Transgenic Crops and Crop Varietal Diversity: The Case of Maize in Mexico

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Transgenic crop varieties are a rapidly expanding and controversial technology. Their effects on biological and cultural diversity are a key issue in an often polarized debate. Here we provide answers to questions about one important example, that of transgenic maize in Mexico. In situ *maize diversity in Mexico is present in traditional varieties in farmers' fields, and in wild and weedy relatives of maize. It is likely that transgenes are present in farmers' local maize varieties, but it is unknown whether they have introgressed. Socioeconomic changes, including migration, trade liberalization, and reduced support for Mexican farmers, may also affect maize diversity. Diversity may increase, decrease, or remain the same, but whether this is viewed as good or bad will depend on subjective values.*

Keywords: GE crops, maize, Mexico, risk, gene flow

The increase in commercial planting of genetically engineered (GE, also known as genetically modified, or GM) crop varieties during the last 10 years has been dramatic, both in the rapidity of its adoption (James 2005) and in the controversy it has sparked (e.g., CEC 2004). But the debate about GE varieties in traditionally based agricultural systems (hereafter "traditional agriculture") did not burst into international headlines until the publication in 2001 of an article reporting evidence of transgenes in farmer varieties (FVs) of maize (*Zea mays* ssp. *mays*) in the state of Oaxaca, in southern Mexico (Quist and Chapela 2001). That paper stimulated much discussion and speculation about the implications of the findings for maize diversity in Mexico. Then, almost four years later, Ortiz-García and colleagues (2005) reported that they had found no detectable evidence of transgenes in the same area, reintensifying the debate.

The polarized positions of proponents and opponents of GE crops often conflate facts and values in research and discussions, frequently adding heat, but not light, to the debate. So what do we know about transgenes and maize diversity in Mexico? We offer an overview of the situation through answers to key questions. Our goal is to integrate the genetic, ecological, and social issues at the farm, regional, Mexican, North American, and global levels, emphasizing the distinction between empirical data and speculation based on unexamined assumptions.

Is maize diversity in Mexico important?

Yes. Although any answer to this question can only be value based, most people, regardless of their position on GE crops, agree about the importance of diversity. Maize was domesticated in southern Mexico, and Mexico is the world center of maize diversity (Matsuoka et al. 2002) and also home to that crop's wild relatives, the teosintes (*Z. mays* sspp.), including the teosinte most closely related to maize (*Z. mays* ssp. *parviglumis*). Much of Mexico's maize diversity is conserved *in situ* in Mexican farmers' fields as FVs (Aragón-Cuevas et al. 2005), which include landraces, traditional varieties selected by farmers, MVs (modern varieties) adapted to the local environments by farmers and by natural selection, and progeny from crosses among these varieties. This *in situ* conservation is recognized as an important complement to the Mexican national gene bank's *ex situ* collection of 10,683 accessions, 83% of which are duplicated in the CIMMYT (Centro Internacional de Mejoramiento de Maíz y Trigo [International Maize and Wheat Improvement Center]) gene bank (Hernández Casillas 2003). Maize diversity plays a central role in the rich agronomic and cultural diversity of Mexico, its culinary traditions, and its national identity (figure 1; Esteva and Marielle 2003). Maize is the staple of most Mexican diets, with over 12.7 million metric tons (equivalent to 126 kilograms per person) consumed directly as food in 2003 (FAOSTAT 2006). Maize occupies more area than any other Mexican crop (8.0 million hectares [ha]), and FVs

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account for 79% of maize area in the nation (Aquino et al. 2001) and approximately 90% in Oaxaca, which has high maize diversity (table 1; Aragón-Cuevas et al. 2005).

Maize is also an important crop globally (first in production and third in consumption, after rice and wheat; FAOSTAT 2006); 56% of global maize production in 2005 occurred in industrial countries using MVs, whose improvement may increasingly depend on the genetic diversity found in FVs (Pollak and Salhuana 2001).

Could transgenic maize affect the genetic diversity of maize in Mexico?

Yes. Transgenic maize could increase or decrease maize diversity, or it could have no lasting effect. This will depend on genetic, ecological, and social processes, which can be empirically understood within the limits of agreement on definitions, methods, and resources (Cleveland and Soleri 2005). We consider the effects of GE varieties per se, as well as effects of transgene flow from those varieties to FVs and to wild and weedy relatives. Seed flow is the first step in (trans)gene flow, followed by pollen flow, hybridization, and introgression (incorporation of the transgene into the host genome with stable inheritance).

Gene flow and its longer-term effects on the diversity of the recipient population depend on a number of variables, including the size of donor and recipient populations, the rate of seed and pollen flow and fertilization, and the relative and absolute fitness of the hybrids, which are determined by the genetic, ecological, and sociocultural processes in specific agricultural systems (Ellstrand 2003). Transgene flow includes not only the gene of interest (e.g., *Bacillus thuringiensis,* or *Bt*) but other genetic elements in the transgenic construct, such as promoter, terminator, and marker genes, as well as linked nontransgenic genes of the host genome that "hitchhike" along with the transgenes (Gepts and Papa 2003). In addition to any effects gene flow might have on allele frequencies in the recipient population, it will increase diversity qualitatively because it adds a new gene or genes. Modern GE crop varieties can also affect diversity by reducing the area planted with FVs, or by replacing FVs (see "Are the potential effects of current GE maize varieties on maize diversity and traditional agricultural systems the same as those of conventional MVs?" and "Will economic globalization affect Mexican maize diversity?" below).

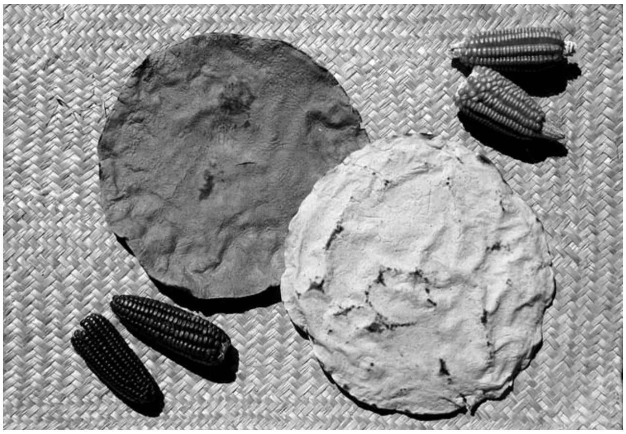

Figure 1. Maize farmer varieties from the Central Valleys of Oaxaca are used to make diverse traditional foods such as yellow and black tlayudas*, the large crisp tortillas of the region. The stacks of* tlayudas *sent by air to Oaxacan migrants working in the United States illustrate the cultural value of traditional maize foods. Photograph: Daniela Soleri.*

Whether any qualitative or quantitative change in diversity will be positive or negative depends entirely on subjective judgments, including those about the role of agriculture in nature and society (Cleveland 2001). For example, conserving the maximum amount of genetic diversity feasible is often the stated goal of conservation. However, maintaining *in situ* the maximum diversity at the crop species, variety, or population level may not always be beneficial for the agricultural communities managing that diversity (e.g., high levels of heterogeneity within any crop can make field management and

Table 1. Maize races present in FVs (farmer varieties) and estimated production area in different regions of the state of Oaxaca, Mexico.

Maize regions	Maize races present in FVs grown in region	Estimated production area of FVs in region (hectares)	Percentage of total Oaxacan maize FV production area
Mixteca	Chalqueño, Cónico	104,000	21.6
Central Valleys	Bolita, Tepecintle, Pepitilla, Tabloncillo	120,000	24.9
Coast	Tuxpeño, Olotillo, Conejito, Tepecintle	80,000	16.6
Istmo de Tehauntepec	Zapalote Chico, Zapalote Grande, Tuxpeño	100,000	20.7
Sierra Juárez–Northern Highlands	Olotón, Cónico, Chalqueño, Bolita, Tuxpeño, Comiteco, Serrano Mixe	17,000	3.5
Cañada–Southern Highlands	Comiteco, Olotón, Tepecintle, Chalqueño	31,000	6.4
Tuxtepec–northern border to the state of Veracruz	Tuxpeño, Tepecintle, Nal-tel, Olotillo	30,000	6.2
Total		482,000	99.9

Note: Percentages do not total 100 because of rounding.
Source: Aragón-Cuevas et al. 2005.

selection for desired traits difficult for farmers, as can high heterozygosity in cross-pollinated species). Even if the amount of diversity does not change, there can be disagreement over which type of diversity (e.g., which alleles, at which loci, from which source) is more valuable, a potential issue when considering the effect of transgene flow on other loci in the genome. Agreement about the value of agricultural transgenes will ultimately require a broad benefit–cost analysis comparing current commercial GE varieties, FVs, and MVs with alternatives, including FVs improved conventionally (see "Are there more diversity-friendly alternatives to current GE crops?" below) or by genetic engineering (Cleveland and Soleri 2005).

Concern over the potential effect of GE varieties and transgenes on maize diversity was important in the Mexican government's decision to ban experimental and commercial planting of transgenic maize in 1998 (Alvarez-Morales 2000), which has since been lifted for experimental plantings. This ban was specifically in response to concern for maize diversity; GE varieties of other species are grown commercially in Mexico, including 0.1 million ha of transgenic soybean and cotton in 2005 (James 2005). Potential effects on maize diversity continue to be the focus of debates about transgenic maize in Mexico (CEC 2004).

Where does transgenic maize in Mexico come from?

The United States. The United States is the world leader in developing, promoting, producing, and regulating GE crops, with 49.8 million ha planted in 2005 (55% of global GE crop area) (James 2005). In 2005, 52% of US maize planted was transgenic—26% *Bt* modified, 17% herbicide resistant, and 9% both *Bt* modified and herbicide resistant (USDA NASS 2005). Transgenic and nontransgenic maize grain are not segregated in the US maize production system (Andow et al. 2004).

Especially since implementation of NAFTA (North American Free Trade Agreement) and other policy changes in the mid-1990s, Mexican imports of US maize have increased (Nadal and Wise 2004). Mexico imports about 25% of its maize from the United States, an average of 5.45 million metric tons per year between 2000 and 2004, including about 500 billion kernels of white *Bt* maize intended for food between 2000 and 2003 (Cleveland and Soleri 2005). Mexico is the second largest recipient of US maize exports (about 11% of total US maize exports), and nearly 100% of Mexican maize grain imports are from the United States (FAOSTAT 2006). In these large-scale movements of grain, some will probably escape accidentally from grain sacks or trucks and be planted unintentionally. Also, farmers often experiment with new seeds, for example, by planting grain intended for eating. In interviews with farmers in four Oaxacan communities, we found that 23% (39 of 169) of those obtaining maize off-farm as grain to eat had also planted some; 8% (13 of 169) were planting grain from government stores, which frequently carried US maize at the time; and 100% of those who planted this grain said it produced pollen.

Does US regulation of transgenic maize include potential effects on Mexican maize diversity?

No. The US Department of Agriculture (USDA) mandate does not include consideration of risk for locations outside the United States (NRC 2002), although this has been recommended (NRC 2002, 2004). However, in a letter accompanying international maize grain exports that include transgenic grain, the USDA strongly implies that because these crops have been approved in the United States, they are without risk for the rest of the world (USDA GIPSA 2002, Cleveland and Soleri 2005). This statement assumes that the US approach can be generalized, complementing the belief that the US government promotes international risk management that is "science-based and is aligned with US safety standards" (USDA APHIS BRS 2004)—this despite evidence that US regulation and enforcement may be inadequate to prevent unintentional transgene flow in the United States (Mellon and Rissler 2004), including gene flow from pharmaceutical and industrial GE crops (USDA 2005).

The risk management process is the main regulatory tool for GE crops in the United States and elsewhere. It consists of four key steps, although they may be organized and labeled in different ways: (1) *identification* of a hazard (potential risk), (2) *analysis* of the probability of *exposure* to the hazard and of *harm* resulting from exposure, (3) *evaluation* (perception, assessment) of harm, and (4) *treatment* (management, regulation) of risk by reducing exposure and harm (e.g., NRC 2002). The risk management process for GE varieties is explicitly based on a preexisting system for invasive alien species (NRC 2002), and genes as well as species can be considered invasive biological entities (Hindar 1999).

As is evident from the steps in risk management outlined above, the extent and effects of biological invasion are context specific. This is why many scientists believe risk assessment for GE crops should be conducted on a case-by-case basis (NRC 2002, Andow and Hilbeck 2004, Snow et al. 2005). To the extent that maize diversity and agriculture in the two countries are different, the US risk management process may not be appropriate in Mexico.

Are maize diversity and agriculture different in Mexico and the United States?

Yes, very different. Key differences are as follows:

Genetic and ecological differences. MVs are sown on a relatively small proportion of Mexican maize area—21% nationally and approximately 10% in Oaxaca, compared with 99% in the United States (Aquino et al. 2001, Aragón-Cuevas et al. 2005). FVs in Mexico are much more genetically diverse than the MVs predominant in the United States; are grown under much more diverse conditions (Aragón-Cuevas et al. 2005); and have high levels of gene flow via pollen and seed due to planting patterns, small field sizes, and extensive seed movement through the informal seed system (Pressoir and Berthaud 2004).

Economic differences. Approximately 50% of Mexico's maize is produced by small-scale farmers (Nadal 2000) receiving few subsidies from the government, using relatively low amounts of external inputs, and planting primarily the seed of FVs they save or obtain through the informal system. These farmers depend on this maize for food. Most maize in the United States is produced by large-scale farmers with subsidies from the government, using relatively high amounts of external inputs (e.g., nitrogen fertilizer, fossil fuel), planting MVs they buy commercially each year, and selling all of their maize, of which only a small amount (2%; Baker and Allen 2005) is consumed directly as grain by US consumers.

Social differences. In Mexico's traditional agricultural systems, the functions of genetic resource conservation, crop improvement, seed multiplication, food production, and food consumption are all integrated within households and communities, whereas in the industrialized maize agricultural systems of the United States, each of these functions is physically and institutionally distinct (figure 2).

Cultural differences. Maize has been a center of cultural values for most of Mexico's diverse ethnic groups for millennia, and today farmers and consumers value different varieties of maize for different growing conditions, foods, and ceremonies (Esteva and Marielle 2003). In the United States, maize has little cultural value except for Native Americans, who cultivate an estimated 0.2% of US maize grain area.

Because of these differences, even if the regulation of transgenic maize in the United States is adequate for that country (see above), it is not appropriate for Mexico.

Figure 2. Winnowing black maize in the Central Valleys of Oaxaca. Maize stored after the harvest is a source of food, of animal feed, and of the genetic diversity from which planting seed is selected for sowing. Here Delfina Castellanos winnows the black maize she has grown, which her household will prepare as food. At planting time she will select desirable ears and shell more of this maize to prepare seeds for sowing. Photograph: David A. Cleveland; used with permission of subject.

Are traditional agricultural systems needed for food production?

Yes. A dominant assumption in economic development for decades has been that traditional agriculture would disappear and food production would shift to large-scale, industrial farms. For example, during the birth of the Green Revolution at CIMMYT and its predecessor organizations in Mexico in the 1960s, there was much discussion about whether the focus should be on improving conditions for small-scale maize farmers or on increasing production by focusing on larger-scale, more industrialized agriculture, with the latter view prevailing (Jennings 1988). Today, in the most environmentally and socially marginal growing areas of Mexico, such as Oaxaca—where most of the population is dependent on maize production—only a small proportion of maize area is planted with MVs (Aragón-Cuevas et al. 2005).

The assumption that traditional agriculture would disappear continues to dominate conventional economic development thinking, as reflected in trade agreements such as NAFTA (Nadal 2000). There is evidence, however, to support the proposition that traditional agricultural systems are essential for meeting the food needs of the future (Heisey and Edmeades 1999), even as the current wave of economic globalization and "free" trade regimes makes it increasingly difficult for them to exist (Narayanan and Gulati 2002, Nadal and Wise 2004). Indeed, according to one study, the expansion of maize area to meet their needs characterizes the poorest rural households' response to reduced subsistence options as government support was withdrawn and cheap, subsidized US maize became available in Mexico (Nadal 2000). Yet even as economic assumptions marginalize Mexican traditional agricultural systems in favor of industrial agriculture, there is growing recognition of traditional systems' importance for food production (Narayanan and Gulati 2002), and increasing research on alternatives to conventional industrial agriculture for all farming systems (e.g., Pimentel et al. 2005). Overall, at least for the near future, the contributions of traditional agriculture to genetic diversity and food production are considered valuable, and are in the hands of the farmers practicing this form of agriculture and their communities.

Will farmers' attitudes and knowledge influence the effects of GE varieties on maize diversity?

Probably. Farmers are not included in policymaking, yet their decisions about what kind of maize to grow, what criteria to use in seed selection, and whether to continue farming will be important. This, in turn, will depend on farmers' values and knowledge, including that concerning GE crops and transgenes, and their ability to make changes.

It has been suggested that an important way in which maize diversity could be reduced is if farmers reject FVs they believe are contaminated with transgenes (Ortiz-García et al. 2005). However, very little is known about Mexican farmers' knowledge and attitudes concerning GE crops. A majority (66%) of 328 farm households interviewed in six communities in Mexico (Oaxaca), Cuba, and Guatemala found genetic engineering per se to be acceptable (Soleri et al. 2005). However, a significantly larger majority (86%) were not willing to accept some of the possible future consequences of a hypothetical GE variety as depicted in a scenario: reliance on the formal seed system, and initially high but declining yields due to evolution of pest resistance. (Although resistance to transgenic *Bt* has not been documented in the field, its occurrence is considered by most scientists to be unavoidable; Bates et al. 2005.) The variety was described by its performance but never identified as being transgenic. Variation in interview responses was present within and across communities and countries where a more modern and more traditional agricultural community was sampled in each country.

In Oaxaca, the number of farmers who found the process of interspecific genetic engineering per se unacceptable was not significantly different ($\chi^2 = 3.7364$, $p = 0.053$) between a more modern, lowland maize-producing community in the Oaxacan Isthmus (18 of 55, or 33%) and a more traditional community cultivating maize on the high plateau of the Central Valleys (28 of 55, or 51%), with substantial variation evident among farmers in each community. However, in other countries included in that international study, there was a significant difference between modern and traditional communities in their attitudes toward genetic engineering per se. There was no significant difference ($\chi^2 = 2.427$, $p = 0.119$) between the Oaxacan communities in their acceptance or rejection of the GE variety described in the scenario. The majority in both the more modern (51 of 54, or 94%) and more traditional (47 of 55, or 85%) communities did not choose the hypothetical GE variety. The variation in attitudes toward GE per se among communities in other countries studied and within Oaxacan communities sampled suggests that acceptance of GE will depend on many factors. However, in all three countries, the potential consequences of a GE variety are a concern for small farmers in both traditional and modern communities.

While our results do not support a common assumption of GE crop opponents that the process of genetic engineering is culturally unacceptable to all farmers in traditional agricultural systems, neither do they support the common assumption of GE crop proponents that farmer acceptance of genetic engineering is tantamount to acceptance of GE varieties. Consequences acceptable in industrial agriculture, such as yields responsive to improved environmental conditions and reliance on the formal crop improvement, seed multiplication, and distribution systems, are perceived differently by farmers in traditional agricultural systems. Significant variation within and between some communities for these responses supports the need for a case-by-case approach.

Farmers' responses to the changing socioeconomic conditions in rural Mexico could have major effects on the extent and diversity of Mexican maize production. However, the details of how this might happen require more investigation. For example, both expansion (Nadal 2000) and contraction (Fitting 2006) of maize area have been reported.

Are traditional farmers in Mexico involved in decisions about transgenic maize?

No. This is in spite of widespread agreement that a successful risk management process requires the involvement of those most affected in decisionmaking at all four steps, and that lack of public trust in GE crops is caused in part by a lack of participation (NRC 2002).

Although traditional farmers have not been formally included in the risk management process in Mexico, or in North America in general, several community and farmer organizations have made statements (e.g., Gonzalez 2005) and have even carried out their own research on transgene presence (ETC Group 2003). At an international meeting in Oaxaca, the discontent of local communities at being left out of decisionmaking was evident. Much of this discontent built on a history of similar exclusion and focused on farmers' rights in their maize FVs, rights that they believed were violated by the presence of transgenes in FVs, which farmers had not authorized (Nadal and Wise 2004). Our surveys of farmers in four Oaxacan communities—including ones close to the capital city, the stage for many of the statements issued about the "maize scandal"—found that only 12% (20 of 168) had heard of transgenic maize.

Have GE maize varieties hybridized with maize FVs or wild relatives in Mexico?

Quite probably. There are good reasons to hypothesize that transgenes are present in Mexican maize FVs as a result of hybridization: wind-borne cross-pollination of maize, high rates of seed and pollen flow in traditional maize agriculture in Mexico, and distribution of large amounts of transgenic maize grain. However, transgene presence in a specific situation depends on many factors about which little is known (e.g., phenological synchrony between GE varieties and FVs and their spatial and temporal distribution, farmer selection criteria, and fitness of GE varieties and GE x FV hybrids) (Gepts and Papa 2003, Ma et al. 2004, Cleveland and Soleri 2005).

Research has documented hybridization between *Bt* maize and nontransgenic maize (Chilcutt and Tabashnik 2004), and there is evidence of similar hybridizations occurring in many of the basic cereal crops (including maize) in the United States during commercial production (Mellon and Rissler 2004). Many crops hybridize with their wild relatives (Ellstrand 2003), and maize and teosinte can form fully fertile hybrids. Thus the potential exists for maize transgenes to move into teosinte, and this has been observed in one teosinte, though not *parviglumis,* the subspecies most closely related to maize (see "Have transgenes introgressed into maize FVs or wild relatives in Mexico?" below).

It has become widely accepted that transgenes are very likely present in some Mexican maize FVs as a result of ongoing hybridizations (e.g., from planting food grain), even if not introgressed, despite the moratorium on planting GE maize in place since July 1998 (Alvarez-Morales 2000). Quist and Chapela's (2001) publication was the first peer-reviewed report of transgenes in FVs. The Mexican government reported transgenes in FVs in 15 of 22 areas in the states of Oaxaca and Puebla (Dalton 2001), but these results have not been published in a peer-reviewed journal (Kaiser 2005). Communities in several Mexican states reported finding transgenes in their maize FVs in 2003 using detection kits applying the DAS (double antibody sandwich) ELISA (enzyme-linked immunosorbent assay) test (ETC Group 2003), though this has not been verified and false positives are possible. Many opponents of GE crops saw these reports as demonstrating the inability to contain transgenes (ETC Group 2003).

The initial reaction by supporters of agricultural genetic engineering was to question the data showing transgene presence in FV populations, and early responses focused on Quist and Chapela's methods and conclusions (e.g., Christou 2002). However, by spring 2002, the majority position of GE crop proponents shifted to one of accepting transgene flow into maize FVs as inevitable, although not accepting Quist and Chapela's claim of introgression. It was accepted that "DNA flies around all over the place down on the farm" and is "as normal and natural, well, as agriculture itself" (Nature Biotechnology 2002).

Have transgenes introgressed into maize FVs or wild relatives in Mexico?

We don't know. Introgression—the stable integration of a gene into the recipient population—is the last stage of gene flow. There is now ample evidence that gene flow and introgression between crops and wild or weedy relatives occurs in many crop species, as between maize and one of its wild teosinte relatives in Mexico (*Z. mays* ssp. *mexicana;* Ellstrand 2003, Baltazar et al. 2005). Extensive gene flow, including introgression, occurs between maize FV populations in Mexico (Pressoir and Berthaud 2004). It seems likely that this will be the same for transgenic MVs as well, but documentation is lacking. However, there are reasons to believe that this is possible. In other crop species, transgenes from GE crop varieties have been successfully backcrossed into wild crop relatives (e.g., sunflower; Snow et al. 2003), and have spontaneously hybridized with nontransgenic and transgenic MVs (e.g., oilseed rape; Hall et al. 2000). There is also recent experimental evidence that introgression can occur between transgenic maize and Mexican FVs (Norman Ellstrand, University of California–Riverside, personal communication, 1 November 2005).

Some proponents of GE crops claim that transgenes will not introgress into FVs if the selection pressure under which they were designed to function is absent. However, a number of studies have found no fitness costs in the absence of the targeted environmental stress (e.g., for insecticidal *Bt* transgenes in the absence of herbivory in wild sunflower; Snow et al. 2003).

If transgenes were present in Oaxacan maize FVs, have they gone away?

We don't know. Ortiz-García and colleagues (2005) reported absence of detectable (> 0.01%) transgenes in maize FVs in the same area where they were reported in 2001 by Quist and Chapela (2001). The response to Ortiz-García and colleagues' report was just as polarized as that to the Quist and Chapela paper, but in the opposite direction. It was hailed by GE crop supporters as evidence of absence—proof that if the 2001 report was accurate, transgenes have since disappeared. *Science* magazine declared that "Mexico's transgenic maize scare appears to be over" (Kaiser 2005). Despite the authors' warning against extrapolating to other locations or into the future (Ortiz-García et al. 2005), they and others have also suggested that the results are important for all Oaxacan or even all Mexican maize FVs (e.g., Kaiser 2005). Opponents of GE crops saw the paper as unscientific and inconclusive (e.g., ETC Group 2005).

Accepting the null hypothesis of absence of transgenes at detectable frequencies, as Ortiz-García and colleagues did, is more open to question and misinterpretation (Andow 2003) than accepting the alternative hypothesis of presence of transgenes. The sample representativeness of farming systems and crop populations is more critical, and requires analysis based on diversity and population structure either empirically measured or theoretically inferred.

A reanalysis of Ortiz-García and colleagues' data (Cleveland et al. 2005) found their conclusions that "the frequency of transgenic seeds from maize grown in the sampled region was near zero" and that there is "no current evidence for transgene introgression into maize landraces in the Sierra de Juárez of Oaxaca" were not scientifically justified. Although Ortiz-García and colleagues' samples were far larger than Quist and Chapela's, they were unrepresentative, and the statistical analysis was inconclusive because it was based on the census population size of the samples instead of their effective population size (N_e). When N_e is used, the binomial probabilities of failing to detect transgenes in landrace populations using Ortiz-García and colleagues' data are much larger than they reported: Transgenes could be present in maize landraces in the Sierra Juárez Region at frequencies of approximately 1% to 4% and still not have been detected (Cleveland et al. 2005). In addition, there may be an even greater probability of transgene presence in landrace populations in the 90% of the maize landrace area of Oaxaca that is not mountainous (in contrast to the mountainous area sampled by both the Quist and Chapela and the Ortiz-Garcia et al. studies), and where GE plants and the offspring resulting from hybridization with FVs would be more likely to survive and reproduce. Thus, because of methodological issues, it is still unclear whether transgenes are present or have introgressed into the maize populations in the communities of the Sierra Juárez Region of Oaxaca, or in the rest of Mexico.

In the absence of more costly research on the variables determining transgene flow and its effects in each specific situation, research on the presence or absence of transgenes, and their frequencies, in landrace populations at different points in space and time can provide important clues for understanding seed and pollen flow, hybridization, and introgression. We suggest that this research be based on (a) understanding local seed systems, including the way farmer practices affect landrace population structure and dynamics; (b) collecting seed samples to optimize the ratio of N_e to census population size, generally by taking a smaller number of seeds from a larger number of ears than has been done; (c) minimizing variance by sampling equal numbers of units at all levels (ear, household, cultivated area, community, etc.); and (d) using N_e, not census population size, to calculate binomial probabilities for the presence of transgenes (Cleveland et al. 2005).

Can maize transgenes always be eliminated from traditional agricultural systems if introgression does occur?

No. It is important to distinguish between transgenes in the food supply and in crop populations. It may be possible to eliminate transgenes from the food supply, that is, to reduce them to acceptable levels (e.g., at or below 0.9% for approved transgenes in the European Union), as in the case of StarLink maize in the United States (NRC 2004). However, eliminating transgenes introgressed into crop populations is a different matter, because they are reproduced every generation, so their fate will depend on population genetic processes. Linkage of transgenes to genes not adapted to local growing environments may cause the transgenes to be selected against, but recombination rates in allogamous crops like maize are high, and the size of linkage regions is relatively small (Gepts and Papa 2003). Fitness-reducing transgenes could persist under ongoing gene flow, especially into smaller recipient populations such as small stands of teosinte. Selectively neutral transgenes may persist until they are lost by genetic drift at a rate dependent on their frequency in the population. If the transgene confers higher fitness, then it will be very difficult, and in some cases probably impossible, to eliminate (NRC 2004).

It might seem that farmers could easily eliminate transgenes from their FVs, since they select seeds each year for planting. However, even if farmers wanted to eliminate a transgene from their FV populations, this would be difficult for a number of reasons. First, if there were no phenotypic expression of the transgene, there would be no basis for selection. Second, it may be difficult for farmers to distinguish some positive or negative forms of phenotypic expression due to transgenes from genetic variation in their FVs and environmental variation in their highly variable growing conditions (Soleri et al. 2000, Soleri and Cleveland 2001), complicating selection efficiencies (figure 3). Third, if, for example, *Bt* genes relevant for important maize pests in a region were present, then transgenic *Bt* x FV hybrids could produce ears with reduced caterpillar damage and associated disease—both valued criteria in farmer seed selection. In this case, whether or not farmers would want to eliminate the transgene would depend on other criteria, including cultural, health, and environmental concerns. At this time there are no commercially available transgenes targeted specifically at major pests of traditional maize production in Mexico (e.g., fall armyworm, *Spodoptera frugiperda;* corn earworm, *Heliothis* spp.; and postharvest pests, including maize weevil, *Sitophilus zeamais*). However, according to CIBIOGEM (Comisión Intersecretarial de Bioseguridad y Organismos Genéticamente Modificados; *http://cibiogem.gob.mx/bases_datos/productos_bioteconologicos.html*), several varieties of *Bt* maize MVs were approved in 2002 and 2003 for commercialization in Mexico (targeted to *Diabrotica* and *Lepidoptera* spp.), though this does not mean they address the problems of greatest import for traditional farmers. Also, a GE cotton including *Bt* genes for resistance to fall armyworm was approved in 2003 for use in Mexico and is being grown, although recent evaluations suggest it eliminates less than 20% of fall armyworm on that crop (Traxler and Godoy-Avila 2004). Finally, because seed systems in traditional Mexican agriculture are open and predominantly informal, with high levels of gene flow via seed (Pressoir and Berthaud

Figure 3. Maize seed selection occurs postharvest from fields with high environmental variation, making it difficult for farmers such as Delfino Jesús Llanez Lopez (from the Central Valleys of Oaxaca, Mexico) to distinguish between genetic and environmental variation. Farmers are aware of this, and many selection criteria focus on characteristics important for seed viability and vigor, not genetic change (Soleri et al. 2000). Photograph: David A. Cleveland; used with permission of subject.

2004), seed purchase could not serve as a locus of transgene control available to private or public institutions, as is envisioned in industrialized agriculture.

Are the potential effects of current GE maize varieties on maize diversity and traditional agricultural systems the same as those of conventional MVs?

Yes and no. If current transgenic MVs are considered substantially equivalent to nontransgenic MVs, as is often the case in US regulatory process (NRC 2002), does this mean that they present no threat to maize diversity? Probably not, though it is often suggested that transgenes will not reduce FV diversity because the effects of transgene flow are similar to gene flow from nontransgenic MVs (Ortiz-García et al. 2005, Raven 2005). MVs have had widespread negative as well as positive effects on traditional agriculture in general (NRC 2002), including changes in intraspecific diversity, so we can expect that current GE crops could have similar effects. MVs, especially of rice (*Oryza sativa*) and wheat (*Triticum* spp.), characterized by traits produced by a small number of genetic changes (increased harvest index, fertilizer response) formed the basis of the Green Revolution. The effects of these self-pollinating MVs have included the replacement or reduction of populations of large numbers of FVs (Plucknett et al. 1987), with widespread environmental and social consequences (NRC 2002). In maize, which is highly outcrossing, varietal replacement has also occurred (though to a lesser extent, for a number of reasons specific to that crop) (Heisey and Edmeades 1999). Because of its reproductive biology and the wide range of environments where it grows, gene flow from MVs to FVs in maize may be a greater possibility. However, few details are known about the effect of gene flow from MVs on FVs (NRC 2002), including maize FVs in Mexico (Serratos et al. 1997). Introgression of a transgene from a GE variety into maize FV populations would be a small genetic change relative to the maize genome size, as was the case in the genetic changes producing the Green Revolution varieties. Therefore, it seems premature to minimize potential effects of transgenic maize on FV diversity by suggesting they would be the same as those of conventional MVs.

However, GE varieties are also fundamentally different in some ways from nontransgenic MVs; for example, genes in GE varieties code for protein production, whereas protein production is silenced in many characteristics of the domestication syndrome (Gepts and Papa 2003). Transgenes like *Bt* backcrossed into FVs could contribute to FV protection and persistence, and thus to the conservation of diversity. Alternatively, transgenes could be linked to disadaptive alleles that could sweep FV populations, causing a loss of locally important alleles. If transgenes allow MVs to grow under conditions where only FVs are currently adapted, they could displace FVs, increasing the probability of gene flow to other FV populations and, in the case of maize in Mexico, to teosinte (Gepts and Papa 2003). In addition, third-generation GE crops producing industrial chemicals and pharmaceuticals may increase the threat to diversity both directly, through the processes outlined above, and perhaps indirectly if concern over transgene presence causes farmers to abandon their FVs (Ortiz-García et al. 2005; see "Will farmers' attitudes and knowledge influence the effects of GE varieties on maize diversity?" above). Maize has been a crop of choice in the development of these third-generation GE crops (Andow et al. 2004).

Will economic globalization affect Mexican maize diversity?

Probably. Maize diversity could be affected by changes in farming practices, as well as by economic and social changes (Cleveland and Soleri 2005), including the same ones that are moving transgenic maize grain into Mexico (Nadal and Wise 2004). Indeed, the current threat to maize diversity in Mexico may not be only, or even primarily, from transgene movement into traditional agriculture systems, but from the national and international policies that are undermining the viability of those systems. As discussed above, the economic assumptions on which NAFTA was based included the assumption that small-scale maize production in Mexico should and would disappear (Nadal and Wise 2004). Tariff protection for Mexican maize farmers, which was intended to be phased out over 15 years under NAFTA, was instead phased out in only 3 years by the Mexican government, and subsidies to farmers in traditional agriculture were reduced, resulting in more transgenic maize entering Mexico as grain and in reduced viability of traditional agricultural systems there (Nadal and Wise 2004), most likely reducing useful maize diversity. Meanwhile, US maize producers received $37.4 billion in government subsidies from 1995 through 2003 (EWG 2005), about $18 per metric ton, or approximately 20% of the average farm price during that period (calculated from Irwin and Good 2004).

These developments may be part of a global process dominated by the assumption that increasing industrialization and concentrated control of agriculture by multinationals is the only means for increasing agricultural sustainability. For example, some see GE crops as the only way to feed the world's growing population (Raven 2005), as a way for traditional farmers to increase their well-being sufficiently to enable them to leave farming altogether (Conway 2003), and as an ethical necessity as promoted by the US government (Nicholson 2004). Indeed, a key argument for regulation by proponents of GE crops is to reassure the world, including developing countries, that those crops are safe (NRC 2002), which many see as important in order to secure and increase the profits of private agricultural biotechnology corporations (e.g., Victor and Runge 2002).

The development of GE crops has fueled multinational consolidation in the seed industry, with a small number of multinational companies dominating the GE crop industry. In the United States, for example, two corporations (Monsanto and Syngenta) held 27% of all agricultural biotechnology patents issued between 1982 and 2001, more than the entire public sector share of 24% (Graff et al. 2003). This consolidation has led to a reduction in crop diversity, including genotypes used for major commercial varieties (Gepts and Papa 2003).

Are there more diversity-friendly alternatives to current GE crops?

Probably. Agricultural biotechnology, including GE crops, could theoretically be used to promote either large-scale industrial agriculture or alternatives that improve traditional systems and support their biological and cultural diversity. GE crops could contribute positively to maize diversity if (a) transgenes were introgressed into existing FVs to improve yield in ways that supported positive functions of traditional systems; (b) this introgression could be accomplished while minimizing any negative consequences on diversity (e.g., by position effects, linkage, and epistasis); (c) companies owning rights in the technologies allowed free use so that seed purchase was not necessary and intellectual property rights were not an issue; (d) a risk management process were specifically designed to evaluate transgenic FVs in the farming systems where they were introduced, and this process explicitly included farmers' participation; and (e) postcommercialization monitoring systems were in place and sufficiently funded to ensure an adequate response to problems such as evolution of pest resistance (Cleveland and Soleri 2005). While all these conditions are feasible, they have not occurred yet and would require substantial investment.

An important question that needs to be answered is, Are there alternatives to GE crops where equal investment of resources might have greater potential benefits for biological and cultural diversity, and for the well-being of farmers and society? For example, Goodman (2004) estimates the "commercial development of a single (trans)gene is now 50x as costly as the development of a commercial inbred by conventional breeding" (approximately $60 million versus approximately $1 million). As the plant breeder Norman Simmonds commented about MVs and the Green Revolution, special care is warranted to ensure that "other possibilities which might accord better with social needs" are not neglected (Simmonds and Smartt 1999).

If it is accepted that traditional agricultural systems in Mexico are valuable for their contributions to biological and

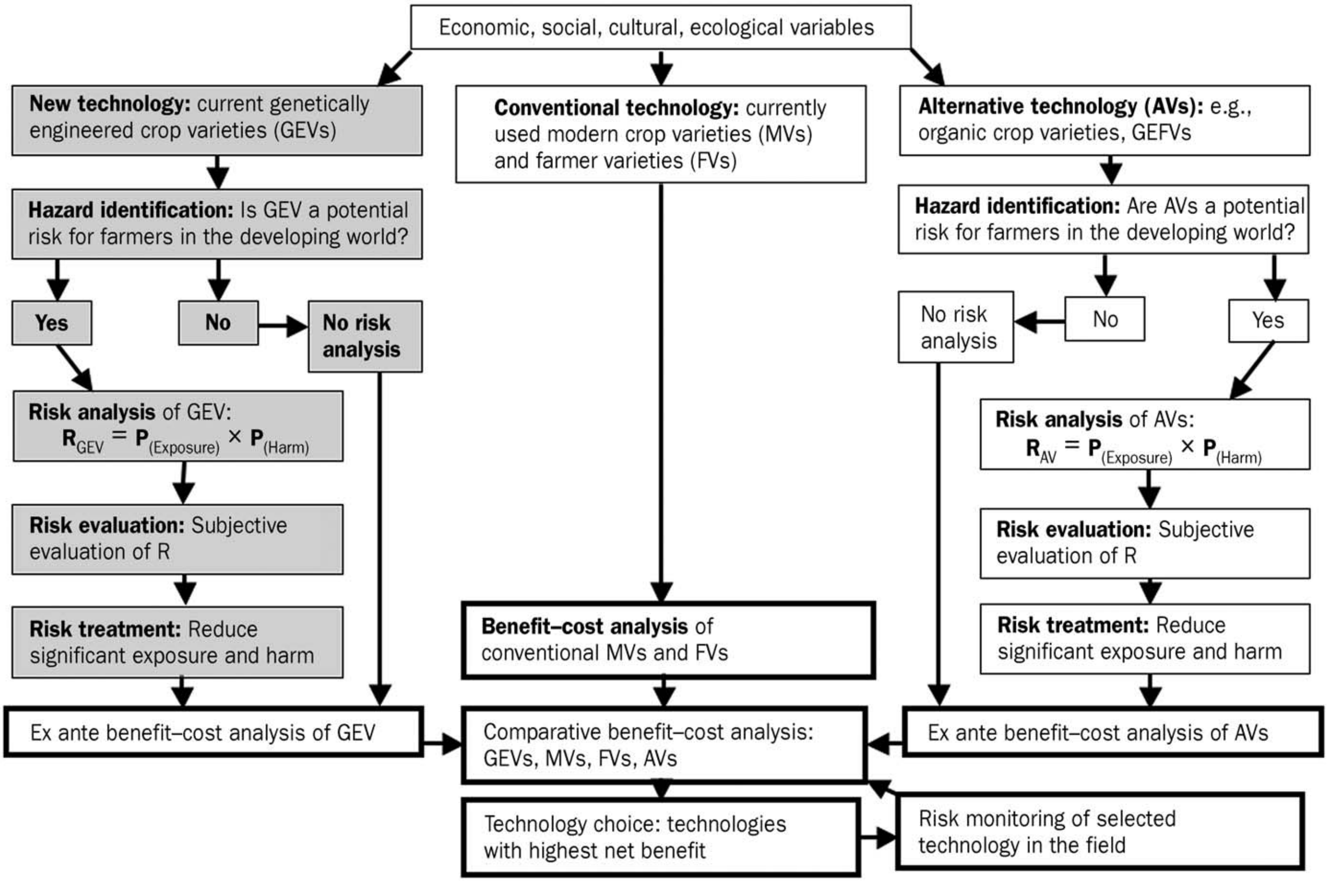

Figure 4. Flow diagram illustrating the combination of risk management for transgenic crops in developing countries (shaded) with a benefit–cost analysis comparing genetically engineered modern varieties (MVs) with other types of crop varieties (bold outline), including integration of new data available through postcommercialization monitoring. Abbreviations: AV, alternative variety; FV, farmer variety; GEFV, genetically engineered farmer variety; GEV, genetically engineered variety; P, probability; R, risk. Modified from Cleveland and Soleri 2005.

cultural diversity, including maize diversity (Aragón-Cuevas et al. 2005), then improving their functioning rather than replacing them is an alternative requiring consideration, and would need to involve the farmers themselves in decision-making to be successful. Alternative approaches, whether or not they include transgenes, will require evaluation not only with a risk management process but also a benefit–cost analysis with clearly stated goals (figure 4; Cleveland and Soleri 2005).

Conclusions

Transgenes are probably present in Mexican maize FVs, and could have introgressed into them, but available data are inadequate for unequivocal conclusions. Though several types of direct effects of GE varieties on maize diversity seem possible, it is difficult to predict their extent, and there is no evidence that maize biodiversity has been affected directly (i.e., through gene flow) by the presence of transgenes in Mexico. Potential negative effects on diversity exist and could increase when GE maize varieties now being developed to produce pharmaceutical and industrial chemicals are commercialized.

Yet at the same time, recent economic policies appear to be reducing the viability of traditional agricultural systems, and if GE maize varieties currently being developed are approved for planting by Mexican farmers, this process is likely to be accelerated. The synergy of all these factors could threaten the biological and social diversity of maize in Mexico. While GE varieties might have positive as well as negative effects on diversity, positive effects seem likely only if those varieties are developed specifically to do this, in collaboration with farmers. More research that considers a wide range of possible approaches, and more unbiased interpretation and application of research results to policy, is urgently needed if we are to make the best choices.

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