Transgenic cotton and sterile insect releases synergize eradication of pink bollworm a century after it invaded the United States

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Invasive organisms pose a global threat and are exceptionally difficult to eradicate after they become abundant in their new habitats. We report a successful multistatic strategy for combating the pink bollworm (Pectinophora gossypiella), one of the world’s most invasive pests. A coordinated program in the southwestern United States and northern Mexico included releases of billions of sterile pink bollworm moths from airplanes and planting of cotton engineered to produce insecticidal proteins from the bacterium Bacillus thuringiensis (Bt). An analysis of computer simulations and 21 y of field data from Arizona demonstrate that the transgenic Bt cotton and sterile insect releases interacted synergistically to reduce the pest’s population size. In Arizona, the program started in 2006 and decreased the pest’s estimated statewide population size from over 2 billion in 2005 to zero in 2013. Complementary regional efforts eradicated this pest throughout the cotton-growing areas of the continental United States and northern Mexico a century after it had invaded both countries. The removal of this pest saved farmers in the United States $192 million from 2014 to 2019. It also eliminated the environmental and safety hazards associated with insecticide sprays that had previously targeted the pink bollworm and facilitated an 82% reduction in insecticides used against all cotton pests in Arizona. The economic and social benefits achieved demonstrate the advantages of using agricultural biotechnology in concert with classical pest control tactics.

Significance

We report eradication of the pink bollworm, one of the world’s most damaging crop pests, from the cotton-growing areas of the continental United States and northern Mexico. A coordinated, multistatic program achieved this success a century after the pest invaded both countries. The program included releases of billions of sterile pink bollworm moths from airplanes and planting of cotton engineered to produce insect-killing proteins from the bacterium Bacillus thuringiensis. Analysis of computer simulations and 21 y of field data from Arizona indicate that these two tactics interacted synergistically to suppress the pest. By eradicating the pink bollworm, the program ended the damage it caused to cotton and the insecticides sprayed to control it, yielding economic, environmental, and social benefits.


Competing interest statement: B.E.T. and J.A.F. are coauthors of patents on engineered insects. B.T. is retired and was previously employed by Monsanto, Bayer CropScience, and BASF.

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3This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2019115118/-/DCSupplemental.
plant up to 100% of their cotton with Bt cotton (28). We previously reported data from 1998 to 2009 showing that this innovative strategy sustained susceptibility of pink bollworm to Bt cotton while reducing the pest’s population density (25). Here, to test the idea of eradicating pink bollworm with the combination of Bt cotton and sterile releases, we conducted computer simulations and analyzed field data collected in Arizona from 1998 to 2018.

**Results**

**Simulated Effects of Bt Cotton and Sterile Insect Releases.** In computer simulations of the eradication program in Arizona from 2006 to 2010, pink bollworm was eliminated by the combination of Bt cotton and sterile insect releases, but not by either of the two tactics used alone (Fig. 2). In a realistic scenario, with all model parameters based on empirical data for pink bollworm in Arizona (SI Appendix, Table S1), the population decreased from 200 million to zero in 3 y with Bt cotton and sterile releases deployed together (Fig. 2A). In this scenario, Bt cotton was the primary factor causing the initial declines. These initial decreases dramatically increased the ratio of sterile to wild moths, spurring the population crash in 2008 and 2009 (Fig. 2A). By contrast, under the hypothetical scenario of sterile releases used without Bt cotton, the population grew until reaching its carrying capacity (Fig. 2A). This simulation result is consistent with previous results showing that sterile releases alone did not effectively suppress established field populations of pink bollworm because the sterile moths did not sufficiently outnumber the wild moths (6, 12–14). Under the hypothetical scenario of Bt cotton used without sterile releases, the population size declined by a factor of 0.78-fold each generation (Fig. 2A). Extrapolating this rate indicates 15.6 y would have been required to reduce the population from 200 million to zero, greatly increasing the probability pink bollworm would evolve resistance to Bt cotton before eradication occurred. Assuming that Bt cotton and sterile insect releases interact additively, the projected time to achieve eradication is also 15.6 y because the sterile insect releases alone did not decrease population size. Thus, the simulated outcome of eradication in 3 y with Bt cotton and sterile releases combined indicates synergy between these two tactics.

In a second set of simulations, we increased the population growth rate per generation (\( R_o \)) from 1.6 to 3.2 and the effective number of sterile moths released per generation (\( S_{eff} \)) from 3 million to 120 million while keeping all other values the same as in the realistic scenario described above. As in the realistic scenario, the combination of Bt cotton and sterile releases caused eradication in 3 y (Fig. 2B). However, with the higher \( R_o \), the population increased to its carrying capacity with either Bt cotton or sterile releases alone (Fig. 2B). Additional sensitivity analyses imply that under a wide range of reasonable assumptions, the combination of Bt cotton and sterile releases can interact synergistically to rapidly eradicate pink bollworm (SI Appendix, Table S1 and Figs. S1–S5).
Observed Effects of the Eradication Program on Pink Bollworm. For 2005, the year before the eradication program began, we calculated that 2.6 billion pink bollworm larvae occurred statewide based on 15.3% of non-Bt cotton bolls infested and 24,754 ha of non-Bt cotton planted in Arizona that year (SI Appendix, Table S1). During the eradication program from 2006 to 2014, 11.4 billion sterile pink bollworm moths were released by airplane over cotton fields throughout Arizona, with a yearly mean of 1.6 billion from 2006 to 2012 (range: 1.1 to 2.0 billion, SI Appendix, Table S2). The mean annual statewide percentage of cotton planted with non-Bt cotton dropped from 36% before the eradication program (1998 to 2005) to 6% during the eradication program (2006 to 2014; SI Appendix, Fig. S6).

Consistent with the simulated effects of Bt cotton and sterile releases combined (Fig. 2), pink bollworm abundance declined to zero during the eradication program (Fig. 3 A and B), and the population growth was negatively associated with the ratio of sterile to wild males (Fig. 4 and SI Appendix, Table S3). The percentage of non-Bt cotton bolls infested with pink bollworm larvae dropped from 15.3% in 2005 to 0.012% in 2009 (two larvae in 16,600 bolls) and then to 0% in 86,413 bolls screened from 2010 to 2018 (Fig. 3A). The mean number of wild pink bollworm male moths caught per trap per week fell from 26.7 in 2005 to 0.000012 in 2012 and then to 0 in 188,881 traps checked from 2013 to 2018 (Fig. 3B). As expected (29), pink bollworm abundance in bolls and traps were correlated (r = 0.96, degrees of freedom (df) = 19, P < 0.0001) and detection was more effective with traps than bolls when the population density was extremely low (Fig. 3 A and B).

The dramatic decrease in abundance during the eradication program contrasts with the period before the eradication program began, when no significant decrease in pink bollworm abundance occurred statewide from 1998 to 2005 (Fig. 3 A and B). The stability of pink bollworm abundance from 1998 to 2005, when non-Bt cotton accounted for a mean of 36% of all cotton (SI Appendix, Fig. S6), is consistent with previous results indicating declines occurred within 15 regions of Arizona only where non-Bt cotton accounted for 35% or less of all cotton (30).

In addition to Bt cotton and sterile insect releases, the eradication program included cultural control tactics for all cotton and the application only in non-Bt cotton fields of pink bollworm female sex pheromone to disrupt mating (18, 25–27 and SI Appendix). The cultural control tactics included constraints on planting and harvesting dates to impose a host-free period and postharvest destruction of cotton residues to reduce pink bollworm overwintering survival (SI Appendix). Even though the cultural control tactics probably contributed to population suppression, they were similar before and during the eradication program. Thus, it is unlikely they were a primary factor causing the dramatic declines during the eradication program. The pheromone treatments were made only in non-Bt cotton fields, which accounted for a mean of 7% of all cotton ha planted statewide from 2006 to 2011 (SI Appendix, Fig. S6). Consistent with the results in Fig. 4, a multiple regression analysis indicated a significant negative association between population growth and sterile insect releases (P = 0.0002), whereas the negative association between population growth and pheromone treatments was not significant (P = 0.49; SI Appendix, Tables S4 and S5).

Economic Impact of Eradication. Concomitant with the dramatic decline in pink bollworm population density, the economic cost associated with the pest plummeted. The mean annual cost of pink bollworm treatments made against pink bollworm and the yield loss caused by the pest decreased to $0 from a mean of $33 per ha of cotton for 1998 to 2005 (y = 0.018x – 34.6, R² = 0.07, df = 6, P = 0.52). The cost of insecticide treatments made against pink bollworm and the yield loss caused by the pest decreased to $0 from a mean of $33 per ha of cotton for 1998 to 2005 (y = 0.018x – 34.6, R² = 0.07, df = 6, P = 0.52). The cost of insecticide treatments made against pink bollworm and the yield loss caused by the pest decreased to $0 from a mean of $33 per ha of cotton for 1998 to 2005 (y = 0.018x – 34.6, R² = 0.07, df = 6, P = 0.52). The cost of insecticide treatments made against pink bollworm and the yield loss caused by the pest decreased to $0 from a mean of $33 per ha of cotton for 1998 to 2005 (y = 0.018x – 34.6, R² = 0.07, df = 6, P = 0.52). The cost of insecticide treatments made against pink bollworm and the yield loss caused by the pest decreased to $0 from a mean of $33 per ha of cotton for 1998 to 2005 (y = 0.018x – 34.6, R² = 0.07, df = 6, P = 0.52).

Discussion
The results here show that the multitactic eradication program reduced the pink bollworm population in Arizona from more than 2 billion in 2005 to zero in 2013 to 2018. Although we cannot exclude potential contributions to population suppression by cultural control tactics or pheromone treatments, the modeling results (Fig. 2 and
and northern Mexico is a threat because this pest still occurs worldwide, nine major pests have evolved practical resistance to Bt crops (24, 39, 40). Has been achieved by a transgenic crop alone or in combination we are not aware of previous examples where pest eradication is associated with decreases in their population density (36–38). This program benefited from a strong grower commitment; cooperation among scientists in government, academia, and industry; a well-developed infrastructure for monitoring pink bollworm; virtually 100% efficacy of Bt cotton against the pest; and the pest’s almost complete dependence on cotton as a larval host plant (6, 18, 25, 27).

We focus here on Arizona because, among the states included in the eradication program, its cotton was most damaged by the pink bollworm and its data collection was most comprehensive. However, parallel efforts in California, New Mexico, and Texas in the United States and Baja California, Chihuahua, and Sonora in Mexico were also essential for regional removal of this pest (18, 27, 33). This program benefited from a strong grower commitment; cooperation among scientists in government, academia, and industry; a well-developed infrastructure for monitoring pink bollworm; virtually 100% efficacy of Bt cotton against the pest; and the pest’s almost complete dependence on cotton as a larval host plant (6, 18, 25, 27).

The program’s success enabled the declaration by the US Department of Agriculture (USDA) in 2018 that the pink bollworm was eradicated from the cotton-growing regions of the continental United States—a century after this agency published a bulletin about preventing the pest’s establishment (34, 35). The program benefited from a strong grower commitment; cooperation among scientists in government, academia, and industry; a well-developed infrastructure for monitoring pink bollworm; virtually 100% efficacy of Bt cotton against the pest; and the pest’s almost complete dependence on cotton as a larval host plant (6, 18, 25, 27).

Materials and Methods

To assess the potential effects on pink bollworm population dynamics of Bt cotton and sterile moth releases used separately or together, we used a deterministic population dynamics model that combined concepts and parameter values we used in simulations, including the standard values and additional values tested in sensitivity analyses where we varied one parameter at a time while holding all other parameters constant. Details about the simulations, eradication program methods, data collection, and statistical analyses are provided in the SI Appendix.

Data Availability. Data are available in the tables of the SI Appendix.


23. V. C. Naik, S. Kumbhare, S. Kranthi, U. Satija, K. R. Kranthi, Field-evolved resistance of Pectinophora gossypiella (Saunders) (Lepidoptera: Gelechiidae), to transgenic Bacillus thuringiensis (Bt) cotton expressing crystal 1Ac (Cry1Ac) and Cry2Ab in India. J. Econ. Entomol. 112, 1543–1565 (2019).

