Regional pest suppression associated with widespread Bt maize adoption benefits vegetable growers

Galen P. Dively[a,1,2], **P. Dilip Venugopal**[a,1,2], **Dick Bean**[b], **Joanne Whalen**[c], **Kristian Holmstrom**[d], **Thomas P. Kuhar**[e], **Hélène B. Doughty**[f], **Terry Patton**[a], **William Cissel**[c], and **William D. Hutchison**[g]

[a]Department of Entomology, University of Maryland, College Park, MD 20742; [b]Office of Plant Industries and Pest Management, Maryland Department of Agriculture, Annapolis, MD 21401; [c]Department of Entomology and Wildlife Ecology, University of Delaware, Newark, DE 19716; [d]New Jersey Agricultural Experiment Station, Rutgers University, New Brunswick, NJ 08901; [e]Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061; [f]Eastern Shore Agricultural Research and Extension Center, Virginia Polytechnic Institute and State University, Painter, VA 23420; and [g]Department of Entomology, University of Minnesota, St. Paul, MN 55108

Edited by Fred L. Gould, North Carolina State University, Raleigh, NC, and approved January 31, 2018 (received for review November 29, 2017)

Transgenic crops containing the bacterium *Bacillus thuringiensis* (Bt) genes reduce pests and insecticide usage, promote biocontrol services, and economically benefit growers. Area-wide Bt adoption suppresses pests regionally, with declines expanding beyond the planted Bt crops into other non-Bt crop fields. However, the offsite benefits to growers of other crops from such regional suppression remain uncertain. With data spanning 1976–2016, we demonstrate that vegetable growers benefit via decreased crop damage and insecticide applications in relation to pest suppression in the Mid-Atlantic United States. We provide evidence for the regional suppression of *Ostrinia nubilalis* (Hübner), European corn borer, and *Helicoverpa zea* (Boddie), corn earworm, populations in association with widespread Bt maize adoption (1996–2016) and decreased economic levels for injury in vegetable crops [peppers (*Capsicum annuum* L.), green beans (*Phaseolus vulgaris* L.), and sweet corn (*Zea mays* L., convar. *saccharata*)] compared with the pre-Bt period (1976–1995). Moth populations of both species significantly declined in association with widespread Bt maize (field corn) adoption, even as increased temperatures buffered the population reduction. We show marked decreases in the number of recommended insecticidal applications, insecticides applied, and *O. nubilalis* damage in vegetable crops in association with widespread Bt maize adoption. These offsite benefits to vegetable growers in the agricultural landscape have not been previously documented, and the positive impacts identified here expand on the reported ecological effects of Bt adoption. Our results also underscore the need to account for offsite economic benefits of pest suppression, in addition to the direct economic benefits of Bt crops.

agricultural biotechnology | pest management | ecological effects | regional pest suppression | offsite benefits

Transgenic crops containing the bacterium *Bacillus thuringiensis* (Bt) genes that express insecticidal proteins are a major pest-management tool. Worldwide Bt crop plantings in 2016 reached 98.5 million hectares (ha), from 1.1 million ha in 1996, primarily as Bt maize (*Zea mays* L.; corn), cotton (*Gossypium* sp. L.), and soybean [*Glycine max* (L.) Merr.] (1). The extensive adoption of Bt crops over the past two decades has enabled control of many economically important insect pests globally (2–6), even as a rise in insect resistance to Bt proteins threatens its sustainability (1, 7). Pest suppression from Bt crop adoption reduces insecticide usage, promotes biocontrol services, and delivers economic benefits (4, 8–13).

The regional pest suppression from area-wide Bt adoption is now well documented, with target pest declines expanding beyond the planted Bt crops into other non-Bt crop fields (2–5, 14, 15). The regional adoption of Bt corn and cotton suppresses pest populations in non-Bt corn and cotton fields in the region. For instance, non-Bt field corn growers in the Midwestern United States benefitted economically from regional suppression of European corn borer, *Ostrinia nubilalis* (Hübner), through area-wide Bt field corn adoption (4). Similarly, adoption of Bt cotton in China suppressed pink bollworm [*Pectinophora gossypiella* (Saunders)] and cotton bollworm [*Helicoverpa armigera* (Hübner)] populations in non-Bt cotton (3, 5). In addition, Bt cotton adoption also suppressed cotton bollworm larval density in other host crops (3). Such regional pest suppression through Bt adoption could also benefit traditional and organic farmers growing other crops through reduced crop damage and insecticide usage (3, 4, 12). However, such benefits to growers of other crops remain unexamined and uncertain, particularly in terms of long-term, regional pest dynamics in relation to Bt adoption. We tested the hypothesis that regional pest suppression through Bt adoption benefits non-Bt growers through reduced crop damage and insecticide applications.

With data spanning four decades and across the Mid-Atlantic US region, we analyzed trends in *O. nubilalis* and corn earworm, *Helicoverpa zea* (Boddie), activity before (1976–1995; pre-Bt) and since (1996–2016) Bt corn introduction and examined potential benefits to vegetable growers through reduced crop damage and recommended insecticide applications. Vegetable crops in the Mid-Atlantic United States represent an ideal cropping system to examine the benefits of regional pest suppression from Bt adoption. Both *O. nubilalis* and *H. zea* have broad feeding and migratory behaviors as economically important pests on many agricultural commodities (16, 17). *O. nubilalis*

Significance

Area-wide *Bacillus thuringiensis* (Bt) adoption suppresses pests regionally, with declines expanding beyond the planted Bt crops into other non-Bt crop fields. The offsite benefits to vegetable crops from such pest suppression have not been documented. We show that widespread Bt field corn adoption is strongly associated with marked decreases in the number of recommended insecticidal applications, insecticides applied, and damage to vegetable crops in the United States. These positive impacts to growers, including organic producers, in the agricultural landscape expands on known ecological effects of Bt adoption.

Author contributions: G.P.D., P.D.V., and W.D.H. designed research; G.P.D., P.D.V., D.B., J.W., K.H., T.P.K., H.B.D., T.P., and W.C. performed research; G.P.D. and P.D.V. contributed new reagents/analytic tools; G.P.D. and P.D.V. analyzed data; and G.P.D., P.D.V., D.B., J.W., K.H., T.P.K., H.B.D., T.P., W.C., and W.D.H. wrote the paper.

Conflict of interest statement: The European corn borer damage data for this study were derived from control plots of pesticide efficacy trials that were part of other unrelated studies funded by various organizations and companies including DuPont Pioneer, Dow AgroSciences, Monsanto, Bayer CropScience, and Syngenta. The pesticide efficacy trials were unrelated to this study, and these companies did not provide funding to support this work, but may be affected financially by publication of this paper and have funded other work by G.P.D., T.P.K., K.H., J.W., and W.D.H.

This article is a PNAS Direct Submission.

[1]G.P.D. and P.D.V. contributed equally to this work.

[2]To whom correspondence may be addressed. Email: galen@umd.edu or venugopal.dilip@gmail.com.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1720692115/-/DCSupplemental.

is a major pest of green beans (*Phaseolus vulgaris* L.) and peppers (*Capsicum annuum* L.), and both insects are major pests of sweet corn (*Z. mays* L., convar. *saccharata*) (18). With New Jersey as a key pepper-producing state in the United States, these vegetable crops are economically important components of the 3,816 farms in New Jersey, Maryland, Delaware, and Virginia (19). In 2016, the three vegetable crops generated $75 million in farm cash receipts on these farms (20). With about one-half of the sweet corn, pepper, and green bean acreage contracted for processing, the six processing companies operating in the Mid-Atlantic region depend on these vegetable crops.

Historically, insecticides have been used extensively on these three crops to control *O. nubilalis* (16, 21, 22). Most plantings of sweet corn receive at least one insecticide application to control whorl/tassel infestations of *O. nubilalis* and multiple applications during silking for ear-invading insects including *H. zea*. *O. nubilalis* has been the most serious pest of peppers and green beans in the Mid-Atlantic region, where crops received three to six insecticide applications to ensure marketable quality as larval feeding within the pod or fruit causes both yield loss and contamination problems in the processed product (18, 21). Direct field sampling for larvae or egg masses of *O. nubilalis* or *H. zea* is not practical for peppers and green beans because of the low damage tolerance level. Recommended insecticide treatment schedules for *O. nubilalis* control on these crops are made primarily based on blacklight trap counts of adult moths (18, 23–25). Existing reports identify the decline of *O. nubilalis* and *H. zea* populations in the Mid-Atlantic region in relation to widespread Bt corn adoption (26–28). This may benefit vegetable growers, as field corn is the primary source of *O. nubilalis* that invade Mid-Atlantic vegetable crops. Hence, the regional suppression of moth populations from Bt corn (field corn) adoption could benefit vegetable growers through both reductions in damage and required insecticide applications.

We examined the regional suppressive effects of Bt field corn adoption on *O. nubilalis* and *H. zea* populations and quantified the reduction in damage and potential reduction in insecticide use in sweet corn, peppers, and green beans due to this suppression. We monitored trends in *O. nubilalis* and *H. zea* activity during 1976–2016 through a regional network of blacklight traps in three states, covering 58,600 km^2 and 10 agricultural crop-reporting districts (CRDs) (https://www.nass.usda.gov/Charts_and_Maps/Crops_County/boundary_maps/indexgif.php) in the Mid-Atlantic United States (*SI Appendix*, Fig. S1 and Table S1). We compared the trends in *O. nubilalis* and *H. zea* captures, reduction in pest damage, and recommended insecticide applications in the three vegetable crops before commercial introduction of Bt corn (1976–1995) with years of Bt corn adoption (1996–2016). We then quantified the role of Bt adoption by analyzing these trends as a function of Bt corn adoption both nationally and by individual CRD. We also analyzed the trends in insecticides applied in peppers and sweet corn in New Jersey during 1992–2016 as a function of national Bt corn adoption.

Mean nightly captures of *O. nubilalis* and *H. zea* declined significantly over the past 21 y, since the introduction of Bt corn. Piecewise linear mixed-model slopes, indicating change in moths trapped per year, were significantly negative during 1996–2016 ($P < 0.0001$), but did not differ significantly from zero during 1976–1995 (Fig. 1 *A* and *B* and *SI Appendix*, Table S2). *O. nubilalis* and *H. zea* captures, respectively, decreased from mean nightly moth captures of 6.8 and 7.5 during 1976–1995 to each 1.9 nightly moth captures during 1996–2016, a net decline of 72% and 75% (raw data means). Additive effects of Bt adoption and environmental factors, temperature and precipitation, were significantly associated with nightly moth captures over the past two decades (*SI Appendix*, *Statistical Analyses*). Moth captures decreased significantly as a function of national average Bt corn (percent) and Bt corn (percent) in CRDs ($P < 0.0001$) (Fig. 1 *C–F* and *SI Appendix*, Table S2).

Conversely, *O. nubilalis* and *H. zea* captures increased as a function of temperature (*SI Appendix*, Fig. S2 *A* and *B* and Table S2). *O. nubilalis* captures also decreased significantly as a function of precipitation (*SI Appendix*, Fig. S2*C* and Table S2), albeit with a weaker strength of association than Bt adoption. The adoption of Bt corn contributed more to the reduced *O. nubilalis* captures during 1996–2016 (proportion of variance explained $R_\beta^2 = 0.66$ for national average Bt corn and $R_\beta^2 = 0.68$ for Bt corn in CRDs) than temperature ($R_\beta^2 = 0.29$ for national average Bt corn and $R_\beta^2 = 0.50$ for Bt corn in CRDs) and rainfall ($R_\beta^2 = 0.04$). Bt adoption reduced *H. zea* captures during 1996–2016 ($R_\beta^2 = 0.47$ for national average Bt corn and $R_\beta^2 = 0.64$ for Bt corn in CRDs), despite its increase with temperature ($R_\beta^2 = 0.43$ for national average Bt corn and $R_\beta^2 = 0.67$ for Bt corn in CRDs). These results indicate that the regional suppression of both moth pests is strongly associated with widespread Bt field corn adoption in the Mid-Atlantic United States, after accounting for the effects of the environmental factors.

We used the time-series data on moth captures within years for each CRD to estimate the potential impact of *O. nubilalis* population declines on recommended control actions in green beans, peppers, and sweet corn. We analyzed the trend in number of recommended insecticidal sprays per crop cycle, calculated based on running 5-d totals of moth captures and action thresholds for determining the need and scheduling of insecticide applications for *O. nubilalis* control on these crops in the Mid-Atlantic region (18, 22, 23, 25, 29) (*Materials and Methods*). Results showed that, concomitant with regional moth suppression, the number of recommended insecticidal sprays per crop cycle in each vegetable has declined since Bt corn introduction. For *O. nubilalis*, piecewise linear mixed-effect models showed that the trend in number of insecticide sprays per crop cycle in peppers, green beans, and sweet corn was significantly negative during 1996–2016 ($P < 0.0001$), but did not differ significantly from zero during 1976–1995 ($P > 0.05$) (Fig. 2 *A–C* and *SI Appendix*, Table S3). For *H. zea* control in sweet corn, the trend in the number of insecticide sprays per crop cycle reversed from significantly positive during 1976–1995 to significantly negative during 1996–2016 ($P < 0.0001$) (Fig. 2*C* and *SI Appendix*, Table S2). The number of recommended insecticide sprays to control *O. nubilalis* in peppers, green beans, and sweet corn, and *H. zea* in sweet corn, significantly decreased as a function of national average Bt corn (percent) and Bt corn (percent) in CRDs ($P < 0.0001$) (Fig. 2 *D–I* and *SI Appendix*, Table S3) based on linear mixed-model results.

We collated long-term data on *O. nubilalis* damage in untreated sweet corn (1984–2017) and peppers (1980–2015) from insecticide efficacy trials in the Mid-Atlantic region (New Jersey, Pennsylvania, Delaware, Maryland, and Virginia), including existing published reports (*Materials and Methods*). *O. nubilalis* damage in control plots of vegetables was reduced, in tandem with insecticide usage, since the introduction of Bt corn. ANOVA-based comparisons of damage levels pre-Bt corn and since Bt corn introduction showed that mean *O. nubilalis* damage in control plots of peppers declined significantly from 35% during 1980–1995 to 8% since Bt introduction in 1996, a 78% decrease ($F_{1,\ 104} = 25.7$, $P < 0.0001$, $r^2 = 0.20$) (Fig. 3*A*). Similarly, mean sweet corn ear damage by *O. nubilalis* significantly declined from 50% during 1984–1995 to 15% since Bt corn introduction, a 70% decrease ($F_{1,\ 152} = 31.3$, $P < 0.0001$, $r^2 = 0.17$) (Fig. 3*B*). *O. nubilalis* damage declined significantly as a function of national average Bt corn (percent) in both peppers ($y = 7.30 - 0.09x$, $F_{1,\ 78} = 121$, $P < 0.0001$, $r^2 = 0.61$) and sweet corn ($y = 6.78 - 0.07x$, $F_{1,\ 133} = 97.6$, $P < 0.0001$, $r^2 = 0.42$) (Fig. 3*C*). These results identify and substantiate the decrease in *O. nubilalis* damage in vegetables coinciding with area-wide deployment of Bt corn.

Farmer-reported usage of insecticides in vegetable crops confirmed the decline in total insecticides applied over the past 25 y. In New Jersey, insecticides (total active ingredient) applied in sweet corn declined from 2.64 kg/ha in 1992 to 0.55 kg/ha in 2016, a 79% decrease. In New Jersey peppers, insecticides applied declined from 4.92 kg/ha in 1992 to 0.75 kg/ha in 2016, an 85% decrease. Insecticide usage in peppers significantly declined as a function of national Bt corn (percent) ($y = 4.19 - 0.04x$, $F_{1,\ 7} = 51.6$, $P < 0.001$, $r^2 = 0.88$; Fig. 3*D*), while in sweet corn, the negative association was marginally significant ($y = 2.01 - 0.02x$, $F_{1,\ 9} = 4.8$, $P = 0.056$, $r^2 = 0.35$) (Fig. 3*D*) based on linear regression.

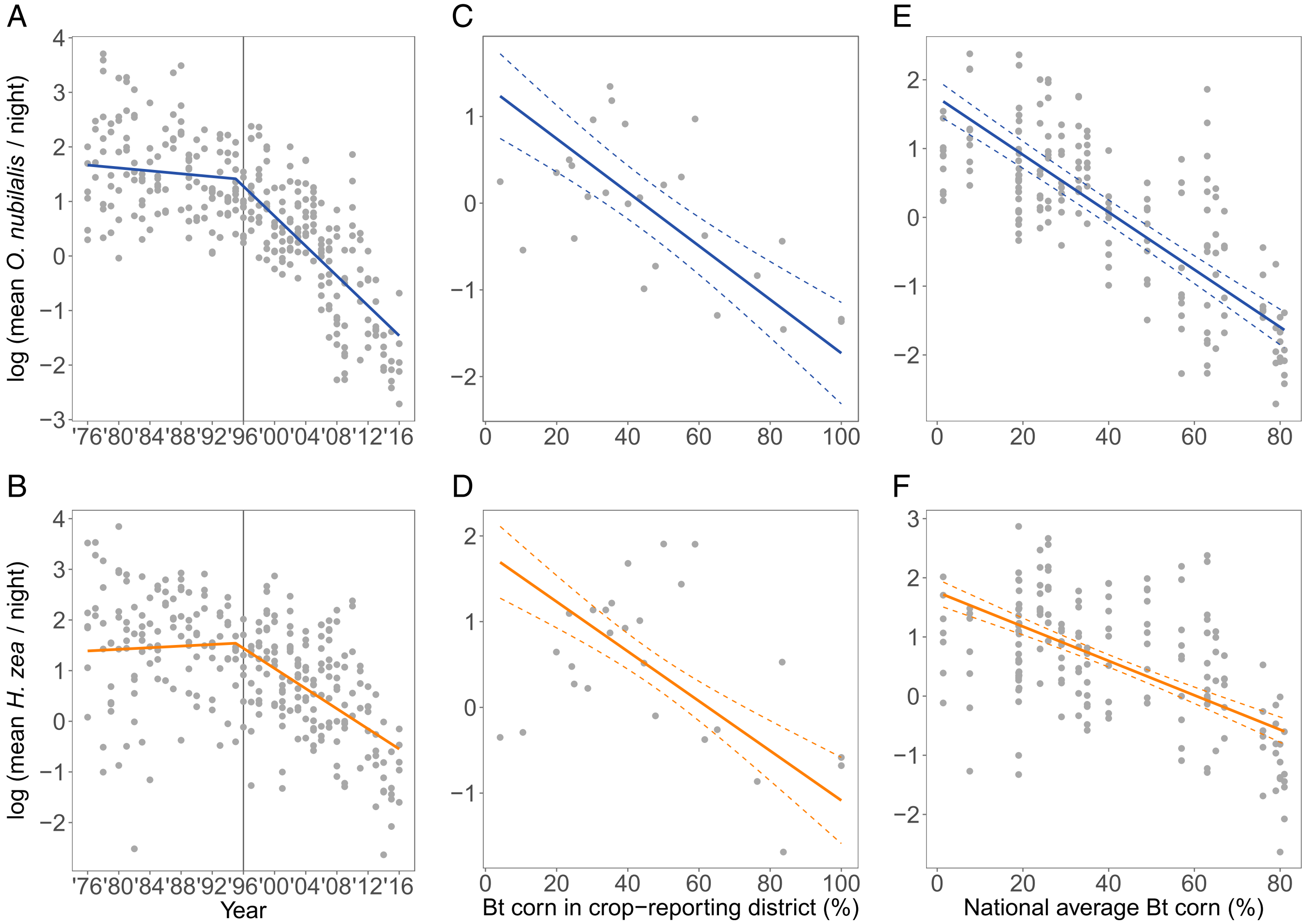

Fig. 1. Activity trends of *O. nubilalis* and *H. zea* in Mid-Atlantic United States (1976–2016) and their association with Bt corn adoption. (*A* and *B*) Trends in mean nightly captures of *O. nubilalis* (*A*) and *H. zea* (*B*) in blacklight traps before and since the beginning of Bt corn use in 1996 (vertical line). (*C*–*F*) Negative linear relationship in mean nightly moth captures and Bt corn adoption (percent) in CRDs (2002, 2006, and 2009) for *O. nubilalis* (*C*) and *H. zea* (*D*) and national average Bt corn adoption (percent) during 1996–2016 for *O. nubilalis* (*E*) and *H. zea* (*F*). Predictions from linear mixed-effects models are plotted (dark lines in all plots) along with upper and lower 95% confidence levels (dotted lines in *C*–*F*), while points represent mean nightly moth captures in the CRDs, all in logarithmic scale.

These results indicate that regional suppression in association with widespread Bt corn adoption may have reduced insecticide usage in vegetable crops.

Through long-term, large-scale analysis, we provide evidence that the regional suppression of both *O. nubilalis* and *H. zea* populations in the Mid-Atlantic region is strongly associated with the area-wide adoption of Bt field corn. Environmental factors and natural enemies also affect the population dynamics of these pest species (27, 30–32). Our results indicate that, after accounting for the environmental factors and their quantified relative influence, the declines in moth populations were strongly related to area-wide Bt field corn adoption, even as increasing temperatures buffered population reduction, consistent with previous reports (3, 27). For *O. nubilalis*, high larval mortality resulted from the high dose of Bt protein expression and the inability of the female to distinguish between Bt and non-Bt corn of similar planting dates for oviposition (4, 33). Thereby, as previous reports identify, Bt crops acted as effective trap crops that induced very high larval mortality, resulting in regional suppression through cumulative years of Bt adoption (3, 4). These results are consistent with previous reports on regional pest suppression (2–6) through Bt adoption in other regions, as well as in the Mid-Atlantic United States (26–28).

An important finding of our study is that the observed regional pest suppression in association with widespread Bt adoption benefits Mid-Atlantic vegetable growers through reduced crop damage and insecticide usage. These offsite benefits to other crops in the agricultural landscape have not been documented previously, so these results expand on the reported ecological effects of regional Bt adoption, including pest suppression in non-Bt crops and promotion of biocontrol services (2–5, 8, 10, 12, 26, 28). Our findings of reduced need for insecticidal treatments to control *O. nubilalis* in Mid-Atlantic vegetables are consistent with those of other vegetable crop studies (34, 35). However, the decline in recommended insecticide sprays reported here represents the potential benefit from Bt field corn adoption that may not translate into actual reduced insecticide applications. The recommendations based on *O. nubilalis* activity in blacklight traps are broad, conservative guidelines for growers who make their own choices and may prophylactically apply insecticides to prevent damage. This is particularly relevant for peppers and green beans for processing that have very low thresholds for damage and high risk of contamination (16).

While the threat of *O. nubilalis* as a pest is diminished, insecticides are applied in Mid-Atlantic vegetable crops to control other pests such as potato leafhoppers [*Empoasca fabae* (Harris)], Mexican bean beetles (*Epilachna varivestis* Mulsant), and other secondary pests. For instance, the increased use of neonicotinoid insecticides applied as seed treatments and foliar sprays in vegetable crops paralleled the adoption of Bt corn. However, these systemic insecticides are labeled mainly for beetle and sucking insect pests and are not effective against lepidopteran larvae.

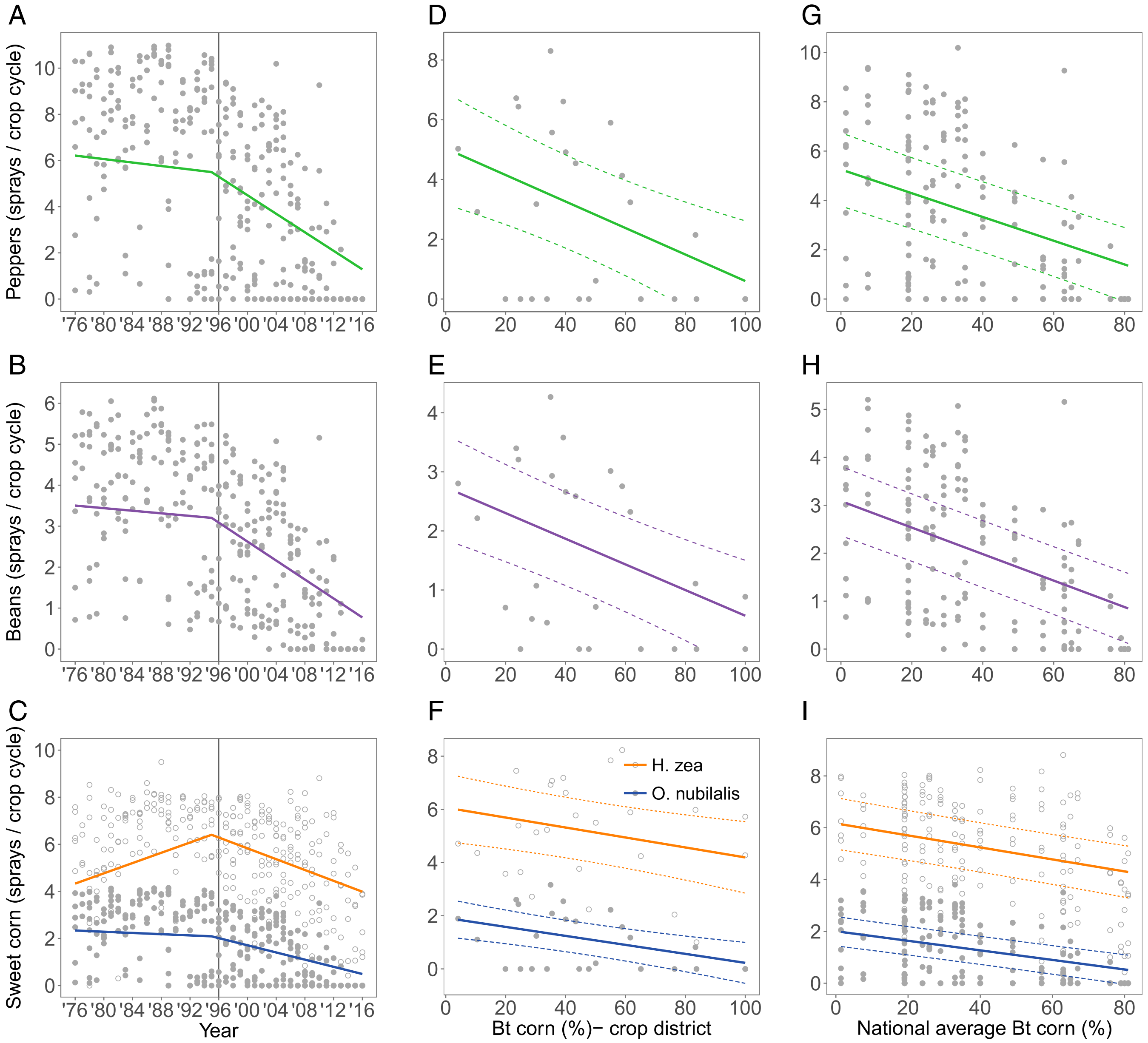

Fig. 2. Trends in recommended insecticidal sprays to control *O. nubilalis* and *H. zea* in vegetable crops of Mid-Atlantic United States (1976–2016) and their association with Bt corn adoption. (*A*–*C*) Recommended number of insecticidal sprays per crop cycle to control *O. nubilalis* during pre-Bt (1976–1995) and Bt (1996–2016) years in peppers (*A*) and green beans (*B*) and to control *O. nubilalis* (black line and gray circles) and *H. zea* (gray line and open circles) in sweet corn (*C*). Vertical line (*A*–*C*) indicates beginning of Bt corn use. (*D*–*F*) Negative linear relationships between insecticidal sprays to control *O. nubilalis* and Bt corn adoption (percent) in CRDs (2002, 2006, and 2009) in peppers (*D*) and green beans (*E*) and to control *O. nubilalis* (blue line and gray circles) and *H. zea* (orange line and open circles) in sweet corn (*F*). (*G*–*I*) Negative linear relationship between insecticidal sprays to control *O. nubilalis* and national average Bt corn adoption (percent) during 1996–2016 in peppers (*G*) and green beans (*H*) and to control *O. nubilalis* (blue line and gray circles) and *H. zea* (orange line and open circles) in sweet corn (*I*). Predictions from linear mixed-effects models are plotted (dark lines in all plots) along with upper and lower 95% confidence levels (dotted lines in *D*–*I*), while points represent average yearly insecticidal sprays in CRDs.

Similarly, the decline in total insecticides applied in New Jersey peppers and sweet corn, as reported by farmers, was also associated with substitution of low use-rate insecticides, namely, pyrethroids and spinosyns, for high-use-rate insecticides such as organophosphates and carbamates (36). Nevertheless, our results indicate that a significant proportion of the decreased insecticide usage in Mid-Atlantic vegetable crops could be attributed to the regional pest suppression associated with widespread Bt field corn adoption.

Regional pest suppression associated with Bt corn adoption may provide substantial economic benefits to vegetable growers. While not quantified here, potential economic benefits include reduced control costs and fewer losses due to contamination at harvest. Particularly for vegetable processing, with a low threshold of infestation tolerated (peppers and green beans) (16), the damage reduction implies less contamination and rejection and greater economic value. Organic growers may also benefit from reduced damages due to the suppression of *O. nubilalis* and *H. zea* populations. Indirect benefits include the reduction in pathogens associated with *O. nubilalis* infestation and damage (37, 38). Regional suppression and the resultant reduced insecticide usage to control *O. nubilalis* in peppers and beans may also promote biocontrol services through an increase in natural enemy populations

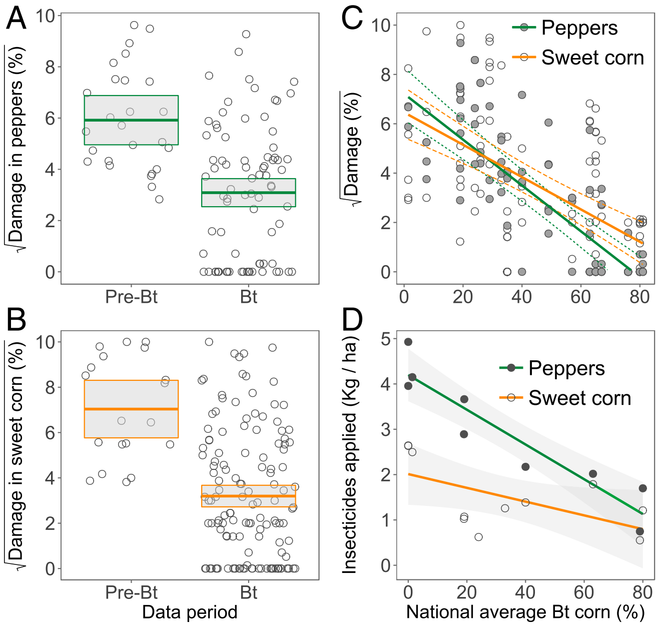

Fig. 3. *O. nubilalis* damage and insecticide usage in Mid-Atlantic vegetable crops (1980–2017) and their relationship with Bt adoption. Significantly reduced *O. nubilalis* damages during Bt years (1996–2017) compared with pre-Bt years in peppers (1980–1995) (*A*) and sweet corn (1984–1995) (*B*). (*C*) Negative linear relationship between national average Bt corn (percent) adoption and *O. nubilalis* damage in peppers (green line and filled circles) and sweet corn (orange line and open circles). (*D*) Negative linear relationship between national average Bt corn (percent) adoption and insecticides applied (total active ingredient) in New Jersey peppers (green line and filled circles) and sweet corn (orange line and open circles). Predictions from linear models (dark lines) are plotted along with upper and lower 95% confidence intervals (gray areas, *A*, *B*, and *D*; dotted lines, *C*), and points represent square root transformed (*A*–*C*) or original (*D*) data values.

(12). Growers of other vegetable crops such as popcorn, potato [*Solanum tuberosum* (L.)], and grain sorghum [*Sorghum bicolor* (L.) Moench], which are host crops of *O. nubilalis*, may also benefit from the regional suppression (35). Vegetable growers in other parts of United States with reduced *O. nubilalis* pressure through high Bt corn acreage are also potential benefactors. Particularly, producers of these vegetables for processing in the North-Central portion of United States (Michigan, Wisconsin, Minnesota, and Ohio) (39) may benefit economically. Our results underscore the need to account for offsite economic benefits of pest suppression, in addition to the direct economic benefits of Bt crops (4, 40).

Overall, our study provides a comprehensive, long-term, and regional-scale documentation of the benefits of transgenic crops. The sustainability of Bt corn in the Mid-Atlantic region and elsewhere, and the associated economic and environmental benefits, is threatened due to the resistance development in *H. zea* to multiple Cry proteins and rise of insect resistance in general (1, 7). While area-wide Bt adoption benefits vegetable growers, these non-Bt vegetable crops in the agricultural landscape are alternate hosts of *O. nubiliblis* and *H. zea* that act as unstructured refuges for Bt resistance management. Utilizing the pyramided combination of Cry1Ab and Vip3A that provides *H. zea* control (7) and strictly adhering to insect-resistance management plans (e.g., non-Bt refuges) to maintain susceptible populations of *O. nubilalis* and *H. zea* may enable continued use of Bt technology as a pest-management tool. Considering Bt technology as another tool in the pest-management toolbox and incorporating insect-resistance management plans into broader integrated pest management strategies (biological control, crop rotation, etc.) could help sustain the Bt technology.

Materials and Methods

Moth Flight Activity. Moth activity data were collected from trap-monitoring networks operated as part of extension integrated pest-management programs across three states in the Mid-Atlantic region of the United States—Delaware, Maryland, and New Jersey (*SI Appendix*, Fig. S1). The database consisted of moth captures recorded by 189 blacklight traps (15-W Elisco type) at multiple locations over 58,600 km^2 in 10 CRDs. Each trap was placed within 60 m of a crop field with the minimum of 180° visibility to that crop. Trap captures of *O. nubilalis* and *H. zea* adults were recorded either daily or thrice weekly (usually Monday, Wednesday, and Friday). We assembled individual trap data recorded over the period from 1976 to 2016 and generated average daily moth captures for each CRD during June 13 to September 17 (*SI Appendix*, Table S1), which is the period during the growing season when moth flights are highest and the majority of control recommendations are made. Trap captures recorded over >1 d were extrapolated on a daily basis by dividing the total catch by the number of trapping days. We monitored trends in moth activity during 1976–2016 in each CRD and examined regional suppression of each insect pest, by comparing average daily moth captures before commercial introduction of Bt corn (1976–1995) with years of Bt corn adoption (1996–2016).

Treatment Thresholds and Recommended Insecticidal Sprays. We used the time-series data on moth captures within years for each CRD to estimate the potential impact of reduced *O. nubilalis* populations on recommended control actions in green beans, peppers, and sweet corn. Existing thresholds based on running 5-d totals of moth captures are well established and have been used to determine the need and scheduling of insecticide applications for *O. nubilalis* control on these crops in the Mid-Atlantic (18, 22, 23, 25, 29). If insecticide control action is needed on a green bean crop, applications begin during bloom to pin pod stage according to the recommended schedules (days between sprays) based on 5-d moth totals as: no control required if <10 moths, 7 d if 10–25 moths, 6 d if 26–50 moths, 5 d if 51–75 moths, 4 d if 76–250 moths, or 3 d if >250 moths. We assumed that insecticides were applied any time during the period of June 14 to September 16 (hereafter referred to as seasonal treatment window), based on the planting dates of consecutive green bean crops in the Mid-Atlantic. The period when insecticides are applied to a green bean crop was assumed to be 21 d (hereafter referred to as the crop treatment window), based on the crop's life cycle and growth pattern.

For peppers, insecticide control is recommended when fruits are about half-developed and applied on a 7-d schedule if *O. nubilalis* moth captures are 25–100 per 5 d or every 5 d if moth captures are >100 per 5 d. Similar to green beans, insecticides are applied anytime during the June 14 to September 16 window, but given the extended length of the fruiting period, we assumed a 60-d treatment window for a pepper crop. Insect control is more complicated in sweet corn because *O. nubilalis* overlaps with other lepidopteran pests, particularly *H. zea*. However, if trap captures call for no control action against *H. zea*, then insecticide applications during the silking stage are recommended for *O. nubilalis* control according to the following thresholds based on blacklight trap captures of moths per 5 d: no control required if <25 moths, or treatments applied every 6 d if 25–50 moths, 5 d if 51–100 moths, or 4 d if >100 moths. Similarly, action thresholds based on blacklight trap catches have been developed and used to schedule silk sprays for *H. zea* control on sweet corn, but control decisions in recent years are mainly determined by pheromone trap monitoring. Nevertheless, we used the following blacklight trap thresholds based on 5-d totals of *H. zea* moth captures for the purpose of comparing trends before and after Bt corn adoption. We assumed no control required if <1 moths, 6 d if 1 to <2 moths, 5 d if 2 to <3 moths, 4 d if 3 to <4 moths, 3 d if 4–30 moths, or 3 d if >30 moths. For fresh market sweet corn, we assumed a seasonal treatment window from June 1 to September 15 and a crop treatment window of 18 d.

To calculate how often treatment thresholds were triggered on each vegetable crop, the time series data of daily moth captures were converted to running 5-d totals within years of each CRD. For each vegetable crop, a tally of days exceeding each threshold level was calculated over the seasonal treatment window and then divided by the total number of days to estimate the probability of *O. nubilalis* moth activity exceeding the threshold for each insecticide treatment schedule. These probabilities were then multiplied by the maximum number of possible applications during the crop treatment window. The summation of these products estimated the average number of applications recommended on each vegetable crop during the entire growing season. For example, the equation for calculating the mean number of insecticide applications recommended on green beans is as follows:

$$S=(Po\times 0)+(P_7\times 3)+(P_6\times 3.5)+(P_5\times 4.2)+(P_4\times 5.25)+(P_3\times 7),$$

where S is the mean total number of recommended sprays per crop cycle, P_o is the probability of no control required, P_7 is the probability of a recommended 7-d treatment schedule, P_6 is the probability of a recommended 6-d treatment schedule, and so on. Numbers in parentheses represent the maximum number of possible applications during the crop treatment window. The same calculations were performed for peppers and sweet corn, but with different probability terms and maximum number of possible applications depending upon the crop treatment window. Trends in the average number of recommended insecticidal treatments for *O. nubilalis* control in each CRD were compared before and after Bt corn adoption, as indicators of potential reduced insecticide usage in each vegetable crop. To provide evidence of actual changes in insecticide usage, we compiled data on insecticide applications in bell peppers and sweet corn for New Jersey from the Agricultural Chemical Use Program (41) during 1992–2016 along with the respective crop acreages (42–44) and calculated trends in total active ingredients applied per unit area.

Trends in *O. nubilalis* Damage in Vegetable Crops. We compiled time-series data on field infestations of *O. nubilalis* in untreated sweet corn (1984–2017) and bell peppers (1980–2015) from various sources to document changes in the Mid-Atlantic population since the introduction of Bt corn. Each data type was compiled in standardized format with the same unit of measurement and averaged by year over periods before and after introduction of Bt corn. We compiled data expressed as the percentage of ears (sweet corn) or pepper fruit damaged by *O. nubilalis* from studies conducted in New Jersey, Pennsylvania, Maryland, Delaware, and Virginia. We present data on *O. nubilalis* damage in both crops from untreated control plots of insecticide efficacy trials and sentinel plots conducted by us over the years. In addition, we reviewed insecticide efficacy trials published in the Arthropod Management Tests since 1976 and extracted data on damage levels in untreated control plots of sweet corn and peppers (*SI Appendix*, Table S4). For both published reports and the insecticide trials, we only included data on *O. nubilalis* damage from June to September crop plantings, coinciding with the second and third generations of *O. nubilalis* that are most damaging to vegetable crops. Details on transgenic corn adoption and environmental data and the statistical analyses are provided in *SI Appendix, SI Materials and Methods*. Data used for the analysis are available in Dataset S1.

ACKNOWLEDGMENTS. We thank Mike Embry and Amy Miller, the numerous research assistants and summer research interns, graduate students, and trap operators for their help in data collection over the past 40 y. We thank the research farm managers, David Armentrout, Mike Newell, Alfred Hawkins, Kevin Conover, and Dave Justice for establishing and maintaining sentinel plots of sweet corn and peppers. We also thank Joseph Ingerson-Mahar and Gerald Ghidiu for providing trap and pepper damage data from New Jersey. This project was funded by US Department of Agriculture National Institute of Food and Agriculture Biotechnology Risk Assessment Grant MD-ENTO-0807, with partial support from the Maryland Integrated Pest Management Extension and Agricultural Experiment Station. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

1. Tabashnik BE, Carrière Y (2017) Surge in insect resistance to transgenic crops and prospects for sustainability. *Nat Biotechnol* 35:926–935.
2. Carrière Y, et al. (2003) Long-term regional suppression of pink bollworm by *Bacillus thuringiensis* cotton. *Proc Natl Acad Sci USA* 100:1519–1523.
3. Wu K-M, Lu Y-H, Feng H-Q, Jiang Y-Y, Zhao J-Z (2008) Suppression of cotton bollworm in multiple crops in China in areas with Bt toxin-containing cotton. *Science* 321: 1676–1678.
4. Hutchison WD, et al. (2010) Areawide suppression of European corn borer with Bt maize reaps savings to non-Bt maize growers. *Science* 330:222–225.
5. Wan P, Huang Y, Tabashnik BE, Huang M, Wu K (2012) The halo effect: Suppression of pink bollworm on non-Bt cotton by Bt cotton in China. *PLoS One* 7:e42004.
6. Downes S, et al. (2017) A perspective on management of *Helicoverpa armigera*: Transgenic Bt cotton, IPM, and landscapes. *Pest Manag Sci* 73:485–492.
7. Dively GP, Venugopal PD, Finkenbinder C (2016) Field-evolved resistance in corn earworm to cry proteins expressed by transgenic sweet corn. *PLoS One* 11:e0169115.
8. Cattaneo MG, et al. (2006) Farm-scale evaluation of the impacts of transgenic cotton on biodiversity, pesticide use, and yield. *Proc Natl Acad Sci USA* 103:7571–7576.
9. Romeis J, Meissle M, Bigler F (2006) Transgenic crops expressing *Bacillus thuringiensis* toxins and biological control. *Nat Biotechnol* 24:63–71.
10. Gatehouse AMR, Ferry N, Edwards MG, Bell HA (2011) Insect-resistant biotech crops and their impacts on beneficial arthropods. *Philos Trans R Soc Lond B Biol Sci* 366: 1438–1452.
11. Kathage J, Qaim M (2012) Economic impacts and impact dynamics of Bt (*Bacillus thuringiensis*) cotton in India. *Proc Natl Acad Sci USA* 109:11652–11656.
12. Lu Y, Wu K, Jiang Y, Guo Y, Desneux N (2012) Widespread adoption of Bt cotton and insecticide decrease promotes biocontrol services. *Nature* 487:362–365.
13. Perry ED, Ciliberto F, Hennessy DA, Moschini G (2016) Genetically engineered crops and pesticide use in U.S. maize and soybeans. *Sci Adv* 2:e1600850.
14. Chu C-C, Natwick ET, López RL, Dessert JR, Henneberry TJ (2006) Pink bollworm moth (Lepidoptera: Gelechiidae) catches in the Imperial Valley, California from 1989 to 2003. *Insect Sci* 13:469–475.
15. Storer NP, Dively GP, Herman RA (2008) Landscape effects of insect-resistant genetically modified crops. *Integration of Insect-Resistant Genetically Modified Crops within IPM Programs*, Progress in Biological Control, eds Romeis J, Shelton AM, Kennedy GG (Springer, Dordrecht, The Netherlands), pp 273–302.
16. Showers WB, et al. (1989) *European Corn Borer–Development and Management* (Iowa State University, Ames, IA).
17. Ditman LP, Cory EN (1931) The corn earworm: Biology and control. *Bull Md Agric Exp Stn* 328:443–482.
18. University of Maryland Extension (2017) *2016-2017 Commercial Vegetable Production Recommendations* (University of Maryland Extension, College Park, MD).
19. USDA - NASS (2014) Census of Agriculture—2012. Available at https://www.agcensus.usda.gov/Publications/2012/. Accessed November 1, 2017.
20. USDA - ERS (2017) Cash receipts by state. Farm income and wealth statistics. Available at https://data.ers.usda.gov/reports.aspx?ID=17843. Accessed November 1, 2017.
21. Dively GP, McCully JE (1979) Nature and distribution of European corn borer feeding injury on snap beans. *J Econ Entomol* 72:152–154.
22. Dively GP (1993) Insect pests of sweet corn I & II. *Vegetable Pest Management–Pest Identification and Biology, Scouting Procedures and Recommended Actions*, Maryland and Delaware Pest Management Programs, eds Dively GP, Whalen J, Linduska J, Patton T, Bean D (Maryland Cooperative Extension Service and Delaware Cooperative Extension Service, College Park, MD), 2nd Ed, pp 10–13.
23. Whalen J, VanGessel M, Mulrooney B (2006) Crop profile for beans (snap) in Delaware (Univ of Delaware, Newark, DE). Available at https://ipmdata.ipmcenters.org/documents/cropprofiles/DEsnapbeans2006.pdf. Accessed November 2, 2017.
24. Fournier A (1999) Crop profile for corn (sweet) in Maryland (Univ of Maryland, College Park, MD). Available at https://ipmdata.ipmcenters.org/documents/cropprofiles/MDcorn-sweet.pdf. Accessed November 2, 2017.
25. Garrison S, Ghidiu G, Kline W, Majek B, Wyenandt CA (2005) *Crop Profile for Peppers (Bell) in New Jersey* (Rutgers Agricultural Research and Extension Center, Bridgeton, NJ). Available at www.ipmcenters.org/CropProfiles/docs/njpeppersbell.pdf. Accessed November 2, 2017.
26. Bohnenblust E, Breining J, Fleischer S, Roth G, Tooker J (2013) Corn earworm (Lepidoptera: Noctuidae) in northeastern field corn: Infestation levels and the value of transgenic hybrids. *J Econ Entomol* 106:1250–1259.
27. Venugopal PD, Dively GP (2017) Climate change, transgenic corn adoption and field-evolved resistance in corn earworm. *R Soc Open Sci* 4:170210.
28. Bohnenblust EW, et al. (2014) Current European corn borer, *Ostrinia nubilalis*, injury levels in the northeastern United States and the value of Bt field corn. *Pest Manag Sci* 70:1711–1719.
29. Richards K (2004) *Crop Profile for Beans (Snap) in Pennsylvania* (Pennsylvania State University, University Park, PA). Available at https://ipmdata.ipmcenters.org/documents/cropprofiles/PAsnapbeans.pdf. Accessed November 2, 2017.
30. Barlow CA, Mutchmor JA (1963) Some effects of rainfall on the population dynamics of the European corn borer, *Ostrinia nubilalis* (Hbn.) (Pyraustidae: Lepidoptera). *Entomol Exp Appl* 6:21–36.
31. Chiang HC, Hodson AC (1972) Population fluctuations of the European corn borer, *Ostrinia nubilalis*, at Waseca, Minnesota, 1948–70. *Environ Entomol* 1:7–16.
32. Lewis LC, Bruck DJ, Prasifka JR, Raun ES (2009) *Nosema pyrausta*: Its biology, history, and potential role in a landscape of transgenic insecticidal crops. *Biol Control* 48:223–231.
33. Hellmich RL, Higgins LS, Witkowski JF, Campbell JE, Lewis LC (1999) Oviposition by European corn borer (Lepidoptera: Crambidae) in response to various transgenic corn events. *J Econ Entomol* 92:1014–1020.
34. Schmidt-Jeffris RA, Huseth AS, Nault BA (2016) Estimating E-Race European corn borer (Lepidoptera: Crambidae) adult activity in snap bean fields based on corn planting intensity and their activity in corn in New York agroecosystems. *J Econ Entomol* 109:2210–2214.
35. Kuhar TP, Ghidiu G, Doughty HB (2010) Decline of European corn borer as a pest of potatoes. *Plant Health Prog*, 10.1094/PHP-2010-0129-01-PS.
36. Stivers-Young LJ, Kuhar TP, Hoffmann MP (2003) Pesticide use changes in New York vegetables: 1978 to 1998. *J Ext* 41:1–9.
37. Anderson TE, Echandi E, Kennedy GG (1981) Transmission of the potato blackleg pathogen by European corn borer larvae. *J Econ Entomol* 74:630–633.
38. Sobek EA, Munkvold GP (1999) European corn borer (Lepidoptera: Pyralidae) larvae as vectors of *Fusarium moniliforme*, causing kernel rot and symptomless infection of maize kernels. *J Econ Entomol* 92:503–509.
39. Hutchison WD, Flood B, Wyman JA (2004) Advances in United States sweet corn and snap bean insect pest management. *Insect Pest Management*, eds Horowitz AR, Ishaaya I (Springer, Berlin), pp 247–278.
40. Brookes G, Barfoot P (2008) Global impact of biotech crops: Socio-economic and environmental effects, 1996-2006. *AgBioForum* 11:21–38.
41. USDA - NASS (2016) Agricultural Chemical Use Program. Available at https://www.nass.usda.gov/Surveys/Guide_to_NASS_Surveys/Chemical_Use/. Accessed June 3, 2017.
42. USDA - ERS (2008) U.S. Bell and Chile Pepper Statistics. Available at usda.mannlib.cornell.edu/MannUsda/viewDocumentInfo.do?documentID=1659. Accessed October 5, 2017.
43. USDA - ERS (2010) U.S. Sweet Corn Statistics. Available at usda.mannlib.cornell.edu/MannUsda/viewDocumentInfo.do?documentID=1564. Accessed October 11, 2017.
44. US Department of Agriculture National Agricultural Statistics Service (2017) QuickStats. Available at https://quickstats.nass.usda.gov/. Accessed August 13, 2017.