2020

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Journal of Economic Entomology, XX(XX), 2020, 1–8
doi: 10.1093/jee/toaa136
Research

Geographic Distribution of *Bacillus thuringiensis* Cry1F Toxin Resistance in Western Bean Cutworm (Lepidoptera: Noctuidae) Populations in the United States

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Subject Editor: Lisa Bird

Received 29 January 2020; Editorial decision 29 May 2020

Abstract

The western bean cutworm (WBC), *Striacosta albicosta* (Lepidoptera: Noctuidae), can be a severe pest of transgenic corn in the western Plains and Great Lakes regions of North America, including on hybrids expressing the *Bacillus thuringiensis* (Bt) Cry1F toxin. The level and geographic distribution of Cry1F resistance are not completely known. Neonate *S. albicosta* from 10 locations between Nebraska and New York state were subjected to dose–response trypsin-activated native Cry1F toxin overlay bioassays. In 2017, the mean estimated lethal concentration causing 50% larval mortality (LC_{50}) ranged from 15.1 to 18.4 µg Cry1F cm^{-2}, and were not significantly different among locations. In 2018, LC_{50} estimates at Scottsbluff, NE (22.0 µg Cry1F cm^{-2}) and Watertown, NY (21.7 µg Cry1F cm^{-2}) were significantly higher when compared to locations in Michigan (15.8 µg Cry1F cm^{-2}). Significantly lower 14-day larval weight among survivors was correlated with higher Cry1F dose. Results from this study indicate that *S. albicosta* survivorship on purified Bt Cry1F toxin shows a relatively even distribution across the native and range expansion areas where seasonal field infestations typically occur.

Key words: insecticidal protein toxin, resistance

The native range of the western bean cutworm (WBC), *Striacosta albicosta* (Smith) (Lepidoptera: Noctuidae), spans the western Great Plains where it remains a pest of cultivated dry beans (*Phaseolus vulgaris* L.) and corn (*Zea mays* L.) (Smith 1887, Hoerner 1948, Keaster 1999). A relatively recent range expansion increased the geographic distribution of *S. albicosta* (Michel et al. 2010, Hutchison et al. 2011) to include portions of Wisconsin by 2005 (Cullen and Jyuotika 2008), followed by movement into Indiana, Michigan, and Ohio (Smith et al. 2019). The current range is as far east as Ontario, Quebec, Pennsylvania, New Jersey, New York, and Nova Scotia (Tooker and Fleischer 2010; Wise 2017; Smith et al. 2018a, 2019), and south into Mexico (Sánchez-Peña et al. 2016). The factors contributing to this range expansion remain unknown. One hypothesis is lack of intra-guild competition following reductions in European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae), and corn earworm, *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae), populations following the widespread adoption of transgenic corn expressing the *Bacillus thuringiensis* (Bt) Cry1Ab toxin (Dorhout and Rice 2010). Reductions in insecticide use following increased Bt adoption and changes in tillage practices, among other reasons, have also been proposed (Hutchison et al. 2011).

Regardless, *S. albicosta* populations are now established in the eastern expansion region of North America (Smith et al. 2018a, 2019) in areas where sandy soils and seasonal temperatures are favorable for overwinter survival (Douglass et al. 1957, Antonelli 1976, Seymour et al. 2010, Hanson et al. 2018).

Striacosta albicosta has a univoltine lifestyle, where moths emerge from diapaused overwintering prepupae in midsummer. Females are attracted to corn in late whorl-stage prior to anthesis, whereupon oviposition occurs mostly on the upper-most leaves and leaf collars (Blickenstaff 1979, Holtzer 1983, Eichenseer et al. 2008). Following eclosion, neonates preferentially feed and develop on tissues of young tassel (Paula-Moraes et al. 2012). After 15 d, larvae are capable of moving several meters between plants within and across rows (Pannuti et al. 2016), but these late instars are primarily found feeding on ears (Appel et al. 1993). The level of ear feeding damage caused by late instars is exacerbated by the fact that *S. albicosta* are not cannibalistic, and multiple larvae can be found per ear. Subsequent feeding on corn kernels causes economically significant damage. In its western range yield loss is of primary concern (Appel et al. 1993; Paula-Moraes et al. 2013). In the Great Lakes and eastern range, the primary concern is that damage can reduce grain quality by providing entry points for molds that release mycotoxins (Parker et al. 2017, Smith et al. 2018a).

Foliar insecticides are used to control larval *S. albicosta* feeding damage, but field efficacy is highly dependent upon rate and timing of applications (Montezano et al. 2017, 2019a; Swoboda-Bhattarai et al. 2018). In general, control with insecticides greatly diminishes after *S. albicosta* larvae enter the ear (Michel et al. 2010). The commercialization of transgenic corn hybrids that express one or more insecticidal Bt proteins can provide season-long control when Bt toxins are efficacious and expressed at a high dose against insect species. However, Bt corn hybrid options are more limited for *S. albicosta* control. For example, studies show that *S. albicosta* is insensitive to and cannot be effectively controlled by Bt corn expressing Cry1Ab and Cry2Ab2 toxins (Catangui and Berg 2006, Eichenseer et al. 2008, Hutchison et al. 2011). In contrast, *S. albicosta* populations maintain susceptibility toward Bt Vip3A toxin (Farhan et al. 2017, Montezano et al. 2019b), but susceptibility is diminished among later instars (Farhan et al. 2019). Regardless, the availability of Vip3A hybrids is currently limited. Cry1F corn hybrids were initially capable of reducing the incidence of feeding damage (Eichenseer et al. 2008, Rule et al. 2014); however, even at the time of initial commercialization, the toxin level was never capable of providing complete suppression of *S. albicosta* feeding damage (Ostrem et al. 2016). Additionally, a majority of growers and crop consultants in Nebraska have observed a decrease in efficacy toward *S. albicosta* (Archibald et al. 2017), the perceived yield loss due to this pest has steadily increased since 2014 (Smith et al. 2017, 2018b, 2019).

Striacosta albicosta resistance to Cry1F transgenic corn is documented. Specifically, Cry1F resistance levels measured by laboratory bioassay have increased ~5.2-fold among field populations following one decade of commercialization (Ostrem et al. 2016), and there currently is no significant differences in ear feeding damage between non-Bt and Cry1F hybrids (Smith et al. 2017, 2019). Additionally, there is an estimated 31.1% mean survival of *S. albicosta* neonates infested on Cry1F hybrids within field plots (Montezano et al. 2019b). This accumulated evidence may have contributed to registrant removal of *S. albicosta* from the list of controlled species on seed corn bags (Unglesbee 2017), recognition of Cry1F resistance by this species in the peer-reviewed literature (Tabashnik and Carrière 2017) and a published regulatory review by the U.S. Environmental Protection Agency (USEPA 2018). Furthermore, the impact of *S. albicosta* Cry1F resistance on insect resistance management (IRM) plans was undertaken by a 2018 EPA Scientific Advisory Panel (SAP; USEPA-SAP 2018). This shift may be due to recent alterations in production practices and the adaptive response of *S. albicosta* has shifted the agricultural pest landscape in recent years (Catarino et al. 2015). Although the increased incidence of documented Cry1F resistance has been shown among populations within the native range of *S. albicosta* in the western Great Plains (Ostrem et al. 2016) and Ontario, Canada (Smith et al. 2017), the prevalence and comparable variation of levels of Cry1F resistance across the current geographic range of *S. albicosta* remains unknown. In the following study, the temporal and spatial distribution of variance in *S. albicosta* Cry1F survivorship was estimated across 10 sample locations from Nebraska to New York in the United States.

Materials and Methods

Field Collections

Striacosta albicosta were collected during mid-July 2017 at nine locations across Nebraska (n = 7), Michigan (n = 1), and New York state (n = 1), and nine locations during this same time period in 2018 from Nebraska (n = 6), Michigan (n = 2), and New York

Table 1. Dose-response of *Striacosta albicosta* larvae from 10 field populations to laboratory *Bacillus thuringiensis* (Bt) Cry1F toxin overlay bioassays given in units of lethal concentration required to cause mortality in 50% of larvae (LC_{50}) at 14 d postinfestation

		2017 bioassays				2018 bioassays			
ID	Location	n	Slope±SE	LC_{50} (95% FL) #	χ^2	n	Slope±SE	LC_{50} (95% FL) #	χ^2
BE	Benkelmen, NE	192	0.74 ± 0.11	8.28 (6.20–11.60)	21.89	0	NA	NA	NA
BR	Brule, NE	250	1.92 ± 0.12	17.49 (15.41–20.59)	1.48	283	1.71 ± 0.10	18.44 (15.36–22.82)^{abc}	13.14
GR	Grant, NE	251	1.81 ± 0.12	16.92 (14.81–20.07)	5.13	284	1.68 ± 0.10	21.33 (18.27–25.85)^{ab}	1.47
KE	Kearney, NE	253	1.60 ± 0.11	17.70 (14.66–23.20)	6.26	285	1.82 ± 0.11	19.38 (17.39–21.88) ^{ab}	3.58
NP	North Platte, NE	249	1.76 ± 0.11	16.92 (14.68–20.35)	4.52	284	1.75 ± 0.10	19.75 (17.47–22.74) ^{ab}	0.97
CN	Central NE pool*	1,003	1.81 ± 0.11	17.26 (15.,98–18.88)	8.26	1,140	1.43 ± 0.11	19.564 (15.,56–26.49)	45.59
ON	O'Neill, NE	250	1.72 ± 0.11	17.31 (14.75–21.47)	1.63	287	1.23 ± 0.09	15.95 (13.27–19.58)^{bc}	3.45
SB	Scottsbluff, NE	253	1.73 ± 0.11	16.79 (14.54–20.19)	3.79	288	2.00 ± 0.11	22.02 (19.68–25.14)^{a}	2.78
EL	East Lansing, MI	253	1.66 ± 0.11	15.12 (13.33–17.57)	2.51	279	1.46 ± 0.10	15.21 (13.63–17.07)^{c}	10.15
ST	Stanton, MI	0	NA	NA	NA	285	1.40 ± 0.09	16.56 (14.31–19,462)^{bc}	8.14
WT	Watertown, NY	251	2.00 ± 0.12	18.44 (16.16–21.97)	3.14	286	1.89 ± 0.11	21.72 (19.17–25.21)^{ab}	7.78

Means (±SE) assigned the same letter in superscripts following fiduciary limit (FL) are not significantly different between populations collected in 2018 according to LSD $P \leq 0.05$.

NA, data not collected; χ^2, Pearson's goodness-of-fit; #, units of µg Bt Cry1F toxin cm^{-2}; *, aggregate analysis of BE, BR, GR, KE and NP by year.

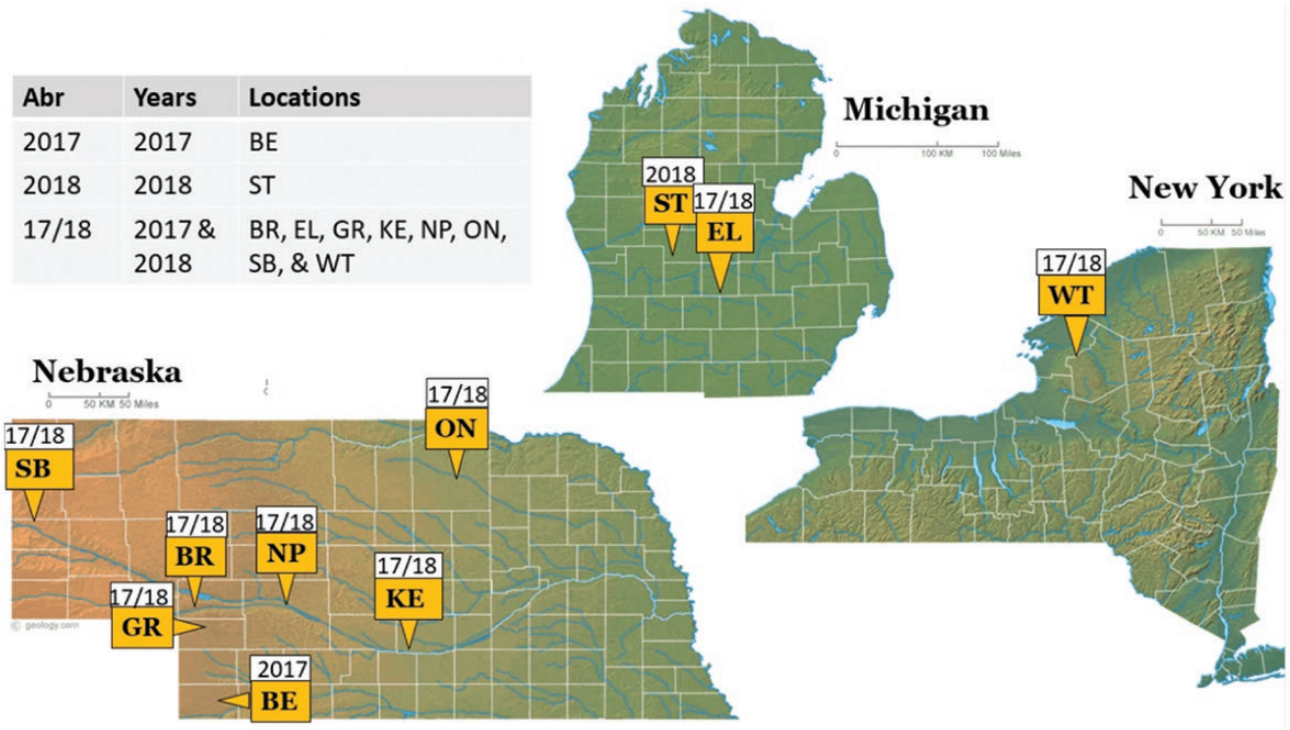

Fig. 1. Location of *Striacosta albicosta* collection sites in Michigan, Nebraska, and New York. Corresponding populations IDs are as in Table 1.

state (n = 1) (Table 1; Fig. 1). Between 100 and 300 egg masses were collected by field scouting at Brule (BR), Grant (GR), and Scottsbluff (SB) locations in Nebraska in both 2017 and 2018 (Fig. 1). For this, a section of leaf or leaf collar with an egg mass was excised from infested corn plants using scissors, individually placed into a self-sealing bag, and stored in a cooler prior to being taken into the Agroecosystems Entomology Laboratory at the University of Nebraska-Lincoln, West Central Research and Extension Center, North Platte (NP), NE (Fig. 1). Neonates from these field-collected eggs were used directly to infects bioassay trays. For all remaining locations, neonates were collected from egg masses laid by field-collected females. For this, adults were collected from 2.13 × 1.17 × 1.17 m screened walk-in 110V blacklight traps with four 5.7 liter planters of ~2- to 3-wk-old pinto bean, *Phaseolus vulgaris* L. (Fabaceae), at the base of each trap to provide shelter and oviposition substrate (Montezano et al. 2019c). Collected adults were transferred to the laboratory, and placed into 63.5 × 63.5 × 63.5 cm rearing cages (Bug Dorm, MegaView Science Co., Ltd., Talchung, Taiwan) containing late vegetative stage *P. vulgaris* for oviposition. Adults were provided a 5% sucrose and 0.2% ascorbic acid solution in a 150 × 15 mm sponge inside a Petri dish. Each mesh cage contained approximately 50–400 field-collected moths. Egg masses were collected daily: leaf cuttings were placed on moistened filter paper inside Petri dishes, held at 26.6 ± 1°C, 70–80% relative humidity (RH), 16:8 (L:D) h photoperiod, and monitored daily for eclosion (Montezano et al. 2019c). For both lab and field collection methods, leaf cuttings with egg masses were surface sterilized by dipping briefly (~2 s) into a solution of 3% bleach, and then placed on trays overlaid with paper towels moistened with 3% bleach, incubated in a Percival E-36HO growth chamber (Percival Scientific, Perry, IA) set at 26.6°C, 70% RH, and 16:8 L:D.

Bacillus thuringiensis Cry1F Toxin Overlay Diet Bioassays

Trays containing *S. albicosta* egg masses were checked two to three times daily, and newly hatched neonates moved to Petri dishes without diet to prevent feeding as larval growth prior to Cry1F exposure can influence bioassay results. Toxin overlay bioassays were conducted as described by Dyer et al. (2013), except the diet formulation used in this study incorporated 500 mg of tetracycline per liter (Sigma–Aldrich, St. Louis, MO). Briefly, 1.0 ml of artificial diet was dispensed into each well of a 128-cell bioassay tray (Frontier Agricultural Sciences, Newark, DE) using a repeater pipette, and then diet overlaid with purified native trypsin digested Cry1F toxin (obtained from Dr. M Pusztai-Carey, Case Western Reserve University, Cincinnati, OH) suspended in 0.1× Triton X (Sigma–Aldrich). Final Cry1F toxin concentrations of 0.0 (control), 1.25, 2.5, 5.0, 7.5, 10.0, 15.0, 20.0, and 30.0 µg Cry1F cm^{-2} were used, which were previously determined to provide sufficient levels of morality to estimate 50% mortality in *S. albicosta* larvae (LC_{50}) using the same protein lot (Dyer et al. 2013) and was within the range of toxin used by other studies (Ostrem et al. 2016; Smith et al. 2017). In total, 16 cells were infested per treatment with a single neonate per cell. Treatments were performed in duplicate for samples from each location at each dose (n = 288 neonates infested per location). At 14-d postinfestation, larval mortality was recorded visually and weights were taken on an Ohaus Adventurer-Pro balance (Ohaus Corporation, Parssipany, NJ). Bioassays were performed and measured using the same method in 2017 and 2018.

For probit analysis, the probability of larval mortality was modeled as a function of Cry1F concentration (dose) at each location and year, with mortality at each dose corrected by control treatment mortalities within location [PSD × (1/PSC), where PSD

denotes proportion surviving on given Cry1F dose and PSC refers to proportion surviving on non-Bt control]. Median Cry1F toxin concentration causing 50% mortality in *S. albicosta* larvae (LC_{50}) across doses were estimated using the PROC PROBIT procedure of SAS 9.4 (SAS Institute 2016) from each location. PROC PROBIT was used with both a normal and logistic distribution with similar results; therefore, a normal distribution was chosen for the final analysis. Comparisons of LC_{50} levels among locations utilized 95% fiducial limits on predicted probabilities. For the analysis of weight of surviving larvae at 14 d, Cry1F concentrations were placed into four groups based on graphed results from 2017 to 2018 data; control (0 µg Cry1F cm^{-2}), low (1.25 and 2.5 µg cm^{-2}), medium (5.0 and 7.5 µg cm^{-2}), and high (10.0, 20.0, and 30.0 µg cm^{-2}). A 2-factor mixed-model replicated experiment ANOVA was performed on fixed-effect factors location group and Cry1F concentration group, replicated over 2 yr (2017 and 2018) using trays nested within year × location group × concentration group. For this model, cell subsamples nested within tray as random effects in the model. Differences of least squares means were conducted for pairwise comparisons when a significant *F*-test value was obtained from ANOVA at $P \leq 0.05$ using PROC GLIMMIX (SAS Institute 2016). Similar to prior studies (Ostrem et al. 2016, Smith et al. 2017), no Cry1F susceptible *S. albicosta* strain exists for comparison. Therefore, resistance ratios were not calculated.

Results

Bacillus thuringiensis Cry1F Toxin Overlay Diet Bioassays

Larval survivorship and weight data were collected from field samples in 2017 (Supp Table 1 [online only]) and 2018 (Supp Table 2 [online only]). A 100% mortality level was not observed for any Cry1F toxin dose at any location after a 14-d exposure, even at the highest dose used in 2017 (20.0 µg cm^{-2}) or 2018 (30.0 µg cm^{-2}). In 2017, there were no significant differences in LC_{50} values across all locations (Table 1). In 2018, the LC_{50} value at East Lansing, MI was significantly lower than Grant, NE; Kearney, NE; North Platte, NE; Scottsbluff, NE; and Watertown, NY. The LC_{50} values at O'Neil, NE, and East Lansing and Stanton, MI were significantly lower than Scottsbluff, NE in 2018 (Table 1).

The distribution of weights among surviving larvae at 14 d demonstrated the significance of differences by year ($F = 82.45$, d.f. = 1, 269, $P \leq 0.01$), collection site ($F = 7.05$, df = 4, 269, $P \leq 0.01$), and Cry1F concentration ($F = 68.24$, d.f. = 3, 269, $P \leq 0.01$). There were no significant differences in the location × concentration groups interaction ($F = 1.32$, d.f. = 12, 269, $P = 0.21$). The difference in the weight distribution of surviving larvae at 14 d between years in 2017 (451.7 ± 12.2 mg) was higher compared to corresponding weights in 2018 (315.4 ± 11.3 mg). This may be due to the addition of testing the 30.0 µg Cry1F cm^{-2} concentration in 2018. Differences were found between overall weights among locations, where significantly higher survivor weights from Michigan (464.0 ± 11.3 mg) compared to the pooled set of locations across Central, NE (366.1 ± 11.3 mg), O'Neill, NE (346.0 ± 11.3 mg), and both New York locations (335.4 ± 11.3 mg), but no difference was detected compared to Scottsbluff, NE (406.4 ± 11.3 mg). Significant differences occurred in the weights of surviving larvae at 14 d among Cry1F concentrations (Fig. 2). In general, larvae weighed significantly less at 14 d as a function of increasing concentrations of Cry1F; control (0 µg Cry1F cm^{-2}; 581.4 ± 23.1 mg), low (1.25 and 2.5 µg Cry1F cm^{-2}; 424.2 ± 16.4 mg), medium (5.0 and 7.5 µg Cry1F cm^{-2}; 312.0 ± 16.7 mg), and high concentration groups (10.0, 20.0, and 30.0 µg Cry1F cm^{-2}; 216.7 ± 15.1 mg).

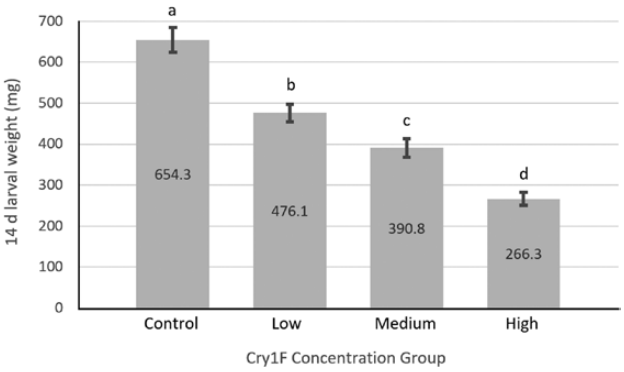

Fig. 2. Differences in mean *Striacosta albicosta* larval weights (mg) among survivors 14 d postinfestation of control diet and diet with an overlay of three levels of native trypsin-activated Cry1F. Cry1F concentration groups: Control, 0 µg cm^{-2}; low = 1.25 and 2.5 µg cm^{-2}; medium = 5.0 and 7.5 µg cm^{-2}; high = 10.0, 20.0 and 30.0 µg cm^{-2}.

Discussion

Varying levels of Bt resistance have been documented among arthropod pest species in the field (Tabashnik and Carrière 2017). These species include ear-feeding noctuid pest insects, corn earworm, *H. zea* (Dively et al. 2016, Reisig and Reay-Jones 2015, Reisig et al. 2018), fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) (Storer et al. 2010, Omoto et al. 2016, Yang et al. 2019, Zhu et al. 2019), and *S. albicosta* (Ostrem et al. 2016, Smith et al. 2017, USEPA 2018). Specifically, *S. albicosta* was listed in the EPA registration of Cry1F transgenic corn as a susceptible target insect (USEPA 2004). Initial field studies reported reduced feeding damage compared to conventional and other Bt hybrids within field trials (Eichenseer et al. 2008, Rule et al. 2014), but levels of resistance have increased ~5.2-fold since the early 2000s (Ostrem et al. 2016), suggesting a response to selection over time. This has resulted in a current scenario where there is no significant decrease in *S. albicosta* damage to Cry1F hybrids compared to conventional non-Bt hybrids (Smith et al. 2017, 2019). Results of the current study agree with prior studies that demonstrate varying degrees of Cry1F resistance within populations of *S. albicosta* (Ostrem et al. 2016, Smith et al. 2017). Specifically, our results estimated an $LC_{50} \geq 8.28$ µg cm^{-2} sample locations and years, but 100% mortality was not achieved even at the highest exposure levels (30.0 µg cm^{-2}; Table 1). Analogous lack of 100% mortality was shown among *S. albicosta* populations from Ontario using 30.0 or 75.0 µg Cry1F cm^{-2} (Smith et al. 2017). Granted the use of a native trypsin-activated Cry1F toxin for bioassays in the current study may not be comparable to prior results that used the purified truncated transgenic version of the Cry1F toxin (Dow AgriSciences, Indianapolis, IN) reported previously (Ostrem et al. 2016, Smith et al. 2017). Furthermore, extrapolation of larval survivorship data in toxin overlay bioassays to analogous survivorship on plants in the field remains difficult due to the lack of toxin expression data in corn tissues and methods to accurately quantify temporal or spatial feeding (i.e., exposure). Regardless, our bioassay results are similar to those previously conducted on *S. albicosta* using Cry1F toxin (Smith et al.

2017). The current study expanded the geographic sampling, and demonstrated that survivorship on the highest Cry1F dose used in this study is widespread across native and expanded ranges.

Across years and locations, the estimated LC_{50} values were significantly higher ($P < 0.05$) at the Scottsbluff, NE (SB) and Watertown, NY (WT) locations in 2018 when compared to the East Lansing, MI location (EL; Table 1). Significant differences were not analogously detected between any locations in 2017, outside of the Benkelmen, NE (BE) location. The cause of the comparative differences in relative LC_{50} in 2018 are not known or investigated further here, but could be due to sampling error despite efforts to randomly sample neonates from each sample site. Alternatively, ≤277-fold differences in LC_{50} estimates were previously observed between sample sites in 2013, where a single location (Perkins County, NE 3) was significanly lower (Ostrem et al. 2016). Differences could potentially be based on random yearly perturbations in resistance allele frequencies based on changes in local production practices or environmental conditions. Despite these outliers, the relatively homogenized level of Cry1F resistance across the Corn Belt (Table 1) and analogous levels of resistance documented in the Great Lakes regions (Smith et al. 2017, 2018a, b), as well as timing of the *S. albicosta* range expansion at a point that largely superseded the Cry1F hybrid commercialization in 2001 (Baktavachalam et al. 2015), might suggest that resistance alleles had been swept eastward during range expansion as opposed to evolving independently. Supporting population genetic evidence shows no significant changes in allele or haplotype frequencies between the native compared to expansion zone (Miller et al. 2009, Lindroth et al. 2012), which may also suggest that no genetic bottlenecks or loss of resistance alleles occurred during the range expansion.

Instances of functional field-evolved resistance, meaning the decrease in susceptibility following exposure to Bt toxins expressed by host plant tissues (Tabashnik et al. 2009), have occurred among ear-feeding noctuids despite the implementation of IRM plans aimed to delay or prevent onset. The high-dose/refuge (HD/R) strategy for IRM incorporates a 'high-dose' of an insecticidal agent (Bt toxin expressed by a transgenic crop plant) that is sufficient to cause 100% mortality of susceptible as well as heterozygous larvae carrying one copy of a resistance allele (USEPA 1998, 2001; USEPA 2009). This 'high-dose' component also assumes that resistance alleles are rare ($<10^{-3}$) and functionally recessive (Gould et al. 1995). The second tenet of the HD/R strategy stipulates that non-Bt expressing refuge plants be in proximity to transgenic plants of the same crop, where these refuges are assumed to provide a source from which numerically overwhelming homozygous Bt susceptible adults will emerge and mate with rare homozygous resistant individuals that survived on Bt crop plants (USEPA-SAP 1998). Thus, resulting heterozygous progeny carrying one recessive resistance allele is functionally susceptible, and target insect populations as a whole theoretically maintain susceptibility. EPA mandates required that refuges be structured into blocks with various configurations prior to 2010, after which non-Bt refuge seed blended at 5 or 10% within Bt seed products were approved for use by growers in the northern United States (i.e., refuge in a bag, RIB). Since computer models predicted greater Bt crop durability when both refuge and high-dose components are effectively implemented (Curtis et al. 1978, Roush 1997, Gould 1998), grower compliance achieved through the use of blended refuge seed products was percieved as a beneficial IRM tactic (Onstad et al. 2011, Carroll et al. 2012).

Slight deviations from assumptions within of the HD/R strategy are predicted to cause increased rates of resistance development (Gould et al. 1994, Roush 1994, Onstad and Gould 1998). Realized exceptions to this include dominant inheritance of Cry1Ab resistance in the African stem borer, *Busseola fusca* (Fuller) (Campagne et al. 2013) and Cry1Ac resistance in *H. armigera* (Hübner) (Jin et al. 2018). In most cases of field-evolved resistance, the factors contributing to the failure of IRM strategies remain unknown (Tabashnik et al. 2015). Regardless, the movement of susceptible larvae between Bt and non-Bt plants within blended refuges is proposed to cause increased mortality of susceptible phenotypes (SS genotypes) thus reducing the effectiveness of refuges (Mallet and Porter 1992, Tabashnik 1994), as shown empirically for *H. zea* (Burkness et al. 2011, 2012, 2015; Crespo et al. 2016). Furthermore, movement and feeding of heterozygous larvae between Bt and non-Bt expressing tissue is hypothesized to increase the effective dominance of resistance alleles by decreasing the exposure (dose), causing an increase in the proportion of heterozygotes that survive and reproduce (Mallet and Porter 1992). Cross pollination of non-Bt refuge kernels by adjacent Bt plants was shown to produce kernels with a mosaic of different Bt toxin expression levels (Chilcutt and Tabashnik 2004, Yang et al. 2014). The movement of larvae among kernels with different levels of Bt toxin expression was predicted to increase the dominance of resistance alleles within computer models (Brévault et al. 2015) and shown in laboratory selection experiments (Yang et al. 2017). Understanding the movement and feeding of larvae on tissues of the same plant or among plants within blended refuges may provide indications of varying exposures among pest species, and risks of low- and sublethal-doses that may exacerbate the rate at which Bt resistance develops. It was shown that early instar *S. albicosta* primarily and preferentially feed upon corn tassel (Paula-Moraes et al. 2013), and later instars are capable of moving up to several meters within a row of maize, and even to plants in adjacent rows (Pannuti et al. 2016). *Striacosta albicosta* larvae may also be more likely to disperse from Bt-expressing plants compared to non-Bt plants (Montezano 2019b). Despite estimates being reported for in-plant expression of the Bt toxins Cry1F (Baktavachalam et al. 2015) and Vip3A (USEPA 2009) not all relevant tissues are represented, and it remains difficult to accurately measure the amount of different tissues actually consumed within field scenarios.

The development of Bt resistance among field populations of pest insects is a threat to the sustainability of current crop production practices (Tabashnik 2008, Heckel 2012, Coates et al. 2015). Cry1F resistance has previously been established for *S. albicosta* (Ostrem et al. 2016, Smith et al. 2017) and recognized by the regulators in the United States (USEPA 2018). This study reports the degree of *S. albicosta* survivorship on Cry1F resistance bioassay from sites across the Corn Belt, including the initial description within the range expansion zone around the Great Lakes regions of the United States, and demonstrates that resistance is relatively homogenized within and across sampling years. These levels of Cry1F resistance estimated from toxin overlay bioassays are analogous with observed levels of damage to transgenic corn (Archibald et al. 2017, Montezano et al. 2019b), but direct correlation to actual exposure levels at which larvae can survive in the field remains difficult to predict. Although prior studies demonstrated that neonate *S. albicosta* are susceptibility to Bt Vip3A toxin (Farhan et al. 2017, Montezano et al. 2019b), later instars show increased tolerance (Farhan et al. 2019), which may have implications in instances when larvae move from refuge to Bt plants. Vip3A resistance alleles are detectable within populations of *H. armigera* (Mahon et al. 2012) and *S. frugiperda* (Yang et al. 2017), and *H. zea* damage to kernels of Vip3A expressing hybrids has been shown in the field (Yang et al. 2019). Regardless, widespread field failures of Vip3A hybrids are yet to be observed for

any lepidopteran pest species. For *S. albicosta*, Vip3A is the only remaining efficacious transgenic Bt toxin, but it remains unclear whether selection pressure imposed by that single toxin will lead to widespread resistance and field failures in the future. The data presented here are useful for making informed control strategy decisions for *S. albicosta*. The implications of widespread Bt Cry1F toxin survivorship of *S. albicosta* exposed to Cry1F suggests that an integrated approach to pest management including other effective Bt toxins in combination with Vip3A, as well as other control tactics, may be a prudent IRM strategy for preserving control technologies and minimizing *S. albicosta* damage to corn.

Supplementary Data

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

Acknowledgments

This work is supported by the Agriculture and Food Research Initiative competitive award no. 2016-33522-25631 from the United States Department of Agriculture (USDA), National Institute of Food and Agriculture (NIFA), Biotechnology Risk Assessment Grant program. Funding was also provided by the USDA, North Central Integrated Pest Management grant #2014-70006-22486, USDA Agricultural Research Service (ARS) (CRIS Project 5030-22000-018-00D) and the Iowa Agriculture and Home Economics Experiment Station, Ames, IA (Project 3543), and the Nebraska Agricultural Experiment Station with funding from the Hatch Multistate Research capacity funding program (Accession Number 1006556) from the USDA NIFA. This article reports the results of research only, and mention of any commercial product or service does not constitute a recommendation for its use by USDA. We thank Fred Springborn for making moth collections from Stanton, MI. We also thank Tina Paque, Samantha Daniel, Miranda Dietz, Grace Hirzel, and Natalie Wertish for work in field collections and running laboratory assays. USDA is an equal opportunity employer and provider.

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