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Suppression of Cotton Bollworm in Multiple Crops in China in Areas with Bt Toxin–Containing Cotton

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Transgenic cotton that has been engineered to produce insecticidal toxins from *Bacillus thuringiensis* (Bt) and so to resist the pest cotton bollworm (*Helicoverpa armigera*) has been widely planted in Asia. Analysis of the population dynamics of *H. armigera* from 1992 to 2007 in China indicated that a marked decrease in regional outbreaks of this pest in multiple crops was associated with the planting of Bt cotton. The study area included six provinces in northern China with an annual total of 3 million hectares of cotton and 22 million hectares of other crops (corn, peanuts, soybeans, and vegetables) grown by more than 10 million resource-poor farmers. Our data suggest that Bt cotton not only controls *H. armigera* on transgenic cotton designed to resist this pest but also may reduce its presence on other host crops and may decrease the need for insecticide sprays in general.

Transgenic crops carrying insecticides have become an important tool for insect pest management worldwide and, in 2007, were grown on a total of 42.1 million ha, accounting for about 37% of all the transgenic crops (*1*). One of these, Bt cotton, produces insecticidal toxins from *Bacillus thuringiensis* (Bt) and occupied 14 million ha worldwide and 3.8 million ha in China in 2007 (*1*). Bt cotton can suppress populations of a target pest with a narrow host range, e.g., pink bollworm (*Pectinophora gossypiella*) (*2*), but its long-term and wider ecological consequences are unknown.

The cotton bollworm, *Helicoverpa armigera,* is one of the most serious insect pests of cotton, corn, vegetables, and other crops throughout Asia. There are four generations of *H. armigera* per year in northern China. In general, wheat is the main host crop of first-generation *H. armigera* larvae, and cotton, corn, peanuts, soybeans, and vegetables are the major hosts for subsequent generations (*3*). Because of its long-distance migrations between provinces and dispersal among different host crops, provincewide outbreaks of *H. armigera* on cotton and other crops were common in the early 1990s in China (*3*). Bt cotton was first approved for commercial use in 1997 in China and remains the only Bt crop registered. By 2001, Bt cotton had been extensively planted, especially in northern China, which resulted in increased yields and decreased use of insecticides (*4*).

We conducted long-term and large-scale field monitoring of *H. armigera* during 1992–2007 in multiple crops in six provinces (Hebei, Shandong, Jiangsu, Shanxi, Henan, and Anhui), covering 38 million ha of farmland in northern China (fig. S1), in which 3 million ha of cotton and 22 million ha of other host crops (corn, peanuts, soybeans, and vegetables) were cultivated annually by more than 10 million small farmers. Our results indicated that both the egg density of *H. armigera* on cotton and the larval density on other major host crops were negatively correlated with the number of years after the introduction of Bt cotton in the period of 1997–2006 (Figs. 1 and 2). Before Bt cotton commercialization, the *H. armigera* population was fairly high on cotton and other host crops over the period from 1992 to 1996. However, population density of *H. armigera* was drastically reduced with the introduction of Bt cotton, especially during the period from 2002 to 2006 (table S1). Using stepwise regression, we evaluated the contribution of temperature, rainfall, and deployment of Bt cotton on the population density of *H. armigera* in six provinces (Table 1). For all six provinces in northern China, Bt cotton acreage correlated best with the reduction in *H. armigera* populations (Table 1). For the second and third generations, the deployment of Bt cotton contributed more to the reduction of *H. armigera* density than temperature and rainfall during 1997–2006 and was the key factor for its long-term suppression in all the six provinces of northern China (R^2 = 0.41 to 0.91, P < 0.05; Table 1). These results indicate that the regional occurrence of *H. armigera* on cotton and other major host crops in northern China was suppressed by the deployment of Bt cotton.

We also sampled *H. armigera* in cotton fields from 1998 to 2007 at Langfang Experiment Station in Hebei Province (*5*). The densities of eggs on Bt and non-Bt cotton and larvae on non-Bt cotton were negatively associated with the number of years after Bt cotton commercialization (R^2 = 0.52 to 0.63, P < 0.05). The population density of *H. armigera* can be described by the linear regression model (Fig. 3). The data also showed that the densities of *H. armigera* eggs were not significantly different between Bt and non-Bt cotton over the period of 1998–2007 (P > 0.05) (Fig. 3A). However, larval densities on non-Bt cotton were significantly higher than those on Bt cotton from 1998 to 2006 (P < 0.05) (Fig. 3B), with an exception in 2007 when the pop-

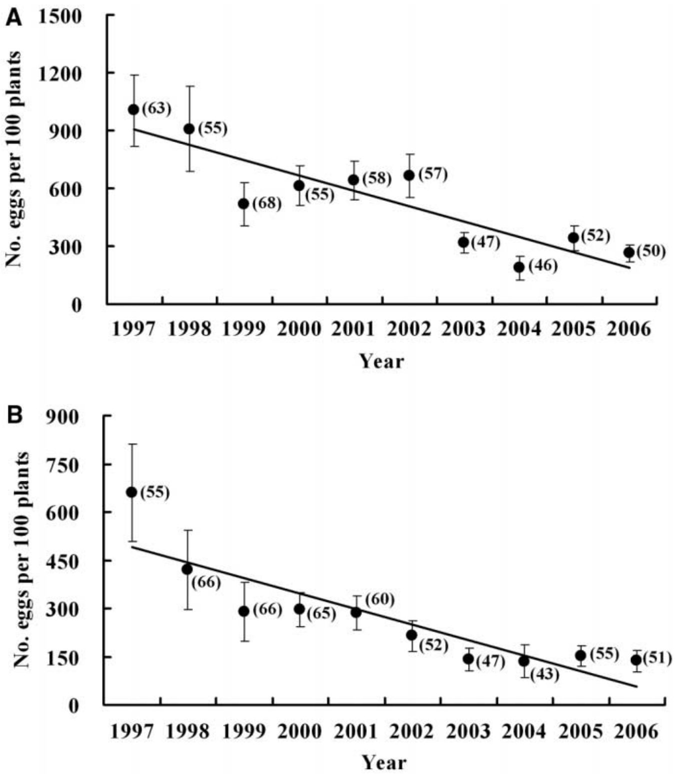

Fig. 1. Egg densities of *H. armigera* from 1997 to 2006 on cotton in northern China. (**A**) Relation between egg density of the second generation (●) and planting year of Bt cotton. Linear model of egg density (black line), y = 157,076.05 − 78.21x, F = 32.16, df = 1,549, P < 0.0001, R^2 = 0.06. (**B**) Relation between egg density of the third generation (●) and planting year of Bt cotton. Linear model of egg density (black line), y = 94,644.36 − 47.15x, F = 26.42, df = 1,558, P < 0.0001, R^2 = 0.05. Data are means ± SEM. Values in parentheses are the numbers of sampling sites for each year.

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ulation density was low and larval density was not significantly different between the two treatments ($P > 0.05$). Using Bt cotton also reduced the duration of *H. armigera*'s oviposition period on cotton, because of decrease of moth density. Three peaks of egg density, representing the second, third, and fourth generations, respectively, were detected each year from 1998 to 2000, and in recent years, there was only one oviposition peak evident in the second generation, and no evident peak in generations 3 or 4 (fig. S2). The abundance of each generation and the peak duration of the third and fourth generations decreased linearly as Bt cotton commercialization proceeded through 1998 to 2007 (fig. S3). Thus, all data indicate that the commercial use of Bt cotton in northern China was associated with long-term areawide suppression of *H. armigera* after 10 years.

Regional control of *H. armigera* in multiple crops in China has been attained in recent years through the use of Bt cotton. Our results suggest that Bt cotton led to reduced populations of *H. armigera* not only on cotton but also on other host crops. This may be because cotton usually is the main host for the moths of the first generation to lay eggs and acts as the source of the subsequent generations on other host crops (*6*). Bt cotton kills most of the larvae of the second generation and, accordingly, works as a dead-end trap crop for *H. armigera* population. Interest in trap cropping, a promising agroecological approach for insect pest control, has increased considerably for modern agriculture (*7*, *8*), but few trap crops were used on such a large scale as that of Bt cotton in northern China, which shows that Bt crop can have a great advantage to expand the traditional view of a trap crop. This dependence on Bt cotton might also contribute to a reduction in both occurrence of *H. armigera* and the need for insecticide sprays in non-Bt host crops such as corn, soybeans, peanuts, and vegetables.

However, a major challenge for planting Bt cotton for pest control is the potential for insects to evolve resistance to Bt. Continuous monoculture of varieties that express the same Bt toxin could select for resistance, particularly when the amount of Bt toxin decreases as the plants age (*9*, *10*). A promising resistance management strategy entails the use of plants with a high dose of toxin in combination with the maintenance of "refuge" crops that encourage proliferation of Bt-susceptible insects within the pest population (*11*–*13*). To this end, the U.S. Environmental Protection Agency requires that each cotton farm set aside some land for cotton that does not produce Bt if farmers plant transgenic Bt cotton producing Cry1Ac toxic protein (*14*–*16*). Although successful in the United States (*17*), this strategy is difficult to implement in China because of the challenges associated with educating and monitoring millions of small

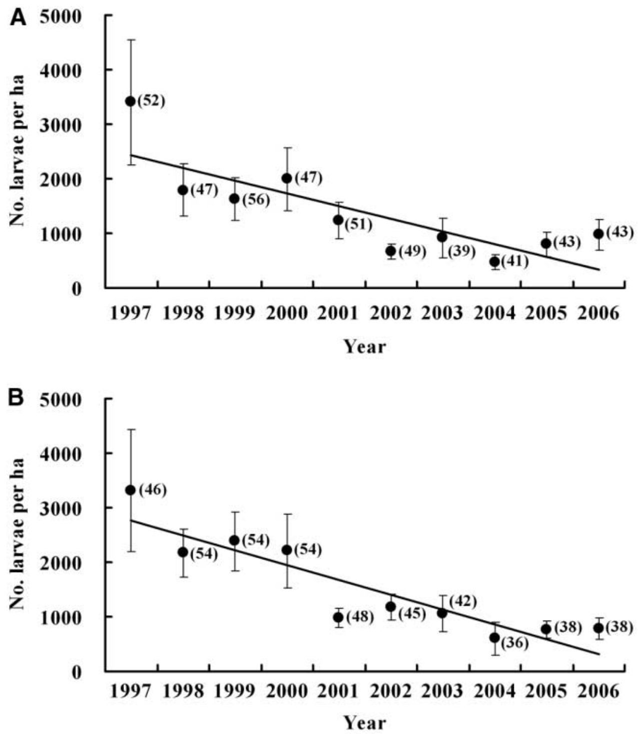

Fig. 2. Larval densities of *H. armigera* from 1997 to 2006 on corn, peanuts, soybeans, and vegetables in northern China. (**A**) Relation between larval density of the second generation (●) and planting year of Bt cotton. Linear model of larval density (black line), $y = 480{,}293.95 - 239.28x$, $F = 16.50$, df = 1,466, $P = 0.0001$, $R^2 = 0.03$. (**B**) Relation between larval density of the third generation (●) and planting year of Bt cotton. Linear model of larval density (black line), $y = 551{,}611.74 - 274.83x$, $F = 21.45$, df = 1,462, $P < 0.0001$, $R^2 = 0.04$. Data are means ± SEM. Values in parentheses are the numbers of sampling sites for each year.

Table 1. Effects of temperature, rainfall, and deployment of Bt cotton on the population density of *H. armigera* in northern China. Stepwise regression analysis was used for analyzing the association between population density (egg density on cotton or larval density on other host crops) of *H. armigera* and temperature (Temp.), rainfall, and deployment of Bt cotton. *F*, generation; R^2, coefficient of determination. Only variables from which the regression coefficient met the criteria of $P < 0.05$ are shown. NS, without significant effects ($P > 0.05$) on population density. + and − represent positive and negative associations between the population density and the factors, respectively. *$P < 0.05$; **$P < 0.01$.

Province	*F*	Egg density of *H. armigera* in cotton fields				Larval density of *H. armigera* on other major host crops			
		Regression coefficient			R^2	Regression coefficient			R^2
		Temp.	Rainfall	% Bt cotton		Temp.	Rainfall	% Bt cotton	
Hebei	2nd	NS	NS	−1.2224*	0.4392*	+0.1767*	NS	−2.4917**	0.8672**
	3rd	NS	NS	−2.1250**	0.7868**	NS	NS	−2.3092**	0.7216**
Shandong	2nd	NS	NS	−1.2932**	0.6023**	+0.1482*	NS	−1.4253**	0.7561**
	3rd	NS	NS	−1.8528*	0.4508*	NS	NS	−1.5658**	0.6724**
Jiangsu	2nd	NS	NS	−1.5974*	0.5617*	NS	NS	−2.3208**	0.6073**
	3rd	NS	NS	−1.2019*	0.4079*	NS	NS	−2.5182**	0.7124**
Shanxi	2nd	NS	−0.0080*	−3.1825**	0.8537**	NS	NS	−3.5959**	0.6308**
	3rd	NS	−0.0023*	−4.3043**	0.9145**	NS	NS	−5.3844*	0.5342*
Henan	2nd	NS	NS	−1.9166**	0.7431**	NS	NS	−1.5024**	0.6065**
	3rd	NS	NS	−1.0534*	0.5236*	NS	NS	−1.8253**	0.6017**
Anhui	2nd	NS	NS	−2.8418*	0.4876*	NS	NS	−2.8676*	0.4568*
	3rd	NS	NS	−2.1755*	0.5831*	NS	NS	−2.2374*	0.4809*
Northern China	2nd	NS	NS	−1.5425**	0.6675**	NS	NS	−1.7971**	0.7866**
	3rd	NS	NS	−2.1414**	0.8973**	NS	NS	−2.2161**	0.8794**

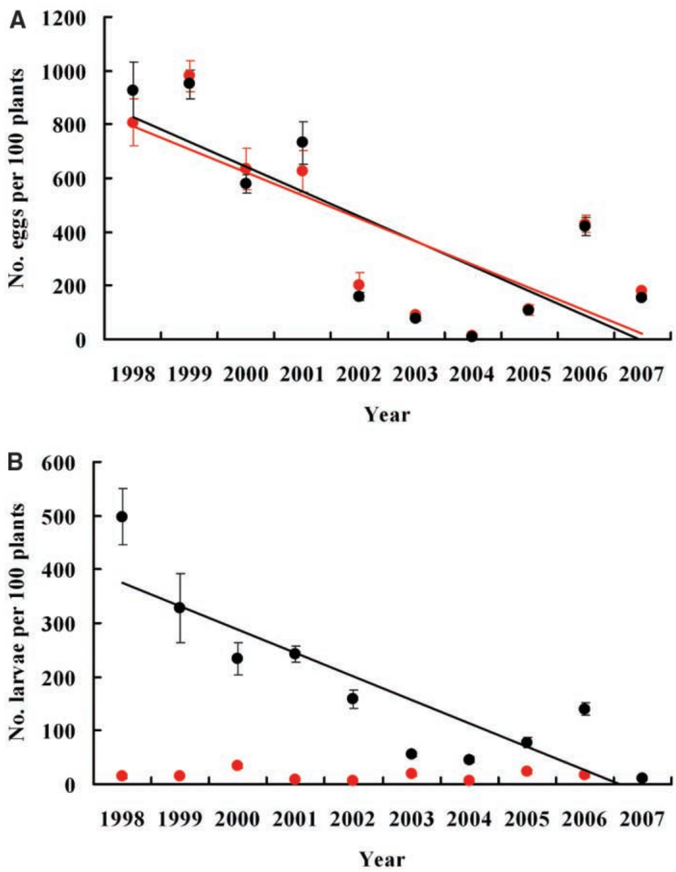

Fig. 3. Egg and larval densities of *H. armigera* on cotton at Langfang site, Hebei Province, China, from 1998 to 2007. (**A**) Relation between egg density on Bt cotton (red circles) and non-Bt cotton (black circles) and planting year of Bt cotton. Linear model on Bt cotton (black line), $y = 185{,}476.90 - 92.42x$, $F = 69.05$, df = 1,58, $P < 0.0001$, $R^2 = 0.54$. Linear model on non-Bt cotton (red line), $y = 171{,}365.94 - 85.37x$, $F = 62.59$, df = 1,58, $P < 0.0001$, $R^2 = 0.52$. (**B**) Relation between larval density on Bt cotton (red circles) and non-Bt cotton (black circles) and survey years. Linear model on non-Bt cotton (black line), $y = 87{,}107.86 - 43.41x$, $F = 97.56$, df = 1,58, $P < 0.0001$, $R^2 = 0.63$. Data are means ± SEM. There are six samples for each point in the graphs.

farmers. In China, a multiple cropping system consisting of soybeans, peanuts, corn, and vegetables is common. These crops also serve as hosts for *H. armigera*, and, because they do not express Bt toxin, they serve as refuges for nonresistant insects (*10*). Because cotton is not the only host crop, Bt cotton comprises about 10% of the major host crops in any province or throughout northern China. This accidental approach to refuge management appears to have, so far, warded off the evolution of resistance (*10*). Nevertheless, as a result of decreased spraying of broad-spectrum pesticides for controlling cotton bollworm in Bt cotton fields, mirids have recently become key pests of cotton in China (*18*, *19*). Therefore, despite its value, Bt cotton should be considered only one component in the overall management of insect pests in the diversified cropping systems common throughout China.

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Can Catch Shares Prevent Fisheries Collapse?

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Recent reports suggest that most of the world's commercial fisheries could collapse within decades. Although poor fisheries governance is often implicated, evaluation of solutions remains rare. Bioeconomic theory and case studies suggest that rights-based catch shares can provide individual incentives for sustainable harvest that is less prone to collapse. To test whether catch-share fishery reforms achieve these hypothetical benefits, we have compiled a global database of fisheries institutions and catch statistics in 11,135 fisheries from 1950 to 2003. Implementation of catch shares halts, and even reverses, the global trend toward widespread collapse. Institutional change has the potential for greatly altering the future of global fisheries.

Although the potentially harmful consequences of mismanaged fisheries were forecast over 50 years ago (*1*, *2*), evidence of global declines has only been seen quite recently. Reports show increasing human impacts (*3*) and global collapses in large predatory fishes (*4*) and other trophic levels (*5*) in all large marine ecosystems (LMEs) (*6*). It is now widely believed that these collapses are primarily the result of the mismanagement of fisheries.

One explanation for the collapse of fish stocks lies in economics: Perhaps it is economically optimal to capture fish stocks now and invest the large windfall revenues in alternative assets, rather than capturing a much smaller harvest on a regular basis. Although this remains a theoretical possibility for extremely slow-growing species

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1. Materials and Methods

1.1 Area-wide population monitoring of *H. armigera* in northern China

Population monitoring. *H. armigera* of the second and third generations on main host crops was monitored from 1992 to 2006 in 6 provinces of China (Fig. S1) through a national area-wide monitoring network of cotton bollworm, which consisted of 100 sites. The population monitoring of cotton bollworm of each site was conducted according to a national standard, which consists of a detailed method for pest population sampling and a host survey (e.g. type of host crop, method of cultivation, cotton variety) at the local sites (*S1*).

Egg density of *H. armigera* on cotton was surveyed every 3 days during the egg-producing periods of the second and third generation. During 1992-2006, 24-68 sites per year were sampled and 10-20 cotton fields were selected per site. Within each field, five points were randomly chosen with a total number of 100 cotton plants. For each sampled plant, a thorough whole-plant survey was conducted in which the eggs of *H. armigera* were counted (*S1*).

Larval densities of *H. armigera* on corn, peanut, soybean, and vegetables, were surveyed once for each generation. The sampling was taken when most of larvae *H. armigera* entered the 4^{th}–6^{th} instar stage in the second and third generations. During 1992-2006, 23-56 sites per year were sampled and 5-10 fields per crop were surveyed at each site. Within each field, five points were randomly chosen with a total number of 50 m^2 plants. For each plant, a thorough whole-plant survey was conducted for sampling the larvae of *H. armigera* (*S1*). The average larval density N (number of larvae per ha) on these host crops was calculated with $N = \sum_{i=1}^{n}(A_i \times B_i) / \sum_{i=1}^{n} B_i$, in which A_i represents the mean larval density on the i^{th} crop, B_i indicates the total planting acreage of the i^{th} crop, and n is the number of host crops.

Host crop information. The annual acreages of the main host crops of *H. armigera*, including cotton, corn, peanut, sesame, legumes, sorghum, vegetables and melons, in each province through 1997 to 2006, were obtained from the China Agriculture Yearbook (*S2*). The annual acreages of Bt cotton for each province through 1997 to 2006 were provided by the Ministry of Agriculture, China. The proportion of Bt cotton was calculated by dividing the acreage of Bt cotton by the total acreage of the main host crops of *H. armigera* in each province.

Meteorological data. Temperature and rainfall data during 1997-2006 at 57 meteorological stations were obtained from the Chinese Meteorological Data Sharing Service System (http://cdc.cma.gov.cn/). The data from the meteorological station in same area were used for the analysis. If there was no meteorological station in the sampling site, we used the data from the nearby stations, which usually were 30-60 km far away. When the distances between the sampling site and several stations were similar, the averages of meteorological data were used.

In general, temperature and rainfall in June are two key climate factors that influence the egg density in the second generation in cotton fields. Both factors during mid July and early August are also critical for the egg density in the third generation. Therefore, we analyzed the effect of the climatic data on egg density of *H. armigera* in cotton fields. Similarly, we analyzed the influence of temperature and rainfall data during June and until July 10 on larval density of the second generation, and of temperature and rainfall from mid July to August 20 were used for the larval density of the third generation in other host crop fields (*S3*).

1.2 Population sampling of *H. armigera* on cotton at Langfang

Two Bt cotton varieties and two conventional cotton varieties were planted each year from 1998 to 2007 at Langfang Experiment Station (39.53 ºN, 116.70 º E) in Hebei Province according to a research protocol (*S4*). A transgenic Bt cotton variety expressing the protein Cry1Ac (NuCOTN33B) and two transgenic Bt cotton varieties expressing the protein Cry1A (GK12 and SGK321) were supplied by China Division of Monsanto Co. (Beijing) and the Biotechnology Research Institute of Chinese Academy of Agricultural Sciences (Beijing), respectively. Three conventional cotton varieties (Shiyuan 321, Simian3 and Zhong12) were obtained from the Institute of Plant Protection, Chinese Academy of Agricultural Sciences (Beijing). Simian3, Zhong12, NuCOTN33B and GK12 were planted during 1998-2000, while Shiyuan 321, Zhong12, SGK321 and NuCOTN33B were used from 2001 to 2007.

The field experimental designs were a randomized complete block, replicated three times. Cotton was managed with standard agronomic practices without insecticide application. Visual sampling was undertaken once every 4-5 d from mid June to early

September. For each sampling, five sites were randomly chosen with a total number of 100 cotton plants from every plot. For each sampled plant, a thorough whole-plant survey was conducted in which eggs and larvae of *H. armigera* were counted and recorded in the field.

1.3 Statistical analysis

Population monitoring in northern China. Simple linear regression model was used to analyze the occurrence trend of *H. armigera*, including egg and larval densities, from 1997 to 2006 *(S5)*. For each site, egg density was the average of the sum of eggs per 100 plants per generation, and larval density was the mean number per ha per generation.

The effects of temperature, rainfall and deployment of Bt cotton on egg and larval densities of *H. armigera* were analyzed by using stepwise regression for each province and the whole northern China *(S5)*. For the analysis, *H. armigera* density was showed as the average of egg and larval density of all the including sites per generation, and that the meteorological data are corresponding to population monitoring. Temperature data was the average of the daily mean temperature at all the selected meteorological stations, and rainfall data was the average of the total rainfall during the whole tested period. The proportions of Bt cotton in the previous and current year were used for analyzing the relationship between deployment of Bt cotton and *H. armigera* density of second and third generations, respectively. Before analysis, the data of *H. armigera* density were log-transformed (lg (n+1)), and the percentage data of Bt cotton deployment were arcsine square root transformed (asin (sqrt (p))). In the analysis, only variables that met the 0.05 significant level were entered into the model.

Statistical significance for population density between different periods of Bt cotton commercialization were determined using analysis of variance (ANOVA) followed by Tukey's honestly significant differences (HSD) test *(S5)*. For each year, the population density was the average of all the survey data per generation. During the same period (1992-1996, 1997-2001, or 2002-2006), the data of each year was regarded as one replicate. Before analysis, the raw data were log-transformed (lg (n+1)) to meet assumptions of normality and homogeneity of variance.

Population sampling at Langfang site. Statistical significance of egg and larval densities of *H. armigera* between on Bt cotton and on non-Bt cotton were determined with using analysis of paired t-test *(S5)*. Before analysis, all the raw data were log-transformed (lg (n+1)) to meet assumptions of normality and homogeneity of variance. Simple linear regression model was used for analyzing the relationship of egg and larval densities and the year of Bt cotton planting *(S5)*.

For examining the change in size and duration of each generation of egg *H. armigera* on cotton between 1998 and 2007, the theoretical abundance A_i and duration δ_i of the i^{th} generation were estimated by fitting a Gaussian function to population density data. Each cotton variety was regarded as one replicate, and the population density for each cotton variety was the mean number of three plots. The Gaussian function used for generation 2 to 4 was $f(t; A, T, \delta) = \frac{A}{\sigma\sqrt{2\pi}} e^{-(t-T)^2/(2\delta^2)}$, where t is the days, A is the area under the curve estimating the abundance of individuals, T is the mean of the distribution corresponding to the date of maximum abundance, and δ is the standard deviation estimating the duration of a generation (Fig. S2A). These parameters were estimated with nonlinear least squares fitting (*S6*), and the significance of regression was tested with F test (*S5*). A_1 was always 0 since the egg densities were available only for the 2-4th generations on cotton. Simple linear regression model was used to analyze the relationship of parameters A and δ estimated above and the year of Bt cotton planting *(S5)*.

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3. Supporting Tables

Table S1. Population density of *H. armigera* in multiple host crop system before and after Bt cotton commercialization in northern China.

Population density	Before Bt cotton commercialization	After Bt cotton commercialization	
	1992-1996	1997-2001	2002-2006
No. *H. armigera eggs* of 2nd generation per 100 plants in cotton field	1398.40 ± 462.38 a † (5) ‡	736.53 ± 92.99 ab (5)	355.10 ± 81.99 b (5)
No. *H. armigera eggs* of 3rd generation per 100 plants in cotton field	429.45 ± 85.84 a (5)	390.64 ± 72.12 a (5)	152.29 ± 16.17 b (5)
No. *H. armigera larvae* of 2nd generation per ha in other host crops	5864.98 ± 1907.85 a (5)	2010.62 ± 369.52 ab (5)	760.77 ± 91.58 b (5)
No. *H. armigera* larvae of 3rd generation per ha in other host crops	4745.26 ± 178.57 a (5)	2212.77 ± 371.58 b (5)	877.46 ± 105.22 c (5)

† Means (± SE) within a row followed by the same letter are not significantly different by Tukey's HSD (P>0.05). ‡ The values in the bracket are the numbers of samples (replicates).

4. Supporting Figures

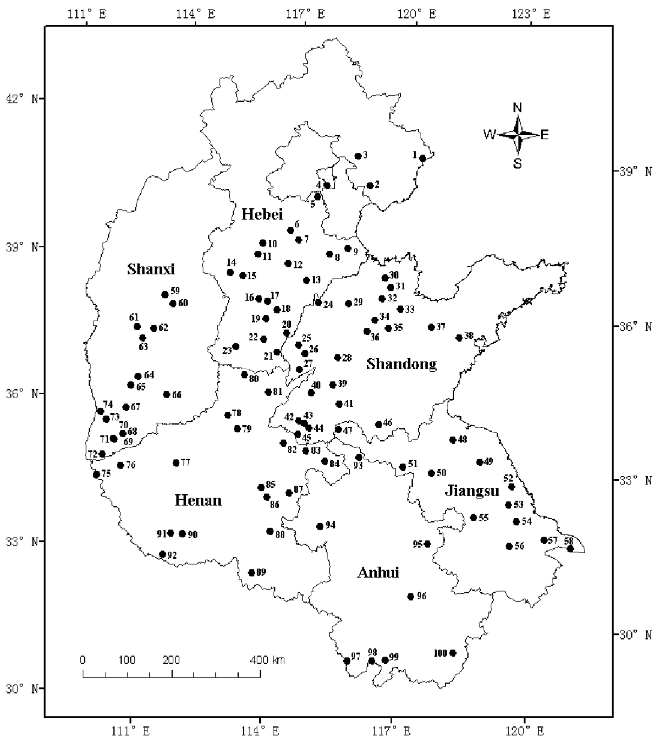
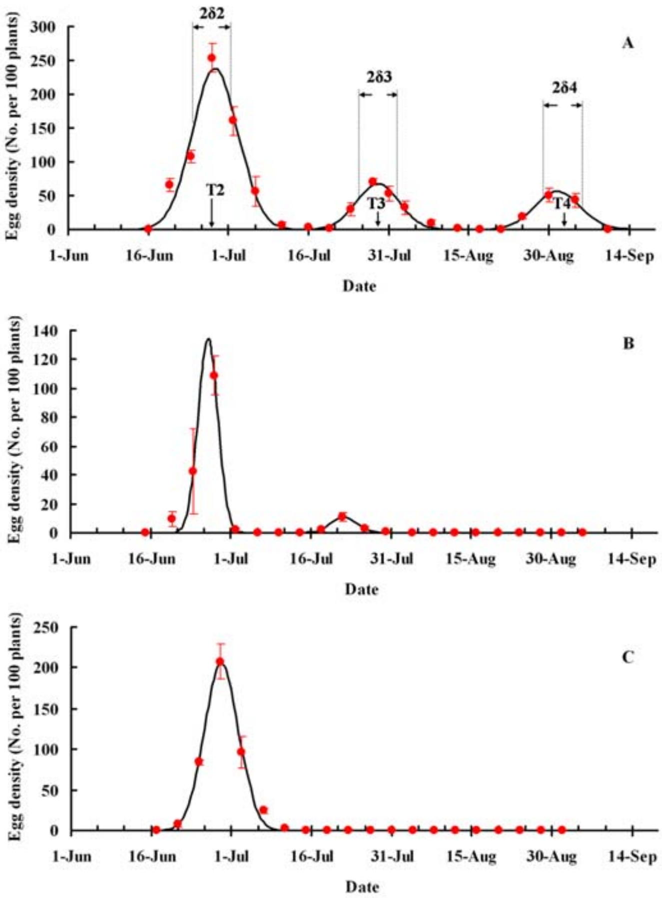


Fig. S1. Site locations for monitoring *H. armigera* in northern China



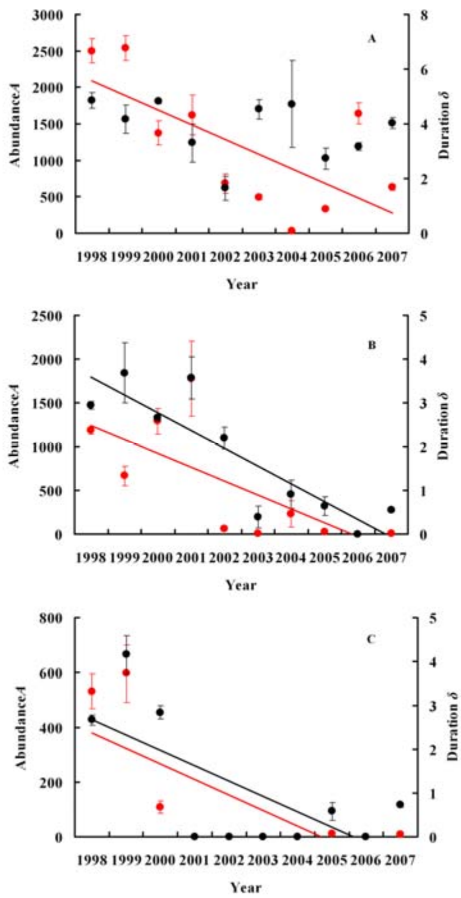


Fig. S2. Variation of egg density of *H. armigera* through time in (**A**) 1999, (**B**) 2002 and (**C**) 2006 at Langfang, Hebei Province. δ_2, δ_3 and δ_4 are the standard deviations estimating the duration of the second, third and forth generation, and T_2, T_3 and T_4 are the means of the distribution corresponding to the date of maximum abundance of the three generations, respectively. Data are showed as Means ± SE. There are four replicates for each point in the graphs.

Fig. S3. Abundance (A) and duration (δ) of *H. armigera* eggs on cotton from 1998 to 2007 at Langfang, Hebei Province. (**A**) Relationship between A (red circles) and δ (black circles) of second generation *H. armigera* and planting year of Bt cotton. Linear model of A (red line), y = 405162.72 – 201.74x, F = 29.52, df = 1,38, P < 0.0001, R^2 = 0.44. (**B**) Relationship between A (red circles) and δ (black circles) of third generation *H. armigera* and planting year of Bt cotton. Linear model of A (red line), y = 319757.54 -159.42x, F = 30.73, df = 1,38, P < 0.0001, R^2 = 0.45. Linear model of δ (black line), y = 815.64 – 0.41x, F = 73.10, df = 1,38, P < 0.0001, R^2 = 0.66. (**C**) Relationship between of A (red circles) and δ (black circles) of forth generation *H. armigera* and planting year of Bt cotton. Linear model of A (red line), y = 113857.87 – 56.80x, F = 37.04, df = 1,38, P < 0.0001, R^2 = 0.49. Linear model of δ (black line), y = 704.09 - 0.35x, F = 32.28, df = 1,38, P < 0.0001, R^2 = 0.46. Data are showed as Means ± SE. There are four replicates for each point in the graphs.