Resistance to Bt Corn by Western Corn Rootworm (Coleoptera: Chrysomelidae) in the U.S. Corn Belt

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Abstract
Transgenic Bt corn hybrids that produce insecticidal proteins from the bacterium Bacillus thuringiensis Berliner have become the standard insect management tactic across the U.S. Corn Belt. Widespread planting of Bt corn places intense selection pressure on target insects to develop resistance, and evolution of resistance threatens to erode benefits associated with Bt corn, such as reduced reliance on conventional insecticides. Recognizing the threat of resistance, the U.S. Environmental Protection Agency requires seed companies to include an insect resistance management (IRM) plan when registering a Bt trait. The goal of IRM plans is to delay Bt resistance in populations of target insects. One element of IRM is the presence of a non-Bt refuge to maintain Bt-susceptible individuals within a population, and growers are required to implement IRM on-farm by planting a refuge. Field-evolved resistance has not been detected for the European corn borer, Ostrinia nubilalis (Hubner), even though this species has been exposed to Bt proteins common in U.S. corn hybrids since 1996. The IRM situation is unfolding differently for Bt corn targeting the western corn rootworm, Diabrotica virgifera virgifera LeConte. In this article, we examine the scientific evidence for D. v. virgifera resistance to Bt rootworm traits and the cropping system practices that have contributed to the first reports of field-evolved resistance to a Bt toxin by D. v. virgifera. We explain why this issue has developed, and emphasize the necessity of an integrated pest management approach to address the issue.

Keywords
Bt corn, IPM, insect resistance management, refuge, western corn rootworm

Disciplines
Agronomy and Crop Sciences | Entomology | Systems Biology

Comments
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Transgenic Bt corn hybrids that produce insecticidal proteins from the bacterium *Bacillus thuringiensis* Berliner have become the standard insect management tactic across the U.S. Corn Belt. In 2012, 67% of 96.4 million acres (39 million hectares) of corn planted in the United States contained at least one Bt trait (U.S. Department of Agriculture–National Agricultural Statistics Service [USDA–NASS] 2012; U.S. Department of Agriculture Economic Research Service [USDA–ERS] 2012a). Bt corn hybrids producing a single Bt protein for European corn borer, *Ostrinia nubilalis* (Hubner), and other lepidopteran pests have been commercially available since 1996 (Tabashnik et al. 2009). Bt corn provides effective control of several key insect pests, with additional benefits of reduced reliance on conventional insecticides. Recognizing the threat of resistance, the U.S. Environmental Protection Agency requires seed companies to include an insect resistance management (IRM) plan when registering a Bt trait. The goal of IRM plans is to delay Bt resistance in populations of target insects. One element of IRM is the presence of a non-Bt refuge to maintain Bt-susceptible individuals within a population, and growers are required to implement IRM on-farm by planting a refuge. Field-evolved resistance has not been detected for the European corn borer, *Ostrinia nubilalis* (Hubner), even though this species has been exposed to Bt proteins common in U.S. corn hybrids since 1996. The IRM situation is unfolding differently for Bt corn targeting the western corn rootworm, *Diabrotica virgifera virgifera* LeConte. In this article, we examine the scientific evidence for *D. v. virgifera* resistance to Bt rootworm traits and the cropping system practices that have contributed to the first reports of field-evolved resistance to a Bt toxin by *D. v. virgifera*. We explain why this issue has developed, and emphasize the necessity of an integrated pest management approach to address the issue.

**Key Words:** Bt corn, western corn rootworm, insect resistance management, IPM, refuge

**ABSTRACT.** Transgenic Bt corn hybrids that produce insecticidal proteins from the bacterium *Bacillus thuringiensis* Berliner have become the standard insect management tactic across the U.S. Corn Belt. Widespread planting of Bt corn places intense selection pressure on target insects to develop resistance, and evolution of resistance threatens to erode benefits associated with Bt corn, such as reduced reliance on conventional insecticides. Recognizing the threat of resistance, the U.S. Environmental Protection Agency requires seed companies to include an insect resistance management (IRM) plan when registering a Bt trait. The goal of IRM plans is to delay Bt resistance in populations of target insects. One element of IRM is the presence of a non-Bt refuge to maintain Bt-susceptible individuals within a population, and growers are required to implement IRM on-farm by planting a refuge. Field-evolved resistance has not been detected for the European corn borer, *Ostrinia nubilalis* (Hubner), even though this species has been exposed to Bt proteins common in U.S. corn hybrids since 1996. The IRM situation is unfolding differently for Bt corn targeting the western corn rootworm, *Diabrotica virgifera virgifera* LeConte. In this article, we examine the scientific evidence for *D. v. virgifera* resistance to Bt rootworm traits and the cropping system practices that have contributed to the first reports of field-evolved resistance to a Bt toxin by *D. v. virgifera*. We explain why this issue has developed, and emphasize the necessity of an integrated pest management approach to address the issue.

**Key Words:** Bt corn, western corn rootworm, insect resistance management, IPM, refuge
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<tr>
<th>Trade name</th>
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<td>20% within half mile</td>
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Insects controlled (bold type) or suppressed (italic): BCW, black cutworm; CEW, corn earworm; CRW, corn rootworm; ECB, European corn borer; FAW, fall armyworm; SB, stalk borer; WBC, western bean cutworm.

Herbicide tolerance traits: GT, glyphosate tolerant; LL, Liberty Link glufosinate tolerant; RR2, Roundup Ready 2 glyphosate tolerant.
The IRM situation is unfolding differently for Bt corn and western corn rootworm, *Diabrotica virgifera virgifera* LeConte (Fig. 1). In this article, we examine the scientific evidence for *D. v. virgifera* resistance to Bt rootworm traits and cropping system practices that contributed to the first reports of field-evolved resistance to a Bt toxin by *D. v. virgifera*. We discuss factors that contributed to the development of resistance, and emphasize the necessity of an integrated pest management (IPM) approach to address the issue.

**Western Corn Rootworm Resistance to Bt Corn in Artificial Selection Studies.** In laboratory and greenhouse selection experiments, *D. v. virgifera* has evolved resistance to all commercially available Bt rootworm proteins. Increased survival of *D. v. virgifera* on transgenic corn producing the Cry3Bb1 protein was found after three generations of on-plant greenhouse selection, and results revealed that resistance to Cry3Bb1 is not inherited recessively (Meihls et al. 2008). Similar studies with other populations confirmed that *D. v. virgifera* resistance to Bt corn can develop quickly when any *D. v. virgifera* population is continuously exposed to selection pressure imposed by the Cry3Bb1 trait (Oswald et al. 2011, Meihls et al. 2012). For Cry34/35Ab1, evolution of resistance by *D. v. virgifera* reared on Bt corn seedlings was observed within five generations, although resistance was not complete or significantly greater after 11 generations of selection (Lefko et al. 2008). Similar values of realized heritability for *D. v. virgifera* resistance to Cry3Bb1 and Cry34/35Ab1 suggest that western corn rootworm can readily evolve resistance to Bt corn (Lefko et al. 2008, Tabashnik and Gould 2012). A laboratory colony of *D. v. virgifera* had a resistance level, similar to those described earlier, to the mCry3A trait within 10 generations of selection (Meihls et al. 2011). Finally, a laboratory colony of *D. v. virgifera* was selected for resistance to noncommercial transgenic corn expressing the eCry3.1Ab protein (Frank et al. 2013).

While artificial selection experiments represent the “worst case” scenario of continual exposure to a Bt rootworm trait, with no supply of unselected (refuge) insects into the population, results from these studies underscore the importance of adhering to IRM refuge plans on-farm to maintain Bt corn efficacy.

**Field-Evolved Resistance by Western Corn Rootworm to Bt Corn in Commercial Fields.** To date, field-evolved resistance to Bt toxin Cry3Bb1 has been confirmed in the refereed literature for 11 populations of *D. v. virgifera* in Iowa. In each of these cases, adults collected from one field constitute a population, and fields from which these populations were collected had been planted to the same single Bt rootworm trait for at least three consecutive years, and as many as seven consecutive years.

In 2011, Iowa State University entomologists found reduced Cry3Bb1 susceptibility of progeny from adult *D. v. virgifera* collected from four fields planted to Cry3Bb1 rootworm hybrids for several consecutive years (Gassmann et al. 2011). In this study, Cry3Bb1 corn had an average of 1.8 nodes of roots pruned (0–3 scale; Oleson et al. 2005). Based on data from U.S. cornfields, it is estimated that one node of root injury causes an average yield loss of ~15% (Dun et al. 2010, Tinsley et al. 2012). *D. v. virgifera* adults also were collected from five control fields not associated with unexpected corn rootworm injury to Bt corn. The control fields had been planted to a greater diversity of crops and a wider array of practices were used to manage corn rootworm. Field-collected adults were held in the laboratory to obtain eggs, and offspring were used in on-plant bioassays to assess survival of *D. v. virgifera* larvae feeding on Cry3Bb1 corn and a near isogenic hybrid lacking a Bt trait. Bioassays also were conducted by using Bt Cry34/35Ab1 corn and its isolate. Results confirmed resistance to the Cry3Bb1 trait for all four *D. v. virgifera* populations from fields with injury to Cry3Bb1 corn. Increased survival was not observed on Cry34/35Ab1, suggesting lack of cross-resistance between these two Bt toxins.

A second study published in 2012 by the same research group reported similar results for seven additional populations of *D. v. virgifera* collected in 2010 (Gassmann et al. 2012a). Laboratory bioassays revealed that these 2010 populations had survival on Cry3Bb1 corn that was 11 times greater than that of control populations, which were brought in to the laboratory before the commercialization of Bt corn for corn rootworm control.

In a related study (Gassmann 2012b), follow-up field experiments were conducted in two of the Iowa fields identified in the 2011 publication as harboring Cry3Bb1-resistant western corn rootworm. Root injury and survival of *D. v. virgifera* to adulthood were measured across eight treatments. Treatments at each site included: 1) non-Bt corn, 2) non-Bt corn with a soil insecticide (active ingredients tebufenpyrim and cyfluthrin; Aztec, AMVAC Chemical Corporation, Los Angeles, CA), 3) non-Bt corn with soil insecticide (active ingredient tefluthrin; Force, Syngenta, Wilmington, DE), 4) Bt Cry3Bb1 corn, 5) Bt Cry3Bb1 corn with a soil insecticide (Aztec), 6) Bt Cry3Bb1 corn with a soil insecticide (Force), 7) Bt Cry34/35Ab1 corn, and 8) a pyramided Bt corn hybrid expressing both Cry3Bb1 and Cry34/35Ab1. Results from the two sites previously confirmed as harboring Cry3Bb1-resistant *D. v. virgifera* found that root injury to Bt Cry3Bb1 corn was higher than injury to other types of Bt corn or to corn roots protected with a soil insecticide, and that survival of *D. v. virgifera* did not differ between Cry3Bb1 and non-Bt corn.

**Factors That Led to Field-Evolved Resistance of Western Corn Rootworm to Bt Corn.** Despite the requirement that growers plant a refuge to delay or prevent resistance development, field-evolved resistance by *D. v. virgifera* to Cry3Bb1 corn occurred in a short period. Why? Insufficient planting of refuges and nonrecessive inheritance of resistance may have contributed to resistance (Gassmann et al. 2011). In addition, none of the Bt hybrids registered for corn rootworm are high-dose events, ensuring some corn rootworm survivors in every field (EPA 2002; Vaughn et al. 2005; Storer et al. 2006; Hibbard et al. 2010a,b; Clark et al. 2012), although eCry3.1Ab has a higher dose than the others (Hibbard et al. 2011). When heterozygotes (individuals with a mixture of alleles for resistance and susceptibility) can survive on a Bt crop, the frequency of Bt resistance alleles within a population can increase rapidly. Furthermore, fitness costs of *D. v. virgifera* resistance to Bt Cry3Bb1 may be low (Meihls et al. 2008, Gassmann et al. 2011, Meihls et al. 2012, Petzold–Maxwell et al. 2012). There is also evidence of nonrandom mating for *D. v. virgifera* within fields, which can diminish mating between susceptible insects from the refuge and resistant insects from Bt corn, and initial resistance allele frequencies may be much higher than initially assumed (Kang and Krupke 2009, Onstad and Meinke 2010).

The 20% structured refuge (separate fields, blocks, or strips) was developed based on the biology, mating behavior, and dispersal patterns of European corn borer coupled with a high dose of Bt proteins.
for European corn borer. For the initial years following commercialization of Bt rootworm traits, the 20% structured refuge and accompanying IRM assumptions applied to European corn borer also were used for corn rootworms. However, one approach to IRM is not necessarily optimal for all insect pests. Even though there is increased use of refuge-in-the-bag seed mixtures and pyramided hybrids with multiple Bt toxins targeting corn rootworms, these products were accompanied by a reduction in refuge size, and it remains unclear whether these recent developments will keep resistant corn rootworm populations in check.

Clarifying the Potential Extent of the Problem. In March 2012, 22 corn entomologists from land-grant universities and the USDA sent a letter to the U.S. EPA expressing concern over the development of field-evolved resistance to the Cry3Bb1 protein by *D. v. virgifera* and providing IPM recommendations to sustain the effective use of Bt corn in the United States (Porter et al. 2012). In particular, these public sector scientists warned that the durability of the Cry3/35Ab1 protein, used in conjunction with the Cry3Bb1, mCry3A, and/or eCry3.1Ab proteins in pyramided Bt corn hybrids, could be compromised in areas where a Cry3Bb1-resistant population of *D. v. virgifera* is present, especially if cross-resistance to mCry3A and/or eCry3.1Ab exists. This concern is heightened because the refuge size has been reduced from 20 to 5% for these pyramided products. Therefore, in an area where a Cry3Bb1-resistant *D. v. virgifera* population has been confirmed, Cry3Bb1 + Cry3/35Ab1 pyramided corn hybrids would effectively function as a single rootworm trait (Cry3/35Ab1) at a 5% refuge, rather than the 20% refuge required for single Bt trait corn. Additional concerns mentioned in the letter include the “insurance-based approach” to insect management—a standard practice across the U.S. Corn Belt in which insecticides are applied at planting to Bt corn targeting rootworms (Gray 2010). Authors of the letter state that pyramided Cry3Bb1 + Cry3/35Ab1 corn should not need insecticidal protection for rootworms, given that the Cry3/35Ab1 toxin is still effective. Although soil insecticides temporarily protect roots from corn rootworm feeding, soil insecticides are not rootworm population management tools and the practice of applying soil insecticide over a Bt corn rootworm hybrid at planting does not lessen the selection pressure imposed by the Bt trait on the rootworm population (Gray et al. 1992). Nonetheless, nearly 47% of Illinois growers who participated in the 2013 regional Corn and Soybean Classics extension meetings held across five locations in Illinois indicated that they intend to use both a soil-applied (at-planting) insecticide and a Bt hybrid for management of corn rootworm (Gray 2013). Reasons for this escalating use of soil insecticide included concerns over secondary insect infestations and higher-than-expected corn rootworm feeding damage to Bt corn (Figs. 2–4). Nearly 27% of the producers who took part in these regional extension meetings indicated that they perceive soil insecticide as cheap insurance (Gray 2013). Continued high commodity prices will likely reinforce these insurance-based decisions (Berry 2013).

Authors of the letter acknowledge challenges faced by U.S. corn growers. For example, Bt rootworm traits are incorporated into elite germplasm that has the highest yield potential, and growers report increasing difficulty obtaining nontransgenic corn seed with equally high yield potential. This can result in Bt rootworm hybrids planted prophylactically in areas where rootworm abundance is low or where a crop-rotation sequence results in little or no rootworm pressure (Gray 2010). Moreover, widespread adoption of Bt technology has left many growers without the equipment necessary to apply soil insecticides to non-Bt corn at planting. The authors state that many growers have used a single-tactic approach for too many years and now unfortunate consequences are beginning to emerge.

What Can Be Done to Stop the Spread of Western Corn Rootworm Resistance to Bt Corn? The letter from land-grant university and USDA entomologists to EPA provides specific IPM recom-
mendations to help corn growers delay further resistance and conserve *D. v. virgifera* susceptibility to Bt corn technology:

- Rotate to soybean or another nonhost crop to break the corn rootworm life cycle.
- Eliminate point sources of resistant populations by crop rotation.
- This may slow development of resistance in, and movement of resistance to, the Eastern Corn Belt, where fewer reports of problem fields have been received compared with the Central Corn Belt (DiFonzo et al. 2013).
- Consider the use of a corn rootworm soil insecticide at-planting with a non-Bt hybrid.
- Consider the use of a Bt hybrid with a different corn rootworm Cry protein than one that may have performed poorly in the past on a particular farm.
- Consider the use of a pyramided Bt hybrid with multiple Cry proteins targeted against corn rootworms.
- Adult suppression may be an appropriate remediation step for one or two growing seasons in fields with confirmed resistance, if crop rotation is not an option or a suitable Bt pyramid is not available. In such cases, soil insecticide applied to non-Bt corn will offer root protection, while adulticides will reduce the number of resistant adults that survive in the field. This should be followed by a long-term IPM approach using a mix of tactics.
- Most importantly, implement a long-term integrated approach to corn rootworm management, based on scouting information and knowledge of corn rootworm densities, that uses multiple tactics such as rotation to a nonhost crop, rotation of Bt toxins, and use of soil insecticides at planting with a non-Bt hybrid.

Other scientists with expertise in Bt crops and IRM published their science-based recommendations to the EPA regarding refuge requirements for Bt hybrids that offer corn rootworm protection (Tabashnik and Gould 2012). The authors conclude that current refuge requirements are not adequate, because Bt rootworm hybrids do not meet the high-dose standard, and *D. v. virgifera* has rapidly evolved resistance to Cry3Bb1 corn in the laboratory, greenhouse, and field. They recommend increasing the minimum refuge for Bt rootworm corn to 50% for plants producing a single Bt rootworm protein (whether the toxin is Cry3Bb1, Cry34/35Ab1, or mCry3Aa) and to 20% for pyramided plants producing two Bt rootworm proteins. These recommendations were offered with the goals of helping delay further corn rootworm resistance, encourage IPM, and promote more sustainable crop protection. The authors acknowledge that enlarging refuges would require more seed without corn rootworm traits (a condition currently limited by availability of corn seed that does not produce a Bt rootworm toxin), and emphasize that these are hypothetical scenarios that, in principle, growers can make less likely by using IPM.

On-farm rootworm management decisions may alter the future course of western corn rootworm resistance evolution. It is critical for seed companies, regulatory agencies, and university/government scientists to work together to provide practical science-based information and recommendations in a timely manner to corn growers, crop consultants, and the agricultural industry. Resistance monitoring is essential to detect resistance evolution in the field, and IPM is essential to ensure effective long-term corn rootworm management and sustainable use of Bt corn (Devos et al. 2013).

Acknowledgments

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