but no chorions were present, perhaps because they had been disloged by rain, blown away by wind, or eaten by predators. The same trees were sampled every month. Trees were divided into three crown levels (Fig. 1): I, crown top, 3.2 m from the ground to the top 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). The height of level III corresponded to that of the first author. Levels II and III were each divided into two positions: positions 3 and 5 = nuts sampled in an area up to 1 m horizontally from the tree trunk; positions 2 and 4 = nuts sampled in an area up to 1 m horizontally 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 data were submitted to Analysis of Variance and T tests (LSD) (Anonymous, 1985). 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 were free of eggs. Nuts were collected every month from five trees per clone, 20 trees in total. In the statistical analysis, crown level I was compared with levels II and III together; level II versus level III; and the inner sampling positions (3 and 5) were compared with the outer sampling positions (2 and 4).

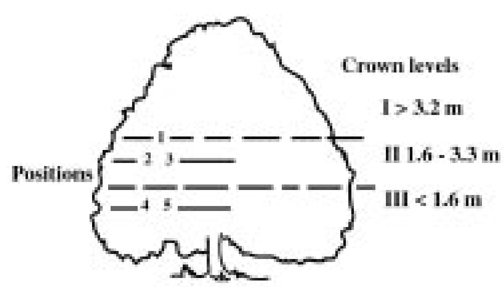

Fig. 1. Diagrammatic representation of the sampling positions and levels used in determining the vertical distribution of the nutborer's eggs on macadamia.

RESULTS

A total of 6 939 nuts were inspected. Newly laid eggs were frequently observed on nuts already bearing eggs or bore-holes. The number of eggs laid per nut varied from cero to eight with a mean of 0.8 (n = 201 nuts). No significant differences were found in the number of eggs per cultivar ($F = 0.69$; d.f. = 3; $p = 0.57$).

Eggs were found on macadamia trees at all heights; however, they were significantly more abundant in crown levels II and III than in level I ($p < 0.001$). The mean number of eggs per nut in top level I was 0.14; in mid level II: 0.29; and in bottom level III: 0.30. There was no significant difference between the number of eggs found on nuts from the lower two levels ($F = 0.22$; d.f. = 1; $p = 0.64$); nor between the mean number of eggs found on nuts on the inner and outer parts of the branches ($F = 2.0$; d.f. = 1; $p = 0.16$) (Table 1). While fewer eggs were found on the inner sampling positions (3 and 5) than on the outer sampling positions (2 and 4), no statistical difference was found between the number of eggs in either positions for levels II and III ($F = 0.22$; g.l. = 1; $p = 0.64$).

TABLE 1

Numbers of Ecdytolopha torticornis *eggs laid per macadamia nut by crown position**

Crown		Number of nuts sampled		Mean number of eggs per nut	
Level	Position	Level	Position	Level	Position
I	1	2233	2223	0.14 b	0.14 b
II	2	2377	1198	0.29 a	0.30 a
	3		1179		0.28 a
III	4	2329	1157	0.30 a	0.32 a
	5		1172		0.28 a

* $p = 0.05$

There was a significant difference ($p < 0.0001$) in the number of eggs per nut over the six months of sampling (Table 2). The number of eggs per nut was highest from July to October, decreased in November (0.2) and dropped steeply to a minimum (0.06) in December (Fig. 2). The decline in the number of eggs per nut paralleled the decline in nut production, but not the decline in the number of damaged nuts which occurred approximately one month earlier (Fig 2).

TABLE 2

Numbers of Ecdytolopha torticornis *eggs laid per macadamia nut over time, 1992**

Month (1992)	Number of nuts sampled	Mean number of eggs per nut
July	1149	0.34 a
August	1000	0.28 a
September	1190	0.29 a
October	1200	0.34 a
November	1200	0.20 b
December	1200	0.06 c

* $p = 0.05$

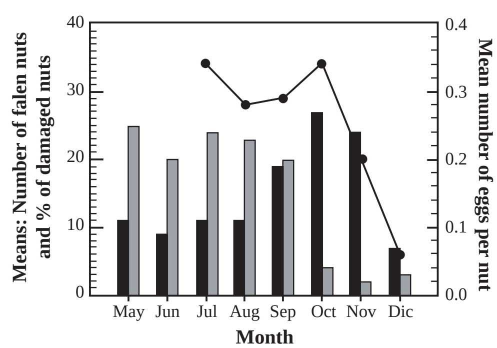

Fig. 2. The mean number of fallen nuts (divided by 10; solid bar); the mean percentage of damaged nuts (hatched bar); and the mean number of eggs per month (line graph).

DISCUSSION

Oviposition site selection is one of the most important aspects of habitat selection in insects. 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 (Blanco-Metzler *et. al*. 1993) might give the larvae the advantage of escaping from parasitoids and predators, or prevent them from being dislodged by the rain. Blanco-Metzler (1994) reported that it took a larva approximately fifty minutes from emerging from the egg to completely bore through the husk. Therefore, if an entrance to the nut has already been made, the first instar larva is more likely to evade detrimental environmental factors and increase its survivorship. Conversely, the females' habit of laying eggs on damaged nuts may lead to intra-specific larval competition for food and/or space. Moreover, larval mortality might increase due to early nut-drop (Blanco-Metzler *et. al*. 1992; Blanco-Metzler 1994). 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. However, cannibalism was not observed in *E. torticornis*: yet early nut-fall was observed and concomitant enhanced larval predation (Blanco-Metzler *et al*. in preparation).

Oviposition in insects has been reported to be influenced by physical properties of the host such as shape of the trees and nuts, colour of leaves and nuts, surface texture of fruits (Prokopy and Bush 1973) and chemical stimulants of the host (Renwick and Radke 1983; Hedin and McCarty 1990). Since no differences were found in the number of eggs between cultivars it is unlikely that during oviposition females were influenced by cultivar variation in shape, size, and colour of the nuts. Thus, the differences in nut damage for cultivars 246, 344, 508 and 660 (C.E. Masís and L.F. Campos 1990; Blanco-Metzler, *et. al*. 1992; Blanco-Metzler 1994) might rather reflect differences in larval survival resulting from cultivar differences in food quality due to variation in secondary plant compounds and husk toughness. Indeed, damage was found to decrease with nut maturation because as the nut dries it provides food of a poorer quality and quantity.

The tendency of finding most eggs in the outer bottom level of the tree crown, followed by the outer middle level, could be because nut production is highest in this part of the tree (Diego Pérez, personal communication), and therefore, the moths lay their eggs where food abundance is highest to ensure the best possible food supply 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 readily from the weeds 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 that could explain the differences in the number of eggs per nut found 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 (oviposition sites) were available and, thus, were thus harder to find. Secondly, a reduction in the number of nuts restricts the available larval food resource and in turn the larval population, hence fewer adults will eventually emerge. Thirdly, the seasonal increase in the abundance of parasitoids (Blanco-Metzler 1994) is also likely to cause a decline in the size of the nutborer population.

Although *Cryptophlebia* females show no preference for laying eggs at different heights in the tree crowns (Jones and Tome 1992) *E. torticornis* females do prefer to oviposit on nuts growing within the first three metres of the ground. We reaffirm comments by Southwood (1978) and Horn (1988) that the identification of host characteristics relevant to oviposition behaviour and insect distribution (both within and between host plants) is important for the design of sampling programmes, the forecasting of insect damage, and for assessment of the effectiveness of control programmes.

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RESUMEN

Se determinó la distribución vertical de los huevos del barrenador de la nuez de macadamia *Ecdytolopha torticornis* Meyrick (Lepidoptera: Tortricidae) y los sitios de preferencia de oviposición en los árboles y entre clones de macadamia. Se detectó la presencia de huevos de *E. torticornis* en todo el árbol, sin embargo, se encontró un menor número de huevos en la parte alta de la corona que en la parte media e inferior. La diferencia en la distribución horizontal de los huevos fue no significativa, a pesar de encontrarse un mayor número de huevos en las posiciones externas. El número de huevos entre clones fue similar, sugiriendo que la polilla del barrenador no tiene preferencias de oviposición entre clones.

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