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Behavior

On-Plant Larval Movement and Feeding Behavior of Fall Armyworm (Lepidoptera: Noctuidae) on Reproductive Corn Stages

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Abstract

Spodoptera frugiperda J.E. Smith (fall armyworm) is considered one of the most destructive pests of corn throughout the Americas. Although this pest has been extensively studied, little is known about its larval movement and feeding behavior on reproductive compared to vegetative corn stages. Thus, we conducted studies with two corn stages (R1 and R3) and four corn plant zones (tassel, above ear, ear zone, and below ear) in the field at Concord, NE (USA), and in the field and greenhouse at Botucatu, SP (Brazil), to investigate on-plant larval movement. The effects of different corn tissues (opened tassel, closed tassel, silk, kernel, and leaf), two feeding sequence scenarios (closed tassel–leaf–silk–kernel and leaf–silk–kernel), and artificial diet (positive control) on larval survival and development were also evaluated in the laboratory. Ear zone has a strong effect on feeding choice and survival of fall armyworm larvae regardless of reproductive corn stage. Feeding site choice is made by first-instar. Corn leaves of reproductive plants were not suitable for early instar development, but silk and kernel tissues had a positive effect on survival and development of fall armyworm larvae on reproductive stage corn.

Key words: larval movement, larval dispersal, *Spodoptera frugiperda*, feeding behavior

The fall armyworm *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae) is considered a major pest of tropical–subtropical origin in the Western Hemisphere ranging from Argentina to southern Canada (Luginbill 1928, Clark et al. 2007, Adamczyk et al. 2008, Farias et al. 2008). It has been reported infesting >80 plant species, including important agricultural crops such as cotton, soybean, and corn (Luginbill 1928, Pogue 2002, Capinera 2008).

In Brazil, the fall armyworm is considered the most destructive and economically important pest in corn (Cruz and Turpin 1983, Cruz et al. 1999, Diez-Rodrigues and Omoto 2001, Carvalho et al. 2013, Huang et al. 2014). In the United States, it has been described as an important yield-limiting pest in southern cornfields (Buntin et al. 2004, Chilcutt et al. 2007, Hardke et al. 2011). This species does not diapause over winter, being vulnerable to low winter temperatures, only surviving year-round in the subtropical climates in the southern regions of Florida and Texas (Sparks 1979, Buntin 1986, Mitchell et al. 1991). Therefore, *S. frugiperda* populations migrate and reinvade corn crops in cooler regions of North America, including Canada, during the summer (Mitchell et al. 1991, Nagoshi et al. 2012). Although fall armyworm can attack all corn stages (Flanders et al. 2007, Cruz et al. 2008, Knutson 2009), its injury is typically

related to foliar consumption and indirect damage to grain production due to reduction in photosynthetic area (Cruz and Turpin 1983, Pitre and Hogg 1983, Buntin 1986, Melo and Silva 1987, Capinera 2000, Vilarinho et al. 2011). Consequently, much *S. frugiperda* research in corn has been directed toward its management on early corn stages, generally when the whorl region is still present, where most fall armyworm larvae are found feeding on the developing leaves (Cruz and Turpin 1983, Harrison 1986, Melo and Silva 1987, Bokonon-Ganta et al. 2003, Siebert et al. 2008).

Although fall armyworm has been reported to behave similarly to corn earworm (*Helicoverpa zea* Boddie, Lepidoptera: Noctuidae), penetrating into the ear and feeding on kernels (Buntin 1986, Capinera 2000, Vilarinho et al. 2011), a better understanding of fall armyworm infestation in reproductive corn stages is still necessary, as well as why the larvae "choose" that feeding site. Such behavior tends to inflict greater damage to corn because of injury to reproductive plant components. It could also limit the use of important control strategies, such as biological and conventional control through pesticide spraying, because the larvae will be protected in the ear.

In this context, knowledge of larval movement is critical to effectively apply pest management strategies (Ross and Ostlie 1990,

Spangler and Calvin 2001, Paula-Moraes et al. 2012). Movement of early instar Lepidoptera within host plants largely determines where feeding sites become established (Zalucki et al. 2002, Perkins et al. 2008). Describing this movement will help in applying these strategies more efficiently, as during their exploration, larvae are vulnerable to predators, parasitoids, pathogens, and insecticides (Zalucki et al. 2002, Johnson et al. 2007, Perkins et al. 2008).

Because fall armyworm reinvades the northern United States during summer every year, usually finding corn in reproductive stages, information on larval movement during these stages is important. In Brazil, factors that affect fall armyworm incidence such as succession of host crops, "off-season" corn and sorghum production, and nearby areas with corn at different phenology have all been increasing (Nagoshi 2009, Barros et al. 2010), which further necessitates a better understanding of this insect's behavior.

Another important reason to better understand larval behavior arises with the advent of transgenic corn that expresses *Bt* toxins. Information on pest movement, as well as larval feeding behavior, is important because the mobility of the insect could impact larval exposure to lethal and sublethal concentrations of Bt toxins in different plant tissues (Paula-Moraes et al. 2012), thus influencing survival and the selection of insect resistance. This information will help in designing strategies to manage resistance (Gould 1998, Dirie et al. 2000), especially in the case of Brazil, where unexpected survival and subsequent resistance of *S. frugiperda* on *Cry*1F and *Cry*1Ab corn has been reported in several regions (Farias et al. 2014, Huang et al. 2014, Niu et al. 2014, Monnerat et al. 2015).

We investigated the on-plant movement of fall armyworm larvae at two different reproductive corn stages under field and greenhouse conditions, as well as feeding behavior on reproductive corn stages. We also evaluated larval performance on different corn tissues in the laboratory.

Materials and Methods

On-Plant Larval Movement

Larval survival, development, and distribution on the corn plant were characterized in the field at the University of Nebraska Northeast Research and Extension Center Haskell Agricultural Laboratory, Concord, NE, during 2013, and in the greenhouse and field at Sao Paulo State University, Department of Crop Protection, Botucatu, SP, Brazil, during the season of 2014–2015. For these studies, two nontransformed corn hybrids Channel 208-71R and Pioneer 30F35 were used in the United States (field) and Brazil (greenhouse and field), respectively.

The treatment design was a 2 by 4 factorial for all studies, with two corn stages (silking or R1 and milk stage or R3; Ritchie et al. 1993), and four different plant zones (tassel, above ear, ear zone, and below ear).

Three experiments were conducted in field conditions, one in the United States and two in Brazil. For all experiments, the experimental areas had two corn stages established using different planting dates. The two corn stages were randomly assigned in a randomized complete block design. There were four plots per corn stage with eight in total. At Concord, NE, each experimental plot consisted of eight 10-m-long rows with 15-cm plant spacing and 0.76 m between rows. At Botucatu, SP (Brazil), each experimental plot consisted of 6 rows by 12 m, with 15-cm plant spacing and 0.45 m between rows. For the second field experiment in Brazil, 10 corn plants of each plot in the field were caged from emergence in order to assure plants remained free of natural infestations and natural enemies. These plants were used to assess the on-plant movement. The cages were 1.0 m wide, 1.3 m long, and 2.5 m high with supports made of PVC pipe (1.9 cm) and the entire structure covered with white insect screen (mesh 16 or holes of 1.19 mm).

In the United States, the plots were irrigated as required with an overhead lateral irrigation system. In Brazil, all plots (except for the field cages) were sprayed with a nonpersistent insecticide deltamethrin Decis 25 EC (Bayer, São Paulo, SP) (S)-α-cyano-3-phenoxybenzyl (1 R,3 R)-3 -(2,2-dibromovinyl)-2,2-dimethylcyclopropane-carboxylate (200 ml ha^{-1} or 5 g of a.i. ha^{-1}) every 3 d until the end of the whorl stage in order to ensure no lepidopteran natural infestations prior to ear formation.

Another on-plant movement trial was conducted in the greenhouse in Brazil. Seeds of conventional Pioneer 30F35 hybrid corn were planted in 8-liter plastic pots containing fertilized soil according to standard cultural recommendations. The study was conducted as a completely randomized design with five replications. Irrigation and standard management practices were used as required to ensure optimum growth until the reproductive corn stages.

Artificial infestation with egg masses was conducted in all studies. In the United States, the egg masses were purchased from a stock colony in a commercial laboratory (Benzon Research, Carlisle, PA). In Brazil, the egg masses were collected from a research colony at the Department of Crop Protection, College of Agronomic Sciences, UNESP, Botucatu, SP (Brazil). The insects were maintained under controlled conditions (temperature = 25 ± 2°C; relative humidity [RH] = 60 ± 10%; photoperiod of 14:10 [L:D] h), and reared according to Parra (2001). The oviposition paper sheets containing egg masses were cut and maintained in growth chamber at temperature of 25°C until the eggs were close to hatching.

The number of eggs were counted using microscope stereoscope (Nikon - Stereo Zoom Microscope SMZ 645). In the United States, 100 eggs were used to infest each plant. In Brazil, 200 eggs per plant were used because of the high number of natural enemies observed and heavy rains that usually occur during the rainfall season that could jeopardize larval survival and recovery. Eggs were selected for uniformity and infested when darkening head capsules became visible through the egg chorion (backhead stage), indicating imminent eclosion.

An artificial infestation method was developed: selected egg masses were transferred into an "envelope" (6 cm in length by 4 cm high) made of organdy tissue with an opening on top, in order to prevent desiccation or excessive moisture. One single "envelope" per plant was stapled on the upper leaf surface, at the end of the first leaf completely extended above the primary ear (above ear zone). The leaf's selection simulated natural oviposition by *S. frugiperda* female moths in reproductive stage corn (preliminary field observations). Ten plants in the central row of each plot were infested in the US and Brazil studies.

Prior to infestation, the plants were inspected for the presence of natural infestations. In the United States, no natural infestation of fall armyworm was detected in the plots during the study. In Brazil, undamaged plants were chosen for the study.

To determine larval movement, the evaluations were performed based on the methods described by Paula-Moraes et al. (2012), where the corn plant was divided in five plant zones (tassel, above ear, primary ear, secondary ear, and below ear). However, in the present study, we decided to combine primary and secondary ear zones in one zone called "ear zone," as many of the corn plants used in our studies had only one ear.

Plant sampling was carried out at 3, 6, 10, 13, and 16 d after infestation (DAI) (eggs hatched within 24 h of infestation). One

plant was evaluated in each plot, on each sampling day. Plants that had no live fall armyworm larvae from the egg masses were discarded, and another plant was sampled. Each corn plant zone was inspected for the presence of larvae (destructive sampling). Larval movement on the corn plant was evaluated based on the number of recovered larvae in each plant zone. Larval survival was calculated by dividing the number of larvae found by the number of eggs infested per plant. The recovered larvae were transferred to 6-ml translucent vials filled with 100% ethyl alcohol for later measurement of head capsule width. Instar classification was based on Pitre and Hogg (1983).

The data were separately analyzed by cultivation system (USA field, Brazil field, field cages, and greenhouse), and tested for normality of the residuals and homogeneity of variance (PROC GLIMMIX PLOT = RESIDUAL PANEL; SAS Institute 2009). The distribution with the best fit was lognormal, which was determined via the DISTRIBUTION option in PROC GLIMMIX (SAS Institute 2009). The relationships and interactions between number of the larvae in different plant zones and corn stages were examined. The Dunnett procedure was used to detect differences from the control (plant zone where the egg mass infestation was done) to the other plant zones (Paula-Moraes et al. 2012).

Larval Feeding

Fall armyworm larval survival and development were evaluated under laboratory conditions (temperature = 25 ± 2°C; RH = 60 ± 10%; photoperiod of 14:10 [L:D] h). Different corn tissues were tested from the same corn hybrid Pioneer 30F35 used in the field studies in Brazil. The different tissues were removed from the field when needed and cleaned with alcohol to avoid contamination and remove foreign material (Dorhout 2007, Paula-Moraes et al. 2012).

Egg masses were obtained from the research colony as previously described for the on-plant study. The eggs were kept in a growth chamber at 25°C until hatching. Fall armyworm neonates (<24 h age) were randomly selected and transferred using a fine paintbrush into vials (100 ml) containing a moistened filter paper in the bottom and sealed with plastic lids. Each vial contained one neonate and ~5 g of each different corn tissue. Corn tissues were replaced every day. The vials were kept in the laboratory at 25 ± 2°C, 60 ± 10% RH, and a photoperiod of 14:10 (L:D) h.

The study was conducted as a completely randomized design with 40 replications. Each vial represented one replication. One diet (positive control), five different corn tissues, and two feeding scenarios were evaluated: diet for fall armyworm made according to Parra (2001), opened tassel (OT), closed tassel (T), silk (S), kernels (K), leaves (L), L–S–K (leaves, silk, and kernel), and T–L–S–K (closed tassel, leaves, silk, and kernels). The opened tassel was collected in tassel stage, when it was already exposed to the air above the other parts, but not completely dried. The closed tassel was collected during pretassel stage, when it was totally green enclosed in the whorl leaves. Silk was removed from the ear during silk stage, when the structures were still green. Kernels were used in milk stage, and the leaves were collected from the upper part of the corn plants (above ear zone). The feeding scenarios were chosen based on fall armyworm damage and possible movement on corn plants. In the feeding scenarios, the type of corn tissue was changed at 5 d after larval exposure to the tissue until the last material, which remained until pupation stage or the end of the assays (e.g., for the L–S–K feeding scenario: 5 d exposed to leaf tissue; 5 d exposed to silk tissue; remaining time to pupation exposed to kernel tissue).

Table 1. Overall larval recovery, total number of recovered larvae, average diameter of head capsule, and instar estimate of fall armyworm from corn plants

Larval recovery[a]	Sampling date				
	First	Second	Third	Fourth	Fifth
USA—field[b]					
Overall recovery (%)	3.50	6.63	7.00	5.50	2.25
Total number of recovered larvae	28	53	56	44	18
Average diameter of head capsule (mm)	0.35	0.46	0.77	1.35	2.29
Estimate instar[e]	1	2	3	4	5
Brazil—field[c,d]					
Overall recovery (%)	4.63	1.81	0.88	0.69	–
Number of recovered larvae	74	29	14	11	–
Average diameter of head capsule (mm)	0.35	0.59	0.89	1.70	–
Estimate instar	1	2	3	4	–
Brazil—field cages[c,d]					
Overall recovery (%)	6.5	2.19	1.06	0.94	–
Number of recovered larvae	104	35	17	15	–
Average diameter of head capsule (mm)	0.32	0.67	1.09	1.68	–
Estimate instar[e]	1	2	3	4	–
Brazil—greenhouse[c]					
Overall recovery (%)	12.25	5.60	1.75	0.90	0.95
Number of recovered larvae	245	112	35	18	19
Average diameter of head capsule (mm)	0.30	0.64	1.26	2.01	2.10
Estimate instar[e]	1	2	3/4	5	5

[a] Larval recovery was calculated by dividing the number of larvae found by the estimate of the number of eggs infested per plant.

[b] Infestated with 100 eggs per plant. Total number of 400 eggs per evaluation.

[c] Infestated with 200 eggs per plant. Total number of 800 eggs per evaluation.

[d] There were no plants evaluated on fifth sampling dates.

[e] Head capsule widths are ~0.35, 0.45, 0.75, 1.3, 2.0, and 2.6 mm, respectively, for instars 1–6 (Pitre and Hogg, 1983).

Larval survival was evaluated at 3, 5, 8, 10, 13, 15, 17, and 20 DAI. After this period, larval survival was checked daily until pupation by recording the number of live larvae. Larval development (time to pupation) was measured daily. Pupal weight was evaluated and conducted on the second day after pupation using a scale (Model Marte AY220, Shimadzu, Kyoto, Japan) to 0.1 mg. Data were analyzed using generalized mixed model (Proc Glimmix, SAS Institute 2009) to detect differences between means. When appropriate, means were separated using Fisher's least significant differences procedures (α = 0.05).

Results

On-Plant Larval Movement

The overall larval recovery in all experiments was low when considering the number of eggs infested, independent of the location or cultivation system. In general, a decrease in the number of recovered larvae was observed from the first to the last sampling date. The percentage of larval recovery was lower than 10% for all sampling dates, except for the first sampling date in the greenhouse study, with a larval recovery of 12.3% (245 recovered individuals; Table 1).

All larvae recovered on the first sampling dates were first instars (Table 1), and on the second date all larvae were second instars. In

Table 2. Corn stage and plant zone effects on mean number of fall armyworm larvae recovered

Effect	df	Sampling date				
		First	Second	Third	Fourth	Fifth
USA—field[a]		P value				
Corn stage	1	0.66	0.70	0.32	0.33	1.00
Plant zone	3	<0.01	<0.01	<0.01	<0.01	<0.01
Corn stage × Plant zone interaction	3	0.50	0.85	0.59	0.81	1.00
Brazil—greenhouse[a,b]		P value				
Corn stage	1	0.08	0.13	0.28	1.00	0.52
Plant zone	3	<0.01	<0.01	<0.01	<0.01	0.02
Corn stage × Plant zone interaction	3	0.11	0.62	0.07	0.88	0.73
Brazil—field[a,b]		P value				
Corn stage	1	0.16	0.07	1.00	0.20	–
Plant zone	3	<0.01	<0.01	<0.01	<0.01	–
Corn stage × Plant zone interaction	3	0.29	0.25	0.71	0.65	–
Brazil—field cages[a,b]		P value				
Corn stage	1	0.92	0.19	0.14	0.32	–
Plant zone	3	0.26	<0.01	<0.01	<0.01	–
Corn stage × Plant zone interaction	3	0.21	0.62	0.53	0.80	–

[a] Infestation of egg mass on leaf above primary ear (above ear zone).

[b] There were no plants evaluated on the fifth sampling dates.

general, on the third, fourth, and fifth sampling dates, most of the larvae were classified as third, fourth, and fifth instars, respectively (Table 1). In the greenhouse, some of the recovered larvae had already reached the fourth instar on the third sampling date, and most of the larvae were fifth instar on the fourth and fifth sampling date. There were no plants evaluated on the fifth sampling dates in the field experiments in Brazil (Brazil—field and field cages), as there were no infested plants. Some plants had no fall armyworm infestation on the earlier sampling dates, and had to be discarded (Table 1).

There was no significant corn stage effect for mean number of fall armyworm larvae for any sampling date for all experiments (Table 2). Likewise, there was no significant interaction between corn stage and plant zone (Table 2). There was a significant plant zone effect on all sampling dates for all experiments ($P < 0.05$), except for the first sampling date in Brazil for caged corn plants (Table 3). There were no plants evaluated for the fifth sampling date in the field areas in Brazil (Brazil—field and field cages) due to the lack of infested plants (Table 2).

No larvae were found in the tassel zone regardless of sampling date or corn stage (Table 3; Fig. 1). In general, most of the larvae were recovered in the above ear and ear zone with a higher concentration in the ear zone on the first and second sampling dates. From the third sampling date, almost all of the infested larvae were recovered in the ear zone in all experiments (Table 3; Fig. 1).

For the US and Brazil field areas (excluding field cage study), the mean number of recovered larvae in the ear zone was significantly higher ($P < 0.001$) when compared to the other plant zones on the first sampling date, including the above ear zone where the egg masses were placed (Table 4). However, the mean number of larvae recovered in the ear zone was the same as in the above ear zone for the experiment in the greenhouse, and did not differ from the same zone in the cage experiment for the same sampling date. Overall, a significantly higher concentration of larvae in the ear zone was observed in all experiments from the second to the last sampling dates (Table 4; Fig. 1).

Table 3. Mean number of fall armyworm larvae recovered in each plant zone

Plant zone	Mean no. of larvae per plant zone				
	Sampling date				
	First	Second	Third	Fourth	Fifth
USA—field					
Tassel	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)
Above ear	0.6 (0.23)	0.1 (0.15)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)
Ear zone	2.9 (0.81)	6.5 (1.57)	8.3 (0.56)	5.5 (0.82)	2.3 (0.25)
Below ear	0.0 (0.00)	0.0 (0.00)	0.1 (0.24)	0.0 (0.00)	0.0 (0.00)
Brazil—greenhouse					
Tassel	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)
Above ear	11.9 (2.32)	3.3 (0.51)	0.2 (0.14)	0.0 (0.00)	0.0 (0.00)
Ear zone	11.9 (1.75)	6.7 (0.51)	2.9 (0.37)	1.7 (0.34)	1.8 (0.29)
Below ear	0.7 (1.75)	1.2 (0.51)	0.4 (0.19)	0.1 (0.17)	0.1 (0.10)
Brazil—field					
Tassel	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	–
Above ear	2.6 (0.44)	0.3 (0.18)	0.1 (0.13)	0.0 (0.00)	–
Ear zone	6.3 (0.69)	3.4 (0.50)	1.6 (0.26)	1.4 (0.18)	–
Below ear	0.4 (0.21)	0.0 (0.00)	0.0 (0.00)	0.0 (0.10)	–
Brazil—field cages					
Tassel	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	–
Above ear	4.3 (1.18)	0.5 (0.19)	0.0 (0.00)	0.0 (0.00)	–
Ear zone	8.1 (1.98)	3.9 (0.62)	2.1 (0.48)	1.9 (0.23)	–
Below ear	0.6 (0.26)	0.0 (0.00)	0.0 (0.00)	0.0 (0.10)	–

Mean number (+SEM) of larvae per plant zone based on the number of larvae recovered.

Larval Feeding

Larval survival was significantly higher for insects reared on diet (85.0%; positive control; $P < 0.001$; Table 5). When comparing the larvae reared on the different corn tissues and feeding scenarios, closed tassel and silk had the highest larval survival (57.50% each). The lowest percentages were observed for larvae feeding on leaf (10.0%) and opened tassel (0%; Table 5). The survival rates in other corn tissues and sequence of feeding scenarios varied from 40.0% (T–L–S–K) to 25.0% (kernel and L–S–K).

The fastest development was observed with larvae reared on kernels (16.5 d) differing from the other corn tissues, sequence of feeding scenarios, and diet (20.2 d; $P < 0.001$; Table 5). Besides resulting in high mortality rates, leaf tissue (24.0 d) delayed the larval development in comparison to the other treatments ($P < 0.001$).

Larvae reared on closed tassel resulted in the lowest pupal weight ($P < 0.001$). Although closed tassel and silk provided highest larval survivals, they resulted in the lowest pupal weights. There was no difference between the T–L–S–K and L–S–K sequence feeding scenarios, kernel, and diet (positive control) for pupal weight (Table 5).

All larvae confined on opened tassel died by 8 DAI (Fig. 2). Likewise, >80% of the larvae feeding on leaf tissue did not survive over the same period. Larvae reared on diet had the lowest mortality at all evaluated days and did not reach 20% of mortality until the end of the trial. No larvae died after 20 DAI.

Discussion

According to Zalucki et al. (2002), mortality in the early larval stages is commonly high in Lepidoptera. The authors reported that almost 40% mortality occurs by egg parasitism attack and other factors during the egg stage, and 50% during the first instar. We expected to find a higher percentage of larval recovery in our studies because the plants
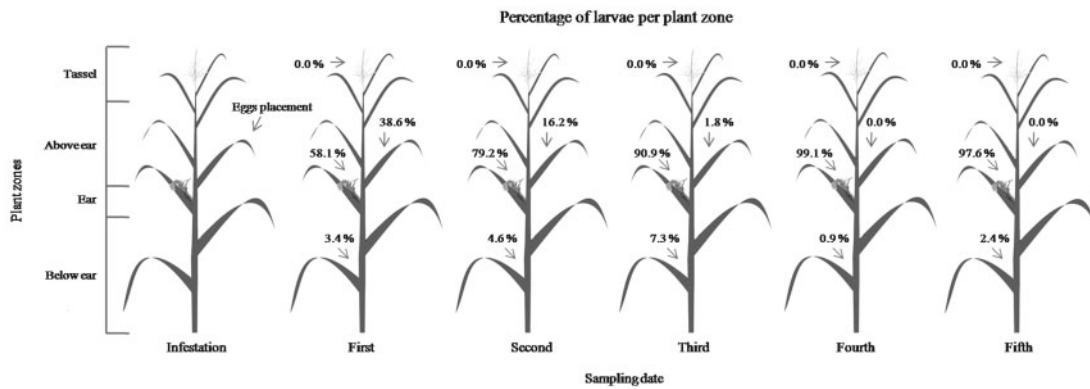
Fig. 1. Mean percentage of fall armyworm larvae recovered in each plant zone for all studies.

Table 4. Comparison of mean number of fall armyworm larvae recovered in each plant zone

Plant zone	Comparison of the mean number of larvae per plant zone									
	Sampling date									
	First		Second		Third		Fourth		Fifth	
USA—field	Mean[a]	P value[b]	Mean[a]	P value[b]	Mean[a]	P value[b]	Mean[a]	P value[b]	Mean[a]	P value[b]
Tassel	0.6 (0.23)	0.03	0.1 (0.15)	0.45	0.0 (0.00)	1.00	0.0 (0.00)	1.00	0.0 (0.00)	1.00
Above ear	0.6 (0.23)	reference	0.1 (0.15)	reference	0.0 (0.00)	reference	0.0 (0.00)	reference	0.0 (0.00)	reference
Ear zone	−2.3 (0.56)	<0.01	−6.4 (0.94)	<0.01	−8.3 (0.56)	<0.01	−5.5 (0.43)	<0.01	−2.3 (0.14)	<0.01
Below ear	0.6 (0.23)	0.03	0.1 (0.15)	0.48	−0.1 (0.24)	0.61	0.0 (0.00)	1.00	0.0 (0.00)	1.00
Brazil—greenhouse										
Tassel	11.9 (2.90)	<0.01	3.3 (0.72)	<0.01	0.2 (0.19)	0.31	0.0 (0.24)	1.00	0.0 (0.11)	1.00
Above ear	11.9 (2.90)	reference	3.3 (0.72)	reference	0.2 (0.19)	reference	0.0 (0.00)	reference	0.0 (0.00)	reference
Ear zone	0.0 (2.90)	1.00	−3.4 (0.72)	<0.01	−2.7 (0.39)	<0.01	−1.7 (0.38)	<0.01	−1.8 (0.41)	0.01
Below ear	11.2 (2.90)	<0.01	2.1 (0.72)	<0.01	−0.2 (0.23)	0.41	−0.1 (0.24)	0.68	−0.1 (0.13)	0.45
Brazil—field										
Tassel	2.6 (0.44)	<0.01	0.3 (0.18)	0.21	0.1 (0.13)	0.38	0.0 (0.00)	1.00		
Above ear	2.6 (0.44)	reference	0.3 (0.18)	reference	0.1 (0.13)	reference	0.0 (0.00)	reference		—
Ear zone	−3.6 (0.82)	<0.01	−3.1 (0.32)	<0.01	−1.5 (0.21)	<0.01	−1.4 (0.10)	<0.01		
Below ear	2.3 (0.49)	<0.01	0.3 (0.18)	0.21	0.1 (0.13)	0.38	−0.0 (0.00)	1.00		
Brazil—field cages										
Tassel	4.3 (30.28)	0.91	0.5 (0.19)	0.03	0.0 (0.00)	1.00	0.0 (0.00)	1.00		
Above ear	4.3 (30.28)	reference	0.5 (0.19)	reference	0.0 (0.00)	reference	0.0 (0.00)	reference		—
Ear zone	−3.9 (31.83)	0.92	−3.4 (0.65)	<0.01	−2.1 (0.25)	<0.01	−1.9 (0.12)	<0.01		
Below ear	3.6 (30.28)	0.92	0.5 (0.19)	0.03	−0.0 (0.00)	1.00	−0.0 (0.00)	1.00		

[a] LSMeans (± SEM).

[b] Mean comparison based on Dunnett test. The reference is the plant zone where the egg mass infestation was done.

were infested with eggs immediately before hatching and were somewhat protected inside a mesh envelope; however, larval recovery was low (3.5 to 12.5%), particularly for first instars at the first sampling date (Table 1). The low percentage of larval recovery may be in part because of larval movement away from the infested plant. This behavior is innate in all species of arthropods (Andrewartha and Birch 1954), including several species from Noctuidae (Zalucki et al. 2002). Such dispersion is an adaptive mechanism by which insects seek resources and acquire mates, oviposition and nesting sites, and refugia (Bell 1990, Price 1997) essential for the growth, development, and maintenance of the individual (Bell 1990).

The causes of larval mortality are not always clear, in part because of the small size of first instars. Likewise, factors such as exposure to natural enemies and weather effects including rainfall and high or low temperatures are also significant mortality factors for first instars (Zalucki et al. 2002). Although more studies are needed

to better define the causes of mortality, the absence of these abiotic factors in our greenhouse study seems to have influenced the number of recovered larvae in Brazil (Table 1). On the first sampling date, the percentages varied from 4.6% in the field area, 6.5% in the field cages, to 12.5% in greenhouse (Table 1). In general, this same pattern was observed for all evaluations in the experiments. In Brazil field areas, we observed a high number of natural enemies, especially *Doru luteipes* Scudder (Dermaptera: Forficulidae), and heavy rains throughout the evaluation period, which may have impacted larval survival. On the other hand, the lack of these biotic and abiotic factors that affected fall armyworm larval survival in Brazil may have been responsible for the higher larval recovery in the US study (Table 1), as fall armyworm do not overwinter in Nebraska and its natural enemies are not as abundant.

In general, a decrease in the number of recovered larvae was observed from the first to the last sampling date (Table 1). Fall

armyworm is known to have cannibalistic behavior. Despite laying egg masses composed of hundreds of eggs, only one or very few larvae per plant are typically found due to this behavior (Sparks 1979, Vilarinho et al. 2011). Although other factors such as environmental effects and an array of potential natural enemies could have contributed to this decrease, relatively high mortality was also observed for the greenhouse and field cage studies (Table 1), which reinforces the possible influence of cannibalism at a shared feeding site (Chapman et al. 2000).

The results of our on-plant studies did not indicate an effect of corn stage or an interaction between corn stage and plant zones on

Table 5. Effects of different corn tissues on fall armyworm larval mortality, larval development, and pupal weight

Corn tissue	Larval survival (%)[a]	Development (d)[b]	Pupal weight (mg)[c]
Diet	85.0 (5.72)a	20.2 (0.53)b	240.0 (7.12)a
Closed tassel	57.5 (7.92)b	18.9 (0.26)c	152.4 (8.58)c
Silk	57.5 (7.92)b	19.7 (0.61)bc	201.1 (8.10)b
T–L–S–K	40.0 (7.84)bc	20.6 (0.25)b	243.4 (7.00)a
Kernel	25.0 (6.93)cd	16.5 (0.45)d	236.4 (5.45)a
L–S–K	25.0 (6.93)cd	20.1 (0.35)bc	251.0 (10.03)a
Leaf	10.0 (4.80)de	24.0 (0.82)a	220.0 (8.84)ab
Opened tassel	0.0 (0.00)e	–	–
P value	<0.01	<0. 01	<0.01

[a] Percentage of larval survival. LSMean (± SEM). The means with the same letter are not significantly different, $P \geq 0.05$.

[b] Larval development. LSMean (± SEM). The means with the same letter are not significantly different, $P \geq 0.05$.

[c] Pupal weight. LSMean (± SEM). The means with the same letter are not significantly different, $P \geq 0.05$.

the distribution of the larvae (Table 2). Our data do indicate significant on-plant movement with a concentration at the ear zone starting from the first sampling date, independent of the reproductive corn stage evaluated (Table 3; Fig. 1). Early-instar movement within host plants is discussed in the literature as the behavior that largely determines where the feeding site becomes established (Zalucki et al. 2002, Johnson and Zalucki 2007, Perkins et al. 2008). However, injury to corn caused by fall armyworm larvae is typically reported as foliar consumption, and sporadically as damage of reproductive parts such as ear structures (Cruz and Turpin 1983, Pitre and Hogg 1983, Buntin 1986, Melo and Silva 1987, Capinera 2000, Vilarinho et al. 2011). In contrast, our findings indicate a strong ear zone effect for fall armyworm larvae during corn reproductive stages, and consequent ear feeding instead of leaf consumption. It is important to emphasize that high leaf consumption is usually reported when corn plants are still in vegetative stages, with significant feeding on developing leaf tissue, and to date little is known about fall armyworm larval choice during corn reproductive stages.

In the Brazil studies, on the first sampling dates, we observed a high number of recovered larvae on the leaf where the egg masses were stapled (Table 3). According to the literature (Zalucki et al. 1986, 2002; Johnson et al. 2007), during the exploration for a suitable feeding site, if larvae probe the substrate and recognize the host or plant part is unsuitable, then exploration is likely to continue (Chang et al. 1985, Hochberg 1987, Varela and Bernays 1988, Terry et al. 1989, Khan et al. 1996, Foster and Howard 1999, Zalucki et al. 2002).

Once the larvae are on a suitable host they will usually settle and establish a feeding site (Chang et al. 1985, Hochberg 1987, Varela and Bernays 1988, Therry et al. 1989, Khan et al. 1996, Foster and Howard 1999, Zalucki et al. 2002). Overall, the highest concentration of larvae was observed in the ear zone from the second to the

I = Infestation; DAI = days after infestation; L-S-K = Leaf - Silk - Kernel; T-L-S-K = Closed tassel - Leaf - Silk - Kernel.

For the feeding scenarios, the type of corn tissue was changed at 5 d after the larvae were exposed to the tissue. The last type of corn tissue remained until the end of the trial.
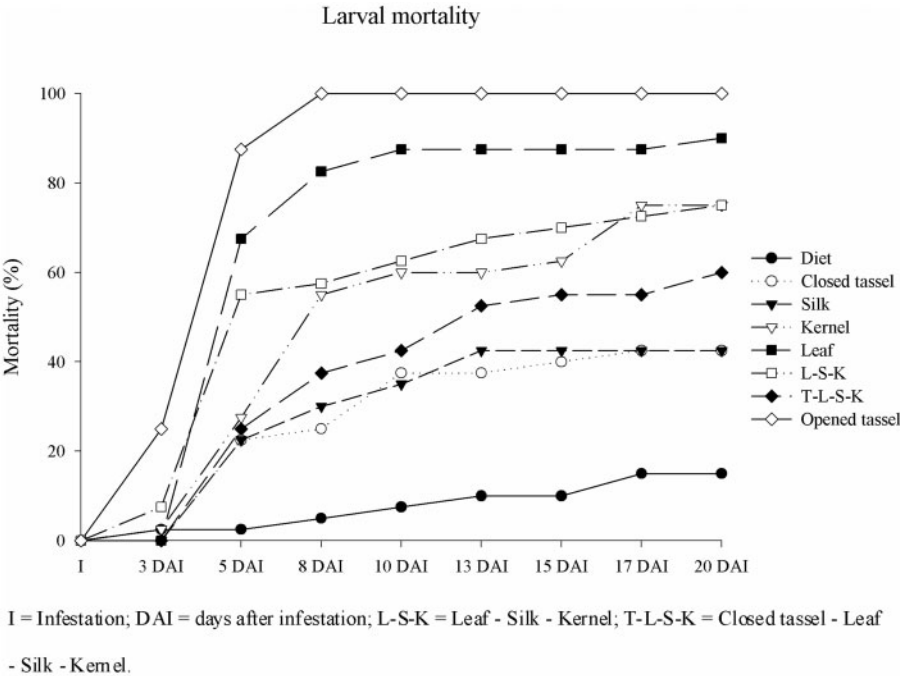
Fig. 2. Fall armyworm larval mortality exposed to different corn tissues and artificial diet up to 20 d after infestation.

last evaluation, independent of corn stage (Table 3; Fig. 1). Thus, after exploration the larvae established their feeding site in the ear zone, more specifically in the silk tissue, where most of the recovered larvae were found until they were able to reach the kernels.

Larval movement on plants can be influenced by several factors both abiotic and biotic, such as age, predators, light, plant architecture, and phototaxis (upward and outward movement; Madge 1964, Alonso and Herrera 1996, Johnson and Zalucki 2007, Johnson et al. 2007). Although these mechanisms by which larvae locate suitable hosts or part of hosts are not clear, the presence of predators did not appear important in our studies. We did not observe any fall armyworm natural enemies on the plants in the US field study or the greenhouse study.

Although the fall armyworm infestation was done above the ear zone, larvae moved downward to the ear zone. Considering the overall results from the field study, we presume that this behavior would be in part because of feeding choice. After hatching, neonates found on the infested plants stayed on the infested leaf for a short period and then moved to find a suitable feeding site (corn ear). Indeed, we observed low larval survival on leaves in the feeding study (Table 5), where at five DAI there was 67.5% mortality, and at eight DAI, ∼82.50% mortality (Fig. 2). Although fall armyworm can be considered a folivore, their larvae may have a mixed feeding habit. According to Scriber and Slansky (1981), and also Bernays and Chapman (1994), for these folivores leaf age and quality are critical factors that affect establishment, growth, and survival of neonates. Generally, some factors change in a leaf as it ages such as water availability, toughness, nitrogen, and another quality factors, which may result in high neonate mortality even if the same leaves are suitable for older instars (Cockfield and Mahr 1993). These changes in leaf quality during the corn reproductive stage probably influenced the neonates' choice and survival in our field study. In addition, the tassel stage (opened tassel) appeared to be unsuitable for fall armyworm larvae, and did not allow development (Table 5). Five DAI, there was 87.5% mortality, and 100% of the larvae were dead after 8 DAI (Fig. 2). This likely explains why no larvae were found in the tassel zone in the on-plant studies (Table 3).

Fall armyworm larvae have been observed feeding on the tassel structure in cornfields by many researchers. However, damage to this structure was always observed when it was enclosed in whorl leaves. For this reason, we decided to include this structure in the feeding study even if the tassel enclosed in whorl leaves, or green tassel, was not available for the larvae in the corn stages evaluated. High larval survival and fast development was confirmed for larvae reared on this structure; however, the remaining pupae had the lowest weight when compared to those reared on the other corn tissues. Likewise, larvae reared on silk tissue had similar results (Table 5). We tested different sources of tissue based on possible feeding scenarios. For L–S–K (leaf–silk–kernel), 5 d of leaf tissue feeding seemed to be excessive for fall armyworm neonates, which resulted in ∼55% of mortality (Fig. 2). For the T–L–S–K (tassel–leaf–silk–kernel) feeding scenario, larval survival had an intermediate value (Table 5). Nevertheless, all larvae that fed on kernels had higher pupal weight (Table 5). Kernels seem to have some positive effect on fall armyworm development, as larvae reared only on this structure exhibited faster development when compared to larvae reared on the other tissues and scenarios (Table 5).

Based on our results, we conclude that corn ear tissue has a strong positive effect on fall armyworm larval feeding choice and survival during reproductive stage corn, and the feeding site choice seems to be done by first instars. It suggests that corn leaves are not suitable for early instar development on reproductive stage corn. It

is also possible that silk and kernel tissues play a role in larval survival and development of fall armyworm larvae. Silk seems to provide shelter and an ideal microclimate for early larval development, and kernels seem to have some positive nutritional quality for larval development.

Considering the implementation for pest management programs, there is a short imterval between fall armyworm egg hatch to larval establishment in the ear on reproductive stage corn. Larval establishment on the corn ear would probably provide shelter for the larvae and consequently reduce the efficiency of some control strategies such as insecticide application (e.g., spraying). Insecticide application, when necessary, should be done before larvae colonize the ear and during larval exploration, when they would be exposed to insecticidal control.

Knowledge about larval on-plant movement and feeding behavior is also necessary for insect resistance management strategies. There is a potential for variability of Bt toxin expression in different corn tissues (Nguyen and Jehle 2007, Székács et al. 2010), and this should be a focus of future studies, especially for insects that have plant stage-specific feeding differences or a mixed feeding behavior, where insects could possibly be exposed to lethal or sublethal doses of toxins (Paula-Moraes et al. 2012).

In the case of fall armyworm, the results indicate that fall armyworm larvae successfully established a feeding site at the ear. Such feeding establishment may expose the larvae to a lower toxin concentration found in corn kernels (Nguyen and Jehle 2007, Székács et al. 2010, Burkness et al. 2011). Likewise, the larvae may be exposed to intermediate levels of toxins in a refuge with cross-pollinated corn ears. Both scenarios can accelerate the selection for resistance (Chilcutt and Tabashnik 2004, Ives et al. 2011, Razze and Mason 2012). In temperate areas, such as in the US Corn Belt, selected populations of fall armyworm would not overwinter, but the pressure of selection can be aggravated in tropical areas, such as Brazil. Fall armyworm can have up to 12 generations a year (Capinera 2000), and several generations occur during corn reproductive stages. These factors require attention in the development of any insect resistance management strategy.

Acknowledgments

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