Intraguild Competition and Enhanced Survival of Western Bean Cutworm (Lepidoptera: Noctuidae) on Transgenic Cry1Ab (MON810) *Bacillus thuringiensis* Corn

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ABSTRACT The effect of genetically modified corn (event MON810, YieldGard Corn Borer) expressing the *Bacillus thuringiensis* sp. *kurstaki* (Berliner) (*Bt*) endotoxin, Cry1Ab, on the survival of western bean cutworm, *Striacosta albicosta* (Smith), larvae was examined during intraguild competition studies with either European corn borer, *Ostrinia nubilalis* (Hübner), or corn earworm, *Helicoverpa zea* (Boddie), larvae. Competition scenarios were constructed by using either a laboratory or field competition arena containing one of five different diets and one of 13 different larval size-by-species scenarios. The survival of western bean cutworms competing with corn earworms in the laboratory arenas on either a meridic diet or isoline corn silk diet was significantly lower ($P \leq 0.01$) than the controls in 13 out of 14 competition scenarios and larval survival was frequently zero. In contrast, the survival of western bean cutworm competing with corn earworm on a Cry1Ab-MON810 corn silk diet was significant higher ($P \leq 0.01$) than the controls in four out of six competition scenarios. The results observed in the three way competitions involving the addition of European corn borers generally did not alter the outcomes observed in the western bean cutworm and corn earworm only two-way competitions. These data suggest that Cry1Ab-MON810 corn may confer a competitive advantage to western bean cutworm larvae during intraguild competition, particularly from corn earworms, and that western bean cutworms become equal competitors only when they are of equal or larger size and the diet is Cry1Ab-MON810 corn.

KEY WORDS intraguild competition, *Striacosta albicosta*, YieldGard, MON810, Cry1Ab

The western bean cutworm, *Striacosta albicosta* (Smith) (Lepidoptera: Noctuidae), is native to North and Central America (Douglass et al. 1957, Lafontaine 2004). The species was originally collected in Arizona (Smith 1887) but was unknown from the northern Rocky Mountain and central Great Plains states. As a pest of agricultural crops, it was first found eating dry beans (*Phaseolus* spp.) in Colorado but later damaged corn (*Zea mays* L.) in Idaho and the western Great Plains states (McCampbell 1941, Hoerner 1948, Hanstbarger 1969). By 1970, it was causing significant damage to corn throughout Nebraska and occasionally small populations were found as far east as counties bordering the Missouri River in western Iowa (Crumb 1956, Keith et al. 1970, U.S. Department of Agriculture [USDA] 1970, Antonelli 1974, USDA 1977, Blickenstaff 1979). However, the western bean cutworm did not become an established pest east of the Missouri River, as it had in Nebraska, and its occurrence was only sporadically documented in Iowa. In 1999, the insect again began a noticeable range expansion into Minnesota and then into Iowa the following year (O'Rourke and Hutchison 2000, Rice 2000). The Minnesota populations examined at seven locations were extremely small and averaged 0.013 larva/ear while the Iowa population, first found in a commercial cornfield near Holstein in west-central Iowa, was heavily infested with western bean cutworm larvae. Kernel damage was noted on 95% of the ears and some ears were infested with up to six larvae per ear (Rice 2000). In the years that followed, the western bean cutworm expanded its distribution eastward across Iowa and by late summer, 2004, it could be found in most eastern Iowa counties that bordered the Mississippi River. The historical significance of this range expansion is that western bean cutworms quickly moved across the central Corn Belt, being captured for the first time in Illinois and Missouri in 2004 (Dorhout and Rice 2004), and 2 yr later, it was documented for the first time in Indiana, Michigan, and Ohio (Rice and Dorhout 2006, Pope 2007, DiFonzo and Hammond 2008).

The range expansion of western bean cutworm across the Corn Belt is a concern to corn producers because larvae damage the crop by directly feeding on the marketable grain (i.e., corn kernels). One larva per corn plant at dent stage reduces yields by 2.32 q/ha

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(3.7 bu/a) (Appel et al. 1993). Larvae can feed on corn for a considerable length of time, taking an average of 55.9 d to complete their larval development at 27°C, 16L:8D (Antonelli 1974); therefore, there is only one generation per year in North America. Larvae are not cannibalistic and large densities of 20 larvae per ear have been documented in heavily infested cornfields (Seymour et al. 1998).

Western bean cutworms, along with European corn borers, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae) and corn earworms, *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae) are the principal Lepidopteran larvae causing economic damage to corn in Iowa. These three moth species represent a feeding guild, which is a group of species that exploits the same class of environmental resources in the same way (i.e., corn kernels being damaged by larval insects) (Root 1967).

The European corn borer is found in all the corn growing regions of North America from the Atlantic coastal states to the Rocky Mountains (Mason et al. 1996, Steffey et al. 1999). Larvae damage corn principally by tunneling through the stalk, thereby disrupting phloem and xylem tissues, or directly feeding on corn kernels. Larvae take ≈16 d to complete their development at 27°C, 16L:8D period (Matteson and Decker 1965). There are two, and occasionally three, generations a year in Iowa with both the second and third generations potentially feeding directly on corn ears (Mason et al. 1996). European corn borer larvae are not cannibalistic and multiple larvae may be found throughout the corn stalk and ear.

The corn earworm is found throughout the United States wherever corn is grown, but it cannot overwinter north of 40° latitude and must migrate into these areas each summer (Steffey et al. 1999). Larvae damage corn by cutting the silks or feeding directly on kernels in the ear. Larval development requires 18.9 d at 27°C, 16L:8D (Butler 1976), which is three times faster than that of the western bean cutworm. There may be two or three generations a year in Iowa (Steffey et al. 1999). Corn earworm larvae are both predatory on other species and cannibalistic (Barber 1936), which typically results in only one late-stage larva per ear.

The recent range expansion by the western bean cutworm across the central and eastern Corn Belt has prompted questions as to possible causes that may be affecting their population dynamics. One significant change in corn production was the introduction of genetically engineered *Bacillus thuringiensis* sp. *kurstaki* (Berliner) (*Bt*) corn in 1996. This transgenic corn, expressing the Cry1Ab protein, was designed principally to control the European corn borer. Corn hybrids were developed by Monsanto Company (St. Louis, MO) expressing the *Bt* endotoxin Cry1Ab (event MON810) and marketed as YieldGard Corn Borer. This MON810 technology, expressed in YieldGard Corn Borer hybrids, is highly toxic and kills nearly 100% of European corn borer larvae and 75–88% of corn earworm larvae (Koziel et al. 1993, Gould 1994, Armstrong et al. 1995, Rice and Pilcher 1998, Burkness et al. 2001, Horner et al. 2003) while not negatively affecting western bean cutworms (Helms and Wedberg 1976, Catangui and Berg 2006, Eichenseer et al. 2008) or the growth and development of beneficial insects (Pilcher et al. 1997). An additional effect is that MON810 corn has also been shown to reduce the cannibalistic behavior of corn earworms (Horner and Dively 2003) and reduces their fitness (Horner et al. 2003). Because MON810 corn effectively controls European corn borer and most corn earworm while not negatively affecting western bean cutworm, it therefore seems plausible that MON810 corn hybrids might be influencing western bean cutworm survival and facilitating their expanding distribution by providing a relatively exclusive habitat that, of these three ear-feeding guild species, only western bean cutworms could effectively use.

The objective of this study was to examine the influence of genetically-modified *Bt* corn (Cry1Ab, event MON810, YieldGard Corn Borer) on the survival of western bean cutworms during intraguild competition with European corn borer and corn earworm larvae.

Method and Materials

Insect Colonies. In 2005, adult western bean cutworm, European corn borer, and corn earworm were collected from black-light traps near Ames, IA, and held in cages until females oviposited. In 2006, corn earworm eggs were commercially purchased (French Agricultural Research Inc., Lamberton, MN) while western bean cutworm and European corn borer adults were again collected from black-light traps near Ames. Before this experiment, the mechanics for continuously rearing western bean cutworms had not been developed and eggs could only be gained by capturing and holding feral moths for oviposition. Captured adult moths during both years were held in screen cages. Laid eggs were collected and transferred to a modified black cutworm diet with aureomycin and benlate omitted (Hendrix et al. 1991, Lewis and Lynch 1969).

Larval Diet. Before experimentation, European corn borers were maintained on a standard wheat germ meridic diet (Lewis and Lynch 1969) while western bean cutworms and corn earworms were maintained on a modified meridic black cutworm diet with aureomycin and benlate deleted (Hendrix et al. 1991). All larvae were held in an environmentally controlled room at 27°C, 16L:8D, and ≈80% RH before experimentation.

Larval diet for intraguild competitions consisted of either the modified black cutworm diet or corn silk. Corn silks from field-grown Cry1Ab-MON810 YieldGard Corn Borer (Corn States 304 YieldGard, Des Moines, IA) plants and a near isoline hybrid (Corn States 304) were removed from the respective ears as needed, washed in a 2% bleach solution for 4 min, and then rinsed in distilled water for 4 min. Only green silks were used to evaluate intraguild competition.

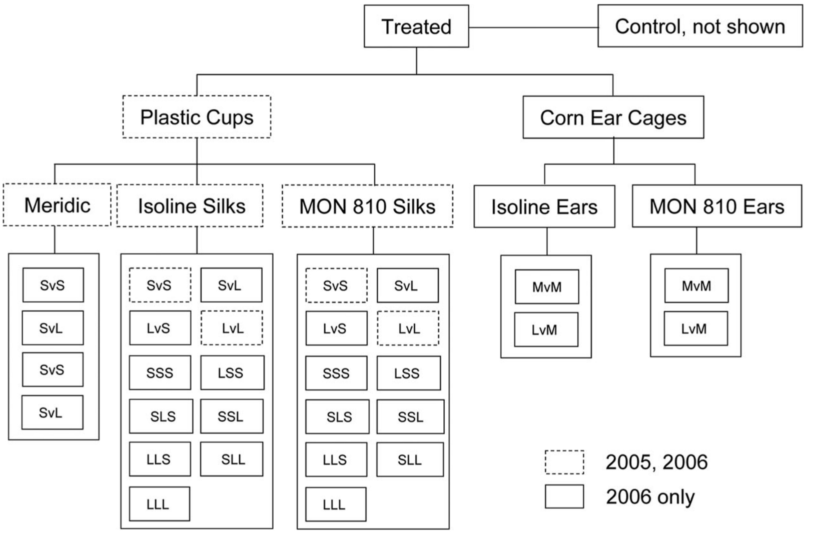

Fig. 1. Flow chart showing the order of the components examined. The order of the components for the control is the same as the treated, but is not shown. First capital letter corresponds to the size of the western bean cutworm larva and the second and third capital letters corresponds to the size of the corn earworm and European corn borer larvae, respectively. S, small; M, medium; L, large; v, versus and denotes a two-way competition.

Experimental Design. A completely randomized design was used with treatments replicated based on availability of western bean cutworm and corn earworm larvae. The experiment had three components and followed a 2 × 5 × 13 treatment design that was unbalanced and incomplete (Fig. 1). The three components were competition arena, larval diet, and intraguild competition.

The first component (competition arena) was divided into field trials using cages on corn ears or laboratory trials using plastic cups containing either meridic or corn silk diet. The field trials used cages constructed from aluminum hardware cloth (4 mm^2 mesh) cut into 30 cm squares. One edge of the hardware cloth was placed halfway along the major axis of the corn ear, which allowed ≈15 cm of the hardware cloth to extend beyond the ear tip. The hardware cloth was then rolled two times around the corn ear, thereby forming a cylinder. The bottom of the cage was held tight around the corn ear by cinching a cable tie over both the hardware cloth and the corn ear. Larvae were placed on the corn silks and then the top of the cage was closed by folding the end back onto itself and stapling it while leaving an internal space of ≈10 cm between the ear tip and the end of the cage. Corn ear cages were used only in 2006 because of limited availability of western bean cutworm larvae in 2005. The laboratory trials used clear plastic cups (18 or 30 ml in 2005 and 2006, respectively) (Fill Rite, Newark, NJ) filled halfway with the respective diet. The smaller cup (18 ml) was an older style container that was unavailable for experimentation the second year of the experiment. However, silk density was nearly identical for both cup sizes.

The second component was divided into five levels based on the type of diet used within the competition arenas. These were a modified meridic black cutworm diet, MON810 corn silks or ears in the field, and near isogenic corn silks or ears in the field.

The third component was divided into 13 levels based on intraguild competition scenarios comprised of different instars and species combinations (Fig. 1). There were a total of eight treatments (2005) or 30 treatments (2006) across all diets and competition arenas.

Treatments. Two-way intraguild competitions were constructed by placing a western bean cutworm larva with a corn earworm larva, each of a particular size, and recording western bean cutworm survival after 9 d. Three-way intraguild competitions included the previous two species plus an European corn borer of a particular size. The larvae for a particular competition were selected from three relative size categories (small, medium, and large). Larvae were placed in a particular size category based on their relative overall body size and their similarity to a larva of a different species within the same relative size category (Table 1). Thus, in a treatment examining a small larva versus a small larva scenario (expressed as sm versus sm or

Table 1. Species, instars, and relative size categories used in intraguild competition studies

Insect	Instar	Relative size
Western bean cutworm	2, 3	Small
	3	Medium
	4, 5	Large
Corn earworm	3, 4	Small
	4	Medium
	5	Large
European corn borer	3, 4	Small
	6	Large

Table 2. Intraguild competition between two sizes of western bean cutworm and corn earworm larvae, 2005

Diet	Competition scenario[a]	df	χ^2 value	*P* value	Treated: Live western bean cutworm	Treated: Reps (*n*)	Control: Live western bean cutworm	Control: Reps (*n*)
Meridic	sm vs sm	1	13.8462	0.0002	1	6	12	12
Meridic	sm vs lg	1	19.0000	<0.0001	0	7	12	12
Meridic	lg vs sm	1	8.1458	0.0043	2	7	11	12
Meridic	lg vs lg	1	19.0000	<0.0001	0	7	12	12
Isoline silks	sm vs sm	1	19.0000	<0.0001	0	7	12	12
Isoline silks	lg vs lg	1	12.3148	0.0004	0	7	10	12
MON810 silks	sm vs sm	1	0.5294	0.4669	6	6	11	12
MON810 silks	lg vs lg	1	0.9167	0.3384	3	3	6	8

[a] sm, small; lg, large; first size, western bean cutworm; second size, corn earworm.

SvS), a second instar western bean cutworm competed with a third instar corn earworm, however, the two species were of approximately equal sizes. Intraguild competitions among larvae are presented as sizes (small, medium, or large) of western bean cutworm versus corn earworm, or in the case of three-way intraguild competitions, the second and third species are the corn earworm and European corn borer, respectively. A three-way intraguild competition, such as MvsMvsL, represents a medium western bean cutworm staged against a medium corn earworm and a large European corn borer.

Controls were constructed by using two (or three) western bean cutworms of the same sizes as the two or three larvae in the intraguild competition treatments. These controls mimicked the effect of resource and spatial competition, but not the interspecies behaviors, thereby allowing the unique effects of corn earworm and European corn borer behavior on western bean cutworm survival to be determined. Each competition in the laboratory was conducted at 27°C, 16L:8D and ≈80% RH for 9 d in a walk-in environmental chamber. The field competitions on corn ears were conducted for 9 d from 27 July to 5 August 2006.

Statistical Analyses. Data from each intraguild competition were analyzed for independence using a χ^2 test (CHISQ option, PROC FREQ; SAS Institute 2007) between the survival of the treated western bean cutworm and its corresponding control. Results are expressed as larval survival (means ± SEM) with treatment differences significant at $P \leq 0.01$.

Results

Larval Competition on Meridic Diet. In 2005, the survival of western bean cutworm in competition with corn earworm was significantly lower than the controls across all size scenarios on the meridic diet (Table 2; Fig. 2). Western bean cutworms in competition with corn earworms had 0% survival in the small versus large and large versus large competition scenarios. There was a small amount of western bean cutworm survival in the small versus small and large versus small scenarios, 16.7 ± 15.2 and 28.6 ± 17.1%, respectively. The survival of western bean cutworm larvae in all of the controls was 100% except for the large versus small scenario, where survival was 91.7 ± 8.0%.

In 2006, survival of western bean cutworms in competition with corn earworms followed the same trends observed in 2005 and were significantly lower than the controls across all size scenarios on the meridic diet (Table 3; Fig. 3). Western bean cutworm larvae paired with corn earworms had 0% survival in the small versus large and large versus large intraguild competition scenarios. There was an increase in the survival of larvae in the small versus small and large versus small scenarios, 16.0 ± 15.0 and 48.0 ± 20.4%, respectively. In contrast, survival of paired western bean cutworms in the controls was very high and ranged from 74.0 ± 17.9–92.0 ± 11.1%.

Larval Competition on Corn Silks. In 2005, intraguild competition (small versus small and large versus large) on the isoline silk diet resulted in no survival of western bean cutworms whereas the paired western bean cutworms in the controls on MON810 silk had 100 and 83.3 ± 15.2% survival, respectively (Table 2; Fig. 2). We observed that mortality in the mixed species competitions was caused by corn earworms attacking, eating, and eventually killing the western

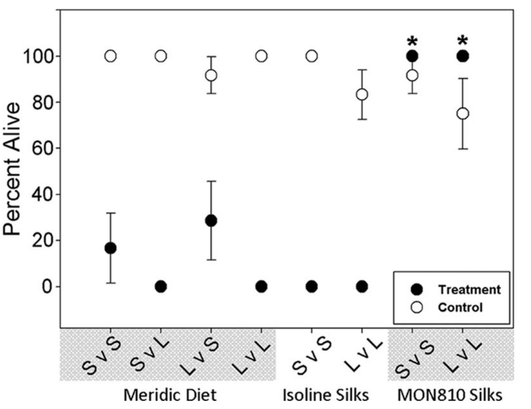

Fig. 2. Survival (means ± SEM) of western bean cutworm larvae competing with corn earworm larvae (black circle) or a conspecific (open circle) in 2005. On the horizontal axis, the first and last capital letters correspond to the relative sizes of the western bean cutworm and corn earworm, respectively. S, small; L, large, v, versus western bean cutworms in the controls were similarly sized. *No significant difference between the survival of the treated and control western bean cutworms, χ^2 test, $P \leq 0.01$.

Table 3. Intraguild competition and survival of western bean cutworm larvae on several diets with corn earworm or European corn borer, 2006

Diet	Competition scenario[a]	χ^2 df	χ^2 value	χ^2 *P* value	Treated: Live western bean cutworm	Treated: Reps (*n*)	Control: Live western bean cutworm	Control: Reps (*n*)
Meridic	sm vs sm	1	26.19	<0.0001	4	25	39	50
Meridic	sm vs lg	1	47.72	<0.0001	0	25	42	50
Meridic	lg vs sm	1	18.41	<0.0001	12	25	46	50
Meridic	lg vs lg	1	36.51	<0.0001	0	25	37	50
Isoline silks	sm vs sm	1	50.89	<0.0001	6	25	50	50
Isoline silks	sm vs lg	1	29.19	<0.0001	1	20	38	50
Isoline silks	lg vs sm	1	2.06	0.1514	15	25	38	50
Isoline silks	lg vs lg	1	35.11	<0.0001	1	20	34	50
MON810 silks	sm vs sm	1	5.63	0.0177	17	25	45	50
MON810 silks	sm vs lg	1	20.00	<0.0001	0	8	15	16
MON810 silks	lg vs sm	1	1.51	0.2196	8	8	15	18
MON810 silks	lg vs lg	1	12.29	0.0005	4	22	27	42
MON810 ear[b]	lg vs md	1	0.12	0.7249	3	5	4	8
MON810 ear[b]	md vs md	1	0.004	0.9493	2	5	5	12
Isoline ear[b]	lg vs md	1	0.26	0.6109	6	11	9	20
Isoline ear[b]	md vs md	1	0.07	0.7888	4	10	7	20
Isoline silks	lg vs lg vs lg	1	13.71	0.0002	0	8	18	24
Isoline silks	lg vs lg vs sm	1	9.41	0.0022	0	8	15	24
Isoline silks	lg vs sm vs sm	1	22.22	<0.0001	1	8	23	24
Isoline silks	sm vs lg vs lg	1	13.71	0.0002	0	8	18	24
Isoline silks	sm vs lg vs sm	1	20.36	<0.0001	0	8	21	24
Isoline silks	sm vs sm vs lg	1	22.22	<0.0001	1	8	23	24
Isoline silks	sm vs sm vs sm	1	26.88	<0.0001	1	8	24	24
MON810 silks	lg vs lg vs lg	1	9.94	0.0016	0	8	16	25
MON810 silks	lg vs lg vs sm	1	11.59	0.0007	2	8	21	24
MON810 silks	lg vs sm vs sm	1	0.61	0.8050	6	8	19	24
MON810 silks	sm vs lg vs lg	1	18.60	<0.0001	1	8	22	24
MON810 silks	sm vs lg vs sm	1	20.36	<0.0001	0	8	21	24
MON810 silks	sm vs sm vs lg	1	7.80	0.0052	2	8	19	24
MON810 silks	sm vs sm vs sm	1	6.10	0.0136	5	8	23	24

[a] sm, small larva; md, medium larva; lg, large larva; first size, western bean cutworm; second size, corn earworm; and third size (if present), European corn borer.
[b] Field exp.

bean cutworms (Fig. 4). In the small versus small competition scenario, all of the western bean cutworms had been consumed by the corn earworms within the first 72 h of the experiment.

Very different results were observed in both mixed species intraguild competitions (small versus small and large versus large) on the MON810 corn silk diet. No difference was observed between the survival of western bean cutworms in the presence of either a corn earworm or conspecific (Table 2; Fig. 2). The western bean cutworms paired with corn earworms had 100% survival in the small versus small and large versus large scenarios, which were not significantly different from the paired controls at 91.7 ± 8.0 and 83.3 ± 10.8%, respectively.

In 2006, two more 2-way intraguild interactions on MON810 and isoline corn silks were added (Fig. 1). On the isoline silk diet (Fig. 3), results similar to 2005 were observed (Table 3; Fig. 3). The survival of western bean cutworm competing with corn earworm was significantly lower than the controls across all scenarios except in the large versus small competition where the treatment was not significantly different from the control, 60.0 ± 20.0 and 76.0 ± 17.4% survival, respectively.

The survival of western bean cutworm in competition with corn earworm on MON810 silk (Table 3; Fig. 3) was again different than the survival of western bean cutworm on the meridic or isoline silk diets. The survival of western bean cutworms in the small versus small or large versus small competition scenarios (68.0 ± 19.0 and 100%, respectively) on the MON810 silk diet was not significantly different from the survival of the controls (90.0 ± 12.3 and 83.3 ± 15.2%, respectively). However, the survival of western bean

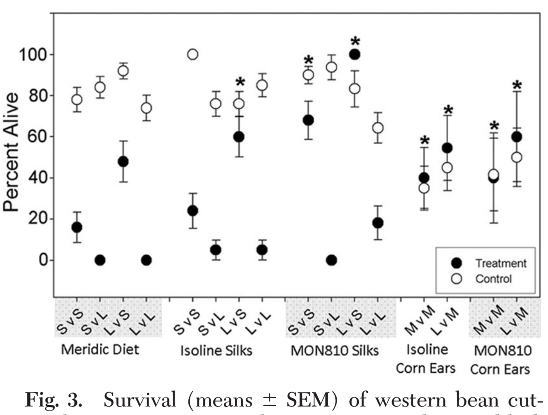

Fig. 3. Survival (means ± SEM) of western bean cutworm larvae competing with corn earworm larvae (black circle) or a conspecific (open circle) in 2006. On the horizontal axis, the first and last capital letters correspond to the relative sizes of the western bean cutworm and corn earworm, respectively. S, small; M, medium; L, large; v, versus Western bean cutworms in the controls were similarly sized. *No significant difference between the survival of the treated and control western bean cutworms, χ^2 test, $P \leq 0.01$.

Fig. 4. Western bean cutworm (top) killed by similar sized corn earworm.

cutworms in the small versus large or large versus large competition scenarios (0 and 18.2 ± 15.8%, respectively) on the MON810 silk diet was significantly different from the controls (93.8 ± 9.9 and 64.3 ± 19.6%, respectively).

In 2006, seven intraguild competitions on silks with European corn borer larvae were added (Fig. 1). The survival of the western bean cutworms in the three-way species competition (Table 3; Fig. 5) on the isoline were significantly lower than the survival of the control western bean cutworms in all scenarios ($P \leq 0.01$, Fig. 5). In contrast, there were two scenarios (sm versus sm versus sm, and lg versus sm versus sm) on the MON810 silk diet where western bean cutworm survival (62.5 ± 19.8 and 75.0 ± 17.7%, respectively) was not significantly different from the controls (95.8 ± 8.2 and 79.2 ± 16.6%, respectively). Adding European corn borer larvae to the three-way intraguild competitions (Table 4) did not significantly affect the survival of the western bean cutworms when compared with the similar two-way competitions (Fig. 3) (i.e., comparing sm versus sm, to sm versus sm versus sm. and sm versus sm versus lg).

Field Trial. During 2005, there were insufficient western bean cutworm larvae available for conducting

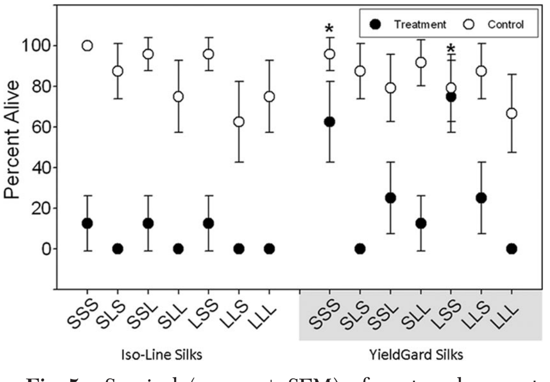

Fig. 5. Survival (means ± SEM) of western bean cutworm larvae competing with both corn earworm larvae and European corn borer larvae (black circle) or two conspecifics (open circle), 2006. On the horizontal axis, the first, second and third capital letters correspond to the relative sizes of the western bean cutworm, corn earworm, and European corn borer, respectively. S, small; M, medium; L, large. Western bean cutworms in the controls were similarly sized. *No significant difference between the survival of the treated and control western bean cutworms, χ^2 test, $P \leq 0.01$.

Table 4. Survival of western bean cutworm in two-way and three-way competitions on isoline and MON810 corn silks where western bean cutworm and corn earworm larval sizes were held constant and European corn borer larvae of two different sizes were added, 2006

Diet	Two-way competition[a]	Three-way competition[a]	df	χ^2 value	χ^2 probability[b]
Isoline silks	sm vs sm	sm vs sm vs sm	1	0.48	0.49
		sm vs sm vs lg	1	0.48	0.49
	lg vs lg	sm vs lg vs sm	1	0.41	0.52
		sm vs lg vs lg	1	0.41	0.52
	lg vs sm	lg vs sm vs sm	1	5.47	0.02
		lg vs sm vs lg		—	—
	lg vs lg	lg vs lg vs sm	1	0.41	0.52
		lg vs lg vs lg	1	0.41	0.52
MON810 silks	sm vs sm	sm vs sm vs sm	1	0.08	0.77
		sm vs sm vs lg	1	4.59	0.03
	sm vs lg	sm vs lg vs sm	1	0.00	1.00
		sm vs lg vs lg	1	1.07	0.30
	lg vs sm	lg vs sm vs sm	1	2.29	0.13
		lg vs sm vs lg		—	—
	lg vs lg	lg vs lg vs sm	1	0.17	0.68
		lg vs lg vs lg	1	1.68	0.20

[a] sm, small; lg, large; vs, versus; "-" indicates competition scenario not performed because of limited numbers of *Striacosta albicosta.* First size, western bean cutworm larvae; second size, corn earworm; and third size, European corn borer larvae.

[b] χ^2 probabilities <0.01 indicate that adding European corn borer larvae significantly altered the survival of western bean cutworm.

experiments in the field. In 2006, larvae on corn ears in the field were added to the experiment. The survival of western bean cutworms in all the treatment competitions on the MON810 and isoline corn hybrids were not significantly different from the controls (Fig. 3, Table 3). At the end of the experiment, we determined that a natural population of western bean cutworms had infested the plot and more western bean cutworms were found in the ear cages than were originally placed in them, thereby confounding the data. We suspect that early instar western bean cutworms were already in the ears before the cages were attached and went undetected at the beginning of the experiment or that neonates were able to craw through the screen holes.

Discussion

The objective of this study was to measure the potential effects of genetically modified corn, specifically event MON810 that expresses the *Bt* endotoxin, Cry1Ab (Koziel et al. 1993, Armstrong et al. 1995), on the survival of western bean cutworm larvae in the presence of potential intraguild competitors—the corn earworm and European corn borer. These three species have been significant pests of corn throughout the western Corn Belt and have co-existed in Nebraska during the last several decades of the previous century. Of these three species, only the western bean cutworm failed to establish itself east of the Missouri River in Iowa, Minnesota, or Missouri. Western bean cutworm larvae had caused significant economic yield loss to corn in eastern Nebraska, but before 1999 or 2000 similar yield losses in Minnesota (O'Rourke and Hutchison 2000) or Iowa (Rice 2000), respectively, had never been documented. The recent expansion of the western bean cutworm into Minnesota and Iowa, and then more quickly into the eastern Corn Belt states, has been cause for alarm for corn producers, but more interestingly it creates an entomological question as to why the western bean cutworm has recently undergone a rapid and significant range expansion occurred.

One of the most significant changes in the production of corn in the Corn Belt was the introduction in 1996 and widespread adoption of transgenic *Bt* corn (U.S. Department of Agriculture–National Agricultural Statistics Service [USDA–NASS] 1997). By 2002, *Bt* corn hybrids containing event MON810 (Cry1Ab) were planted on 6.555 million ha (16.2 million a), or 26.1% of the acreage, in the top 10 corn-producing states (USDA–NASS 2003). MON810 corn is extremely lethal to European corn borer larvae but is mildly toxic to corn earworm larvae. We hypothesized that this significant landscape change in corn production might possibly be *one* of the several biological and environmental reasons that potentially influenced the rapid range expansion of western bean cutworms, specifically as it might have affected intraguild competition of ear-feeding Lepidopteran larvae.

We examined in the laboratory hypothetical intraguild competition scenarios involving the western bean cutworm, corn earworm, and European corn borer. Both a natural diet of corn silks and a modified meridic diet were used. The survival of western bean cutworms in the presence of corn earworm larvae on either a meridic diet or isoline corn silks was near zero and significantly lower than the western bean cutworm control survival of almost 100%. Corn earworm larvae are more aggressive, even against conspecifics (Barber 1936), and stronger competitor species than western bean cutworms, often killing them, even if the western bean cutworm was initially larger than the corn earworm. This intraguild competitive advantage is probably partially because of the three times faster development rate of the corn earworm under the same conditions (Antonelli 1974, Butler 1976). In contrast, western bean cutworm survival on MON810 corn silks was near 100% when the larvae were of equal or larger size than the corn earworms. The results also show that European corn borer larvae, in the three-way competitions, generally did not alter the intraguild outcomes observed in the two-way interactions and are probably not the primarily guild species responsible for reducing the survival of western bean cutworms.

These data suggest that MON810 corn confers a competitive advantage to western bean cutworm larvae in the presence of intraguild competition from corn earworms and European corn borer larvae. This is especially true with the aggressive corn earworm (Barber 1936) that become much less aggressive (Horner and Dively 2003) and less fit (Horner et al. 2003) on MON810 silks. Western bean cutworms become equal competitors only when they are of equal or larger size than corn earworms on MON810 silks. Thus, if competition from corn earworm populations had been significantly suppressing either the movement or population increase of western bean cutworms east of Nebraska and into the central Corn Belt, then the recent introduction and widespread planting of MON810 (Cry1Ab) corn could have acted as part of an ecological release for western bean cutworms, thereby expanding their range into the central and eastern Corn Belt. A historical review of past and recent corn earworm populations across the Corn Belt would be needed to help substantiate or disprove this hypothetical field interaction between corn earworm and western bean cutworm. Unfortunately, we know of no such data set.

This artificial laboratory experiment does not answer the question of intraguild competition in corn with western bean cutworms and other species in the field, but it does suggests a potential direction for future field research to determine the importance of intraguild competition in the recent range expansion of western bean cutworm.

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