Yield Effects of Genetically Modified Crops in Developing Countries

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Onfarm field trials carried out with *Bacillus thuringiensis* (Bt) cotton in different states of India show that the technology substantially reduces pest damage and increases yields. The yield gains are much higher than what has been reported for other countries where genetically modified crops were used mostly to replace and enhance chemical pest control. In many developing countries, small-scale farmers especially suffer big pest-related yield losses because of technical and economic constraints. Pest-resistant genetically modified crops can contribute to increased yields and agricultural growth in those situations, as the case of Bt cotton in India demonstrates.

Discussions on whether modern agricultural biotechnology is appropriate for developing countries have been controversial in the recent past (*1*, *2*). Can genetically modified (GM) crops, especially those that have been developed in the industrialized world, solve the pressing agricultural problems of developing countries? Thus far, 99% of the global GM crop acreage relates to insect-resistance and herbicide-tolerance traits (*3*). Recent studies point out that these technologies mainly substitute for pesticides but that yield effects are generally small. Yield advantages of insect-resistant cotton in the United States and China, for instance, are less than 10% on average (*4–6*). For insect-resistant maize in the United States and herbicide-tolerant soybeans in the United States and Argentina, average yield effects are negligible and in some cases even slightly negative (*7–9*). The economic and environmental gains of pesticide savings and reduced effort for pest control have been documented in the literature (*4–6*, *9*); yet some argue that the potential of GM crops in developing countries is limited without a substantial yield effect, especially in regions with strong population growth (*10*).

We maintain that the limited experience with GM crops so far is insufficient to make broad generalizations about their impacts. We use the example of *Bacillus thuringiensis* (Bt) cotton in India to suggest that currently existing GM crops can have significant yield effects that are most likely to occur in the developing world, especially in the tropics and subtropics.

Bt cotton contains the gene for Cry1Ac, which provides a fairly high degree of resistance to the American bollworm (*Helicoverpa armigera*), the spotted bollworm (*Earias vittella*), and the pink bollworm (*Pectinophora gossypiella*), all of which are major insect pests in India. The technology was developed by the U.S. company Monsanto and was introduced into several Indian hybrids in collaboration with the Maharashtra Hybrid Seed Company (Mahyco). The first contained field trials with Bt hybrids in India were conducted in 1997. In subsequent years, field tests were extended to collect agronomic data and information for bio- and food-safety evaluation. In 2002, Bt cotton technology was commercially approved, and farmers have started to adopt the new hybrids (*11*).

In 2001, field trials were carried out on 395 farms in seven states of India. These trials were initiated by Mahyco and supervised by regulatory authorities. Although the sites were visited by agronomists in regular intervals for pest scouting and data collection, the trials were managed by the farmers themselves using customary practices. Three adjacent 646-m^2 plots were planted: the first with a Bt cotton hybrid, the second with the same hybrid but without the Bt gene (non-Bt counterpart), and the third with a different hybrid commonly used in the particular location (popular check). This setup reduces the effects of differences in agroecological conditions and managerial abilities when making technological comparisons.

In addition to the regular trial records, more comprehensive information was collected for 157 farms on agronomic aspects and farm and household characteristics. Observations from these 157 farms constitute the data basis for this analysis (*12*). They cover 25 districts in three major cotton-producing states: Maharashtra and Madhya Pradesh in Central India and Tamil Nadu in the South. Plot-level input and output data were extrapolated to 1 ha to facilitate comparisons.

On average, Bt hybrids were sprayed against bollworms three times less often than were non-Bt counterparts and popular checks (Table 1). Individual bollworm control applications were still carried out, because, especially for *H. armigera*, the Cry1Ac protein does not cause 100% mortality and toxin production decreases in aging plants (*13*, *14*). There was no significant difference in the number of sprays against sucking pests such as aphids (*Aphis gossypii*), jassids (*Amrasca bigutulla*), and whitefly (*Bemisia tabaci*). Bt does not provide resistance to these insect species. Insecticide amounts on Bt plots were reduced by almost 70%, both in terms of commercial products and active ingredients. Most of these reductions occurred in highly hazardous chemicals, such as organophosphates, carbamates, and synthetic pyrethroids, belonging to international toxicity classes I and II. In financial terms, the pesticide savings were worth about U.S. $30 per ha.

Yet the more sizeable benefits are due to yield advantages. Average yields of Bt hybrids exceeded those of non-Bt counterparts and popular checks by 80% and 87%, respectively (*15*). The density functions in Fig. 1 demonstrate that the whole yield distribution experienced a notable shift to the right. The similarity of the curves for non-Bt counterparts and popular checks indicates that a general germ-plasm effect is more or less negligible. The yield gains are largely due to the Bt gene itself. Bollworm pressure in India

Table 1. Comparison of insecticide use and yields on Bt and conventional cotton plots. Mean values are shown with standard deviations in parentheses; *n* is the number of plot observations. Yield values refer to the amount of seed cotton before ginning. Data was obtained from 2001 trials.

	Bt (n = 157)		Non-Bt counterpart (n = 157)		Popular check (n = 157)	
No. of sprays against bollworm	0.62*	(1.28)	3.68	(1.98)	3.63	(1.98)
No. of sprays against sucking pests	3.57	(1.70)	3.51	(1.66)	3.45	(1.62)
Amount of insecticide (kg/ha)	1.74*	(1.86)	5.56	(3.15)	5.43	(3.07)
which is in						
Toxicity class I	0.64*	(1.10)	1.98	(1.78)	1.94	(1.78)
Toxicity class II	1.07*	(1.27)	3.55	(2.66)	3.46	(2.60)
Toxicity class III	0.03	(0.08)	0.03	(0.08)	0.03	(0.08)
Amount of active ingredients (kg/ha)	0.48*	(0.55)	1.55	(0.96)	1.52	(0.95)
Yield (kg/ha)	1501*	(857)	833	(572)	802	(571)

*Mean values are different from those of non-Bt counterparts and popular checks at a 5% significance level.

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was exceptionally high in 2001; nonetheless, previous onfarm trials that were carried out in fewer locations but with the same experimental design showed considerable yield advantages in earlier seasons, too. Over the 4-year period from 1998 to 2001, Bt hybrids showed an average advantage of 60% (*16*).

Analysis of factors influencing yield impacts of new, effective pest-control technologies suggests that they depend on local pest pressure and damage, availability of alternatives for pest control, and farmers' adoption of these alternatives (*17*, *18*). Under Indian conditions, bollworms have a high destructive capacity that is not well controlled in conventional cotton (Fig. 2). On average, pest damage was about 60% on the conventional trial plots in 2001. This result is consistent with earlier studies by entomologists in India, who found that average pest-related losses are 50 to 60% (*19*). In the United States and China, estimated losses in conventional cotton due to insect pests account for only 12% and 15%, respectively (*20*), because of lower pest pressure and higher adoption of pesticides. This explains why yield effects of Bt technology are smaller in those countries.

The higher pesticide adoption in spite of lower pest pressure in the United States and China is because of more favorable soil and climatic conditions, and thus higher yield potentials. Furthermore, pesticides in China have been subsidized, so they are more affordable (*21*). Indian farmers, in contrast, are often indebted and credit constrained and do not have access to chemicals at the right point in time (*22*, *23*). Bollworms have also developed resistance to many of the insecticides available on the market, so that ever-increasing amounts have to be sprayed. Indian farmers would have to triple their current pesticide use in conventional cotton in order to achieve a level of damage control similar to that provided by Bt technology (Fig. 2).

Although the field trials were managed by farmers, it might be possible that average technology gains will be somewhat lower in commercial agriculture. Still, given the magnitude, the yield effects of Bt cotton in India should remain sizeable. So far, only three Bt hybrids have been approved by regulatory authorities. It will be important to release additional Bt cotton hybrids, which are well adapted to diverse agroecological conditions, so that the technology yield gains for farmers are not curbed by a general germ-plasm disadvantage.

Many developing countries are currently in the process of assessing the costs and benefits of importing GM crop technologies from abroad for adaptation and use in their domestic agricultural sectors. Therefore, some projections based on the Indian results might be instructive. Pest pressure and related crop damage vary greatly from region to region and even across individual locations. Generally, however, pest pressure in developed countries and other temperate zones is moderate, whereas in tropical and subtropical regions it is high. Especially in the noncommercial and semicommercial crop sectors, where technical and economic constraints impede a more widespread use of chemicals, pest-related crop losses are often 50% and higher (*20*).

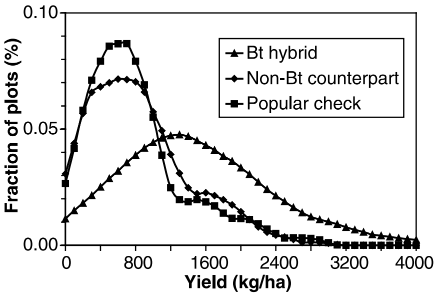

Fig. 1. Yield-density functions for Bt and conventional cotton hybrids. Functions were estimated nonparametrically using the Epanechnikov kernel with 157 observations each. Data was obtained from 2001 trials.

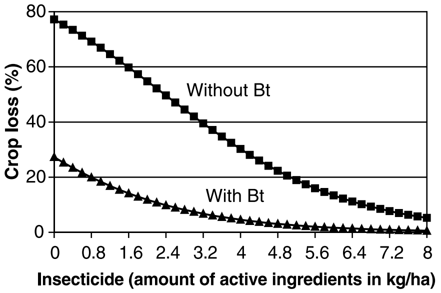

Fig. 2. Relationship between insecticide use and crop losses with and without Bt technology. Curves are predictions based on econometric estimation of a logistic damage-control function. See table S1 for details and results of the estimation procedure. Data was obtained from 2001 trials.

Table 2. Expected yield effects of pest-resistant GM crops in different regions. Assessments of pest pressure and use of chemical alternatives refer to approximate regional averages (*20*) and neglect existing intraregional variation.

Region	Pest pressure	Availability of chemical alternatives	Adoption of chemical alternatives	Yield effect of GM crops
Developed countries	Low to medium	High	High	Low
Latin America (commercial)	Medium	Medium	High	Low to medium
China	Medium	Medium	High	Low to medium
Latin America (noncommercial)	Medium	Low to medium	Low	Medium to high
South and Southeast Asia	High	Low to medium	Low to medium	High
Africa	High	Low	Low	High

Incorporating lessons of the crop-protection literature (*17*, *18*), Table 2 assesses the actual and expected yield effects of GM crops in different regions. Because of intraregional variation in the underlying determinants, the statements should only be interpreted as approximate trends. Almost all GM crop technologies were initiated by commercial firms in the industrialized world, targeting the needs of farmers who are able to pay for them. Some varieties were transferred to the commercial sectors of Latin America and China, where agroecological conditions and pesticide application rates are similar. In all cases, yield effects have been low to medium, although there have been sizeable gains from pesticide substitution. But with careful adaptation and effective regulation, these same technologies can also be introduced to other developing regions, where yield effects will be more pronounced. Pest-resistant GM crops are easy to manage at the farm level, and they could substantially reduce current gaps between attainable and actual yields, especially in small-holder farming systems.

On the basis of pest pressure and current crop protection, the biggest yield gains are expected in South and Southeast Asia and Subsaharan Africa. The field-trial results from India and preliminary evidence from Indonesia and South Africa are in line with this hypothesis (*24*, *25*). South and Southeast Asia and Subsaharan Africa are also the regions with highest population growth, so increases in agricultural output per unit area are vital for poverty alleviation and food security. Bt cotton, Bt maize, and Bt potatoes, which have already been commercialized in some countries, have direct relevance to the developing world. Bt rice, Bt sweet potatoes, and a number of food crops with other pest-resistance mechanisms will further broaden the portfolio in the near future (*26*, *27*). Agricultural biotechnology offers many more applications for developing countries beyond pest control, but we show that the GM crops developed so far can already have important impacts.

Reservations related to actual and perceived environmental and health risks, intermingled with broader concerns about intellectual property rights (IPRs) and corporate dominance, have led to limited acceptance of GM crops among the public and policy makers (*28*). Although there is mounting evidence on the benefit side, the technological potentials are not widely acknowledged. Responsible risk management and balanced science communication are prerequisites for overcoming acceptance problems and ensuring sustainable use of GM crops. Furthermore, public-sector research investments will need to be expanded and mechanisms for technology transfer and handling of IPRs established so that promising biotechnologies can reach the poor at affordable prices on a larger scale.

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Table S1
References

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GUN4, a Regulator of Chlorophyll Synthesis and Intracellular Signaling

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Nuclear genes control plastid differentiation in response to developmental signals, environmental signals, and retrograde signals from plastids themselves. In return, plastids emit signals that are essential for proper expression of many nuclear photosynthetic genes. Accumulation of magnesium-protoporphyrin IX (Mg-Proto), an intermediate in chlorophyll biosynthesis, is a plastid signal that represses nuclear transcription through a signaling pathway that, in *Arabidopsis*, requires the *GUN4* gene. GUN4 binds the product and substrate of Mg-chelatase, an enzyme that produces Mg-Proto, and activates Mg-chelatase. Thus, GUN4 participates in plastid-to-nucleus signaling by regulating Mg-Proto synthesis or trafficking.

Plastids are semiautonomous organelles such as the chloroplast. Plastid genomes encode 60 to 80 proteins in higher plants, and more than 3500 nuclear genes are predicted to encode chloroplast proteins in *Arabidopsis* (*1*, *2*). The developmental and metabolic status of plastids affects the expression of nuclear genes that encode plastid proteins, and distinct plastid-to-nucleus signaling pathways have been hypothesized on the basis of physiological, genetic, and molecular studies. Plastid signals are also important for efficient metabolism and proper leaf development (*3*, *4*).

We carried out a genetic screen in *Arabidopsis* to identify components of the plastid-to-nucleus signaling pathways. Our screen employed the herbicide Norflurazon, which blocks chloroplast development, and the use of *Lhcb* reporter genes, which are severely repressed in tissues lacking mature chloroplasts. We identified five mutants (*gun1* to *gun5*) that derepress *Lhcb* in the absence of normal chloroplast development. *gun2* through *gun5* mutations act in one pathway, whereas *gun1* defines a separate pathway (*5*). *gun2*, *gun3*, and *gun5* mutations affect plastid enzymes that synthesize tetrapyrroles (such as heme, chlorophyll, and phytochromobilin) and reduce levels of the chlorophyll precursor magnesium-protoporphyrin IX (Mg-Proto) (*5*, *6*). Buildup of Mg-Proto in the plastid is sufficient to regulate the expression of a large number of nuclear-encoded chloroplastic proteins whose functions are associated with photosynthesis (*4*, *6*). *gun4* is a chlorophyll-deficient mutant that also affects the Mg-Proto pathway (*5*).

We mapped the *gun4-1* allele to a 99-kb interval on the bottom of chromosome 3. A bacterial artificial chromosome (BAC) fragment was used to rescue the pigmentation and gene expression phenotypes of *gun4-1* (Fig. 1A) (*7*). An open reading frame (ORF) was identified on the complementing BAC fragment (GenBank accession no. NM_115802) that encoded a previously uncharacterized protein with a putative chloroplast transit peptide (Fig. 1B). A missense mutation that caused a Leu^{88} → Phe^{88} (L88F) substitution in the derived amino acid sequence was identified in *gun4-1* (Fig. 1B) (*7*). GUN4-related proteins were found only in species that carry out oxygenic photosynthesis (*7*). *Arabidopsis* and rice GUN4 proteins have small divergent COOH-terminal extensions that are absent in bacterial and red algae chloroplast relatives (Fig. 1B). Most species have one GUN4-related gene, but *Synechocystis* and *Nostoc* have three and four, respectively. One of the *Synechocystis* ho-

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