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Plant-to-Plant Movement of *Striacosta albicosta* (Lepidoptera: Noctuidae) and *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Maize (*Zea mays*)

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Received 5 January 2016; Accepted 17 February 2016

Abstract

Integrated pest management (IPM) and insect resistance management (IRM) in various cropping systems demand a comprehensive understanding of insect behavior. Among the needed information is basic characterizations of larval movement and dispersion of some insect-pests, such as the noctuids *Striacosta albicosta* (Smith) and *Spodoptera frugiperda* (J.E. Smith). We investigated the plant-to-plant movement of western bean cutworm and fall armyworm larvae in field of maize. Experiments on *S. albicosta* were conducted between 2008 and 2010. A main study with this pest was performed in 2012 in a randomized complete block design (RCBD) with nine replications. An *S. frugiperda* study was performed in 2013 in an RCBD with eight replications. The plant-to-plant movement and larval survival were measured in plots with maize nontoxic to the insects. The larval survival of *S. albicosta* presented high variety throughout the years. Although *S. frugiperda* survival was relatively low during 2013, it did not compromise the larval assessment. Larvae of both species dispersed governed by nondirectional sensory information, and presented aggregated and symmetrical distribution; however, fall armyworm remained nearer the release point. These results may help the IPM components, such as scouting and economic threshold, as well as the implementation of refuge and seed mixture strategies for IRM.

Key words: larval dispersal, larval movement, western bean cutworm, fall armyworm, *Zea mays*

Dispersal is defined as the movement away from a densely populated place that results in the spreading of part of the original individuals (Price 1997). This behavior is an adaptive mechanism by which insects seek resources and thereby acquire food, mates, and refuge (Bell 1990, Price 1997), which are essential for the establishment, growth, and development of the insect (Bell 1990).

An inherent tendency to disperse seems to be present at some level in all species of arthropods (Andrewartha and Birch 1954). Most Lepidoptera disperse as winged adults, but many groups can also disperse as larvae. Larval dispersal commonly occurs by crawling or ballooning. Ballooning is the movement where larvae use silk to hang off of plant structures to come in contact with another structure or be taken by wind. This behavior is recorded for several lepidopteran families, including Noctuidae. As caterpillars grow, ballooning becomes impossible due to their increased weight, and dispersal mostly occurs by walking. However, walking movement may happen at any moment when parts of the host plant are unsuitable for larval establishment (Zalucki et al. 2002).

Environmental factors may also influence the rate and success of dispersal (Bell 1990, Tikkanen et al. 1999, Zalucki et al. 2002). However, it is unclear how the insects perceive their environment (Baker 1978, Harris and O'Miller 1982). According to Bell (1990), the types of information used by insects are governed by nondirectional or directional sensory information, recognized from the external environment and internally derived kinesthetic or stored genetic information.

Western bean cutworm [*Striacosta albicosta* (Smith)] (Lepidoptera: Noctuidae) is considered an important pest of maize (*Zea mays* L.) in the U.S. Corn Belt and parts of Canada (O'Rourke and Hutchison 2000, DiFonzo and Hammond 2008, Michel et al. 2010, Tooker and Fleischer 2010, Paula-Moraes et al. 2012). Likewise, fall armyworm [*Spodoptera frugiperda* (J.E. Smith)] (Lepidoptera: Noctuidae) is considered an important yield-limiting pest in the United States and indeed throughout North and South American maize fields (Buntin et al. 2004, Chilcutt et al. 2007, Farias et al. 2008, Hardke et al. 2011). Although important maize

pests, some aspects on their behavior are unclear. Such aspects are critical to the application of management strategies. One of the less understood aspects is the extent of larval dispersal.

Larval dispersal can directly influence the accuracy of scouting methods (Ross and Ostlie 1990); however, scouting methods have often been developed without considering the dispersion of larvae among plants. Knowledge of western bean cutworm and fall armyworm behavior and dispersion in field maize would contribute to the development of more effective sampling methods. In addition, knowledge of larval survival would increase precision of economic thresholds (Ostlie and Pedigo 1987, Ross and Ostlie 1990).

Another important reason to examine such behavior is associated with the widespread use of *Bt* transgenic maize (Shelton et al. 2002, Brooks and Barfoot 2005, Tabashnik et al. 2008, Murphy et al. 2010). The fast adoption of this technology can jeopardize its long-term durability (Tabashnik et al. 2008, 2013). The major concern is the possibility of rapid selection for resistance to *Bt* toxins because the target pests are continually exposed to the toxins. This scenario produces a high and constant selection pressure for resistance (Gould 1998, Guse et al. 2002, Bates et al. 2005, Onstad 2008, Tabashnik et al. 2009, Head and Greenplate 2012).

The use of refuge is one of the main recommended components of an insect resistance management (IRM) plan for *Bt* crops (Alstad and Andow 1995, Macintosh 2009). Initially, for Lepidoptera the refuge was required to be no more than 0.8 km away from the *Bt* maizefield. The percentage of refuge area is variable depending on the trait and region. In the U.S. Corn Belt, it must be 20% of a grower's *Bt* maizefield, and in defined cotton-growing regions, 50% (Environmental Protection Agency [EPA] 1998). In recent years, the pyramiding of *Bt* traits allowed the reduction of some refuges from 20% to 10% or 5%, depending on the trait (DiFonzo 2015). The design of the refuge can take many forms: in blocks, strips, a separate field, or border around *Bt* maizefields (Cullen et al. 2008). In those refuges where *Bt* and non-*Bt* plants are in close proximity, the movement of the target pests between *Bt* and non-*Bt* maize (refuge) can accelerate the selection of resistant insects (Goldstein et al. 2010).

There is a concern, however, that growers may not comply with refuge requirements due to the additional effort associated with planting refuge and lower returns of refuge crops compared to transgenic (Mallet and Porter 1992, Hurley et al. 2006, Murphy et al. 2010). A seed mixture or "refuge-in-the-bag" (RIB strategy) has been suggested as an alternative strategy to counter the low adoption of refuge by some growers (Gould 1996, Wangila et al. 2013). Recently, seed mixtures for pyramided transgenic maize was approved for some traits in the U.S. Corn Belt (DiFonzo 2015).

Designing an appropriate refuge directly depends on the behavior and biology of each target pest for each crop. Considering larval movement, seed mixtures would not be recommended as an appropriate refuge strategy for species that have a high dispersal capacity (Davis and Onstad 2000). Insects that tend to disperse within rows would be better suited to structured refuges than to integrated refuges (e.g., seed mixtures), as the insects would likely meet the same type of plant in block or strip refuges (Petzold-Maxwell et al. 2013). For example, according to Davis and Onstad (2000) and Siegfried and Hellmich (2012), the European corn borer is a good candidate for structured refuges in maize, as most of larvae usually disperse within the infested row.

Due to the complexity in designing studies capable of representing the suite of refuge configurations, probabilistic models have been developed and reported in the literature (Onstad and Gould 1998, Peck et al. 1999, Davis and Onstad 2000, Ives et al. 2011,

Carrol et al. 2012). However, many aspects necessary for increased accuracy of these models are still unclear and depend upon assumptions, such as larval movement of the target pest (Onstad 2006). In the case of western bean cutworm and fall armyworm, information on larval movement is relatively limited. Prior to modeling refuge configurations, it is necessary to understand the pest's larval movement in conventional crop systems.

In short, information on larval behavior and biology of western bean cutworm and fall armyworm is critical to improve pest management strategies, manage resistance, and to provide reliable data to support insect resistance modeling efforts. Thus, the objective of this research was to further describe the plant-to-plant movement and survival of western bean cutworm and fall armyworm larvae in field maize.

Material and Methods

Larval Movement of Western Bean Cutworm

The study of western bean cutworm larval movement was conducted in field maize at the University of Nebraska Northeast Research and Extension Center Haskell Agricultural Laboratory, Concord, NE. Field experiments were conducted during 2008, 2009, 2010, and 2012. A maize hybrid (DKC 61-72 RR) expressing *Bacillus thuringiensis* (*Bt*) protein Cry1Ab (YieldGard, Monsanto, St Louis, MO) that is not toxic to western bean cutworm was used to minimize the confounding effect of European corn borer [*Ostrinia nubilalis* (Hübner)] (Catangui and Berg 2006). The maize stage evaluated was R1 (silking) (Ritchie et al. 1993). All fields were under lateral-arm irrigation and conventional agronomic practices were followed for the region.

Exploratory Trials of Western Bean Cutworm Larval Movement

Prior to the main experiment of western bean cutworm larval movement, several trials on a smaller scale were performed in order to better understand the movement pattern of the insect.

Three consecutive trials were evaluated in 2008, 2009, and 2010. In 2008, two plots with five rows of 17 plants each (3.04 by 2.88 m) were evaluated. In 2009, two plots with three rows of 21 plants per row (1.52 by 3.6 m) were evaluated. In 2010, three plots with five rows of nine plants each (3.04 by 1.44 m) were evaluated. In all years, row spacing was 0.76 m and average plant spacing within rows of 0.18 m.

Artificial infestation was conducted in all exploratory trials by using egg masses collected from commercial maizefields. The "egg mass sandwich infestation" methodology was used as described by Paula-Moraes et al. (2013). An overall mean number of 50 eggs were infested per plant. The central plant from the central row of each plot was infested.

Main Experiment of Western Bean Cutworm Larval Movement

Based on the movement pattern observed in the exploratory trials, the main experiment was performed in 2012. For this study, nine plots with 13 rows of 41 plants (9.12 by 6 m) per plot were evaluated. Row spacing was 0.76 m and average plant spacing within rows of 0.15 m. Plants were inspected for the presence of natural infestations. No natural infestation of western bean cutworm or other ear feeding Lepidoptera was detected in all plots of the exploratory trials and main experiment.

The "wild moths" methodology described by Paula-Moraes et al. (2013) was used to infest the plots for this experiment. One male and two females were confined on the top part of the maize

plant within a large flat mesh pollination bag. Two days after infestation, the presence of egg masses was determined and thinned so that two egg masses were left per plant. Egg masses were photographed to later count the number of the eggs (Paula-Moraes et al. 2013). Due to the low larval survival of western bean cutworm observed in preliminary tests, we decided to use two egg masses per plant. Approximately 170 eggs were infested per plant. Infested plants were identified with flagging tape. The central plant from the central row of each plot was infested.

For the exploratory and main experiments of western bean cutworm larval movement, all experimental plots were arranged in a randomized complete block design. A five-row border of maize plants was maintained at the edges of each plot to separate and avoid interaction between plots. Plants were inspected for the presence of western bean cutworm egg masses prior to artificial infestation. No natural infestation was observed in the experimental plots during all years.

For all experimental plots, destructive sampling was carried out and larval presence was recorded on all maize ears in all plants. An injured ear was counted as larval presence. Western bean cutworm larval dispersion and distance from the release point was evaluated ~15 d after infestation (DAI). The number of recovered larvae was recorded and percentage of larval survival was calculated. Position of the larval presence was recorded in each plot. Plants were oriented as North (N)–South (S) in the same row related the infested plant, and East (E)–West (W) across rows. Larval position was designated as 0 for the infested plant. The maize rows were in a N–S orientation.

Based on the position of the recovered larvae, the maximum distance covered by the larvae and number of larvae were evaluated for: different quadrants (Northeast [NE], Southeast [SE], Northwest [NW], and Southwest [SW]; plants from the center row and center across row were not included), two orientations (N and S; plants from the center across row were not included), movement across rows (E and W axes; plants from the center row were not included), and movement within infested row (N and S axes). Distance was calculated by Euclidean distance, where distance between plants or rows is the length of the line segment connecting them (ordinary distance). The Euclidean distance of the farthest detected larva in each quadrant was the maximum distance.

Larval Movement of Fall Armyworm

The fall armyworm larval movement study was conducted at the University of Nebraska Northeast Research and Extension Center Haskell Agricultural Laboratory, Concord, NE, in 2013. A conventional maize hybrid (Channel 208-71R) was used for this experiment. All plots were under lateral-arm irrigation and conventional agronomic practices were followed for the region. The maize stage evaluated was R1 (silking) (Ritchie et al. 1993), which was selected in order to simulate late infestation of fall armyworm in the north-central United States during summer months. This species does not overwinter in the north-central United States because of harsh winter conditions. The infesting populations are from the subtropical climates of south Florida and Texas that migrate to and infest crops in the northern United States (Mitchell et al. 1991).

Row spacing was 0.76 m and plant spacing within rows 0.15 m. Each plot consisted in 16 rows of 30 plants per row (11.4 by 4.5 m). There were a total of eight plots in a randomized complete block design. A five-row border of maize plants was maintained at the edges of each plot to separate and avoid interaction between plots. Plants were inspected for the presence of natural infestations. No natural

infestation of fall armyworm or other ear feeding Lepidoptera was detected in all plots.

Artificial infestation was conducted by using egg masses purchased from a stock colony from Benzon Research, Carlisle, PA. The oviposition paper sheets containing egg masses were held in a growth chamber at 25°C until darkening head capsules became visible through the egg chorion (blackhead stage). The number of eggs were counted using microscope stereoscope (Nikon - Stereo Zoom Microscope SMZ 645, Tokyo, Japan). A mean number of 200 eggs were used to infest each plant. Eggs were selected for uniformity and transferred into an “envelope” (6 cm in length by 4 cm high) made of organdy tissue in order to prevent desiccation or eggs from being washed off plants by irrigation or rain. The “envelope” had an opening on top allowing the larvae to leave. One “envelope” was stapled per plant (Pannuti et al. 2015).

Marking and position of infested plants, and egg mass position on the plant was conducted using the same methodology as described in the western bean cutworm larval movement study.

Destructive sampling was carried out and larval presence was recorded on all maize plant parts. Fall armyworm larval movement was based on larval presence. Fall armyworm larval dispersion and distance from the release points were evaluated 14 DAI in order to observe late instars established in a feeding site. Percentage of larval survival was calculated. Position of the fall armyworm larvae was recorded in each plot. Plant location and orientation from the infested plant, as well as evaluated parameters followed the same methodology described for the western bean cutworm study.

Statistical Analysis

The data were separately analyzed by species and year. Results were tested for normality and homogeneity of variance. A normal distribution was assumed. Data were analyzed using generalized mixed model to detect differences between means (SAS Institute 2009). When appropriate, means were separated using Tukey’s test significant differences procedures ($\alpha = 0.05$).

Results

Larval Survivorship of Western Bean Cutworm and Fall Armyworm in Field Maize

Larval survival was low and few western bean cutworm larvae were observed in all experimental plots in 2008 and 2009 (Table 1). In 2010 and 2012, larval survival of western bean cutworm increased considerably, 23.31 and 17.49%, respectively. Western bean cutworm larval survival varied from 6.12% (season of 2008) to 23.31% (season of 2010). For the fall armyworm, larval survival was 5.06% in 2013 (Table 1).

Table 1. Western bean cutworm and fall armyworm larval survival in maize, Concord, NE, from 2008 to 2013

Year	% Larval survival ^a	Number of larvae
Western bean cutworm		
2008	6.12	6
2009	6.94	5
2010	23.31	107
2012	17.49	263
Fall armyworm		
2013	5.06	81

^a Larval survival percentage based on total number of eggs infested.

Table 2. Mean number (\pm SE) of western bean cutworm larvae in different positions related to the infested plant in maize, Concord, NE, from 2008 to 2010

Position	Concord 2008			Concord 2009			Concord 2010		
	WBC recovered larvae/damage								
	Mean ^a			Mean ^a			Mean ^a		
NE	0.50 (0.50)a	1.00 (1.00)a	5.00 (1.00)a						
NW	0.00 (0.00)a	0.50 (0.50)a	1.67 (1.67)a						
SE	0.50 (0.50)a	0.50 (0.50)a	3.67 (1.76)a						
SW	0.00 (0.00)a	0.00 (0.00)a	2.67 (0.88)a						
P value	0.6151	0.7344	0.4190						
N	1.50 (0.50)a	1.00 (1.00)a	11.67 (3.67)a						
S	0.50 (0.50)a	1.00 (0.00)a	11.67 (2.91)a						
P value	0.2929	1.0000	1.0000						
Within rows (0.18 m between plants)									
N	1.00 (1.00)a	0.00	5.00 (1.00)a						
S	0.00 (0.00)a	0.00	5.33 (0.33)a						
P value	0.4226	–	0.7676						
Across rows (0.76 m between rows)									
W	0.00	0.00	0.33 (0.33)a						
E	0.00	0.00	0.33 (0.33)a						
P value	–	–	1.0000						

^a Mean number of western bean cutworm larvae. Tukey (\pm SEM). The means with the same letter are not significantly different, $P \geq 0.05$.

Exploratory Trials of Western Bean Cutworm Larval Movement

In 2008, only two larvae were recovered in both axes (across and within rows). In 2009, no larvae were found in the axes with respect to the infested plant (across and within rows) and did not allow statistical comparison (Table 2).

There were no significant differences for larval presence among the different quadrants (NE, SE, NW, and SW), N and S orientations, across rows (E and W axes), or within infested row (N and S axes) for all years (Table 2).

No significant differences were observed for maximum distance between the quadrants (NE, SE, NW, and SW) in all experiments, except for 2010 ($P = 0.0336$; Table 3). In 2010, the maximum distance for larvae in the NE quadrant was significantly higher (2.48 m) than for larvae in the NW quadrant (0.61 m). The mean maximum distances in SW and SE quadrants were intermediate values (2.19 m and 2.13 m, respectively) and did not differ significantly from NE and NW quadrants. There were no significant differences between N and S orientations or axes (across rows and within row) regardless of year (Table 3). In all years, larvae reached the total maximum distance in the plots.

Main Experiment of Western Bean Cutworm Larval Movement

There were no significant differences for number of larvae among the different quadrants (NE, SE, NW, and SW), orientations (N and S), within infested row, and across rows with respect to the infested plant (Table 4). The larval frequency varied from 31.4% (SW) to 15.7% (NW) between quadrants. Considering N and S orientations, within row (N and S axes), and across rows (W and E axes), larval frequency was similar and did not vary more than 12% (Table 4).

Regarding the mean maximum distance covered by the western bean cutworm larvae in the different quadrants, the highest value was observed in the SE quadrant (3.54 m), but did not differ significantly from the others (Table 4).

Table 3. Mean value (\pm SE) of maximum distance covered by western bean cutworm larvae in different positions related to the infested plant in maize, Concord, NE, from 2008 to 2010

Position	Concord 2008			Concord 2009			Concord 2010		
	Maximum distance (m)								
	Mean ^a			Mean ^a			Mean ^a		
NE	1.10 (1.10)a	1.27 (1.27)a	2.48 (0.06)a						
NW	0.00 (0.00)a	0.00 (0.00)a	0.61 (0.61)b						
SE	1.48 (1.48)a	0.92 (0.92)a	2.13 (0.41)ab						
SW	0.00 (0.00)a	0.74 (0.74)a	2.19 (0.20)ab						
P value	0.6083	0.7718	0.03336						
N	1.45 (0.74)a	1.27 (1.27)a	2.48 (0.06)a						
S	1.48 (1.48)a	1.65 (0.18)a	2.30 (0.24)a						
P value	0.9893	0.7950	0.5094						
Within rows (0.15 m between plants)									
N	0.36 (0.36)a	0.00 (0.00)a	1.19 (0.26)a						
S	0.00 (0.00)a	0.00 (0.00)a	1.66 (0.06)a						
P value	0.4226	–	0.1495						
Across rows (0.76 m between rows)									
W	0.00 (0.00)a	0.00 (0.00)a	0.25 (0.25)a						
E	0.00 (0.00)a	0.00 (0.00)a	0.25 (0.25)a						
P value	–	–	1.0000						

^a Maximum distance covered by western bean cutworm larvae. Distance was calculated by Euclidean distance, where distance between plants or rows is the length of the line segment connecting them (ordinary distance). Tukey (\pm SEM). The means with the same letter are not significantly different, $P \geq 0.05$.

Table 4. Mean value (\pm SE) of recovered larvae, frequency, and maximum distance covered by western bean cutworm larvae in different positions related to the infested plant in maize, Concord, NE, 2012

Position	Concord 2012		
	Recovered larvae/damage		Maximum distance
	Mean ^a	Frequency (%) ^b	
NE	3.67 (1.12)a	23.6	2.96 (0.60)a
NW	2.44 (0.84)a	15.7	1.41 (0.46)a
SE	4.56 (1.21)a	29.3	3.54 (0.84)a
SW	4.89 (2.03)a	31.4	1.86 (0.48)a
P value	0.5994	–	0.0727
N	10.78 (2.58)a	44.3	3.29 (0.53)a
S	13.56 (3.63)a	55.7	3.71 (0.81)a
P value	0.6664	–	0.9048
Within rows (0.15 m between plants)			
N	4.67 (1.18)a	53.2	0.91 (0.18)a
S	4.11 (0.90)a	46.8	1.19 (0.33)a
P value	0.7133	–	0.4226
Across rows (0.76 m between rows)			
W	0.78 (0.28)a	53.8	0.51 (0.33)a
E	0.67 (0.24)a	46.2	0.68 (0.32)a
P value	0.7643	–	0.6525

^a Number of western bean cutworm recovered larvae. Tukey (\pm SEM). The means with the same letter are not significantly different, $P \geq 0.05$.

^b Frequency (%) of western bean cutworm larvae in each position.

^c Maximum distance covered by western bean cutworm larvae. Distance was calculated by Euclidean distance, where distance between plants or rows is the length of the line segment connecting them (ordinary distance). Tukey (\pm SEM). The means with the same letter are not significantly different, $P \geq 0.05$.

The western bean cutworm larvae moved similarly for N and S orientations, and no significant differences for mean maximum distance were observed between orientations (Table 4).

Considering the within infested row (N and S axes) and across rows (E and W axes) with respect to the infested plant, there were no statistical differences between the compared positions (Table 4).

Most of recovered larvae of western bean cutworm were observed on the infested plant, or neighboring plants within the same row and neighboring rows. Eighty-four out of 263 larvae were recovered within the infested row and 198 out of 263 in an area of ~ 9 m² (radius of 1.7 m) around the infested plant. The maximum distance was 6.8 m (NE quadrant) from the infested plant (Supp. Fig. 1 [online only]).

Fall Armyworm Larval Movement

There were no statistical differences for number of fall armyworm larvae recovered between the different quadrants (NE, SE, NW, and SW), N and S orientations, across rows (E and W axes), or within infested row (N and S axes; Table 5). The larval frequency varied from 45.4% (SW quadrant) to 15.2% (NE and SE quadrants). With respect to N and S orientations, the larvae were distributed similarly, with frequencies of 54.2 and 45.8%, respectively. Within the infested row (N and S axes), 73% of the larvae moved North. Considering the movement of larvae across rows (W and E axes), 56.8% of the larvae were recovered on the Western axis (Table 5).

No significant differences were observed for maximum distance between the different quadrants, N and S orientations, and across rows. For within the infested row (N and S axes), the mean maximum distance was significantly greater for the North axis (0.68 m) than the South axis (0.17 m; $P = 0.0048$; Table 5).

Table 5. Mean value (\pm SE) of recovered larvae, frequency, and maximum distance covered by fall armyworm larvae in different positions related to the infested plant in maize, Concord, NE, 2013

Position	Concord 2013		
	Recovered larvae		Maximum distance Mean (m) ^c
	Mean ^a	Frequency (%) ^b	
NE	0.63 (0.32)a	15.2	0.44 (0.22)a
NW	1.00 (0.33)a	24.2	0.89 (0.28)a
SE	0.63 (0.32)a	15.2	0.57 (0.28)a
SW	1.88 (0.40)a	45.4	1.34 (0.21)a
<i>P</i> value	0.0511	–	0.0658
N	4.00 (1.24)a	54.2	1.00 (0.25)a
S	3.38 (0.68)a	45.8	1.40 (0.21)a
<i>P</i> value	0.6651	–	0.2905
Within rows (0.15 m between plants)			
N	2.38 (0.73)a	73	0.68 (0.13)a
S	0.88 (0.35)a	27	0.17 (0.07)b
<i>P</i> value	0.0853	–	0.0048
Across rows (0.76 m between rows)			
W	0.50 (0.19)a	56.8	0.48 (0.20)a
E	0.38 (0.26)a	43.2	0.19 (0.12)a
<i>P</i> value	0.7054	–	0.2462

^a Mean number of fall armyworm recovered larvae. Tukey (\pm SEM). The means with the same letter are not significantly different, $P \geq 0.05$.

^b Frequency (%) of fall armyworm larvae in each position.

^c Maximum distance covered by fall armyworm larvae. Distance was calculated by Euclidean distance, where distance between plants or rows is the length of the line segment connecting them (ordinary distance). Tukey (\pm SEM). The means with the same letter are not significantly different, $P \geq 0.05$.

Most of recovered fall armyworm larvae were observed on the infested plant or the neighboring plants within the same row and neighboring rows. No larvae were recovered three or four rows away from the infested row. Forty-one out of 81 larvae were recovered within the infested row and 74 out of 81 in an area of ~ 3.8 m² (radius of 1.1 m) around the infested plant. The maximum distance of larval detection was 1.9 m (SE quadrant) from the infested plant (Supp. Fig. 2 [online only]).

Discussion

Information on larval movement of western bean cutworm and fall armyworm is very limited. Challenges include the difficulty to design such studies and the analysis of the data. Larval recovery is typically low, primarily because of high mortality for early instar Lepidoptera (Zalucki et al. 2002). We observed low larval survival in 2010 for fall armyworm and in 2009 for western bean cutworm. High western bean cutworm mortality has been reported in the literature (Paula-Moraes et al. 2013), where although egg survival is high, only a few larvae survive to maturity. Abiotic and biotic factors (e.g., weather, natural enemies) may increase mortality (Zalucki et al. 2002). However, in 2010 and 2012, we observed relatively high western bean cutworm larval survival. Paula-Moraes et al. (2013) similarly reported variability in larval survival in maizefields during three years across three ecoregions of Nebraska. According to the authors, differences in temperature and humidity during egg hatch may have had a significant affect on larval survival, particularly for neonates. Zalucki et al. (2002) also reports the range of larval mortality is quite variable, depending on species. Although these data are difficult to obtain, knowledge of larval survival is necessary in order to design larval behavior studies, and also is critical for designing pest management strategies and tools such as economic thresholds (Paula-Moraes et al. 2013).

In the exploratory trials of western bean cutworm larval movement, the larvae were observed to move similarly in all directions (nondirectional movement) and reached the edge of the evaluation area in almost all plot sizes, independent of year. Based on exploratory trials plot size was increased in 2012. The larger plots appear to have been adequate, as few larvae were observed near plot edges.

Western bean cutworm exhibited nondirectional movement in all years. Fall armyworm larvae exhibited greater movement to the North within the infested row. However, no significant differences were observed when considering general N and S orientations, so it appears that fall armyworm also exhibited nondirectional movement, and this northern movement may have been influenced by wind or another environmental factor. In Nebraska, prevailing winds in summer are often from southwest, which may have influenced the northern movement within row of the fall armyworm larvae in our study. Insect movement between or within plants (resources) is commonly related to an active mechanism by which insects seek resources (Bell 1990). There are several possible types of information described in the literature that are used by insects to guide search orientation. Among many factors, sensory information can be directionally (Baker 1978, Harris and O'Miller 1982) or nondirectionally oriented (Barrows 1975, Bell 1990). For example, a puff of pheromone may "alert" the insect of the presence of a resource; however, the source of the pheromone cannot be localized (Bell 1990). On the other hand, directional information from biotic sources may happen by several clues, such as chemical gradients of pheromone or food odor, sound waves, and direct visual localization (Baker 1978, Bell 1990). This type of perception allows the insect to have control of its direction toward the biotic source

(Bell 1990). Thus, the movement patterns of both species in this study appear to be nondirectionally oriented.

Many refuge configurations for *Bt* crops have already been proposed based on the target insect's behavior. Based on the results for western bean cutworm and fall armyworm, the structured refuge's placement position (e.g., on North or South sides of the *Bt* crop) does not interfere in its effectiveness. However, its distance from the *Bt* crop field is more likely to interfere when considering the larval movement observed in our study.

Western bean cutworm larvae exhibited symmetrical and aggregated spatial dispersion in the maize field, with most of the recovered larvae observed on the plant infested with eggs or the neighboring plants within the same row and neighboring rows. Likewise, fall armyworm exhibited the same pattern. However, western bean cutworm larvae dispersed further from the infested plant than fall armyworm larvae. About 32% of the western bean cutworm larvae were recovered within the infested row and 75.3% within a radius of 1.7 m of the infested plant. Conversely, Blickenstaff (1983) observed more within row western bean cutworm dispersal than across row dispersal in common beans (*Phaseolus vulgaris* L.). However, characterization of plant-to-plant larval movement must be considered individually for each crop and cultivation system. Depending on various factors, the larvae may be able to disperse differently, or more rapidly and successfully, depending on crop or cultivar. For example, movement within rows is more likely to happen where more leaves are in contact within a row than than across rows, such as with common beans (Blickenstaff 1983).

For fall armyworm, almost 50% of the larvae were recovered within the infested row and 91.4% within a radius of 1.1 m. A similar pattern has been reported for fall armyworm in cotton where larvae remain predominantly within average distances of 1 to 2.4 plants from the original infested plant, not dispersing more than five plants from the site of release (Ali et al. 1990). Ross and Ostlie (1990) reported that about 50% of European corn borer larvae infesting whorl stage maize remained on the infested plant and 90% remained within the infested row.

Besides having significant value for ecological understanding, larval movement of each insect species can influence several factors concerning its management, such as scouting methodology. Western bean cutworm and fall armyworm exhibited a symmetrical and aggregated spatial dispersion in maize, and such behavior should be considered when developing sampling methodology. Insect dispersion and distribution in a crop can directly influence the number and size of samples required to be reliable and representative.

With respect to insect resistance management and refuge configuration, western bean cutworm exhibited a greater larval dispersion across rows compared to several other species in the literature (Blickenstaff 1983, Ali et al. 1990, Ross and Ostlie 1990, Davis and Onstad 2000, Siegfried and Hellmich 2012). Although fall armyworm seems to move less than western bean cutworm, the insect also exhibited significant larval dispersion across rows. Therefore, based on the results in this study, structured refuges may be more appropriate than integrated refuges (e.g., RIB strategy) for both species. According to Mallet and Porter (1992), insects with low plant-to-plant movement are considered the best candidates for successful implementation of a RIB strategy. Insects that have higher plant-to-plant movement would be the worst candidates for the use of seed mixtures (Davis and Onstad 2000). In addition, the present results corroborate Onstad et al. (2011), who presume that each species must be considered independently and one should not expect a one-size-fits-all IRM plan to be ideally suited for all pest species.

We believe the results of this study can inform not only IPM and IRM for western bean cutworm and fall armyworm in maize, but also present a useful method to characterize and compare the dispersion of various pest species within their respective host crops.

Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

Acknowledgments

We thank the Coordination for the Improvement of Higher Education Personnel (CAPES) for a doctoral scholarship granted to the first author and to the National Council for Scientific and Technological Development (CNPq) for the Productivity in Research Fellowship granted to the fourth author.

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