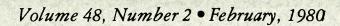
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Within-plant Distribution of Predators on Cotton: Comments on Sampling and Predator Efficiencies L. T. Wilson and A. P. Gutierrez

Within-plant Distribution of the Immatures of Heliothis zea (Boddie) on Cotton L. T. Wilson, A. P. Gutierrez, and T. F. Leigh

Fruit Predation Submodel: Heliothis Larvae Feeding **Upon Cotton Fruiting Structures** L. T. Wilson and A. P. Gutierrez

Within-plant Distribution of Predators on Cotton: Comments on Sampling and Predator Efficiencies (Wilson and Gutierrez)

Within-plant distribution of four predators found in California cotton fields is described. Adult stages of all predators were found in greatest frequency in the terminal portions of the plant, and, within that region, adults tended to be more common on fruiting parts than the same species of larvae. In general, the smaller predators, Geocoris and Orius, were found higher on the plant than the larger predators Chrysopa (larvae) and Nabis. Their respective areas of activity corresponded to the location of suitably sized (stages) prey. Those predators closest to the plant terminal were more effectively sampled with the standard University of California sweepnet.

Within-plant Distribution of the Immatures of Heliothis zea (Boddie) on Cotton (Wilson, Gutierrez, and Leigh)

A detailed study of the within-plant distribution of cotton bollworm (*Heliothis zea* (Boddie)), its eggs and larvae, was conducted in the field, and sampling schemes for them were developed.

The average location of bollworm eggs was approximately one-third of the distance in nodes from the terminal, while older larvae were found lower on the plant than younger larvae. The sampling scheme for bollworm eggs relies on the finding that the mainstem leaves are the preferred oviposition site. Field observations indicate that early first instar larvae can be detected in squares by the presence of frass and the flaring of the bracts. These criteria are used in a suggested sampling scheme for first-through-third instar larvae.

Fruit Predation Submodel: Heliothis Larvae Feeding Upon Cotton Fruiting Structures (Wilson and Gutierrez)

Field and laboratory data on the numbers and age distribution of two varieties of cotton fruits, the association of various-age bollworm larvae (Heliothis zea (Boddie)) and various age fruit, as well as the attack rates of the larvae on the fruits were used to develop a submodel describing predation of bollworm larvae on cotton fruits. The submodel will be used in the coupling of bollworm- and cotton-plant population models. This model is an important step in the development of dynamic economic threshold levels for bollworm in cotton.

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Within-plant Distribution of the Immatures of Heliothis zea (Boddie) on cotton^{1, 2} INTRODUCTION

In the san Joaquin valley of California, lepidopterous larvae are believed to be insecticide-induced pests of cotton (Falcon et al. 1971; Gutierrez et al. 1975). The amount of damage produced by the larvae of a pest species depends not only upon the timing and density (intensity) of the infestation, but upon the ages of the damaged plant structures.

In insecticide-free fields, lepidopterous populations normally are kept in check by an abundance of general predators (Falcon *et al.* 1971; Ehler, Eveleens, and van den Bosch 1973; and Eveleens, van den Bosch, and Ehler 1973).

Many papers have examined the within-plant distribution of *Heliothis* spp. in cotton (Quaintance and Brues 1905; Parsons 1940; Fye, Kuehl, and Bonham 1969; Beeden 1974; Hillhouse and Pitre 1976). Most papers describe the location of the organisms by vertical distribution or by structure (fruit, leaf surface, stems, etc.), but none adequately describes the changes in egg and larval distributions through time, or how this distribution is determined by adult moth preferences for oviposition sites.

This paper describes the changing vertical within-plant distribution through time of bollworm (*Heliothis zea* Boddie)) eggs and larvae on various parts. Sampling schemes were developed for eggs and larvae based upon the observed within plant distributions.

METHODS

The experiments were conducted at the USDA Cotton Research Station at Shafter, California, and at the J. G. Boswell Ranch near Corcoran, California, during the summers of 1974 and 1975, respectively. Acala SJ-1 (6.38 plants/meter-row) and Acala SJ-2 (11.95 plants/meter-row) cottons were grown during 1974 and 1975, respectively.

The distribution of bollworm eggs was determined by confining females and males (2 each) in each of six field cages on 18 dates (six time periods) from June 17 to September 8. Each wooden frame field cage was 1.00 × 0.96 meter at the base and 1.82 meters in height, covered with 0.36-cm mesh galvanized wire screen, and placed over 1 meter-row of plants. The moths were held in oviposition cages in the laboratory until they began laying eggs (Olivares-Mongrut 1971), and placed in the field cages from 4 to 8 p.m., allowed to oviposit for 2 days, after which they and the cages were removed. The location of each egg was recorded by mainstem (cotyledon equals one) and branch node, the type of branch (vegetative or primary fruiting), and plant part. Eggs deposited on leaves were also recorded by surfaces. The vertical within-plant distribution of bollworm larvae on fruits was studied in a similar manner. (N.B. The larvae rarely attack other plant parts.)

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During 1975, the dispersal of first instar larvae within the plant was studied by placing larvae on the mainstem node leaf and first branch leaf in the preferred areas of the plants and recording their directions of travel. The within- and between-plant movements of 2nd through 5th instar larvae were observed, and changes in feeding sites were determined through time.

RESULTS

Within-plant distribution of H. zea eggs

Oviposition site preference by plant part—The adult moths oviposited on both surfaces of leaves, on fruit and on the stem of the cotton plant. A total of 12,941 eggs were found in the six time experiments. Of these, 89.6 percent were found on leaves (i.e., 48.2 percent on primary mainstem leaves (MSNL), 23.1 percent on primary fruiting branch leaves (FBL), and 18.3 percent on vegetative branch leaves (VBL), 9.9 percent were found on fruits and only 0.5 percent on stems). The obvious preference for leaves was rather surprising since the larvae fed primarily on fruits (but see below). The proportion of eggs deposited on FBL, fruits, and MSNL remained fairly constant throughout the season (80.3 percent), and were used as the benchmark *total* for the remaining analyses.

The proportion of eggs deposited on fruits was greatest during the peak squaring period (see Fig. 1a-b), and there was an apparent decreased preference for the top surface of leaves as the season progressed (see Fig. 1c).

An obvious hypothesis to test was whether the eggs were distributed at random on leaves and fruits. Equation 1 shows the relationship between the proportion of eggs (Y) which are on MSNL, and the proportion of oviposition sites which were MSNL.

$$Y = 0.3627 + 0.6056X, r^2 = 0.994, F = 632.7, n = 6, P < .001$$
 [1]

An average 48.2 percent of the eggs were deposited on MSNL, hence [1] implies that mainstem leaves were more preferred than expected. This may be due to:

- 1. MSNL near the terminal where the eggs are deposited are larger than the corresponding branch leaves, hence, on the basis of area, MSNL should receive more eggs.
- 2. MSNL near the terminal shade branch leaves and fruits on the same branch which would further enhance the availability of MSNL to ovipositing moths.

Moths also showed differential preference for the upper (T) and lower (B) leaf surfaces. Regressions of the average number of eggs/leaf surface (T and B) against the average proportion of leaves with eggs (X) provide estimates on the effect of egg density on moth oviposition.

$$\overline{\text{Egg}_{\text{T}}}$$
 = 1.40 + 1.72X, F = 27.4, N = 11, .001 < P < .002

$$\overline{\text{Egg}_{\text{B}}}$$
 = 2.07 + 1.60x, F = 8.1, N = 1, .02 < P < .05

The intercepts estimate the average number of eggs deposited during each oviposition (i.e., 1.40 and 2.07 on the top and bottom surface, respectively). The slopes of the two regressions were not significantly different.

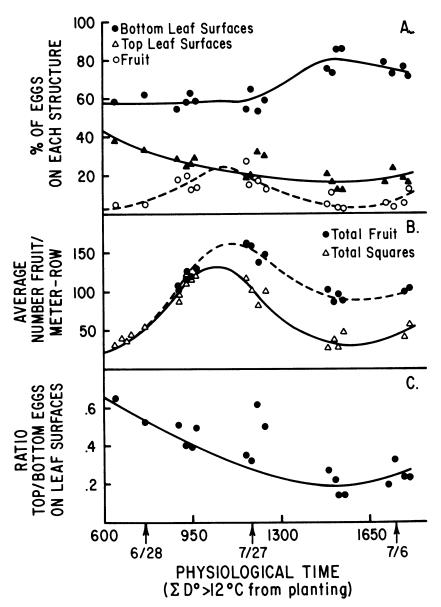


Fig. 1. Plots of (a) the observed trends (proportions) for eggs deposited on top and bottom leaf surfaces and on fruits through the season, (b) the average number of fruits (total squares and total fruits) found per meter-row of cotton through the season, and (c) ratio of eggs on top per bottom leaf surfaces through the season. Shafter, California, 1974.

Equation 2 describes the relationship between the proportion of eggs (\hat{p}) deposited on the top leaf surfaces and the proportion of leaves with eggs (X).

$$\hat{p}$$
 = 0.210 + 0.221X, r^2 = .669, n = 11, 0.002 < P < .005 [2] and \hat{q} = 1 - \hat{p} is the proportion of eggs on the bottom leaf surfaces.

Apparently bollworm moths had a decreasing preference for the bottom surfaces at higher egg densities (i.e., the surface that initially had the greater number of bollworm eggs). This suggests that the presence of eggs at a given position may decrease the likelihood that others will be deposited there. This behavior would be advantageous to the survival of bollworm eggs and larvae by reducing the probability of cannibalism (Stinner, Rabb, and Bradley 1974).

The eggs were not distributed at random on leaf surfaces, but the non-random distribution may not hold for whole leaves. Figure 2a is a plot of the proportion of leaves with eggs on both surfaces against the proportion of leaves with eggs. These data were compared with an expected cumulative Poisson distribution function (E1) modified by the probability of oviposition occurring on both the top and bottom surfaces. The curve is described by Equations 3 and 4.

$$E_1 = f(X) = \sum_{k=2}^{\infty} m^k e^{-m} (1 - p^k - q^k)/k!$$
 [3]

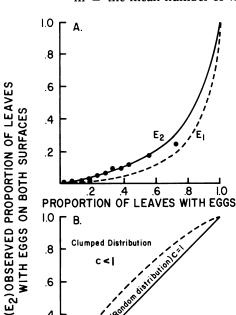
and

$$X = \sum_{k=0}^{\infty} p[k] - p[0] = 1 - e^{-m}$$
 [4]

where

k = frequency class for the number of times a leaf is visited by a moth(s) during oviposition.

m = the mean number of visits per leaf.



Uniform Distribution

1.0

c > |

.6

(E1) EXPECTED PROPORTION OF LEAVES WITH EGGS ON BOTH SURFACES

.4

.2

0

Fig. 2. Plot of (a) the proportion of leaves with eggs on both leaf surfaces against the proportion of leaves with eggs, and (b) the regression of E₂ (curve fitted to data) on E₁ (the expected cumulative Poisson distribution function which has been modified by the probability of oviposition occurring on both the top and bottom leaf surfaces). Shafter, California, 1974.

 E_1 underestimated the data, but essentially had the same pattern as the fitted line E_2 . The curves were extended beyond the observed range of the data only for theoretical purposes. If $E_1 = E_2$, then oviposition was random with respect to leaves. A regression of E_2 on E_1 produced a symmetrical curve (---, Figure 2b) above the line $E_1 = E_2$. Deviation above $E_1 = E_2$ would imply that the eggs had a clumped distribution, while deviations below would imply a tendency towards a uniform distribution of the eggs. The observed departure from randomness towards a clumped distribution was the result of the adult moth's preference for the upper strata of the plant (see following sections), and appeared to overcome the slight bias against leaf surfaces with eggs (see above), or the fact that moths on average deposit more than one egg per visit.

The line fitted to E_1 regressed against E_2 can be described by Equation 5.

$$\hat{E}_2 = E_1/(E_1 + (1 - E_1)c)$$
 [5]

where

$$c = \sum_{i=1}^{n} (E_{1i} - E_{1i}E_{2i})/\Sigma(E_{2i} - E_{1i}E_{2i}), n = the number$$
of data points

The constant c describes the type of deviation from a random distribution. If c > 1, the eggs appear to be located uniformly on the plant, but if c < 1, the eggs have a clumped distribution. For the bollworm egg distribution, c equals .54081. Equation 3 multiplied by Equation 5 (i.e., a correction for weighted Poisson) reproduces the fitted curve (E₂) for the observed proportion of leaves with eggs upon both surfaces (Figure 2a).

Moths also discriminated between leaves and fruit, as a cursory analysis showed that oviposition on fruit was lower than expected on relative abundance. The ratio of eggs/fruit to eggs/leaves for each sampling date would estimate this lower preference. On average, 74.5 percent as many eggs were deposited per fruit as per leaf.

The numbers of squares and bolls change throughout the season and analysis of preference for either must be corrected for the difference. A regression of the proportion of squares with eggs (Y) against the proportion of fruit which are squares (X) was used to test the hypothesis examined that squares and bolls were receiving eggs in proportion to their abundance (H_0 : b = 1). In this case b = 0.997, and the hypothesis was accepted (see Equation 6).

$$\hat{Y} = 0.01098 + .997X, r^2 = .903, n = 12, F = 93.1,$$
 [6]

Vertical within-plant distribution of *H. zea* eggs—As the season progressed, the plants got larger and the choice of strata for oviposition became much greater. At sparse plant densities, vegetative branches low on the plant grew large enough so that they penetrated to the top of the crop canopy, and many produced fruits. In addition, the position of the first fruiting branch was also influenced by plant density (Gutierrez et al. 1975). Thus, the identification of oviposition sites by mainstem node may not reflect the true position of eggs in the crop canopy.

Figure 3b shows over time the average mainstem node position of all eggs; those oviposited only on primary fruiting branches and mainstem leaves, and the average number of mainstem nodes. Recording egg position simply by mainstem node without

regard to the kind of branch is shown by the lower average position for total eggs. In general, the moths oviposited in the top of the plant, as indicated by the regression of the average mainstem location for eggs (\overline{T}) against the average number of mainstem nodes (\overline{H}) per plant (see Equation 7, and Fig. 3a).

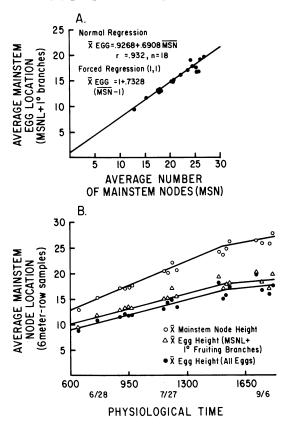


Fig. 3. Regression of the (a) average mainstem location for eggs (primary fruiting branches and mainstem leaves only) against the average number of mainstem nodes per plant, and (b) a comparison of the average mainstem node position of all eggs through time, those oviposited only on primary fruit ing branches and mainstem leaves, and the average number of mainstem nodes. Shafter, California, 1974.

$$\overline{T} = .9268 + .6908\overline{H}, r^2 = .932, n = 18, F = 220.0, P < .001$$
 [7]

The regression equation should be forced through (1,1) because plants are one node tall when they germinate, hence eggs laid on the cotyledon leaves are recorded as node 1 (see Equation 8).

$$\overline{T}$$
* = 1.0 + .7328 (H - 1) [8]

Within-plant dispersal and distribution of bollworm larvae.—In contrast to the immobile egg stage, larvae may move from one site to another to find food or more favorable micro-habitats. The dispersal of larvae of different ages may have a profound effect on the age structure of the fruit population and on yields. In general, larvae moving up or out in the plant have younger fruit to attack and vice versa.

In a 1975 test, newly hatched larvae less than 10 minutes old were placed either on mainstem leaves or on fruit branch leaves in the terminal of the plant. The position of each larva was checked every 15 to 30 minutes until they ceased moving and began feeding continuously. Of 131 newly hatched larvae tested, only 71 survived to initiate feeding upon fruit. Of these, 6 remained at the same node (branch and mainstem),

while the other 65 travelled up the mainstem of the plant and/or out on the same branch. The remaining 60 larvae were either not found and/or were killed by predators.

Table 1 presents estimates for age-specific bollworm mortality for 1974. During August, 2,675 or 100 percent of the bollworms were destroyed before they reached the third instar. During September, 1,669 or 100 percent were destroyed before reaching the second instar. In both cases, the field was untreated, and egg samples revealed that egg viability was near 95 percent. Of 86 observed cases of bollworm egg and larvae predation, 67.4 percent were by *Orius tristicolor* (White) adults and nymphs, while *Chrysopa* and *Geocoris* spp. were responsible for most of the remaining mortality.

Table 1.

CUMULATIVE PERCENT MORTALITY OF BOLLWORM IMMATURES TO THE END OF EACH STAGE. SHAFTER, CALIFORNIA 1974.

Date	Instar							
	1	2	3	4	5	n		
6/18-28	67.5	84.1	85.5	87.0	87.6	1674		
7/8-11	82.7	87.0	88.6	89.1	89.8	3965		
7/26-29	89.9	94.0	96.0	96.1	96.3	2675		
8/18-21	95.4	>98	100	100	100	2958		
9/6-11	>99	100	100	100	100	1669		

In a second test, larvae were checked to determine the location of successive feeding sites during their lives (Table 2). The larvae in the first three instars tended to move up the plant, while those in the last two instars moved down. Figure 4 shows the position of the various age larvae regressed against the number of mainstem nodes per plant. These data indicate that older larvae are found lower in the plant.

Bollworm larvae search for food (i.e., fruit), hence the actual location of the larvae within the plant is strongly determined by the position and age structure of the fruit. Figure 5 shows that as the larvae got older, there was a corresponding widening of the age (i.e., size) of fruit which they accepted. While squares were preferred over bolls as feeding sites by all bollworm instars, a greater proportion of older fruit was included in the larval diet of all instars as the season progressed.

Some observations on the effects of irrigation intensity, soil profile, and the cultural practice of terminal topping (to facilitate hand picking) on bollworm oviposition were made and indicated that factors that delayed the termination of plant growth (due to fruit maturation) resulted in the plant's being more favorable to ovipositing moths. Increased irrigation resulted in lusher, later maturing plants, while sandy soils and terminal topping resulted in less favorable plants. In the 1974 studies 3219, 4187 and 5535 eggs were laid on the low-, normal- and high-irrigation level plants, respectively. In August of 1976 no eggs were found on plants that had been topped or which were on sandy soil, while plants growing normally in heavier well watered soils had egg counts of ca. 6 per 100 terminals. (N.B. The same field may have streaks of different soil types.)

Sampling bollworm populations—The differences in within-plant distribution of eggs and larvae required that separate sampling schemes be developed for each.

A majority of the bollworm eggs were deposited on mainstem leaves (MSNL), and

because these leaves can be easily identified and quickly sampled, a sampling scheme for eggs is based upon MSNL.

The value of an MSNL sampling scheme depends upon our ability to estimate total population densities from MSNL egg samples with high accuracy and small effort.

Table 2.
DISPLACEMENT OF BOLLWORM LARVAE FOR EACH INSTAR.*

	Instar					
Item	1	2	3	4	5	
Mainstem direction x	.52	1.32	.21	29	76	
sd	.82	1.36	2.31	2.82	2.65	
n	25	22	42	133	94	

^{*}Positive values mean an upward movement while negative values mean a downward movement.

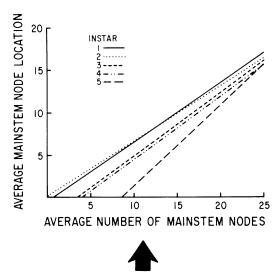
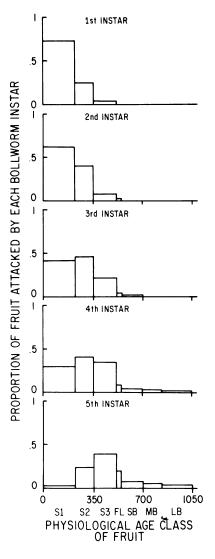


Fig. 4. Regression of the average node location in cotton of the first through fifth instar larvae against the average number of mainstem nodes per plant observed at Shafter, California during 1974.

Fig. 5. Proportion of attacks (seasonal average) by the different instar larvae against the various age categories of fruits. Costa de Hermosillo, Sonora, Mexico, 1976.





Regression Equation 9 describes the relationship on a meter-row basis between the number of eggs on MSNL (\bar{E}_{MSNL}) to the total number of eggs (TE) at a plant density of 6.38 plants/meter-row. The population of eggs was high in these tests.

$$\overline{E}_{MSNI}$$
 = 43.62 + .4645TE, r^2 = .939, $n = 6$, $F = 61.2$, $P < .001$ [9]

The regression should be forced through the origin as zero total eggs should result in zero MSNL eggs (Equation 10).

$$E_{MSNI}^{*} = .4805TE$$
 [10]

Gutierrez³ (unpublished data) found in another noctuild moth *Trichoplusia ni* (Hubner) that the fraction of eggs (β) deposited on MSNL was proportional to plant density (d) expressed as plants per meter-row (Equation 11). A similar relationship probably holds for bollworm (see previous sections).

$$\beta = .3314 + .02200d \tag{11}$$

Plant density also influences the average mainstem node location of bollworm eggs (see section on vertical distribution). The average location of the MSNL eggs (Ê) was estimated by Equation 12.

$$\hat{E} = 1 + \hat{b} (H - 1)$$
 [12]

where

H = the average number of mainstem nodes

 $\hat{b} = 0.7471 + 0.00531d$, the regression coefficient for MSNL egg locations as influenced by plant density (Gutierrez, unpublished).

Equation 12 assumes linearity with the regression forced through (1,1).

Given Ê, 50 percent of the MSNL eggs can be sampled by taking all leaves from the terminal to Ê. However, if a different proportion of the MNSL eggs is to be sampled, the within-plant distribution of eggs on mainstem leaves must be known.

The standard deviation (sd) of egg locations was linearly related to (H-Ê) and to the number of mainstem nodes above the cotyledon (H-1), and some algebra yields H-Ê = (1-b) (H-1). Therefore, sd must be proportional (\$\phi\$) to (H-Ê) / (H-1) = 1-b. Equation 13 describes the relationship between \$\phi\$ and 1-b.

$$\phi = .72306 \ (1-b)$$
 [13]

A sampling scheme using this information would have the following form.

$$\hat{N}_{(1-\alpha)\beta} = H - (b \pm \phi t_{(\alpha,\infty)} \times (H-1) + 1), \text{ where } b = [14]$$

$$- \text{ if } \alpha < .5$$

 $\hat{N}_{(1-\alpha)\beta}$ = the number of mainstem node leaves counting from the terminal which have to be sampled to account for $(1-\alpha)\beta$ percent of the population, t is student's t, and β is estimated from Equation 11. The total population density per meter row is then estimated by Equation 15.

Total eggs = MSNL eggs/
$$(1-\alpha)\beta$$
 × (plant density/ sample size)

³ A copy of this unpublished manuscript is available from the second author.

The increased efficiency of MSNL sampling can be easily seen. During late July and early August, before the plants have reached advanced maturity, sampling whole plants (6.38 plants/meter-row) often took in excess of 15 minutes, while meter-row samples took an average of 70 minutes. In contrast, sampling just the mainstem leaves during this same period required about 10 minutes per meter-row, or ca. 14 percent of the time required by the whole plant method. Only half of the eggs were found on MSNL, but the total can be estimated from [15].

Sampling part of the mainstem leaves takes further advantage of our knowledge of the egg distribution pattern. Sampling approximately the upper 20 percent of the mainstem leaves yields half of the MSNL eggs, (i.e., 24.1 percent of all eggs are sampled). Figure 6 shows the relationship between the percent of mainstem eggs sampled and the percent of mainstem leaves sampled (6.38 plants/meter-row). The greatest sampling efficiency occurs when approximately 30 percent of MSNL are sampled. Beyond this point the efficiency begins to decrease.

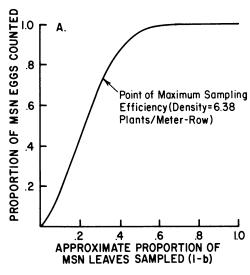


Fig. 6a-b. The relationship (a) between the percent of mainstem eggs sampled and the percent of mainstem leaves sampled (6.38 plants/meter-row). Shafter, California, 1974.

Bollworm larvae—Unlike bollworm eggs, larvae were much easier to sample. A sampling plan to estimate bollworm larvae should be directed only at the first three instars, as older larvae are safe from attack by most predators and are located far enough down the plant so that chemical control is unlikely to be effective. Early instar larvae could usually be determined by the flaring of squares and the presence of feces. Sampling the squares in the upper modes usually gave a good estimate of early instar larval population densities. Similar conclusions were reached by Boyer, Warren, and Lincoln (1962).

DISCUSSION

The majority of bollworm eggs are laid on the bottom surface of leaves near the terminal. Under high levels of bollworm infestation, the proportion of eggs oviposited on the bottom surface lessens. The greatest proportion of eggs found on fruit coincides with the peak period of fruit production.

Many studies have been conducted on the distribution of bollworm eggs on cotton (Heliothis zea (Boddie) in the United States and H. armigera (Hbn.) in Africa). An

examination of six such studies showed no consistency in the rate of bollworm oviposition preference as a function of plant structures. Two studies found leaves (Parsons 1940; Reed 1965), two found fruits (Quaintance and Brues 1905; Beeden 1974) and two found that stems (Tunstall, Matthews, and McKinley 1966; Matthews and Tunstall 1968) were the most preferred oviposition sites, respectively. *Trichoplusia ni* (Hubner), a noctuid that exhibits oviposition behavior similar to bollworm, oviposits approximately 95 percent of its eggs on the bottom leaf surface of older leaves (Gutierrez, unpublished data).

Moths lay a variable number of eggs during each oviposition visit. During this study, the top and bottom leaf surfaces received an average of 1.40 and 2.07 eggs, while squares and bolls received 1.67 and 2.32 eggs per oviposition visit, respectively. Data of Fye, Kuehl, and Bonham (1969) indicated that an average of 1.3 eggs were oviposited each time a female visited a plant for oviposition. This value probably underestimates actual numbers of eggs oviposited per visit because of the difficulty involved with sampling low density natural field populations. Using field observaion on 34 ovipositing moths, Quaintance and Brues (1905) recorded 1,141 eggs oviposited upon 1,175 visited plants (.97 egg/visit), but moths land on plants to feed as well as to oviposit, hence the eggs laid per oviposition visit is higher. Our estimate was 1.89 eggs per oviposition visit, which would imply that half of the visit recorded by Quaintance and Brues (1905) was for other reasons.

In this study, the average node position of bollworm eggs was approximately one-third of the distance in nodes from the terminal. Mowlam (1972) cited in Beeden (1974) found that *H. armigera* (Hbn.) eggs were on average deposited one-fourth of the way down the plant while Beeden (1974) found the value to be one-fifth. Considering that internode elongation is minimal near the terminal nodes, on a linear scale the average egg location observed in this study would probably be very close to the value presented by Beeden (1974). Other authors have reached similar conclusions concerning the distribution of bollworm eggs near the plant terminal (Boyer *et al.* 1962; Matthews and Tunstall 1968; Fye 1972; and Hillhouse and Pitre 1976).

Bollworm larvae move towards the terminal during the first three instars, but each instar is generally found further from the terminal than the previous one, because the mainstern node production rate exceeds the larval dispersal rate.

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