2006

Dispersal of Adult *Diatraea grandiosella* (Lepidoptera: Crambidae) and Its Implications for Corn Borer Resistance Management in *Bacillus thuringiensis* Maize

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Qureshi, Jawwad A.; Buschman, Lawrent L.; Throne, James E.; and Ramaswamy, Sonny B., "Dispersal of Adult *Diatraea grandiosella* (Lepidoptera: Crambidae) and Its Implications for Corn Borer Resistance Management in *Bacillus thuringiensis* Maize" (2006). *Publications from USDA-ARS / UNL Faculty*. 1991.
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Dispersal of Adult *Diatraea grandiosella* (Lepidoptera: Crambidae) and Its Implications for Corn Borer Resistance Management in *Bacillus thuringiensis* Maize

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Ann. Entomol. Soc. Am. 99(2): 279–291 (2006)

ABSTRACT Dispersal of the southwestern corn borer, *Diatraea grandiosella* Dyar, was examined by release and recapture of dye-marked adults and by capture of feral adults in and around 50-ha center pivot irrigated fields of *Bacillus thuringiensis* (Bt) maize. Pheromone and blacklight traps were used to capture the adults. In 1999, 2000, and 2001, a total of 177, 602, and 1,292 marked males, and 87, 231, and 1,045 marked females were released in four irrigated Bt maize fields, respectively. Recapture beyond release point was 2.13, 6.17, 3.16, and 17.91% for males and 0, 0, 2.23, and 4.18% for females in the four fields, respectively. One male was recaptured over native vegetation outside the field perimeter, and one was caught in a neighboring maize field, 457 m from the release point. An exponential decay function explained recapture of marked adults across the dispersal distance. More than 90% of adults were recaptured within 300 m of the release point. Large numbers of feral adults were captured throughout the study fields and over native vegetation between fields. The feral adult dispersal could be described with a linear model. Virgin females (38% marked and 14% feral) were captured throughout the study fields. The recapture of marked insects suggests that the dispersal was limited. However, capture of feral adults throughout Bt maize fields indicates that the actual dispersal may be more extensive than indicated by recapture of marked adults. Potential refuge sources for the feral adults were 587–1,387 m from the edge of the fields. There seems to be some dispersal of *D. grandiosella* from the nontransgenic "refuge" fields into the transgenic fields, which may allow for some genetic mixing of the Bt-resistant and -susceptible insects to help suppress potential evolution of pest resistance to transgenic maize. However, it is not clear whether the dispersal recorded in this study is sufficient to support the current resistance management strategy for corn borers.

KEY WORDS Bt corn, insect dispersal, resistance management, southwestern corn borer, transgenic crops

DISPERSAL BEHAVIOR OF HIGHLY MOBILE pest insects must be understood to explain their biology and ecology and to develop an effective pest management strategy (Turchin and Thoeny 1993). Understanding dispersal behavior of pests targeted by transgenic crops is also important in the development of sound management strategies to avoid the evolution of pest resistance to the transgenic crop. Theoretical population and genetic models have been used to forecast the development of resistance in target pests, but these models include assumptions about biological parameters such as dispersal (Gould 1994). Some models for the development of resistance suggest dispersal parameters were important in determining the time to resistance (Guse et al. 2002, Onstad et al. 2002).

The southwestern corn borer, *Diatraea grandiosella* Dyar, is a destructive pest of maize, *Zea mays* L., in the southern parts of North America (Davis 1965, Chippendale 1979, Knutson and Davis 1999), where the annual cost of control and damage is in the millions of dollars. The southwestern corn borer and the European corn borer, *Ostrinia nubilalis* (Hübner), are primary targets of transgenic *Bacillus thuringiensis* Berliner maize (Bt maize). Bt maize hybrids are extremely effective in controlling both of these species (Koziel et al. 1993, Ostlie et al. 1997). However, there is concern that Bt maize acreage will continue to increase and that the corn borers will develop resistance (or virulence) to the insecticidal protein in

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0013-8746/06/0279–0291$04.00/0 © 2006 Entomological Society of America

the transgenic plants. Selection pressure is much more intense for populations exposed to Bt maize than it is for populations exposed to standard pesticides because the toxin is continuously present in the plants. This means corn borers are at high risk of developing resistance to Bt maize. The success of the Bt maize technology will be short-lived if corn borers develop resistance to the toxins expressed in transgenic plants (Ostlie et al. 1997). Moderate to high levels of resistance to various Bt proteins have been observed in laboratory populations of the European corn borer reared on diets with low doses of Bt proteins (Huang et al. 1999). However, we do not know whether such a phenomenon would occur in the southwestern corn borer, because such studies have not been performed.

The United States Environmental Protection Agency (USEPA) has addressed the concern for the potential development of resistance by requiring transgenic seed companies to develop and implement an effective resistance management plan (Ostlie et al. 1997, USEPA 2001). They have mandated the use of the high dose/refuge strategy as a prophylactic insect resistance management (IRM) plan (Ostlie et al. 1997, Shelton et al. 2000, USEPA 2001), which requires high dose Bt plants to kill all homozygous susceptible (SS) and most or all potential heterozygous resistant insects (RS). A refuge of susceptible maize must be planted nearby and is expected to produce susceptible insects (SS) that can mate with any potentially resistant insects (RR or RS) that might develop in the Bt maize field. As long as the resistance gene frequency is low and resistance is inherited as a recessive trait, all resulting offspring (SS or RS) should be susceptible to the high dose Bt maize plants. For this strategy to work, the adult insects must be able to disperse from the "refuge" field into the Bt maize field for mating to occur between the two populations (Gould 1994, Ostlie et al. 1997, Shelton et al. 2000).

Studies on dispersal of the European corn borer have recently been undertaken in Iowa, Nebraska, and Kansas (Hunt et al. 2001, Showers et al. 2001, Qureshi et al. 2005). However, information on dispersal of the southwestern corn borer is limited to inferences based on the biology of the insect. Its precopulatory dispersal was reported to be mostly limited to the natal field (Langille and Keaster 1973); other observations, however, suggest that southwestern corn borer dispersal may be more extensive. For example, Rolston (1955) reported dispersal to and oviposition in maize fields 2.4 km away from source fields. He also reported that at least 91% of females mated within 24 h of emergence and that 66% of females mated on the night of emergence. The latter also was reported by Davis and Henderson (1967). However, Langille and Keaster (1973) reported that mating occurred within 48 h of emergence. Rolston (1955) reported that two-thirds of females mated on the night of emergence and that three-quarters of the eggs were oviposited 1 d after mating and that the rest were laid on the second and third day after mating. Similarly, Davis et al. (1933) observed that eggs were laid near the natal site on the first night but that the mobility of the female increased as the egg load decreased over the next 2 to 3 nights. Guse et al. (2002) and Onstad et al. (2002) developed IRM models for southwestern corn borer. They found that the time required for resistance to develop was sensitive to assumptions about egg distribution. However, there is limited empirical dispersal information to support the model assumptions.

The current study was designed to develop dispersal parameters for the southwestern corn borer in western Kansas where maize is grown under irrigation in a semiarid climate. Additionally, we wanted to compare dispersal of southwestern corn borer with that of the European corn borer (Qureshi et al. 2005), because IRM plans have been developed for the European corn borer and they need to be validated for use with the southwestern corn borer. The same IRM plan is being used for the two species in the regions where they are sympatric.

Materials and Methods

The southwestern corn borers used in the mark–release–recapture experiments were reared at the Kansas State University Southwest Research and Extension Center (SWREC), Garden City, KS. The laboratory colonies were established every fall from larvae collected in non-Bt maize in southwestern Kansas. The insects were reared on a wheat germ-based meridic diet (Davis 1976) (BioServe, Frenchtown, NJ) with aureomycin and formaldehyde (in 1999 and 2000) or neomycin sulfate (in 2001) as antibiotics. Voucher specimens no. 149 are located in the Kansas State University Museum of Entomological and Prairie Arthropod Research. The insects were marked by incorporating oil-soluble dyes (Sudan Red 7B [C.I. 26050] and Sudan Blue 670 [C.I. 61554], Aldrich, Milwaukee, WI) in the diet (Qureshi et al. 2004). Dye-marked southwestern corn borer pupae were placed in petri dishes in 19-liters plastic buckets with a wet sponge. The buckets were covered with corrugated roofing steel to protect pupae from rain and irrigation but to allow the adults to emerge and disperse as they eclosed. This was done to reduce physical agitation that occurs when large numbers of adults are held in cages until release.

Marked and feral adults were captured using two types of traps: Ellisco-type battery-operated black light traps (15 W) (Gemplers, Bellville, WI) and plastic bucket traps (yellow and white) (Gemplers) with southwestern corn borer pheromone lures (Trécé lures supplied by Gemplers). A DDVP Vaportape II (Gemplers) was added to each bucket (both traps) to kill the trapped adults. Pheromone lures were replaced every 14 d, whereas bulbs in the blacklight traps were replaced only when they burned out. The pheromone traps captured males only, whereas blacklight traps captured both genders. The traps were monitored daily during feral adult flights and when marked pupae were in the field. Adults captured at each location were counted and identified as marked or unmarked. This was done in the field when possible; however, there were times when the adults were

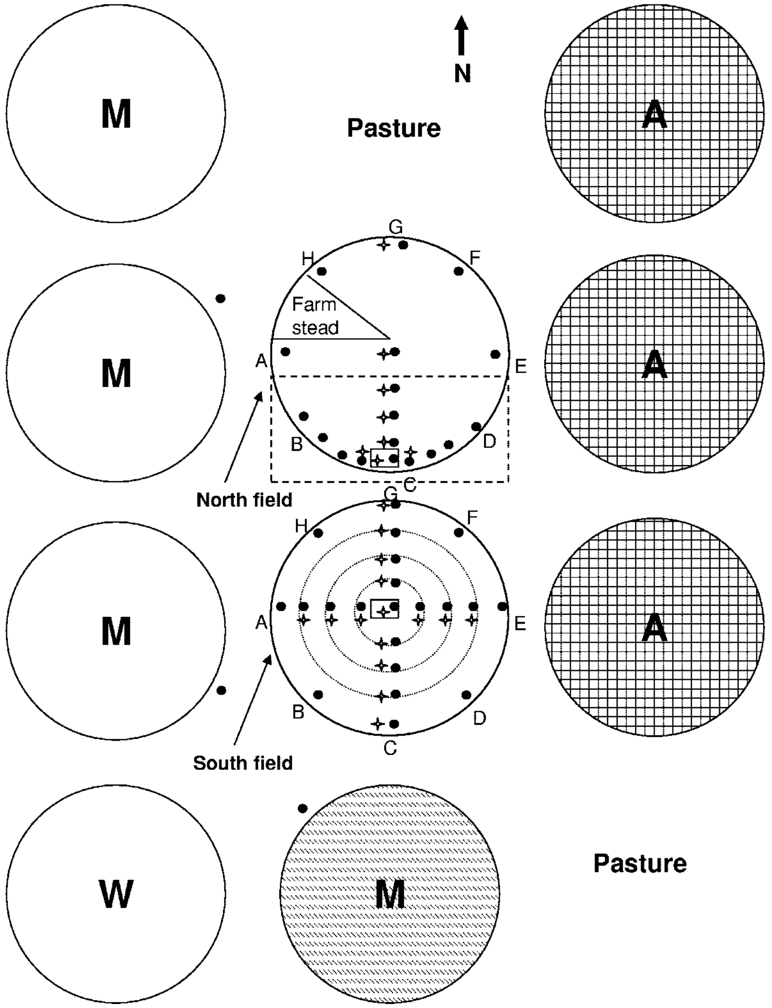

Fig. 1. Study fields, release point, and trap locations (□, release point; ●, pheromone trap; ✦, light trap; ⬚, replanted part) in 1999 with neighborhood fields and crop covers for 1998 and 1999. Study fields were in Bt maize during both years. Each circle is a field of ≈40–50 ha represented by a letter for 1998 crop (A, alfalfa; M, maize; W, wheat) and background for 1999 crop (○, maize; ▨, wheat; ⊕, alfalfa). Trap symbols are not scaled to the actual distances from the release points or neighborhood fields.

placed in resealable plastic bags, labeled, and taken to the laboratory where they were refrigerated until they could be identified and counted. All marked and some unmarked females were dissected in the laboratory to determine mating status based on the presence or absence of a spermatophore in the bursa copulatrix.

The 1999 and 2001 study fields were selected to avoid fields that might have corn borer-infested maize stubble from the previous year. This was done to avoid production of feral first generation southwestern corn borers within the field. The study fields also were planted to Bt maize (YieldGard) to avoid production of feral second generation southwestern corn borers within the field. This reduced the number of local feral adults that would be collected in the traps. It also allowed us to determine how many feral adults dispersed into the study fields from neighboring fields. The 2000 study field did not meet these requirements so only the data for marked adults could be used to describe dispersal.

1999 Experiment. Two neighboring (5 m apart) center pivot irrigated circles of Bt maize were selected 12 km southeast of Garden City, KS (37° N, 101° E), referred to as north field (≈44 ha) and south field (≈50 ha) or study fields (Fig. 1). Both fields were planted to YieldGard Bt maize. The fields had YieldGard Bt maize stubble from the previous year (we assumed no corn borer production occurred). The release site for the south field was located in the center of the field, but the release site for the north field was along the south margin of the field near the south field (Fig. 1). A small nursery of non-Bt maize (0.2 ha) was planted at the release site in each field to obtain corn borers on plants treated with RbCl and CsCl for a companion dispersal study by using these elemental markers. However, the intended RbCl and CsCl treatments and corn borer inoculations did not occur. Because the plants were exposed to feral first generation adults, there could have been a few feral second generation adults produced in this nursery. We did not find corn borer-infested plants, and there was no increase in the catch of feral insects in the traps near the release site. However, regression analysis was not performed on feral captures from the second flight.

The neighborhood of the two study fields is illustrated in Fig. 1. The corners beyond the reach of the center pivot sprinklers had fallow wheat stubble with very few weeds. There were four non-Bt maize fields to the south and west of the study fields that were potential sources of feral adults during the second generation flight. There also was a circle to the south that had maize stubble from the previous summer, but it was planted to wheat. There were no other maize fields within several miles to the north and east, but there were other maize fields scattered to the west. The non-Bt maize fields were probably sprayed with insecticides to control second generation maize borers (both in 1999 and in 1998). The study fields were not sprayed during the experiments.

The two test fields were planted on successive days so development was similar in the two fields. The south part of the north field needed to be replanted about a month later, so development of that section was considerably later than that of the rest of the maize in the two study fields. The first planting in both fields was at the 12- to 14-leaf stage (≈60 cm in height) during the first generation flight of feral adults, whereas the replanted maize was at the two-leaf stage. A severe hailstorm on 1 July caused serious plant and trap damage and terminated captures for the first corn borer flight. The north half of the north field was abandoned because of the hail damage and the traps were removed. During the release of marked adults the first planting was at the silking stage, whereas the replanted maize was at the 18-leaf to tassel stage. In total, 170 blue pupae and 210 red pupae were placed in the north and south fields, respectively, starting on 25 July. Dispersal of marked adults coincided with the second generation flight of feral adults.

During the first generation flight of feral adults there were eight pheromone traps installed at sites A–H around the perimeter of each field (Fig. 1). During the release of marked southwestern corn borer, additional pheromone and blacklight traps were installed on the north–south and east–west transects (Fig. 1). Three southwestern corn borer pheromone traps were installed outside the study fields near non-Bt maize fields that were potential sources of feral adults (Fig. 1). The blacklight and southwestern corn borer pheromone traps were installed 2 m apart but equidistant from the release site. One southwestern corn borer pheromone trap and one blacklight trap were installed at each release point to record the emergence pattern and to calculate the proportions of dispersing males and females. In the north field, the perimeter traps A to H were installed at 550, 274, 60, 366, 610, 732, 762, and 732 m from the release point, respectively (Fig. 1). In the south field, the traps were installed at 30, 61, 152, and 366 m on the north, south, east, and west transects from the release point (Fig. 1). The perimeter traps A to H were installed 6 m from the field edge and between 366 and 396 m from the release point. During the release of marked adults and second generation flight of feral adults, there were a total of 18 and 21 pheromone traps and eight and 15 blacklight traps installed in the north and south fields, respectively.

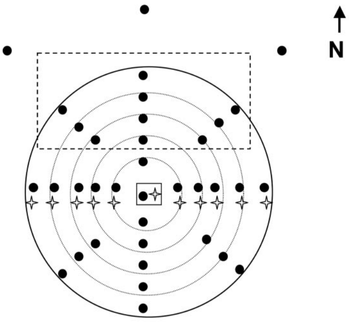

Fig. 2. Study field, release point, and trap locations in 2000 (□, release point; ●, pheromone trap; ✧, light trap; ⬚, wheat stubble). This field did not meet the selection criteria for plantation to Bt maize during study year and the previous year; therefore, studies on feral captures were not conducted.

2000 Experiment. A study field that met our selection criteria could not be found. Therefore, we used a half-pivot irrigated maize field (18 ha) at the Kansas State University Southwest Research and Extension Center, Garden City, KS (37° N, 101° E). The study field was planted to both YieldGard Bt maize (10 ha) and non-Bt maize (8 ha). The north part of the circle was in wheat stubble (Fig. 2), and there was dryland maize planted in the unirrigated corners of the field to the north. However, the field had been in non-Bt maize the previous year, so there was substantial production of feral adults within the study field. Therefore, feral adult capture data are not reported. The study field was not sprayed with insecticide.

The release site was located in the center of the field (Fig. 2). In total, 1,235 red and blue southwestern corn borer pupae were placed in the field for adult dispersal between 22 July and 20 August. The dispersal of marked adults coincided with the second generation flight of feral adults.

There were a total of 36 southwestern corn borer pheromone traps installed along eight transects from the release site. There were 11 blacklight traps installed along east and west transects from the release point (Fig. 2). The blacklight and southwestern corn borer pheromone traps were installed 2 m apart, equidistant from the release site. The traps were installed at 15, 46, 107, 229, and 366 m on the north, south, east, and west transects from the release point. One southwestern corn borer pheromone trap and one blacklight trap were installed at the release point to record the emergence pattern and to record the recapture

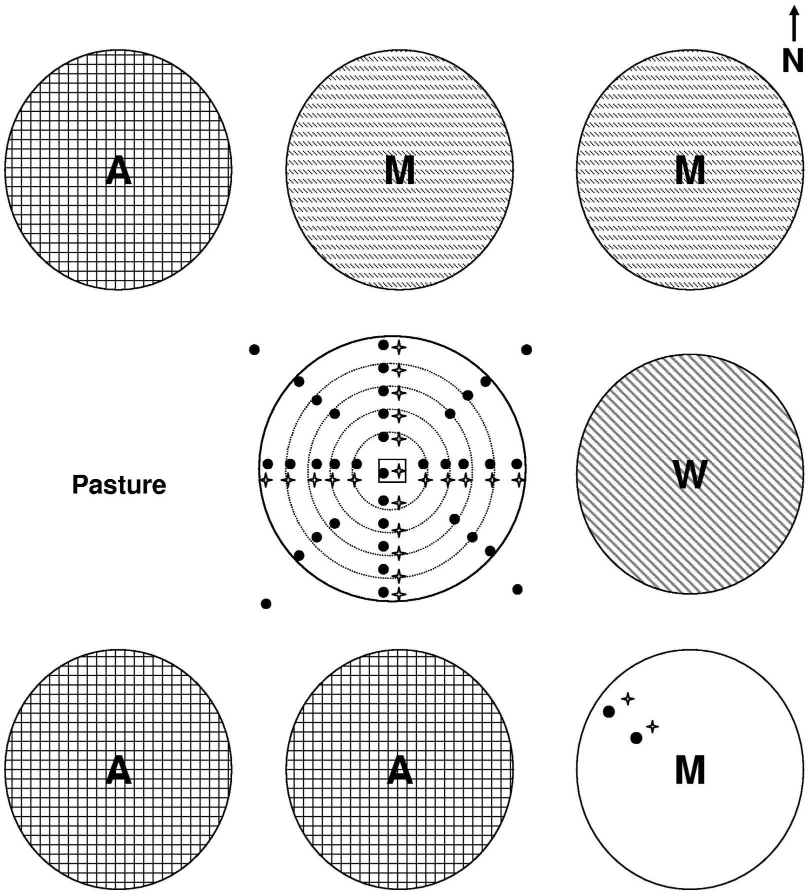

Fig. 3. Study field, release point, and trap locations (□, release point; ●, pheromone trap; ✧, light trap) in 2001 with neighborhood fields and crop covers for 2000 and 2001. Study field was in Bt maize during both years. Each circle is a field of ≈40–50 ha represented by a letter for 2000 crop (A, alfalfa; M, maize; W, wheat) and background for 2001 crop (○, maize; ▨, wheat; ⊕, alfalfa; ⊘, potato). Trap symbols are not scaled to the actual distances from the release points or neighborhood fields.

rate of dispersing males and females where the number of available insects was known independently (emergence numbers). Three pheromone traps were installed in dryland maize 396–483 m from the release point to the north, northwest, and northeast (Fig. 2). Transects to the west, southwest, south, southeast, and east were in maize, whereas transects to the northwest, north (except the 15 m trap), and northeast were over the wheat stubble. Four of the eight transects had only the outside three positions installed. The perimeter traps were placed ≈6 m from the field edge and the distance to the release point averaged 366 m. One temperature and humidity sensor (Hobo Pro, Onset Computer Co., Bourne, MA) was installed at each of the eight trap locations in the perimeter and near the release point.

2001 Experiment. A center pivot irrigated circle of Bt maize (≈50 ha) was located 16 km southwest of Garden City, KS (37°N, 101° E) (Fig. 3) that was planted to YieldGard Bt maize hybrid. This study field had been in winter wheat and grazed down before maize was planted. The release site was located in the center of the study field (Fig. 3). A small nursery of non-Bt maize (0.2 ha) was planted at the release site to obtain corn borers on plants treated with RbCl and CsCl for a companion dispersal study by using elemental markers. These plants were inoculated with southwestern corn borers neonates, which entered the pupal stage by 25 July. Therefore, data for feral adults collected after 25 July was not used to evaluate feral adult dispersal into the field. The neighborhood of the study field is illustrated in Fig. 3. The corners beyond the reach of the center pivot sprinklers remained in native sand hill vegetation (grass and sagebrush). The surrounding crop fields were wheat, potato, alfalfa, maize, and native grass pasture. The only known non-Bt maize field was located ≈0.2 km to the southeast of the study field. Non-Bt maize fields in the neighborhood were probably sprayed with insecticides to control corn borers, but field records were not available. The study field was not sprayed.

In total, 4,265 red and blue pupae were taken to the field for adult emergence from 6 July to 17 August. Most of the adults dispersed during the second gen-

Table 1. Summary of dispersed and recaptured marked southwestern corn borer males and females from four study fields, 1999–2001

Yr/Field	Date	No. pupae producing adults and pupal color	Gender	No. dispersed at release bucket	Beyond release point	% recaptured at release bucket	Beyond release point
1999 North field	25 July	170	Male	60	47	22.00	2.13
		Blue	Female	41	33	22.00	0.00
1999 South field	25 July	205	Male	117	81	31.00	6.17
		Red	Female	46	32	30.00	0.00
2000 Field	22 July–20 Aug.	1235	Male	602	569	5.50	3.16
		Red and blue	Female	237	224	5.50	2.23
2001 Field	6 July–17 Aug.	4265	Male	1,292	949	26.55	17.91
		Red and blue	Female	1,045	956	8.51	4.18

eration flight of feral southwestern corn borers. The pupae were sexed and held in separate dishes so emergence of each sex could be recorded. The numbers of adult males and females that eclosed and dispersed from the container were recorded each day by counting the viable pupae in the bucket and recording the difference. There were 21 blacklight traps and 21–36 pheromone traps installed inside the study field. Both trap types were installed at 15, 46, 107, 229, and 366 m on the north, south, east, and west transects from the release point (Fig. 3). Only pheromone traps were installed on the diagonal transects at 107, 229, and 366 m from the release point, respectively (Fig. 3). The blacklight traps were installed 2 m from the pheromone traps, but equidistant from the release site. One pheromone and one blacklight trap were installed at the release point. The perimeter traps were 6–15 m inside from the field edge, and the distance to the release point averaged 366 m. There were four pheromone traps installed outside the study field over the native sand hill vegetation. Two pheromone traps were installed in the non-Bt maize field to the southeast that was a potential source of feral southwestern corn borers (Fig. 3). One temperature and humidity sensor was installed near the release site and at each of the eight trap locations on the perimeter of the field.

Data Analysis. Feral capture data from the perimeter traps of 1999 study fields were evaluated using regression analysis for the relationship with the distance from potential refuge fields in the neighborhood. Mark–recapture data within study fields of 2000 and 2001 were analyzed for relationship with dispersal distance from field center to the perimeter, whereas feral capture data of 2001 were analyzed for the same relationship but from the field perimeter to the center. Five data variables were tested: males recaptured in pheromone traps, males recaptured in light traps, females recaptured in light traps, combined males and females recaptured in light traps, and total recapture of all males and females in both pheromone and light traps. The actual number of adults caught in each trap along the four major transects (north, south, east, and west) were summed for each year or generation. All five variables for marked recapture data for 2000 and 2001, and feral capture data for second generation flight of 2001 (before 25 July) were analyzed through TableCurve 2D software (Jandel Scientific 1996). TableCurve 2D automatically fits several thousand families of equations to the data (Systat Software Inc. 2002). We selected equations that best described the data based on the magnitude and pattern of residuals, lack-of-fit tests, and whether the equations were biologically reasonable for describing the data. The model equations $[\hat{y} = a/(1 + 2a^2bx)^{0.5}]$ for mark–recapture data from 2000 and 2001 were integrated and the integrals were solved for a number of distances (x) between 0 and 366 m to determine the area under the curve corresponding to the distances within which 50, 90, 95, and 99% of the dispersed insects would be found. The slope and intercept values of model equations for particular data sets were used to calculate the estimated dispersal ranges.

The 2000 and the 2001 recapture data from pheromone and light trap catches on the main transects were tested for normality by using Shapiro–Wilk test and then analyzed for male catch difference using a paired *t*-test (Snedecor and Cochran 1989) in SAS (SAS Institute 1999–2000). Data with non-normal distribution were analyzed using Wilcoxon signed rank test (Snedecor and Cochran 1989). Feral catch data for the second generation flight from 1999 (south field) and 2001 also were analyzed using the same method. To determine whether light traps installed near the pheromone traps had a significant influence on the capture of males in pheromone traps, the capture data for solo pheromone traps (107, 229, and 366 m on the diagonal transects) were compared with capture data from pheromone traps installed near light traps. We used only the comparable traps at the same distances from the release site on the cardinal direction transects.

Results

1999 Experiment. The total recapture of marked adults for light and pheromone traps at the release point varied from 22 to 31% (Table 1). In the north field, only one male was recaptured and that was at 30 m from the release point. Five marked males released in the south field were recaptured at 30 ($n = 2$), 61 ($n = 1$), and 366 ($n = 1$) m, and one was recaptured in the north field 457 m from the release point. No marked females were recaptured beyond the release point, and the marked females that were recaptured at the release point were all mated. Unfortunately, our southwestern corn borer colonies were not very productive this summer, so the numbers of pupae avail-

Table 2. Mating status of the marked and feral southwestern corn borer females that dispersed between the field center and the perimeter or vice versa in two study fields in 2000 and 2001

Distance (m)[a]	Marked females (distance from release point to the perimeter trap)												
	2000				2001				Total				
	No. ct.	No. dis.	M	V	No. ct.	No. dis.	M	V	No. ct.	No. dis.	M	V	V (%)
0	13	13	8	5	89	80	51	29	102	93	59	34	36.56
15	3	3	2	1	17	17	10	7	20	20	12	8	40.00
46	0	0	0	0	11	11	8	3	11	11	8	3	27.27
107	2	2	1	1	7	7	2	5	9	9	3	6	66.67
229	0	0	0	0	3	3	2	1	3	3	2	1	33.33
366	0	0	0	0	2	2	2	0	2	2	2	0	0.00
	Feral females (distance from perimeter trap to the center of field)[b]												
	2001 Generation 1				2001 Generation 2[c]				Total				
0	1	1	1	0	60	59	52	7	61	60	53	7	11.67
137	3	3	2	1	31	31	29	2	34	34	31	3	8.82
259	0	0	0	0	50	46	36	10	50	46	36	10	21.74
320	1	1	1	0	45	43	38	5	46	44	39	5	11.36
351	1	1	1	0	26	25	20	5	27	26	21	5	19.23
366	0	0	0	0	8	8	7	1	8	8	7	1	12.50

M, mated; V, virgin; ct, caught; dis, dissected.

[a] 0 is release point and 366 is the perimeter.

[b] 0 is perimeter and 366 is the release point.

[c] Numbers that were caught before 25 July to avoid potential emergence from non-Bt nursery block.

able were very small. However, there were some recaptures so we have included these data.

During the first flight, catches of feral males in pheromone traps around the perimeter of the two study fields were highest along the south perimeter, suggesting the maize stubble south of the south field was the source of many of the feral southwestern corn borers. However, there was no significant correlation ($P > 0.05$) between feral adults and distance from potential refuge fields in the neighborhood for either the first or second generation flights. In total, 3,318 males and 342 females were captured across the south field during the second generation flight. Feral male captures during the second generation flight were higher in the pheromone traps than in the light traps in the south field ($S = 95.5$; $P = 0.001$).

2000 Experiment. In the 2000 study, the recapture of marked adults at the release point was 5.50% ($n = 33$ and 13 for males and females, respectively) (Table 1). In total, 18 marked males and five marked females were recaptured beyond the release point. Marked males were recaptured at 15 ($n = 11$), 46 ($n = 3$), 107 ($n = 2$), 229 ($n = 1$), and 366 ($n = 1$) m from the release point. No marked males were recaptured over the wheat stubble in the three north transects nor in other maize fields to the north and west. Five marked females were recaptured at 15 ($n = 3$) and 107 ($n = 2$) m from the release point, and 40% were virgin (Table 2).

The regression between recaptured adults with distance from the release point was described well by an empirical model with negative exponential decay $\hat{y} = a/(1 + 2a^2bx)^{0.5}$ (Table 3). There was a smooth decline in recapture with increasing distance from the release point to the perimeter of the field (Fig. 4). Based on the above-described dispersal equation, the radius of the circle that included 50% of the recaptured insects averaged only 93–94 m (Table 4). The radius of a circle that included 90–99% of the recaptured insects averaged 296–360 m (Table 4).

Marked male recapture was not significantly different for pheromone and light traps on the two transects that had both traps ($t = 1.88$, $P = 0.090$). Many feral males were caught in the pheromone traps over wheat stubble, although no marked males were recaptured in these traps.

2001 Experiment. In the 2001 study, the recapture of marked adults at the release point averaged 26.55% for the males and 8.51% for the females (Table 1). In total, 170 marked males and 40 marked females were recaptured beyond the release point. Marked males were recaptured at 15 ($n = 87$), 46 ($n = 22$), 107 ($n = 26$), 229 ($n = 19$), and 366 ($n = 15$) m from the release point inside the study field. One marked male was recaptured outside the study field over the native vegetation. Marked females were recaptured at 15 ($n = 17$), 46 ($n = 11$), 107 ($n = 7$), 229 ($n = 3$), and 366 ($n = 2$) m from the release point inside the study field and 40% ($n = 16$) were virgin (Table 2). No marked males or females were recaptured in the neighboring non-Bt maize field.

In total, 18 feral males and six feral females were captured during the first generation flight, and 9,809 feral males and 2,989 feral females were captured during second generation flight inside the study field. However, 515 feral males and 220 feral females were captured before 25 July and were included in the regression analysis for second generation flight. Of the 212 feral females dissected, 14% were virgin, and the percentage remained consistent across the field (Table 2). Feral males also were captured in high

Table 3. Parameters of the regression models describing the relationship between southwestern corn borer adult catch over distance for two study fields, 2000 and 2001, using TableCurve 2D

Yr	Model[a]	Trap	Gender	Marked adults (dispersal from release point to the perimeter trap)				Lack of model fit[c]
				a ± SE	b ± SE	R^2	Maximum[b] attainable R^2	
2000	1	P	M	15.00 ± 0.48	0.0074 ± 0.002500	0.98	0.99	0.10
	1	BL	M	18.00 ± 0.71	0.0118 ± 0.007300	0.97	0.97	0.65
	1	BL	F	13.00 ± 0.75	0.0285 ± 0.028800	0.93	0.94	0.81
	1	BL	MF	31.02 ± 1.29	0.0044 ± 0.003000	0.97	0.97	0.81
	1	P, BL	MF	46.00 ± 1.25	0.0014 ± 0.000500	0.99	0.99	0.33
2001	1	P	M	46.01 ± 2.91	0.0002 ± 0.000060	0.92	0.93	0.77
	1	BL	M	297.00 ± 4.25	0.0001 ± 0.000030	0.99	0.99	0.65
	1	BL	F	89.00 ± 0.96	0.0005 ± 0.000100	0.99	0.99	0.85
	1	BL	MF	386.00 ± 4.65	0.00005 ± 0.000010	0.99	0.99	0.76
	1	P, BL	MF	432.00 ± 6.37	0.00002 ± 0.000005	0.99	0.99	0.76
				Feral adults (dispersal from perimeter trap to the center of field) second generation flight before 25 July				
2001	1	P	M	16.76 ± 1.61	0.00003 ± 0.0000100	0.73	0.76	0.82
	2	BL	M	16.87 ± 3.30	−0.0114 ± 0.0040000	0.31	0.52	0.21
	2	BL	F	13.50 ± 2.70	−0.0042 ± 0.0032000	0.08	0.24	0.54
	2	BL	MF	30.37 ± 5.56	−0.0155 ± 0.0066000	0.23	0.42	0.33
	1	P, BL	MF	52.21 ± 6.96	0.000001 ± 0.0000005	0.48	0.55	0.68

P, pheromone; BL, blacklight; F, female; M, male.

[a] Model 1: $\hat{y} = a/(1 + 2a^2bx)^{0.5}$; model 2, $\hat{y} = a + bx$.

[b] Maximum attainable R^2 indicates the maximum amount of variation that any equation fit to the data could explain, allowing for the pure error in the data (Draper and Smith 1981). The pure error is the variation in the data that occurs when repeated measurements are made at identical values of the independent variable.

[c] Probability of 0.05 or below indicates lack of model fit.

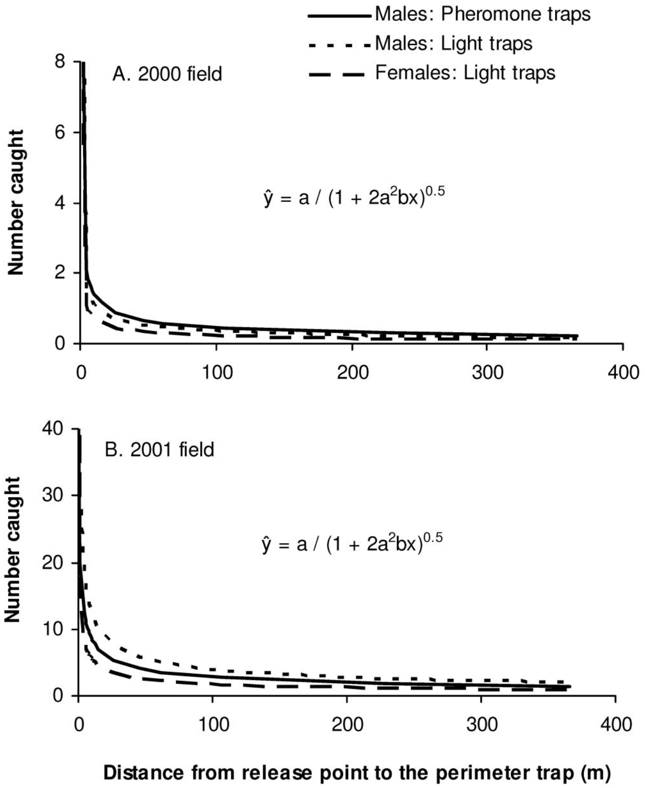

Fig. 4. Relationship between the numbers of marked male and female adults of southwestern corn borer recaptured within the study fields and the distance from the release point in the field center to the perimeter traps during 2000 and 2001.

Table 4. Estimated dispersal ranges of marked southwestern corn borer adults based on model $\hat{y} = a/(1 + 2a^2bx)^{0.5}$ for recapture distance relationship during 2000 and 2001

Yr	Model parameter		Estimated dispersal ranges (m)[a]			
	a	b	50%	90%	95%	99%
		Males from pheromone traps				
2000	15	0.0074	94	298	333	359
2001	46	0.0002	97	298	331	359
		Males from light traps				
2000	18	0.0118	93	296	331	359
2001	297	0.0001	93	297	330	358
		Females from light traps				
2000	13	0.0285	94	297	333	360
2001	89	0.0005	94	297	331	359

[a] Estimated dispersal ranges are the distances from the field centers within which 50, 90, 95, and 99% of the dispersed adults are expected to remain, respectively.

numbers in traps outside the field over the native vegetation.

The regression between recaptured marked males and females with distance from the release point was well described by an empirical model with a negative exponential decay $\hat{y} = a/(1 + 2a^2bx)^{0.5}$ (Table 3). There was a smooth decline in recapture with increasing distance from the release point out to the perimeter of the field (Fig. 4). The same model also explained the regression of second generation feral male captures in pheromone traps before 25 July across distance from perimeter to the field center (Table 3; Fig. 5). Based on the above-described dispersal equation the radius of the circle that included 50% of the recaptured insects averaged only 93–97 m (Table 4). The radius of the circle that included 90–99% of the recaptured insects averaged 297–359 m (Table 4). The data for feral males and females captured in the light traps were described by the linear model $\hat{y}$; = a + bx (Table 3; Fig. 5), although the slope was not significant ($P > 0.05$) for the female captures.

Marked male recapture was significantly higher in light traps than in the pheromone traps ($t = 3.00$, $P = 0.015$), but feral male capture during the second-generation flight was not significantly different for pheromone and light traps ($S = 1.00$, $P = 0.988$). The marked male recapture in pheromone traps placed together with light traps was significantly higher than for pheromone traps placed alone ($S = -38.5$, $P = 0.030$); however, the feral male capture during second generation was not significantly different for the two types of pheromone traps ($t = -1.51$, $P = 0.230$).

Discussion

Dispersal distance seemed to be the only variable needed to describe the dispersal of marked and feral southwestern corn borers. Such one-dimensional dispersal can best be described with a mathematical equation (Plant and Cunningham 1991). Two different equations were found appropriate to describe the dispersal patterns of marked and feral southwestern

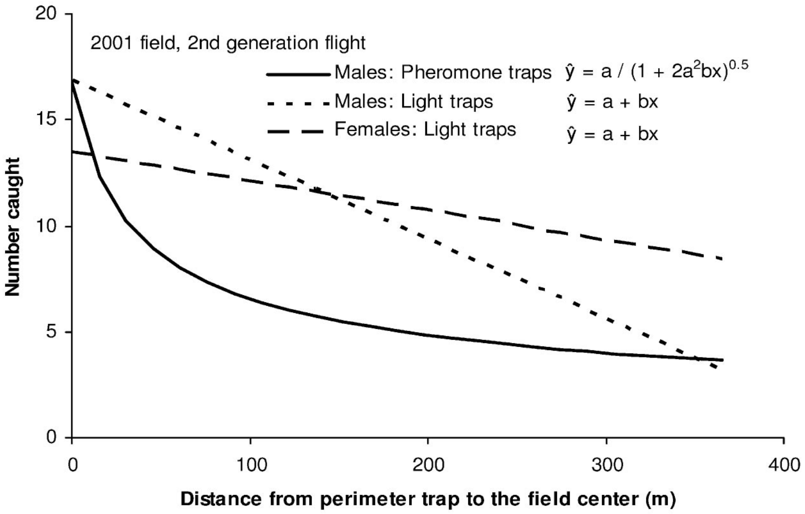

Fig. 5. Relationship between the numbers of feral male and female adults of southwestern corn borer captured within the study field during second generation flight before 25 July and the distance from the perimeter traps to the field center during 2001.

corn borer adults. The dispersal of marked adults was best explained with an exponential decay model with smooth but rapid decline over increasing distance from the release point. The recapture of marked males over the native vegetation ($n = 1$) and in neighborhood maize fields ($n = 1$) was not high enough to draw conclusions about dispersal between corn fields. Because there were no light traps installed over native vegetation outside the two study fields in 1999 and 2001, so there are no data for female dispersal outside the release field. The dispersal data of feral adults was best explained with a linear model except for the data set for males captured in the pheromone traps, which was best explained with an exponential decay model. There was substantial capture of feral males over the native vegetation or wheat stubble between neighborhood fields and study fields. The capture of feral males in the study fields suggests extensive adult dispersal because there was a general lack of a slope with distance from potential refuge fields and large numbers of both males and females were captured in the study fields. The feral adults seemed to come from refuge fields in the neighborhood or from more distant sources. The nearest possible refuge fields were at a distance of 587–1,387 m from the perimeter of the study fields and feral adults were captured all the way to the center of study fields, an additional 366 m from the field perimeter. The directional dispersal of marked southwestern corn borers was not analyzed because dispersal occurred over a long period and daily counts were small. Additionally, the local environment must have been rather uniform in the center pivot irrigated study fields of corn with no spatial anisotropy except in 2000. The feral adults captured at all locations in the study fields were not significantly correlated with the distance from the neighboring potential refuge fields located in different directions from study fields.

When similar models can be used to explain the dispersal of both genders of marked (exponential decay) or feral (linear) adults, this indicates that both males and females follow similar dispersal patterns. However, when two different models can be used to explain the dispersal of marked and feral adults this may mean that the released marked insects and the feral insects likely represent two subpopulations or age groups. One group may settle down within the release field (short distance dispersers), and the other group leaves the field immediately upon eclosion (long distance dispersers). Such divergence has been reported for the pink bollworm, *Pectinophora gossypiella* (Saunders) (Tabashnik et al. 1999); western corn rootworm, *Diabrotica virgifera virgifera* LeConte (Coats et al. 1986); and European corn borer (Qureshi et al. 2005). Low recapture rates of marked populations are very common and recaptures are usually highest in the vicinity of release points (Qureshi et al. 2005). However, another explanation might be that the linear distribution of feral insects may represent the extended tail of the exponential decay equation when it gets beyond 100 to 200 m from the point of dispersal.

In modeling resistance development in southwestern corn borer, Guse et al. (2002) used dispersal parameters that assumed a relatively extensive dispersal (0.4%) and they found that resistance did not develop in 100-yr simulations. However, resistance developed within 33–40 yr when up to 50% of the oviposition was distributed in proportion to the landscape. In the current study, mark–recapture data suggest that male dispersal may be more limited than assumed above because only 1% of marked males were recaptured outside the release field. However, large numbers of feral males from non-Bt maize fields were captured in the Bt maize study fields, and this suggests that male dispersal was more extensive than suggested by mark recapture data. In 1999, the number of feral males captured in the study fields seemed to be 4–6% of the number captured in potential source fields. It is not clear whether this dispersal was extensive enough to be helpful with corn borer resistance management in Bt maize.

In winged insects, it is mainly the mated female that redistributes the population beyond the natal field. The extent of precopulatory dispersal and the location of mating seem to be important considerations in resistance management. The IRM plan for Bt maize assumes that surviving females in a Bt maize field will mate with susceptible males that disperse from refuge plantings in the neighborhood. Rolston (1955) and Langille and Keaster (1973) reported that 66–91% of southwestern corn borer females mated within 24 or 48 h of emergence. In our experiments, marked males and females eclosed together in the buckets and may have mated before dispersing. However, mating success seemed to be poor; 38% of all recaptured females were virgin, whereas 14% of the feral females were virgin. There may be physiological reasons that account for females remaining virgin or there were too few males around when some females eclosed. Johnson (1963) suggested that for many insects females disperse more extensively before they reach the egg-laying stage, and insect flight often becomes more local and presumably less dispersive as females age and the need to lay eggs increases. However, southwestern corn borers females are very heavy upon eclosion and usually oviposit within 24–48 h of eclosion. There would seem to be little time for preovipositional dispersal. Additionally, the favorable environmental conditions within the irrigated maize fields would seem to encourage them to stay in the natal field. Only in 1999 were there any blacklight traps installed outside the release fields, but the numbers released were small, so we cannot say that females did not disperse beyond the study field. Large numbers of feral females captured throughout the study fields may have flown from possible source fields in the neighborhood of 587–1,387 m from the perimeter of study fields or from more distant sources. This suggests that female dispersal may be fairly extensive. This would be a serious concern for resistance management as it enhances the flow of resistance genes out of natal fields and it could decrease the time to development of resistance. However, we did not examine the egg load of the captured females. It is possible that they had laid most of their eggs in their natal fields. Schenck and Poston (1979) reported that peak female capture occurred 2 d after peak oviposition. Feral female captures were always lower than the male captures, which suggests that females may be less dispersive than males. Rolston (1955) reported a sex ratio in southwestern corn borer of 40:60 male/female. However, Schenck and Poston (1979) reported that female captures were lower than male captures. It was not clear whether that was because of the females being less attracted to the light traps or females being less dispersive and thus less likely to fly into the area of the influence of light traps. Therefore, further studies are needed to obtain more information on female dispersal and oviposition because the model for insect resistance development was very sensitive to these parameters (Guse et al. 2002).

Trap competition or interference between the traps did not seem to be a factor in these studies. The minimum distance between light traps in this study was 15 m. This is well beyond the 1–3 m area of influence for light traps with 125-W MV lamps reported for the capture of *Noctua pronuba* L. and *Agrotis exclamationis* L. (Baker and Sadovy 1978). There was no significant difference in the rate of capture for marked or feral southwestern corn borers for light traps with 15-W lamps placed 1.5, 3, or 5 m apart (J.A.Q., unpublished data). This study also was used to collect data on European corn borers, and the capture of feral European corn borer adults also was also suppressed in these traps (Qureshi et al. 2005). This suggests that even traps placed at 1.5 m apart did not interfere with each other. There was no clear patten that pheromone traps captured more southwestern corn borers than did light traps. In 1999, feral male capture was higher in the pheromone traps than in the light traps, but in 2001 the capture was higher in light traps than in pheromone traps. Recapture of marked males was not significantly different between the two types of traps in 2000, but it was higher in the light traps than in pheromone traps in 2001. This inconsistency was surprising because we normally captured many more males in pheromone traps than in light traps. This variability may have been associated with the freshness of the pheromone lures. The lures were stored in a freezer, but no effort was made to standardize the time they were in storage. The presence of light traps in the vicinity of some of the pheromone traps also did not seem to influence capture of southwestern corn borers. The recapture of marked males in 2001 was significantly higher in pheromone traps sited with light traps than in the pheromone traps sited alone, but the capture of feral males was not significantly different. There were many more feral than marked male captures, so they are probably a more reliable indicator on this question.

The recapture rate was slightly higher for the southwestern corn borer than for the European corn borer (Qureshi et al. 2005). For the southwestern corn borer, the proportion recaptured at the release point averaged 6–31% for males and 6–22% for females, and the proportion recaptured beyond the release point averaged 2–18% for males and 0–4% for females. For the European corn borer, the proportion recaptured at the release point averaged 0.9–11% for males and 0.5–11% for females, and the proportion recaptured beyond the release point averaged 0.2–10% for males and 0.1–4.3% for females (Qureshi et al. 2005). The higher recapture rate could in part be because of the southwestern corn borer pheromone traps being more effective than those of the European corn borers. Alternatively, it may be that the southwestern corn borer had more of a tendency to stay in the release field than did European corn borer. The higher recaptures of southwestern corn borer may also be associated with the crop maturity. Some of the low recapture rates for European corn borers occurred during the early season releases in whorl-stage maize, whereas recapture rates were higher in reproductive maize. All southwestern corn borer releases were made in reproductive stage maize.

The dispersal of the southwestern corn borer in this study was similar to that described for the European corn borer (Qureshi et al. 2005). Similar models described the dispersal of both species and the radius of the circle that included 50 and 99% of recaptured corn borers was ≈100 and ≈350 m, respectively. However, the number of southwestern corn borer males that were recaptured in neighboring maize fields seemed to be lower. Only one of 193 (0.5%) recaptured males was outside the release field over the 3 yr (releases) of this study. However, 14 of 430 (3.3%) recaptured European corn borer males were outside the release field over the 2 yr (five releases) of the study (Qureshi et al. 2005). Large numbers of both genders of feral adults of both species were recorded in the study fields. Unlike the European corn borer (Qureshi et al. 2005), the feral southwestern corn borer males were captured in traps installed over the native vegetation in the nonirrigated areas between the irrigated fields. These dry areas did not seem to be barriers for the feral populations of southwestern corn borer. Also the European corn borer has a longer preovipositional period than does the southwestern corn borer, so it is more likely that there is preovipositional dispersal of the European than there is for the southwestern corn borer which has a shorter preovipositional period.

The current resistance management program for European and southwestern corn borers in Bt maize requires that the non-Bt maize refuge field be within 800 m (0.5 mile) of the Bt maize field (USEPA 2001). However, there is no agreement yet on how to use dispersal data to select the maximum separation distance between Bt maize and non-Bt maize refuge plantings that would allow adequate mixing of the potentially resistant and susceptible populations of corn borers for their resistance management. Mo et al. (2003) suggested a maximum separation of <50 m for cauliflower and broccoli fields for resistance management of diamondback moth, *Plutella xylostella* (L). This was based on the average dispersal distances for adults, which they reported to be between 13 and 35 m. They also reported that the radius of an ellipse that would include 99% of the dispersed adults was ≈200 m. In this study and in the study with European corn borer (Qureshi et al. 2005), the radius of the circle that included 50 and 99% of marked corn borers was ≈100 and 350 m, respectively. This is considerably less than the 800 m currently recommended maximum separation distance between Bt maize and non-Bt maize fields. However, it should be noted that the dispersal of feral adults seemed to be more extensive than that of marked adults for both species. Therefore, the actual dispersal between fields may well be considerably greater than the data for marked insects suggest. However, it is not clear whether the dispersal recorded in these studies is extensive enough to support the current resistance management strategy for corn borers. There seems to be some dispersal of corn borers from the nontransgenic refuge fields into the transgenic maize fields and that would allow for some genetic mixing of the Bt-resistant and -susceptible populations. If many corn borers engage in long distance dispersal, then the distance between Bt maize fields and refuge fields will not need to be as restrictive as it is now. Because dispersal patterns of both the European and southwestern corn borers seem to be similar, it is possible that similar resistance management plans may be suitable for the two species in the regions of their sympatric occurrence.

Acknowledgments

We thank R. Long and C. Cole for help with rearing southwestern corn borers; and J. Guzman, A. Nonhof, and other temporary staff for help with field studies. This article is Contribution No. 05-296-J from the Kansas Agricultural Experiment Station and represents work sponsored by F-205, NC-205, Monsanto Co., and AgrEvo Co.

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Received 16 May 2005; accepted 19 October 2005.