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Current European corn borer, *Ostrinia nubilalis*, injury levels in the northeastern United States and the value of *Bt* field corn†

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Abstract

BACKGROUND: Recent evidence indicates that some populations of European corn borer (ECB), *Ostrinia nubilalis* (Hübner), have declined to historic lows owing to widespread adoption of *Bt* corn hybrids. To understand current ECB populations in Pennsylvania field corn, the authors assessed larval damage in *Bt* and non-*Bt* corn hybrids at 29 sites over 3 years. The influence of *Bt* adoption rates, land cover types and moth activity on levels of ECB damage was also considered.

RESULTS: *Bt* hybrids reduced ECB damage when compared with non-*Bt*, but these differences inconsistently translated to higher yields and, because of higher seed costs, rarely improved profits. No relationships were detected between land use or *Bt* adoption and ECB damage rates, but positive relationships were found between plant damage and captures of *Z*-race ECB moths in pheromone traps in the PestWatch network.

CONCLUSIONS: ECB damage levels were generally low and appear to be declining across Pennsylvania. In many locations, farmers may gain greater profits by planting competitive non-*Bt* hybrids; however, *Bt* hybrids remain valuable control options, particularly in the parts of Pennsylvania where ECB populations persist. Moth captures from PestWatch appear to provide insight into where *Bt* hybrids are most valuable.

Supporting information may be found in the online version of this article.

Keywords: *Bt* adoption; *E*-race; *Z*-race; transgenics

1 INTRODUCTION

Transgenic crop species expressing insecticidal *Bacillus thuringiensis* (*Bt*) toxins have been commercially available for nearly 20 years.[1] Since being introduced, farmer adoption of *Bt* crops has steadily increased, resulting in large-scale reductions in populations of at least three insect pest species worldwide, including the European corn borer (ECB) *Ostrinia nubilalis* (Hübner).[2–4] In addition to insect control, *Bt* crops have provided benefits by increasing yield,[5] reducing the risk of yield loss,[6] reducing the quantity of insecticides applied to farm fields[7] and improving farm worker safety.[8]

In the United States, farmers plant *Bt* corn (*Zea mays* L.) mostly to control two insect pest species, western corn rootworm (WCR) *Diabrotica virgifera virgifera* (LeConte) and ECB. Western corn rootworm is native to the Great Plains region of North America and is a specialist root-feeding coleopteran that annually causes losses of around $US 1 billion.[9] In the midwestern United States, growers typically control WCR with corn hybrids expressing *Bt* toxins in the roots, but recent evidence of *Bt*-resistant populations of WCR are forcing growers to reconsider their management strategies.[10] In contrast, ECB is a highly polyphagous above-ground pest species that was accidentally introduced into North America in the early 1900s.[11] Prior to introduction of *Bt* corn hybrids, ECB caused crop losses that annually approached $US 1 billion nationwide, and $US 35 million in the northeastern United States.[4,5] Of the numerous plant species that ECB attacks, corn is the most widely grown host in the United States, covering over 35 million ha of cropland in 2011 (National Agricultural Statistical Service: http://www.nass.usda.gov/Charts_and_Maps/Field_Crops/cornac.asp.), 65% of which was planted with *Bt* hybrids (United States Department of Agriculture Economic Research Service: http://www.ers.usda.gov/data-products/adoption-of-genetically-engineered-crops-in-the-us/recent-trends-in-ge-adoption.aspx). *Bt* corn hybrids have been widely adopted because they are exceptional for managing ECB: 99.9% of larvae are expected to

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die when they feed on plants expressing *Bt* toxins.[12] Prior to transgenic technology, farmers relied on natural enemies and insecticides to control ECB damage; however, natural enemies rarely provided complete control,[13] and insecticide applications were logistically challenging because of crop height, large acreage and the small window of opportunity to kill larvae before they enter the stalk or ear.[14] In addition to field corn, ECB can be problematic for sweet corn,[15] which has fewer and more expensive *Bt* hybrids available than field corn, and most sweet corn growers continue to rely on broadcast applications of insecticides to control ear-feeding caterpillars.

To time insecticide treatments for sweet corn and other vegetable crops, agricultural professionals can track moth flight activity using pheromone traps. In Pennsylvania and much of the northeastern United States, many farmers rely on moth capture data shared through the PestWatch system (www.pestwatch.psu.edu),[16] which presents data from a network of sex pheromone traps located near vegetable farms and is managed by extension educators and other agricultural professionals. While traps within the PestWatch network provide insight into ECB population size and periods of activity, their utility as a predictive tool, particularly for field corn, has been limited because the previously reported relationships between ECB captures and crop damage have been variable.

Owing to variability similar to that associated with moth captures, spatial land cover variables also do not appear to be consistently associated with herbivore populations.[17] Often, the lack of detectable effects of land use on herbivore populations can be linked to insect life-history factors, such as increased prevalence of host plants for generalist insects, or increasing emigration rates from non-crop hosts to crop hosts.[18,19] However, increases in biological control of herbivorous pests and decreases in insecticide use have been detected as landscape heterogeneity increases,[20] so it is clear that landscape can influence insect management tactics.[17] For ECB, landscape complexity, or even the proportion of a landscape planted to corn, may influence populations, but this relationship has been explored only on a limited basis.[17]

Here, the authors present an integrated effort to understand ECB populations, potential influences on these populations and the value of *Bt* field corn hybrids given the current ECB population size. With recent widespread declines in ECB populations in the midwestern United States,[4] there is now reason to consider whether *Bt* hybrids, which continue to provide excellent control of ECB but cost more than non-*Bt* hybrids, still provide a strong return on investment. To understand current ECB populations and the value of *Bt* hybrids, an assessment was made of larval damage and yield of *Bt* and non-*Bt* hybrids across Pennsylvania over 3 years. Whether spatial land cover characteristics and current *Bt* adoption rates predict ECB damage was also tested to gain an understanding of some of the factors that influence ECB populations in Pennsylvania. Lastly, the data reported to PestWatch were used to explore whether using pheromone traps can have a wider predictive value for ECB infestations in field corn.

2 MATERIALS AND METHODS

2.1 European corn borer damage in *Bt* and non-*Bt* hybrids

To assess ECB damage and the value of *Bt* corn, *Bt* and non-*Bt* corn hybrids were planted on 16 farm sites across four growing zones in Pennsylvania in 2010, ten sites in 2011 and three sites in 2012 (supporting information Table S1). In 2010, eleven of the 16 sites were planted into fields that were not planted to corn the previous year (i.e. rotated fields), and the other five were continuous corn. Of the 16 sites, three were in corn maturity zone 1, five were in zone 2 and there were four each in zones 3 and 4.[21] In 2011, challenging spring and fall conditions limited the sites that could be planted or harvested; thus, there was only one site in zone 1, and three sites in each of zones 2, 3 and 4. Eight of the ten sites were planted in rotated fields, and two fields were continuous corn. To gain a better understanding of a few local ECB populations, this study was repeated in 2012 at only three sites, the two Penn State research farms and a commercial site in York County adjacent to the 2010 site (all rotated fields). In all 3 years, five *Bt* and five non-*Bt* hybrids (isolines when possible) were planted at each site in zones 1, 3 and 4, and six *Bt* and six non-*Bt* hybrids in zone 2 (supporting information Tables S2, S3 and S4). Those hybrids containing *Bt* toxins targeted ECB (among other lepidopteran species) and WCR and were representative of corn hybrids planted as part of a crop rotation by farmers in Pennsylvania. Five replicates of each hybrid were planted in 2010 and 2011, and four replicates in 2012 in a randomized complete block design in 2.4×5.3 m plots. Soil insecticides were not applied. At least four rows of *Bt* corn surrounding the outside plots were planted to minimize edge effects.

During September of each season, an assessment was made of ECB damage on ten random plants in an outside row of each plot in four replicates at each site. Stalks were sliced open using knives, and the numbers of ECB tunnels and larvae per stalk were counted. Ears were also evaluated for ECB damage, and ear damage was differentiated by the presence of live larvae and location and type of feeding.[21] Using an Almaco SPC-40 (Almaco, Nevada, IA) research plot combine, yield data were collected from the middle two rows in each plot from all five replicates at each site in 2010 and 2011, and four replicates in 2012. A HarvestMaster grain monitor (HarvestMaster Inc., Logan, UT) on the combine collected yield, moisture and test weight data for each plot. It was assumed that larval ECB damage in non-*Bt* hybrids represented local ECB populations, and that differences in yield and profits between *Bt* and non-*Bt* varieties would provide insight into the value of *Bt* hybrids for ECB control.

Harvest mass and moisture were used to calculate yield per hectare, corrected to 15.0% moisture. Economic returns for 2010 and 2011 were estimated by multiplying yield by the price of corn for each year ($US 0.21 kg^{-1} in 2010, $US 0.28 kg^{-1} in 2011; National Agricultural Statistical Service: http://www.nass.usda.gov/Charts_and_Maps/Agricultural_Prices/pricecn.asp), and net returns were calculated by subtracting the seed cost of each hybrid and drying cost from the gross returns. Prices for individual hybrids were received from local seed dealers, and the average cost of *Bt* hybrids was about $US 50 ha^{-1} more than for non-*Bt* seeds. Drying cost was calculated using a price of $US 0.04 per percent above 15.0% moisture per 25.4 kg of corn. An economic analysis for 2012 was not pursued because of the limited number of sites.

To assess the potential relationship between ECB infestations and *Bt* adoption rates,[4] *Bt* corn adoption rates were obtained for the crop-reporting districts in Pennsylvania for 2002, 2006 and 2009 from the Agricultural Biotechnology Stewardship Technical Committee, a consortium of representatives from each of the major companies that develop and sell transgenic traits and seeds. Because Pennsylvania has some areas with two generations of ECB per year and others with only one, ECB tunnels per stalk was used as a representation of local populations over the entire season. The 2009 *Bt* adoption data, the latest year available, were used to test for a relationship between *Bt* adoption and current ECB populations.

All combined data were analyzed by analysis of variance (ANOVA).[22] The combined analysis found interactions between ECB damage and site and zone; therefore, data (tunnels and larvae per stalk, percentage of ears and stalks damaged, yield and profit) from all sites were analyzed separately.[22] To determine the relationship between ECB tunnels per stalk and 2009 *Bt* adoption rates, linear regression was used.[22]

2.2 Landscape analysis

To determine whether land use characteristics influenced ECB damage, with the aid of the 2006 National Land Cover Database (http://www.mrlc.gov/nlcd2006.php) the percentage of land area each year in cultivated crops within a 0.5 and 10 km radius of each of the sampling sites was calculated in ArcMap 10.1 (Environmental Systems Resource Institute, Redlands, CA). The number of ECB tunnels per stalk each year was then regressed on this amount of cultivated cropland.[22]

2.3 European corn borer trapping

To relate male ECB captures in pheromone traps to in-field damage, the authors relied on data reported to PestWatch. Pheromone traps have been used to track insect pest populations as part of this system since 1998, and participants use Harstack wire cone traps to capture ECB.[16] The ECB traps from which data were used occurred in the same or adjacent county for nine of 16 sites in 2010, and for nine of ten sites in 2011. Sites that did not have a trap in the same or adjacent county were excluded from the analysis. Traps averaged 25.1 $\pm$ 5.8 km from damage evaluation sites in 2010, and 14.5 $\pm$ 6.2 km in 2011 (supporting information Table S5). The closest trap was 0.5 km and the farthest trap 57.2 km from their respective damage evaluation site over both years.

In Pennsylvania there are two separate pheromone races of ECB, the *E*- and *Z*-races.[23] To understand the relationships between moth captures of the two races and damage, a linear regression was used to relate cumulative male captures (each race separately and both races combined) to the present field assessments of ECB damage (tunnels per stalk, percentage of stalks damaged and percentage of ears damaged in non-*Bt* hybrids), with year as a covariate.[22] Data from the 2012 sites were not included in the analysis because injury was assessed at only three sites.

3 RESULTS

3.1 European corn borer damage in *Bt* and non-*Bt* hybrids

As expected, *Bt* corn hybrids were very effective at controlling ECB. Fewer than 0.1 tunnels per stalk were found in *Bt* hybrids at all sites over 3 years, and 72% of sites experienced 0.01 or fewer tunnels per *Bt* stalk (Tables 1, 2 and 3). European corn borer damage in non-*Bt* hybrids, which should reflect local populations of ECB, was low. At 17 sites, fewer than 0.25 tunnels per stalk were found, and 19 sites had less than 25% of stalks damaged. Only three sites had European corn borer injury levels in non-*Bt* hybrids of over one tunnel per stalk (Tables 1 and 3), a level that reduces yield by about 3%.[24] Moreover, fewer than 10% of ears in non-*Bt* hybrids were found to be damaged by European corn borer at all but three sites (Tables 1, 2 and 3).

When compared with non-*Bt* hybrids, *Bt* hybrids at 24 of the 29 sites significantly reduced the number of ECB tunnels per stalk and the percentage of damaged stalks (Tables 1, 2 and 3; supporting information Tables S6, S7 and S8). At the five sites where the number of tunnels per stalk and the percentage of stalks damaged in *Bt* hybrids were not reduced relative to non-*Bt*, damage in the non-*Bt* hybrids was very low (<0.1 tunnels per stalk). At 20 of the 29 sites, the number of larvae per stalk and the percentage of ears damaged was significantly lower in *Bt* than in non-*Bt* hybrids (Tables 1, 2 and 3; supporting information Tables S6, S7 and S8); at the nine other sites, fewer than 0.02 larvae per stalk were found, and less than 5% of ears were damaged in non-*Bt* hybrids. Only the site in Westmoreland County experienced over 5% of ears injured in *Bt* hybrids.

Yield from *Bt* hybrids was significantly higher than yield from non-*Bt* hybrids at 11 of the 29 sites, whereas non-*Bt* hybrids yielded statistically better at four sites (Tables 1, 2 and 3; supporting information Tables S6, S7 and S8). At the remaining 14 locations, yields from *Bt* and non-*Bt* hybrids were similar (Tables 1, 2 and 3; supporting information Tables S6, S7 and S8). Overall, *Bt* hybrids yielded 1.9% higher than non-*Bt* hybrids (Table 4), lower than in a previous study where the average yield from *Bt* hybrids was 5.5% higher than from non-*Bt*.[5] Among the seven sites that were planted as continuous corn, yield was similar at three locations, *Bt* hybrids yielded higher than non-*Bt* at three sites and non-*Bt* hybrids yielded higher than *Bt* at one site (Tables 1 and 2). Notably, when seed and drying costs were considered, *Bt* hybrids only returned significantly greater profits than non-*Bt* hybrids at one of 26 locations, and this site was planted to continuous corn (Table 1; supporting information Table S6). Meanwhile, non-*Bt* hybrids returned greater profits than *Bt* hybrids at seven of 26 sites (Tables 1 and 2; supporting information Tables S6 and S7). Net income at the remaining sites was highly variable and statistically similar between *Bt* and non-*Bt* hybrids (Tables 1 and 2; supporting information Tables S6 and S7).

No significant relationship was found between ECB tunnels per stalk and current *Bt* adoption rates (best-fit regression line: $Y = 0.10X - 0.166$, $F = 0.766$, $R^2 = 0.04$, $P = 0.392$) (Fig. 1). Nevertheless, *Bt* adoption rates increased from 40% in 2002 to nearly 70% in 2009 in parts of southeastern Pennsylvania, where there were three sites (Dauphin, Lancaster and York counties), in common with a previous study.[5] At two of these three sites, ECB stalk damage appears to have substantially declined over the last decade (Dauphin: from 2.5 to 0.1 tunnels per stalk; Lancaster: from 1.8 to 0.5 tunnels per stalk), while stalk damage at the third site (York: 1.0–1.4 tunnels per stalk) remained similar to levels found a decade ago.[5] There was also another common site (Lycoming County) in north-central Pennsylvania, where ECB damage also declined from 2.1 to 0.3 tunnels per stalk in the same time period.[5] Additionally, ECB damage at the Centre County site declined from 3.5 tunnels per plant in 2004 and 2005 to less than 0.2 tunnels per stalk for the entire season (Calvin D, private communication). Moreover, ECB damage across Pennsylvania appears to have substantially decreased from 1.68 to 0.35 tunnels per stalk in the last decade (Table 4).[5]

3.2 Landscape analysis

When the percentage of cropland within a 0.5 or 10 km radius of the sampling sites was related to the number of ECB tunnels per stalk, no significant relationships could be found (best-fit regression lines: 0.5 km, $Y = 0.0005X + 0.327$, $F = 0.02$, $R^2 = 0.00$, $P = 0.885$; 10 km: $Y = 0.001X + 0.318$, $F = 0.14$, $R^2 = 0.01$, $P = 0.716$), suggesting that finer-scale landscape factors or other aspects

Table 1. Prior year crop, yield (Mg), net income (\$ ha^{-1}), European corn borer larvae and tunnels per stalk and the percentage of stalks and ears damaged (± SEM) in *Bt* and non-*Bt* corn for 16 sites in four different growing zones across Pennsylvania in 2010[a]

Location (zone number)	Previous crop	Type	Yield (Mg)	Net income	Larvae per stalk	Tunnels per stalk	Percentage of stalks damaged	Percentage of ears damaged
Mercer (1)	Hay	*Bt*	11.62(0.17)	2104.39(35.22)	0.00**	0.01(0.01)**	0.50(0.50)**	0.50(0.50)**
		Non-*Bt*	11.55(0.18)	2146.09(35.00)	0.11(0.01)**	0.23(0.04)**	20.50(2.85)**	7.00(1.64)**
Tioga (1)	Corn	Bt	10.09(0.28)	1818.16(56.55)	0.00	0.00	0.00*	0.00
		Non-*Bt*	10.06(0.23)	1867.10(45.72)	0.01(0.01)	0.02(0.01)	1.85(0.82)*	0.00
Cambria (1)	Corn	Bt	9.98(0.20)*	1808.54(41.71)	0.00	0.00	0.00	0.50(0.50)
		Non-*Bt*	9.40(0.24)*	1741.62(46.18)	0.01(0.01)	0.01(0.01)	0.50(0.50)	1.00(0.69)
Bradford (1)	Corn	*Bt*	11.97(0.22)**	2210.54(45.53)*	0.00**	0.00**	0.00**	0.00**
		Non-*Bt*	11.37(0.22)**	2130.51(43.99)*	0.07(0.03)**	0.47(0.15)**	29.00(4.92)**	7.50(7.50)**
Westmoreland (2)	Corn	*Bt*	9.10(0.14)**	1641.58(28.43)	0.00**	0.00**	0.83(0.58)**	7.92(2.33)
		Non-*Bt*	8.52(0.22)**	1584.41(45.45)	0.06(0.02)**	0.13(0.03)**	4.58(1.34)**	6.67(1.87)
Centre (2)	Corn	*Bt*	10.83(0.14)	1872.16(25.97)	0.00**	0.00**	0.00**	0.00**
		Non-*Bt*	10.66(0.14)	1907.52(25.65)	0.08(0.02)**	0.19(0.02)**	14.86(2.26)**	5.69(1.87)**
Indiana (2)	Soybean	*Bt*	9.11(0.19)**	1611.22(39.11)	0.00**	0.01(0.01)**	0.83(0.58)**	0.83(0.58)**
		Non-*Bt*	8.42(0.35)**	1534.06(70.21)	0.11(0.03)**	0.37(0.06)**	27.92(2.96)**	4.17(1.19)**
Clinton (2)	Soybean	*Bt*	10.03(0.22)*	1805.66(44.80)	0.00**	0.00**	0.00**	0.00**
		Non-*Bt*	9.55(0.24)*	1774.97(48.96)	0.15(0.06)**	0.42(0.03)**	30.00(2.89)**	3.33(1.30)**
Columbia (2)	Soybean	Bt	10.81(0.17)	1940.39(33.58)**	0.01(0.01)**	0.01(0.01)**	2.08(1.34)**	0.00**
		Non-*Bt*	10.87(0.16)	2016.94(34.09)**	0.06(0.01)**	0.13(0.03)**	10.00(2.00)**	2.50(1.09)**
Clinton (3)	Soybean	*Bt*	11.51(0.15)*	2112.95(33.90)**	0.00**	0.01(0.01)**	1.00(0.68)**	0.00
		Non-*Bt*	11.77(0.16)*	2215.33(30.76)**	0.04(0.01)**	0.12(0.01)**	9.50(1.70)**	1.00(0.69)
Lycoming (3)	Soybean	*Bt*	13.14(0.10)**	2373.43(21.79)**	0.00	0.00**	0.00**	1.00(1.00)**
		Non-*Bt*	13.55(0.22)**	2516.35(42.41)**	0.01(0.01)	0.49(0.07)**	38.50(3.42)**	7.00(1.64)**
Union (3)	Soybean	*Bt*	11.32(0.12)	2001.85(24.82)	0.00**	0.01(0.01)**	0.50(0.50)**	0.50(0.50)**
		Non-*Bt*	11.40(0.14)	2017.26(27.37)	0.15(0.01)**	0.31(0.10)**	22.50(3.69)**	3.00(1.28)**
Perry (3)	Soybean	*Bt*	10.81(0.18)	1964.85(35.89)	0.00**	0.02(0.01)**	2.00(0.92)**	0.00**
		Non-*Bt*	10.75(0.22)	2012.77(43.31)	0.27(0.03)**	1.10(0.07)**	64.00(3.11)**	9.50(2.56)**
York (4)	Soybean	*Bt*	12.26(0.15)	2216.59(30.23)*	0.03(0.01)**	0.08(0.03)**	7.50(2.60)**	1.00(0.69)**
		Non-*Bt*	12.35(0.14)	2280.56(29.39)*	0.38(0.06)**	1.43(0.14)**	60.00(5.33)**	21.00(3.32)**
Lancaster (4)	Soybean	*Bt*	10.45(0.16)*	1892.93(32.62)	0.05(0.01)**	0.11(0.01)**	12.00(2.96)**	1.50(0.80)**
		Non-*Bt*	10.14(0.16)*	1871.32(34.74)	0.23(0.02)**	0.84(0.09)**	54.50(4.44)**	21.50(3.02)**
Franklin (4)	Soybean	*Bt*	5.21(0.25)*	838.37(52.42)	0.00**	0.01(0.01)**	0.50(0.50)**	0.00*
		Non-*Bt*	4.64(0.21)*	770.28(45.27)	0.09(0.02)**	0.59(0.07)**	38.50(5.04)**	1.50(0.82)*

[a] * Mean within a column within each site significantly different at $\alpha = 0.10$; **mean within a column within each site significantly different at $\alpha = 0.05$.

Table 2. Prior year crop, yield (Mg), net income (\$ ha^{-1}), European corn borer larvae per stalk, tunnels per stalk and percentage of stalks and ears damaged (± SEM) in *Bt* and non-*Bt* corn for ten locations in four different growing zones across Pennsylvania in 2011[a]

County (zone number)	Previous crop	Type	Yield (Mg)	Net income	Larvae per stalk	Tunnels per stalk	Percentage of stalks damaged	Percentage of ears damaged
Mercer (1)	Hay	*Bt*	10.61 (0.21)*	2648.97 (54.72)	0.00**	0.01 (0.01)**	0.50 (0.50)**	0.50 (0.50)
		Non-*Bt*	10.20 (0.17)*	2622.31 (46.60)	0.07 (0.02)**	0.23 (0.05)**	21.00 (3.90)**	1.50 (0.82)
Centre (2)	Soybean	*Bt*	7.93 (0.24)	1928.13 (65.12)	0.00**	0.01 (0.01)**	1.67 (0.98)**	2.50 (1.38)**
		Non-*Bt*	7.76 (0.30)	1946.11 (79.66)	0.08 (0.02)**	0.21 (0.04)**	15.83 (2.25)**	7.92 (1.99)**
Indiana (2)	Soybean	*Bt*	10.51 (0.17)	2539.85 (45.31)	0.01 (0.01)**	0.01 (0.01)**	0.42 (0.42)**	0.83 (0.83)**
		Non-*Bt*	10.48 (0.19)	2577.47 (48.31)	0.20 (0.03)**	0.26 (0.03)**	21.25 (2.65)**	7.50 (1.83)**
Columbia (2)	Wheat	*Bt*	4.70 (0.26)	1027.96 (70.36)	0.02 (0.01)	0.03 (0.02)*	2.92 (1.41)*	0.83 (0.57)
		Non-*Bt*	4.49 (0.30)	1034.83 (83.11)	0.01 (0.01)	0.10 (0.03)*	7.64 (2.26)*	2.50 (1.09)
Clinton (3)	Soybean	*Bt*	8.02 (0.16)	1910.52 (42.29)**	0.00	0.00	0.00	0.00
		Non-*Bt*	8.10 (0.20)	2019.68 (54.37)**	0.00	0.02 (0.01)	2.00 (1.56)	0.50 (0.50)
Lycoming (3)	Corn	*Bt*	12.66 (0.20)**	3100.81 (55.47)**	0.00	0.01 (0.01)	0.50 (0.50)	0.00
		Non-*Bt*	13.14 (0.31)**	3309.66 (81.25)**	0.01 (0.01)	0.04 (0.02)	3.50 (1.82)	0.00
Dauphin (3)	Soybean	*Bt*	3.92 (0.18)**	833.77 (52.03)**	0.01 (0.01)	0.06 (0.04)	4.21 (2.21)	0.00
		Non-*Bt*	4.33 (0.14)**	1030.52 (40.49)**	0.01 (0.01)	0.08 (0.03)	6.50 (2.54)	0.50 (0.50)
York (4)	Soybean	*Bt*	10.84 (0.30)	2726.35 (81.31)	0.00	0.02 (0.01)*	2.00 (1.17)	0.00
		Non-*Bt*	10.94 (0.19)	2833.39 (55.16)	0.00	0.06 (0.02)*	5.00 (1.53)	0.50 (0.50)
Berks (4)	Corn	*Bt*	5.69 (0.37)	1260.19 (133.33)	0.00	0.01 (0.01)*	0.50 (0.50)**	0.00*
		Non-*Bt*	5.58 (0.49)	1328.69 (100.82)	0.02 (0.01)	0.07 (0.03)*	6.00 (3.11)**	3.00 (1.05)*
Lehigh (4)	Soybean	*Bt*	9.19 (0.35)**	2201.64 (91.31)	0.00**	0.02 (0.01)**	1.50 (0.82)**	0.00**
		Non-*Bt*	8.62 (0.35)**	2131.05 (93.40)	0.14 (0.03)**	0.60 (0.09)**	42.00 (5.36)**	6.00 (1.52)**

[a] * Mean within a column within each site significantly different at $\alpha = 0.10$; **mean within a column within each site significantly different at $\alpha = 0.05$.

Table 3. Yield (Mg), European corn borer larvae per stalk, tunnels per stalk and the percentage of stalks and ears damaged (± SEM) in *Bt* and non-*Bt* corn for three locations in two different growing zones in Pennsylvania in 2012

County (zone number)	Previous crop	Type	Yield (Mg)	Larvae per stalk	Tunnels per stalk	Percentage of stalks damaged	Percentage of ears damaged
Centre (2)	Soybean	*Bt*	8.24(0.17)	0.00**	0.01(0.01)**	0.42(0.42)**	0.00
		Non-*Bt*	8.04(0.23)	0.05(0.02)**	0.10(0.05)**	9.17(2.40)**	2.08(1.20)
Lancaster (4)	Soybean	*Bt*	9.90(0.15)**	0.00**	0.01(0.01)**	1.00(0.68)**	0.50(0.50)**
		Non-*Bt*	9.34(0.32)**	0.05(0.02)**	0.12(0.05)**	9.50(3.52)**	9.00(2.50)**
York (4)	Soybean	*Bt*	11.83(0.19)**	0.00**	0.02(0.01)**	2.00(0.92)**	1.50(1.50)**
		Non-*Bt*	10.84(0.26)**	0.47(0.05)**	1.43(0.10)**	76.50(2.64)**	21.50(5.30)**

[a] **Mean within a column within each site significantly different at $\alpha = 0.05$.

Table 4. Yield (Mg), European corn borer larvae per stalk, tunnels per stalk and the percentage of ears damaged (± SEM) in *Bt* and non-*Bt* corn in Pennsylvania averaged over all sites and years

Hybrid type	Yield (Mg)	Larvae per stalk	Tunnels per stalk	Percentage of ears damaged
Bt	9.73 (0.44)	0.01 (0.01)	0.02 (0.01)	0.70 (0.28)
Non-*Bt*	9.54 (0.45)	0.10 (0.02)	0.35 (0.07)	5.68 (1.14)

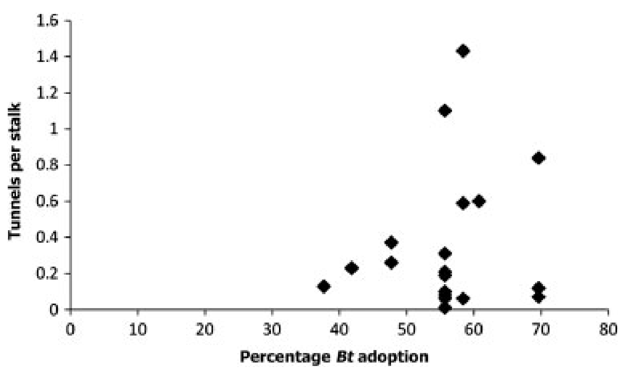

Figure 1. Linear regression between 2009 *Bt* adoption rates and the number of European corn borer tunnels per stalk in non-*Bt* hybrids ($Y = 0.10X - 0.166$, $F = 0.766$, $R^2 = 0.037$, $P = 0.392$).

of the landscape may be driving local populations. Alternatively, factors other than landscape may be influencing ECB populations.

3.3 European corn borer trapping

When ECB damage at each site was related to the cumulative number of male moths in pheromone traps, significant positive relationships between captures of *Z*-race ECB and the percentage of ears damaged were found for 2010 and 2011 (Fig. 2, Table 5). Additionally, captures of *Z*-race ECB were found to be a marginal predictor of the number of tunnels per stalk (Fig. 3), but not the percentage of stalks damaged (Table 5). No significant relationships were detected between capture of *E*-race ECB moths and the number of tunnels per stalk (Fig. 4) or the percentage of damaged ears or stalks (Table 5). Combined capture of *E*- and *Z*-race moths was a marginal predictor of the percentage of damaged ears (Fig. 5), but not the number of tunnels per stalk or the percentage of damaged stalks (Table 5). These latter results clearly indicate that *Z*-race ECB drove the relationships that were detected.

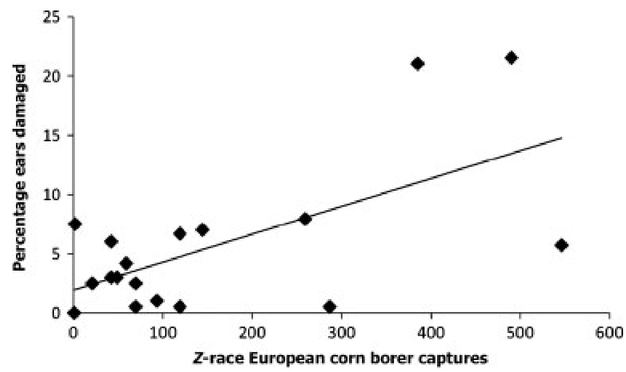

Figure 2. Linear regression between cumulative *Z*-race European corn borer captures in pheromone traps and the percentage of damaged ears due to European corn borer in non-*Bt* hybrids during 2010 and 2011 ($Y = 0.24X - 1.59$, $R^2 = 0.362$, $P = 0.008$).

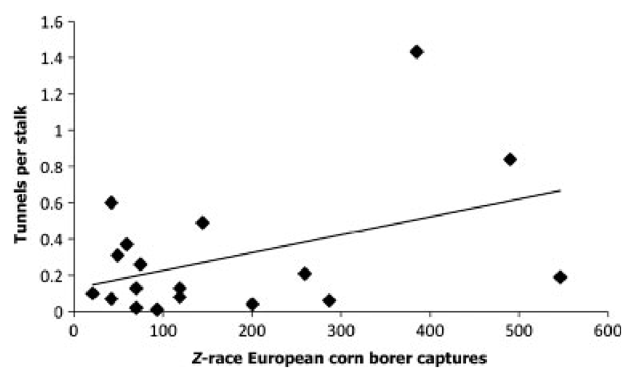

Figure 3. Linear regression between cumulative *Z*-race European corn borer captures in pheromone traps and the number of European corn borer tunnels per stalk in non-*Bt* hybrids during 2010 and 2011 ($Y = 0.001X - 0.129$, $R^2 = 0.191$, $P = 0.070$).

4 DISCUSSION

As expected, *Bt* hybrids continued to be very effective at reducing stalk damage caused by ECB. Damage was significantly lower in *Bt* than in non-*Bt* hybrids at 83% of the sites over all 3 years (Tables 1, 2 and 3). This result was expected because *Bt* hybrids are well known to be very effective at controlling ECB.[4,5,25,26] At sites where the degree of damage to *Bt* hybrids and non-*Bt* hybrids was similar, non-*Bt* hybrids had fewer than 0.1 tunnels per stalk. Notably, 66% of sites had less than 25% of stalks damaged in non-*Bt* hybrids, suggesting that European corn borer populations are relatively low across the state. In a previous Pennsylvania study, only one of

Table 5. Linear regressions between the number of European corn borer *E*-races, *Z*-races and $E+Z$-races captured in sex pheromone traps and the number of tunnels per stalk and the percentage of damaged ears and stalks in non-*Bt* field corn during 2010 and 2011

Pheromone race	*Y*	Model	*F*	R^2	*P*
E-race	Tunnels per stalk	$Y=0.0005X+0.24$	0.69	0.041	0.419
	% Damaged stalks	$Y=0.012X+17.51$	0.36	0.022	0.555
	% Damaged ears	$Y=0.007X+4.59$	1.14	0.066	0.302
Z-race	Tunnels per stalk	$Y=0.001X+0.129$	3.78	0.191	0.070
	% Damaged stalks	$Y=0.045X+11.58$	2.91	0.154	0.108
	% Damaged ears	$Y=0.24X+1.59$	9.06	0.362	0.008
$E+Z$-races	Tunnels per stalk	$Y=0.0002X+0.15$	2.51	0.173	0.139
	% Damaged stalks	$Y=0.017X+10.63$	2.98	0.199	0.110
	% Damaged ears	$Y=0.006X+2.41$	3.60	0.231	0.082

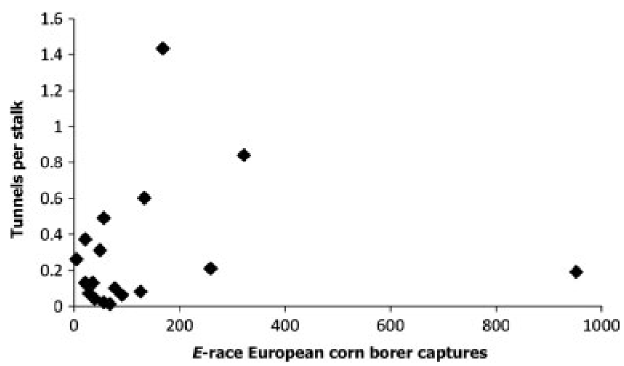

Figure 4. Linear regression between cumulative *E*-race European corn borer captures in pheromone traps and the number of European corn borer tunnels per stalk in non-*Bt* hybrids during 2010 and 2011 ($Y=0.0005X+0.24$, $R^2=0.041$, $P=0.419$).

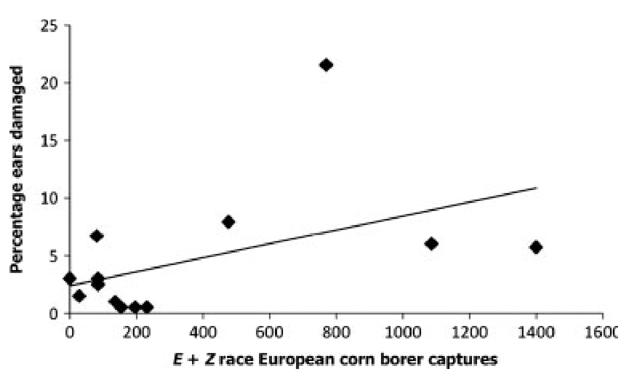

Figure 5. Linear regression between cumulative *E*- and *Z*-race European corn borer captures in pheromone traps and the percentage of damaged ears due to European corn borer in non-*Bt* hybrids during 2010 and 2011 ($Y=0.006X-2.41$, $R^2=0.231$, $P=0.082$).

12 locations had about 25% of stalks damaged in non-*Bt* hybrids; the remaining sites had at least 50% of stalks damaged.[5]

Across Pennsylvania, infestations of ECB in non-*Bt* hybrids appear to have decreased substantially, particularly at the Centre County location and at three of the four sites (Dauphin, Lancaster, Lycoming and York counties) that were shared with a previous effort.[5] The reason for this decline is unclear, but may be related to local *Bt* adoption rates (see below for further discussion of this issue). Surprisingly, in 2010 and 2012 a high population of ECB persisted near the York County site, an area that anecdotally has a relatively high *Bt* adoption rate. In 2011, the field was located about 8 km west of the 2010 site, and much lower ECB injury in the non-*Bt* hybrids was found. This evidence of local ECB population fluctuations reinforces the need for farmers to scout their non-*Bt* plantings to understand ECB population changes and the associated threat to their fields. However, as *Bt*/non-*Bt* seed mixtures (also known as 'refuge-in-a-bag') become increasingly popular, they will complicate assessment of pest populations on non-*Bt* plants.[27]

Ear damage caused by ECB was low across the sites, with only three locations over 3 years having greater than 10% of ears damaged in non-*Bt* hybrids, indicating that ECB is not a major pest of field corn ears in Pennsylvania. At 63% of the sites, lower levels of ear injury from ECB were found in *Bt* compared with non-*Bt* ears (Tables 1, 2 and 3), indicating that *Bt* hybrids can effectively reduce ear damage, as documented in other studies.[28] In a related study, the present authors also found low levels of corn earworm (*Helicoverpa zea* Boddie) damage in these plots, suggesting that ear pests are generally not problematic in Pennsylvania field corn.[21] Moreover, at the three sites with ECB ear damage of over 10%, corn earworm damage was low, suggesting that the threat of ear damage caused by a combination of the two species in field corn is low, but this threat probably varies with planting date because earworm populations largely depend on when the corn was established.[21]

In spite of experiencing lower rates of ECB injury across the 3 years of the present study, *Bt* hybrids only produced significantly higher yields than non-*Bt* hybrids at 38% of the sites (11 of the 29 sites) (Tables 1, 2 and 3). Three of the sites where *Bt* hybrids yielded better were planted as continuous corn, and at these locations the yield could have potentially been influenced by corn rootworm populations and rootworm-specific *Bt* toxins; however, corn rootworm populations were not assessed. In contrast to the higher yields from *Bt* hybrids at some sites, non-*Bt* hybrids produced significantly greater yields at 14% of the sites (4 of the 29 sites), while yields among *Bt* and non-*Bt* hybrids were similar at the remaining 48% of the sites (14 of the 29 sites). Previous results indicated that *Bt* hybrids increased yields in Pennsylvania and Maryland by about 5.5% when ECB injury averaged 1.7 tunnels per stalk;[5] however, at the current level of ECB damage (0.35 tunnels per stalk), yields may only be expected to increase 1.9% when using *Bt* hybrids, suggesting that at many of the sites the ECB damage is low enough for growers to be able to produce competitive yields with some non-*Bt* hybrids. Similarly, the area-wide suppression of ECB in the midwestern United States is providing economic benefits for non-*Bt* growers.[4]

Although *Bt* hybrids produced higher yields than non-*Bt* hybrids at 11 locations, the higher-priced transgenic hybrids only returned significantly greater profits at one of these sites. This result emphasizes that yield increases associated with *Bt* traits do not consistently translate into greater net profits, especially when the higher-priced hybrids targeting both ECB and CRW are used on rotated fields for ECB control, as is common now in the northeast.[29] Grain moisture levels among *Bt* and non-*Bt* hybrids were similar (Bohnenblust EW, unpublished data), indicating that differences in drying costs were negligible, in contrast to previous work.[5,29] To maximize profits, these results suggest that growers should choose competitive hybrids that grow well in their area and are appropriate for their local insect pest populations. In the present study, many growers with low ECB pressure could probably have achieved competitive yields and greater profits with non-*Bt* hybrids that had lower seed costs. Indeed, at the four sites where non-*Bt* hybrids yielded better and at the three sites where yield was similar, a significant profit advantage was seen for non-*Bt* hybrids (Tables 1 and 2). Nevertheless, some of the locations had ECB damage high enough to warrant caution, and at these locations the authors would still recommend *Bt* hybrids to reduce risk and maintain profitability.

Additionally, because ECB populations appear to be low across much of the state, growers would have the option of switching between *Bt* and non-*Bt* hybrids to take advantage of their respective strengths. For example, a grower could reduce input costs by planting non-*Bt* hybrids for several years, and then, if scouting or Pestwatch reports revealed increases in ECB populations, the grower could switch much of the acreage to *Bt* hybrids to control ECB damage. Once the ECB population was low again, the grower could then return to non-*Bt* hybrids. Such an approach would balance a grower's position, to take advantage of lower-cost seed with the need to control ECB populations, although the details of such an approach would need to be developed.

Moreover, planting non-*Bt* hybrids when possible would also reduce selection for individuals resistant to *Bt* toxins, thereby delaying development of resistance to *Bt* by ECB.

Owing to larval movement within the present small-plot, field-trial design, ECB damage, yield and profit estimates may have been biased by control provided by neighboring *Bt* plants. For instance, ECB larvae will move between plants within a field,[30] and if larvae moved from non-*Bt* plants to *Bt* plants in adjacent plots, they would have died when feeding on the *Bt* plants, resulting in the ECB damage estimates being lower in non-*Bt* hybrids than might be expected in a field consisting of a single non-*Bt* hybrid. The present yield and profit estimates for the non-*Bt* plots might therefore be higher than expected in a non-*Bt* field; however, neonate ECB larvae can perceive *Bt* toxins and move away at higher rates from *Bt* plants than from non-*Bt* plants,[30,31] suggesting that some larvae moving to *Bt* plants may be balanced by larvae moving from *Bt* to non-*Bt* plants, possibly mitigating some of this potential bias.

Neither coarse-scale land use nor the latest available *Bt* adoption rates at the scale of crop-reporting district appeared to influence the levels of ECB damage measured in non-*Bt* varieties. If these variables do influence ECB populations, they may be detectable using finer-scale measurements of land use, crop-specific acreage or *Bt* adoption. Nevertheless, other studies have also shown that crop area is not predictive of ECB damage levels,[17] but the present authors explored land use patterns as a potential predictor of ECB damage when it was found that the ECB populations were not explained by *Bt* adoption rates. While ECB injury was high (more than one tunnel per stalk) at three sites in southeastern Pennsylvania, the area of the state with the highest concentration of crop land, this result could be driven by the presence of more non-*Bt* corn than in other regions of the state, or by higher proportions of bivoltine ECB populations, which are found in that part of the state.[32] In contrast, the more northerly sites with shorter growing seasons are likely to have higher proportions of the univoltine strain of ECB.[32] The presence of the bivoltine ECB strain at the more southerly sites provides a greater opportunity for ECB populations to grow quickly, possibly resulting in more variable and higher population levels.

When considering *Bt* adoption rates, it does not seem too surprising that no relationship was detected between ECB populations and *Bt* adoption, as midwestern researchers found.[4] These midwestern data were based on statewide averages of ECB populations generated in long-term sampling efforts. The present data are far less comprehensive; they are based on site averages with only a few years of data. Nevertheless, the data suggest that ECB populations have declined by 72–96% over the last 10 years in several parts of Pennsylvania, and one of the most parsimonious possible explanations is that local *Bt* adoption has played a role.

In each of 2 years, cumulative captures of *Z*-race ECB in pheromone traps predicted the percentage of ears damaged, and marginally predicted the number of tunnels per stalk in non-*Bt* corn. A similar relationship between ECB captures and ear damage has been seen in traps baited with pheromone and a maize kairomone, phenylacetaldehyde.[33] Others found a weak positive relationship between ECB captures in pheromone traps and leaf damage.[34] The relationship between ECB captures and larvae per plant appears to be variable, however, depending on site and population density.[35] ECB captures have previously been shown to be positively correlated with in-field damage when larval densities were low (<0.75 larvae per plant),[35] and at most of the present sites the number of tunnels per stalk was similarly low, suggesting that ECB monitoring with pheromone traps may be most effective when in-field populations are low. Although the relationship between ECB captures and the number of tunnels per stalk in the present study is weak, it suggests that the PestWatch network can provide growers with relative population densities that can complement scouting efforts to help them to decide whether *Bt* hybrids might be economical in future years. Further, because a complementary study also found significant relationships between in-field infestations of corn earworm and moth captures in PestWatch,[21] data from PestWatch or similar networks may be more robust and widely applicable to management decisions than currently recognized.

In summary, it was found that damage from ECB tends to be low across Pennsylvania, with a few localized exceptions. The authors failed to identify environmental factors associated with damage levels because the analyses may have been too coarse to detect a relationship between injury and regional *Bt* adoption or the intensity of agricultural land use. The data suggest that, at least in several locations, ECB populations have declined substantially. *Bt* hybrids yielded more than non-*Bt* hybrids at only 38% of the sites, and, because of higher seed costs associated with multiple-gene *Bt* hybrids, at only one of these sites did yield translate into a significantly greater profit. Nevertheless, *Bt* hybrids continue to provide excellent control of ECB and are still valuable in areas where ECB damage is high, but, in areas with low ECB populations, some non-*Bt* hybrids can yield competitively and result in higher profits. Notably, it was found that captures of *Z*-race ECB moths in the PestWatch network were associated with ECB damage to field corn in Pennsylvania; therefore, information from this trapping network may help growers to determine whether the risk ECB poses to their fields is significant enough to warrant the use of *Bt* hybrids in subsequent years or whether they have an opportunity to increase profitability by planting lower-cost non-*Bt* hybrids.

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SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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