WITHIN-PLANT DISTRIBUTION OF FALL ARMYWORM (LEPIDOPTERA: NOCTUIDAE) LARVAE ON CORN DURING WHORL-STAGE INFESTATION

J. M. LABATTE
INRA Station de Zoologie
rte de St cyr
78000 Versailles, France

ABSTRACT

Field experiments on the within-plant distribution of larvae of the fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), on the early-whorl to late-whorl stage of corn, *Zea mays* L., revealed that most larvae were found in the wrapped leaves of the whorl. Beta density function for describing larval distribution showed that larval instar, infestation date and environmental conditions did not influence this process. Larval distribution and its time course was accurately described with a single Beta density function for all infestations. This function gave 64%, 25%, 8%, 2% and 1% of larvae in the highest visible leaf and leaves just above, respectively. When the tassel began development in the whorl (pre-tasseling corn stage), most larvae (80%) were found in this location. After tasseling, larvae moved down to the lower leaves and into the ear (75%).

Key Words: *Spodoptera frugiperda*, *Zea mays*, mathematical model.

RESUMEN

Los ensayos en campo, sobre la distribución de las larvas de *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) durante las etapas de crecimiento vegetativo del maíz, *Zea mays* L. han demostrado que la mayoría de las larvas se encuentran en las hojas del cogollo. La utilización de una función de densidad Beta, para describir la distribución de las larvas, ha mostrado que el estado de las larvas, el período de infestación y las condiciones del medio no influyen la distribución de las larvas. La distribución de las larvas y su cinética fueron descritas apropiadamente por con una función simple de densidad Beta para cada infestación. Esta función ha dado 64%, 25%, 8%, 2% y 1% de larvas en la hoja más alta y las hojas immediatamente inferiores. Cuando la panícula comienza su desarrollo, la majoría de las larvas (80%) fueron encontradas en ella. Despues de floración, las larvas bajaron hasta las hojas bajas y hasta la mazorca (75%).

The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), is a major pest of corn, *Zea mays* L., in the southeastern United States, Central America and the Caribbean islands. Typically, damage to corn is caused by foliar feeding of FAW larvae during the whorl stage (Buntin 1986). Yield losses may reach 50% (Cruz & Turpin 1983). Chemical control has been used successfully to control FAW larvae in corn fields (Pitre 1986) and is currently the main control practice. Nevertheless, insecticidal control requires as many as 8 applications to be effective (Hruska & Gladstone 1988), and development of resistance to selected insecticides has been reported (Young 1979, Leeper 1984, Pitre 1986, Young 1986, Guillebeau & All 1991). Improvement of FAW management requires: (1) a better knowledge of dynamic FAW biological processes relative to feeding damage and their influence on the use and the impact of control practices (Lewis & Nordlund 1984, Gardner et al. 1984), and (2) development of alternative, effective control practices based on host plant resistance and microbial control (Gardner et al. 1984, Hamm & Wiseman 1986, Carpenter & Wiseman 1992).

To achieve this goal, research should be directed towards a better understanding of larval dynamics and the quantitative description of the natural relationships between FAW larval biology, the corn crop, and environmental factors (Fig. 1). A description of larval dynamics in relation to foliar damage is important because larvae are the main target of control practices. Quantification of these processes under natural conditions is necessary to describe the impact of host plant resistance and other interactions on microbial control.

This paper deals with the study of FAW larval within-plant distribution in whorl-stage corn. Larval within-plant distribution has an influence on two important processes: (1) location of damage, and (2) impact of control practices whose efficiency depends on larval distribution (contact probability) (Gardner et al. 1977). Several studies on larval distribution have been reported. Luginbill (1928) observed positive phototropism, which may account for the presence of young larvae on the topmost portions of the plants. Vickery (1929) reported that young larvae feed in the shade or in protected situations, such as between the young leaves of corn. Morrill & Greene (1973a) determined that most larvae were present in plant whorls in pre-tassel field corn, and in husks and ears in post-tassel corn. They explained these results by a negative geotropism and/or positive phototropism, and a positive thigmotactism (Morrill & Greene 1973b). Despite this work, changes in the distribution of FAW larvae over time and the effects of larval age and environmental conditions on larval distribution within the corn plant, are still unknown. In addition, previous studies have not resulted in a quantitative description of FAW

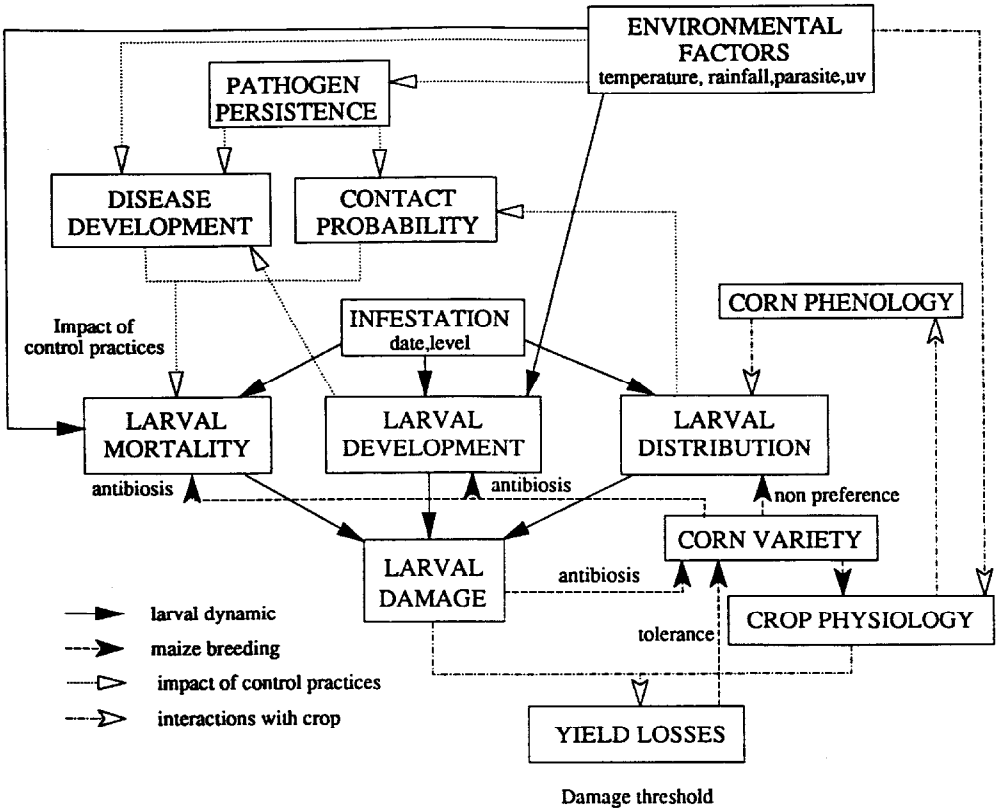

Fig. 1. Diagram showing the different processes on which control practices, breeding, yield losses and their relationships depend.

larval within-plant distribution. This paper presents a model which quantifies the proportion of larvae on the different internodes and organs of the corn plant during the pre-tasseling period.

Materials and Methods

All field studies were conducted at Petit-Bourg, Guadeloupe in corn fields of the 'Spectral' corn variety sown at the usual density of 50,000 plants per hectare with an inter-row distance of 0.75 m. All corn field study sites were at least 0.1 ha in size.

Plants were artificially infested with FAW egg masses obtained from the laboratory after two to five generations. FAW egg masses were initially collected from Guadeloupe field corn and reared using Poitout's diet (Poitout & Bues 1974). FAW egg masses and adults were identified by J. Etienne (Dept. Zoology, INRA Guadeloupe). Egg masses were pinned to the undersides of the uppermost expanded leaves. Artificial infestation made it possible to choose different infestation dates and to evaluate the effects of different weather conditions. A total of eleven infestations were examined over a wide range of plant maturity stages and environmental conditions (Table 1).

Determination of larval development and distribution required the dissection of plant samples. Sampling began from a few hours to two days after egg hatch. At least five corn plants were dissected daily until no larvae were found (due either to mortality or pupation). The head capsule width and the position of each larva (organ and internode) were recorded. The development stage and the number of visible and expanded leaves of dissected plants were also recorded. Larval instar was determined based on capsule width. Vertical distribution of larvae was compared using Smirnov's test (Sokal & Rohlf 1981).

Results and Discussion

The vertical distribution of larval FAW over time within various vegetative parts of the corn plant is presented in Fig. 2. Except for infestation 9, where larvae were found in the ear and tassel, most larvae were found in the leaves of the whorl in the early-whorl to late-whorl stages (Fig. 2, infestations 1 to 8). No larvae were found on or in the stalk.

Early- to Late-Whorl Infestation

Typically, larvae fed in the wrapped-up leaves of the whorl; few larvae were found in unprotected areas. Dissections carried out a few hours after egg hatch indicated that

TABLE 1. FAW INFESTATION CONDITIONS DURING DIFFERENT EXPERIMENTS.

Plot Number	Infestation Date	No. of Days After Sowing	Corn Stage	Daily Mean Temp. (°C)	Total Rainfall (mm)
1	1 Feb 1992	15	Whorl-4 leaves	23.6	20.4
2	9 Oct 1991	18	Whorl-6 leaves	25.3	74.0
3	13 May 1992	20	Whorl-5 leaves	25.5	—
4	29 Aug 1991	23	Whorl-7 leaves	26.1	26.5
5	11 May 1992	29	Whorl-7 leaves	25.5	—
6	24 Feb 1992	30	Whorl-7 leaves	23.6	101.5
7	7 Mar 1992	35	Whorl-8 leaves	23.7	17.8
8	25 Dec 1991	37	Whorl-10 leaves	23.4	144.6
9	14 Jan 1992	55	Perceptible tassel	23.4	61.0

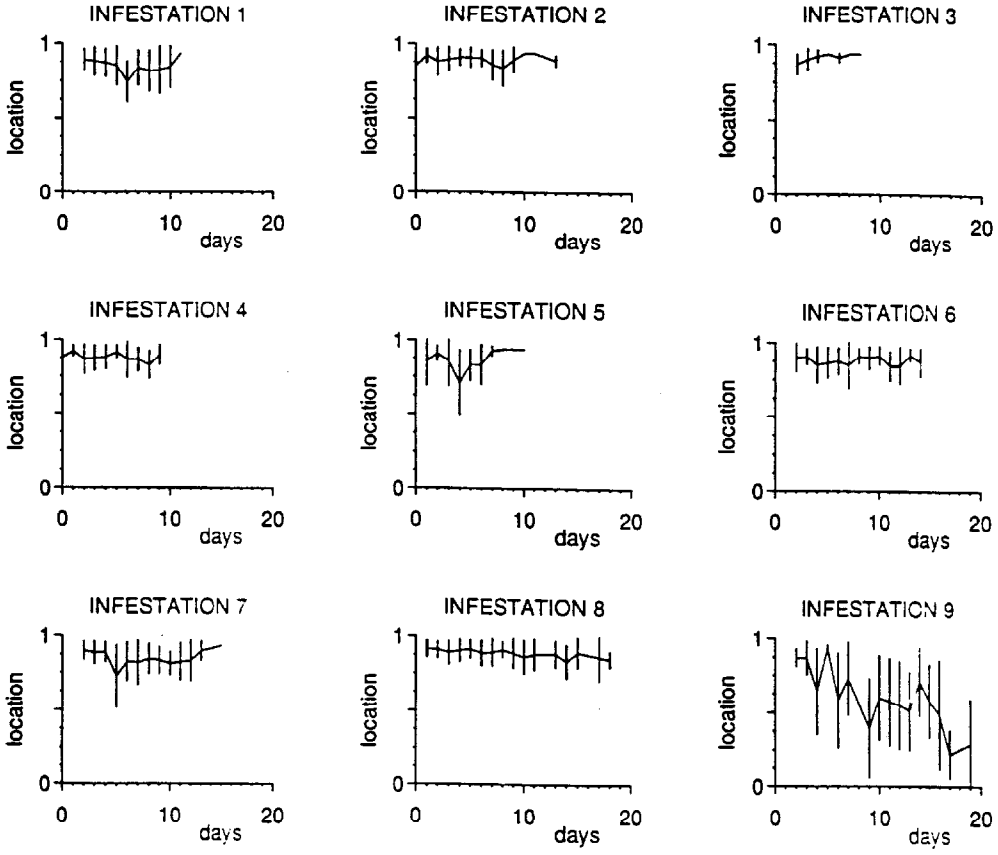

Fig. 2. Time course of FAW larval distribution in nine stages of infestation in corn. Solid line represents mean larval location, vertical line is the standard deviation. The X-axis represents days after egg hatch. The Y-axis represents the normalized vertical location of larvae, with 0 being the seventh leaf below the highest visible leaf and 1 the highest visible leaf (see text).

newly-hatched larvae moved quickly into the topmost portions of the plant (Fig. 2, infestations 2 and 4). More than 85% of larvae were found in the two highest visible leaves within 12 h after egg hatch. A similar distribution was observed in infestations 1, 3, and 5 to 8 when dissections began the first or second day after egg hatch (Fig. 2). Lack of foliar damage on the leaves below the whorl during the initial days after infestation confirmed this observation.

The time course of larval distribution showed that larvae fed in the topmost part of the plant from a few hours after egg hatch until the end of larval development (Fig. 2). Thus, no important change in larval location was observed for different instars. This observation was confirmed by Smirnov's test analysis (Table 2). The pattern of larval location on the plant was similar with most of the infestations (Table 3), except in infestations 1 and 7 where fewer larvae were found in the highest visible leaf, and infestation 9 where larvae moved down when the tassel became visible.

Density functions were used to quantify larval vertical distribution on corn. Beta density functions (Johnson & Kotz 1972) were chosen because they are defined on a finite interval (0-1), their parameters are easily interpreted (the mean and standard deviation of the distribution), and they have been adapted to describe the vertical

TABLE 2. ANALYSIS OF DIFFERENCES IN THE VERTICAL WITHIN-PLANT DISTRIBUTION OF DIFFERENT FAW INSTARS.

Instar	No. Larvae[1]	Instar 2	3	4	5	6
1	521	NS[3]	S[2]	NS	NS	NS
2	730		S	NS	NS	NS
3	596			NS	NS	NS
4	379				NS	NS
5	283					NS
6	51					

[1]Data for infestations 1 to 8 were combined.
[2]S = significantly different at 5% level (Smirnov's test).
[3]NS = not significantly different at 5% level (Smirnov's test).

distribution of insects (Labatte & Got 1993). Analytical expression of these density functions (f(X)) is as follows:

$$f(X) = X^{(p-1)}\,(1-X)^{(q-1)}/B(p,q)$$
$$E = p/(p+q)$$
$$SD = \left[\frac{(\quad p*q \quad)}{(p+q)^2(p+q+1)}\right]^{0.5}$$

where p,q are the function parameters; B(p,q) = G(p)G(q)/G(p+q) (G=Gamma function); X is the vertical position; E is the mean larval location; and SD is its standard deviation.

Larval vertical distribution was defined on the interval 0-1, with eight possible locations from 0, the seventh leaf below the highest visible leaf, to 1, the highest visible leaf. No larvae were found below the first location.

The density function parameters, E and SD, were estimated by minimization of the sums of squares of the residuals with the S programs (Chambers & Hastie 1992), a programming environment for users of UNIX systems.

These functions were used to compare inter-instar and inter-plot larval distribution (Fig. 3 and 4). Development of the distribution model required the assumption that the model was valid under different environmental conditions. To test this, we generated

TABLE 3. ANALYSIS OF DIFFERENCES IN THE VERTICAL WITHIN-PLANT DISTRIBUTION OF FAW LARVAE AMONG DIFFERENT PLOTS (INFESTATION DATES).

No. Plot	Larvae	Plot 2	3	4	5	6	7	8	9
1	552	S[1]	S	S	S	S	NS[2]	S	S
2	618		S	NS	NS	NS	S	NS	S
3	122			NS	NS	NS	S	NS	S
4	284				NS	NS	S	NS	S
5	146					NS	S	NS	S
6	298						S	NS	S
7	408							S	S
8	657								S
9	588								

[1]S = significantly different at 5% level (Smirnov's test).
[2]NS = not significantly different at 5% level (Smirnov's test).

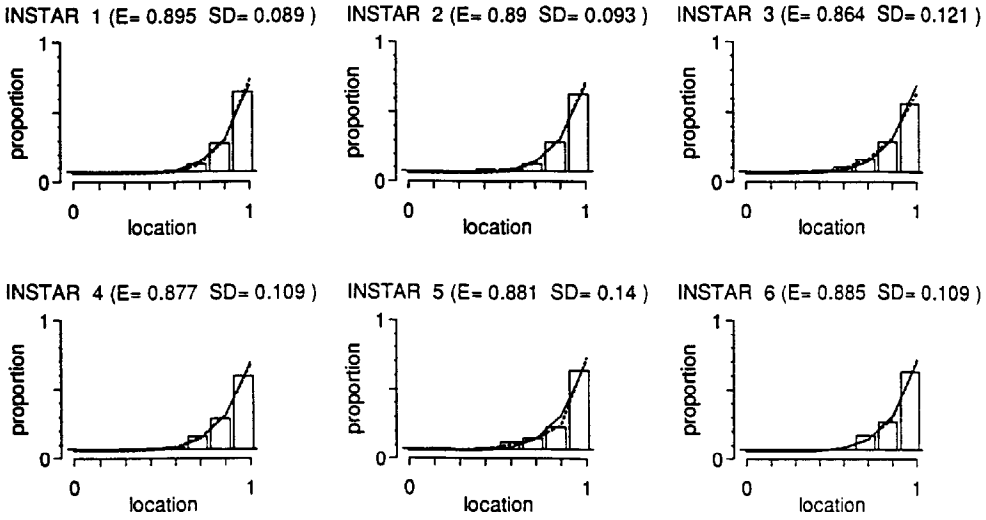

Fig. 3. Mean larval location for each instar with Beta density function fittings. The X-axis represents the normalized vertical location, with 0 being the seventh leaf below the highest visible leaf and 1 the highest visible leaf (see text). Histograms represent the proportion of larvae in each of the eight locations. The dotted line represents the fitting of the Beta density function estimated for each instar. Beta density function parameters are given in each graph. The solid line represents the fitting of the Beta density function estimated for all the instars ($E = 0.89 \pm 0.003$, $SD = 0.102 \pm 0.037$).

distribution estimates for different conditions. To evaluate the effects on the model of different plots (stages of infestation) or instars, we carried out model estimations by assigning identical values to the parameters. A comparison of the goodness-of-fit of the model, when estimated plot-by-plot or instar by instar, by assigning identical parameters for all the plots or instars, makes it possible to evaluate the accuracy of the model under different conditions.

The density functions estimated for each observation (dotted lines of Figs. 3 and 4) describe the larval vertical distribution well, with less than a 10% difference between observed and fitted distributions. These fittings provided a graphical reference for the goodness-of-fit. In order to evaluate the influence of larval instar or infestation date, a single density function (solid line) was estimated by first assigning identical parameters for all the instars (Fig. 3) and then for all the infestations (Fig. 4). The goodness-of-fit of the single functions allowed a similar description of larval distribution compared to observation-by-observation fittings. These results indicate that differences in larval instar, corn stage or environmental conditions did not influence larval distribution in early- to late-whorl of corn. The single function estimated for all the infestations was used to describe larval distribution over time for infestations in early- to late-whorl corn. Fig. 5 presents an illustration of the fittings obtained with this function for each infestation. Larval distribution is accurately described with only small differences between observed and fitted distributions.

Pre-tasseling Infestation

Infestation 9 was carried out at the pre-tasseling stage of corn. The tassel was well developed in the whorl at the beginning of the infestation and most larvae were attracted to it (Fig. 6). The percentage of larvae in the tassel reached up to 80% before the tassel emerged. This percentage progressively decreased until tasseling, when few larvae were found in this location.

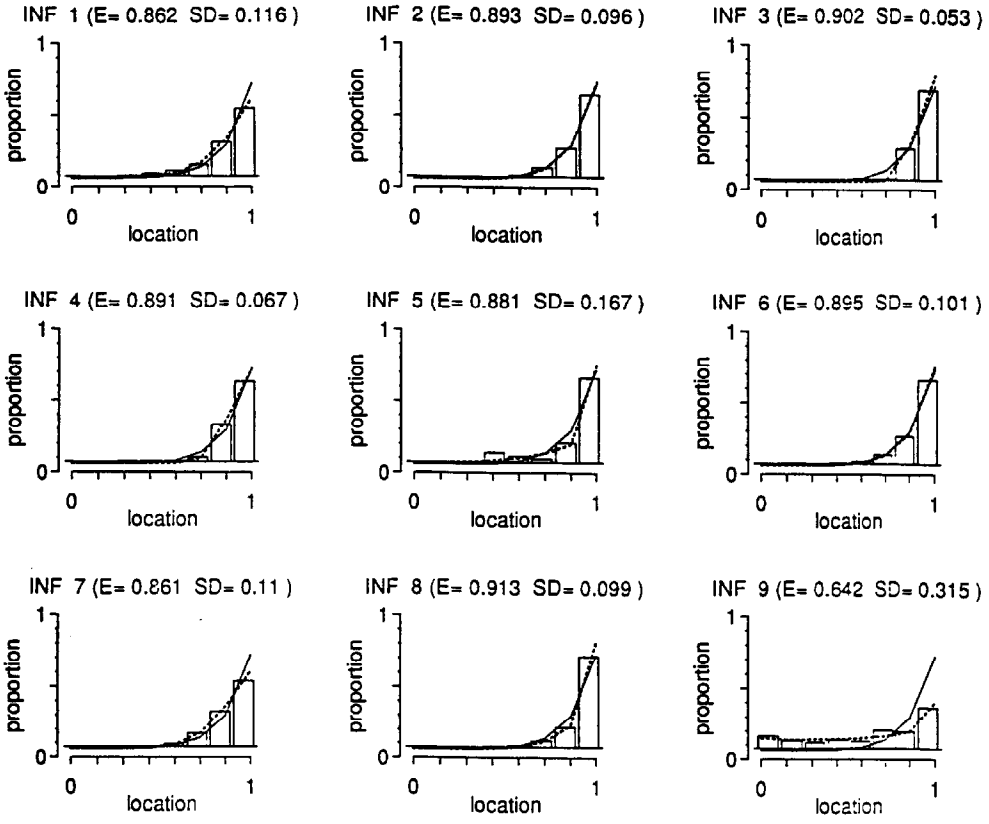

Fig. 4. Mean larval location for each infestation stage with Beta density function fittings. For legends see Fig. 3, except that the instar is replaced by time of infestation. Parameters of the single Beta density function estimated for all the infestations are $E = 0.88 \pm 0.002$ and $SD = 0.104 \pm 0.028$.

When the tassel emerged, the larvae moved to the lower leaves and the ear (Figs. 2, 6). The percentage of larvae in the ear increased progressively after tasseling and reached up to 75% at the end of the larval development, a few days after female flowering. This time course is in agreement with the observations of Morrill & Greene (1973a).

Conclusions

This study demonstrated that the within-plant distribution of FAW larvae in the leaves remained constant from the early- to late-whorl stages of corn development. The fitting of a single density function for all the larval instars and all stages of corn development permitted a good description of the FAW larval distribution with few discrepancies. The average percentages of larvae in all infestations were 64%, 25%, 8%, 2%, and 1% on the highest visible leaf and on the successive leaves just below, respectively. This distribution remained constant until the tassel became well developed in the whorl, whereupon most larvae were found in this structure. After tasseling, most larvae moved to lower leaves and to the ear.

This study demonstrated that, for early- to late-whorl stage corn, FAW larvae were in unprotected areas for less than one day, immediately after egg hatch. They were subsequently found in the wrapped-up leaves of the whorl and remained in this protected area until the end of their development. This behavior could explain the variable results

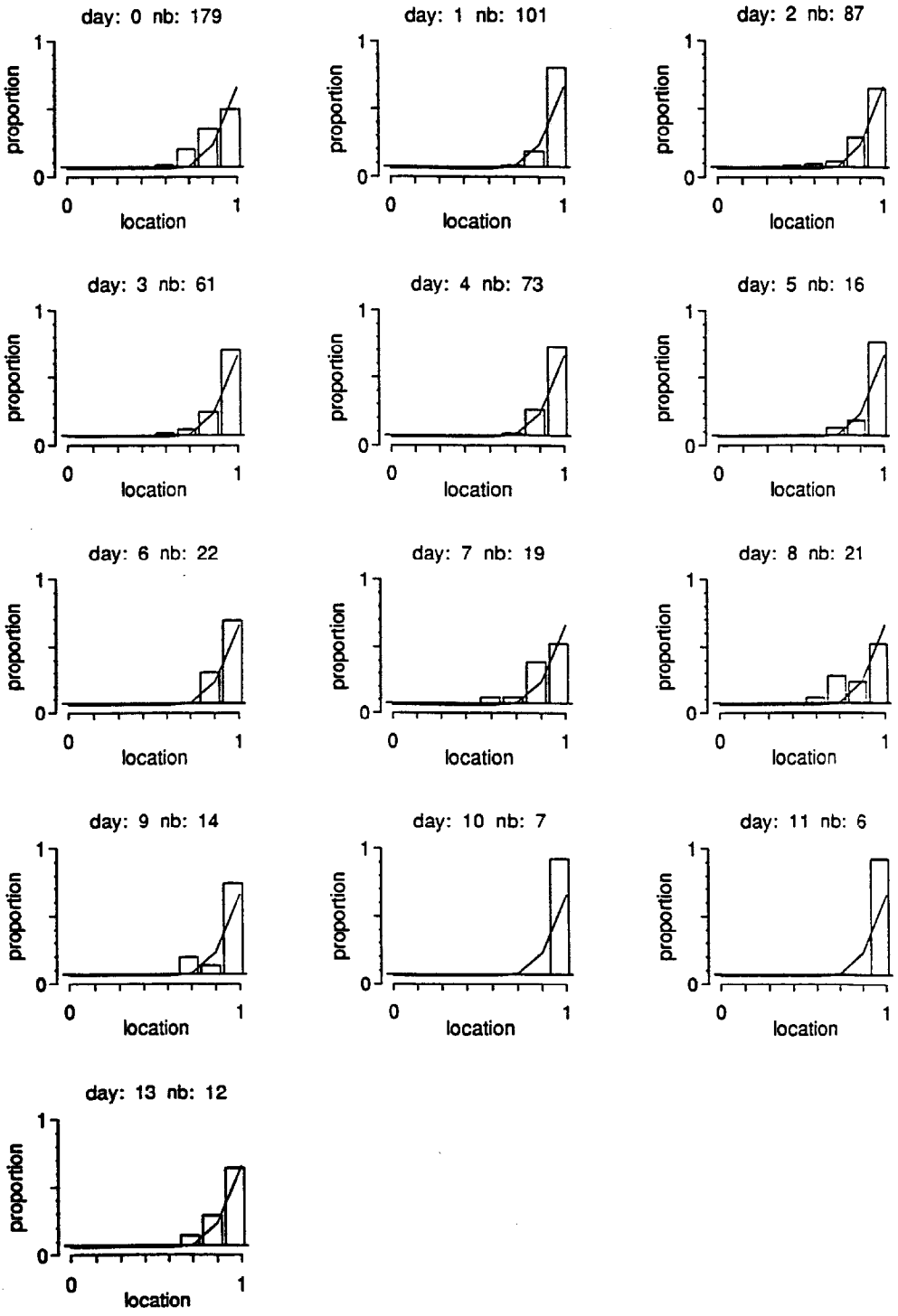

Fig. 5. Description of the time course of larval within-plant distribution for infestation 2 using the Beta density function parameters. For legends see Fig. 3. Each graph represents a daily observation. The numbers indicate the observation day after egg hatch and the numbers of larvae found.

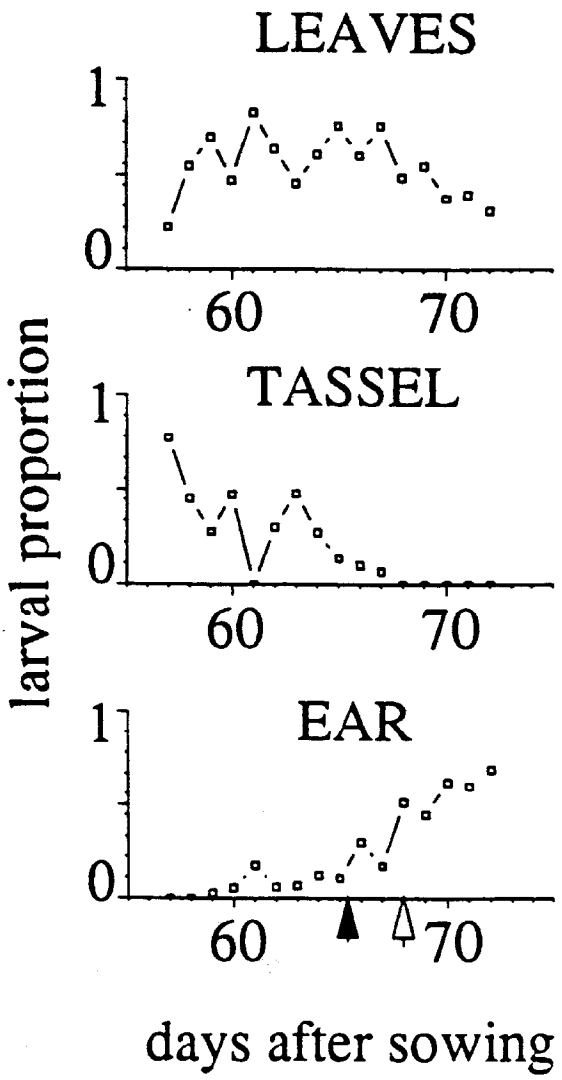

Fig. 6. Time course of the larval inter-organ distribution for infestation 9. The full arrow indicates the day when 50% of plants were in tassel, the empty arrow the day when 50% of female plants were in flower.

obtained with some microbial controls such as *Bacillus thurigiensis* (Gardner & Fuxa 1980), and the necessity to apply microbial insecticides with a high clearance sprayer or in granular formulations to direct the treatment into the leaves of the whorl (Gardner et al. 1984).

Quantitative studies on other biololical control agents, including the entomopathogenic hyphomycete, *Paecilomyces fumosoroseus*, and the nuclear polyhedrosis virus, SfNPV, are currently in progress in order to describe the persistence of these microbial agents within the plant and their relationships with larval dynamic processes (Maniania & Fargues 1985, Fargues et al. 1991, Biache et al. 1991). The present study of FAW within plant distribution over time will enable a better understanding of the probability of contact between the microbial agent and FAW larvae, and the impact of the microbial agent on larval mortality. This will result in improved methods

for evaluation of the effectiveness of microbial control, will help to explain variable results, and will ultimately lead to improvements in microbial control strategies.

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THE NATURAL HOST PLANTS OF *ANASTREPHA* (DIPTERA: TEPHRITIDAE) IN A TROPICAL RAIN FOREST OF MEXICO

VICENTE HERNÁNDEZ-ORTIZ[1] AND ROGELIO PÉREZ-ALONSO[2]
[1]Instituto de Ecología A. C. Apartado Postal 63
91000 Xalapa, Veracruz, México

[2]Facultad de Ciencias, Universidad Nacional Autónoma
de México. Cd. Universitaria, México D. F., México

ABSTRACT

The relationships between *Anastrepha* species and their host plants are recorded and analyzed from a study carried out in a natural tropical community of Mexico (Estación de Biología Tropical Los Tuxtlas, Veracruz). We sampled fruits of 55 plant species of the tropical rain forest and found the following associations: *Tapirira mexicana* Marchand was infested with *A.* sp. and *A. obliqua* (Macquart); *Spondias radlkoferi* J. D. Smith with *A. obliqua*; *Tabernaemontana alba* Mill. with *A. cordata* Aldrich; *Quararibea funebris* (Llave) Vischer with *A. crebra* Stone; *Inga sapindoides* Willd. with *A. distincta* Greene; *Brosimum alicastrum* Sw. and *Pseudolmedia oxyphyllaria* J. D. Smith with *A. bahiensis* Costa Lima; *Psidium guajava* L. with *A. striata* Schiner and *A. fraterculus* (Wiedemann); *Citrus aurantium* L. and *C. maxima* (Burm.) Merrill with *A. ludens* (Loew); *Chrysophyllum mexicanum* Brandegee ex Standley, *Pouteria sapota* (Jacq.) H. Moore & Stearn and *Pouteria* sp. with *A. serpentina* (Wiedemann). Also, we found the species *A. hamata* (Loew), *A. leptozona* Hendel and *A. minuta* Stone, whose hosts in the Los Tuxtlas region are still unknown.

We sampled infestation rates in 10 of the 13 host plants. Of the 3704 fruits examined, 23.1% were infested. We encountered 2290 larvae, of which 1600 pupated. Parasitoids or adult flies emerged from 85% of these. Infestation percentages of the different fruit species were highly variable, ranging from 1.5% for *P. oxyphyllaria* to 66.7% for *Pouteria sapota*. The mean number of larvae per fruit usually was between 1.25 and 2.59, and in only the largest and heaviest fruits (such as *C. aurantium*, *P. sapota* and *P.* sp.) were there more than 9.0 larvae present. Some fruit characteristics affecting the degree of infestation are discussed, and the possible existence of a diapause period in some *Anastrepha* species is noted.

Key Words: Fruit flies, fruit infestation, behavior, food preference.