

Traditional Mexican agricultural systems and the potential impacts of transgenic varieties on maize diversity¹

Mauricio R. Bellon¹ and Julien Berthaud²

¹*International Maize and Wheat Improvement Center (CIMMYT), Mexico DF, Mexico;* ²*Institut de Recherche pour le Développement (IRD), Montpellier, France*

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Abstract. The discovery of transgenes in maize landraces in Mexico, a center of diversity for this crop, raises questions about the potential impact of transgene diffusion on maize diversity. The concept of diversity and farmers' role in maintaining diversity is quite complex. Farmers' behavior is expected to have a significant influence on causing transgenes to diffuse, to be expressed differently, and to accumulate within landraces. Farmers' or consumers' perceptions that transgenes are "contaminants" and that landraces containing transgenes are "contaminated" could cause these landraces to be rejected and trigger a direct loss of diversity.

Key words: Biosafety, Center of diversity, Genetic erosion, Latin America, Maize, Mexico, Small-scale farmers, Transgenic varieties

Mauricio R. Bellon is a human ecologist working in the Economics Program of the International Maize and Wheat Improvement Center (CIMMYT) in Texcoco, Mexico. He received his MSc and PhD in ecology at the University of California, Davis. His current research includes projects that deal with on-farm conservation of maize, gene flow in traditional farming systems, and the impact of improved germplasm in the livelihoods of poor farmers.

Julien Berthaud is a population geneticist working for the Institut de Recherche pour le Développement (IRD). He received his PhD in plant science at the University of Paris 11. His current research includes projects related with the dynamics of genetic diversity, especially in traditional maize farming systems.

Introduction

The discovery of transgenic products in maize landraces² planted by small-scale Mexican farmers has caused great controversy (Carpentier and Herrman, 2003; Christou, 2002; Editorial Note, 2002; Kaplinsky et al., 2002; Metz and Fütterer, 2002; Quist and Chapela, 2001, 2002). It has raised the issue of whether the commercial introduction of transgenic maize varieties may have a deleterious effect on the diversity of maize landraces. This issue is significant because Mexico is a center of maize domestication and maize diversity.

Maize diversity in Mexico is found in traditional agricultural systems, but it is not a natural phenomenon. It results from the complex interaction between biological and sociocultural factors. In traditional agricultural systems,³ small-scale farmers generally produce maize for their own consumption, though some may sell a high proportion of their production. These farmers plant landraces and also improved varieties, which may be managed as landraces. Through their knowledge, preferences, and practices, they have developed and continue to

maintain maize diversity, making this region a center of diversity.

Transgenic maize has been grown commercially since 1996 and occupied 19.3 million hectares globally in 2004, mostly in the United States (ISAAA, 2005). Transgenic maize varieties possess one or several foreign genes (transgenes) inserted through genetic engineering. The foreign gene(s) come from various sources, including completely different species. Currently there are two major types of commercial transgenic maize: Bt maize (which produces an insecticide for certain types of insects) and herbicide-tolerant maize (which carries a transgene that allows it to survive even if sprayed with a particular herbicide), as well as combinations of both. Future transgenic varieties will have other traits, such as improved tolerance to drought and frost and better nutritional quality. Transgenic maize that is not designed for human consumption but rather for the production of industrial and pharmaceutical products, such as oils, plastics, and vaccines, is under development. Mexico's moratorium on planting transgenic maize, in place since 1998, has just recently been lifted for research purposes

but not for commercial planting. However non-segregated maize grain from countries where transgenic varieties are planted can be imported. There is a debate on whether transgenic maize varieties should or should not be allowed to be grown commercially in the country.

This paper explores the potential impacts of transgenic varieties on maize diversity. We examine definitions and means of analyzing maize diversity and describe mechanisms that may cause transgenes to diffuse into traditional agricultural systems. We present three models based on the behavior of traditional farmers that explore how transgenes might impact the maize diversity they maintain. We discuss the implications of the specificity of traditional agricultural systems for biosafety regulations in Mexico.

Maize diversity

Mexico is within the primary center of domestication and diversity of maize (*Zea mays* L.). The most recent evidence indicates that maize was domesticated in a single event in southern Mexico about 9,000 years ago. Molecular data indicate that Mexican maize diverged from Mexican annual teosinte (*Z. mays* ssp. *parviglumis*) between 5,689 and 10,093 BP (Matsuoka et al., 2002), which is consistent with the date of the oldest fossil maize of 6,250 BP (Piperno and Flannery, 2001). The early diversification probably occurred in the highlands between the present-day states of Oaxaca and Jalisco, before maize spread into the lowlands (Matsuoka et al., 2002).

Diversity exists in wild species and in crops. It has its origin in the history of each species and the management by farmers in the case of crops. Diversity is expressed through many traits and has its base in the variation of the many genes (and alleles)⁴ that are involved in their expression. The origin of this variation is mutation, which occurs constantly and naturally and can accumulate in the genome. When these mutations affect the expression of recognized traits, selection helps to modify (increase or decrease) their frequency in the populations. Mutations migrate from one population to another, promoting diversity within populations.

The evaluation of genetic diversity is complex because “diversity” is a multidimensional concept that can be applied to a population of plants, a group of populations, a plant species, and specific traits of interest. Diversity can be studied at the level of genes and DNA (i.e., by using molecular markers to analyze genotypes). This analysis reveals “neutral” diversity, which is not selected for because it is based on a variation in DNA that is not necessarily translated into a selective advantage. Neutral diversity reflects the demography and history of maize populations, such as expansions or contractions of populations or migration between populations (i.e., through seed or pollen exchange).

Diversity can also be studied at the level of morphology – the phenotype – which is the level to which farmers and breeders have immediate access. Historically, diversity in maize in Mexico has been described at the level of the phenotype, using the concept of “race.” Anderson and Cutler (1942: 17) first proposed classifying maize by races and defined a race as “a group of related individuals with enough characteristics in common to permit their recognition as a group.” Wellhausen et al. (1952) refined this concept and used it to describe the diversity of maize types cultivated in Mexico. Currently, 59 races have been described in Mexico (Sanchez et al., 2000). Phenotypic diversity is quite obvious in kernel color, ear and kernel shape and size, and agronomic traits such as plant height and length of the growing cycle. The concept of race rests on the hypothesis that diversity is restricted **within** a given race and exists mostly **between** races.

In a recent analysis using molecular markers, Matsuoka et al., (2002) found that races of maize are differentiated at the continental level according to an isolation-by-distance scheme, in which the races that are the farthest apart geographically are also the most genetically distinct. At the country level (in Mexico, for example), the genetic relationships between races of maize are not very clear or well defined, possibly because “most of the isozyme (and this can be true for other markers) variation in the races of maize in Mexico occurs within, rather than between races” (Sanchez et al., 2000: 57). This statement is also true of farmers’ populations and lowers the precision with which we can detect significant differences in the diversity of races of maize over time and space.

Another issue in the analysis of diversity arises from the fact that different markers (morphological and molecular) relate different information about diversity because they reflect different processes involved in the evolution of populations. Pressoir and Berthaud (2004), analyzing the diversity of maize in the Central Valleys of Oaxaca, showed that while the same neutral diversity (detected through molecular markers) is found in each population, morphological diversity is found within and among populations. As mentioned earlier, neutral diversity reflects the demography and history of maize populations. The morphological diversity observed in local maize populations reflects the history of farmers’ selection.

Individual farmers or groups of farmers have different interests. They value different traits (many of them not commercially valuable) and different options for the same trait. Through their choices and selection practices, they create the types we observe in their fields. Small-scale maize farmers provide long lists of traits that they value, mainly related to agronomic, consumption, and management characteristics (see Bellon and Risopoulous, 2001; Smale et al., 1999).⁵ Evaluating this diversity as farmers do is difficult and requires the use of social and

biological methodologies, as well as sampling farmers' fields and undertaking agronomic evaluations on experiment stations (see Bellon et al., 2003a; Pressoir and Berthaud, 2004).

Changes in diversity are related mostly to selection and migration. Selection occurs naturally or is imposed by farmers. Migration is associated mostly with farmers' decisions to mix seeds or to plant two types of maize side by side. In the next paragraphs we will explain how farmers' management of landraces can interact with diversity.

Traditional maize agricultural systems in Mexico

Mexico is a center of diversity because farmers domesticated maize and since then have been able to diversify the crop through constant divergent selection into many landraces and populations to fit their own needs, both cultural and agronomic. Traditional maize systems are thought to comprise more than two million farmers planting approximately 5.8 million hectares during the rainy season of 2002.⁶ Traditional agricultural systems are characterized by a series of practices and conditions – described below – that differ strongly, both genetically and socially, from those of commercial agriculture for which transgenes have been developed and are commercialized.

Landscapes with multiple maize populations

Many small-scale maize farmers simultaneously plant more than one maize population to meet different needs and preferences (Bellon, 1996). This strategy is important because most farmers consume what they produce, so their decisions about what to plant are influenced not only by the agronomic performance of a population, but also by the quality of the food products, such as tortillas, tamales, or atole (traditional maize preparations in Mexico). Because farmers are not homogenous even within a single community, they may plant different populations, which create a landscape in which numerous maize populations coexist (Bellon and Brush, 1994; Louette et al., 1997; Perales et al., 2003a). These farmers usually own several small plots scattered throughout an area and cannot prevent the exchange of pollen between populations (Bellon and Brush, 1994). This practice creates an environment that is conducive for pollen flow among different maize populations.

Seed recycling

Saving seed from one season to the next (also known as seed recycling) is an almost universal practice among small-scale Mexican farmers. Farmers usually follow strict procedures to select seed to retain for the next

season (Anderson, 1947; Wellhausen et al., 1952). Farmers save seed not only of landraces, but also of hybrids, a practice that is much more prevalent than generally believed (Morris et al., 1999).

Seed selection has important genetic implications. It defines which individuals pass their genes to the next generation and hence their traits and alleles, thereby affecting the genetic structure of the population. Because seed is selected in the household and not in the field, farm families exert direct selection pressure on ear characteristics but only indirect pressure on related plant characteristics such as plant height, which are rarely taken into account (Louette and Smale, 2000; Smale et al., 1999). At least from the farmer's perspective, seed selection may also be fundamental to maintaining the integrity of a landrace, which can be lost easily through hybridization (Bellon and Brush, 1994; Louette et al., 1997).

Seed flows

Besides maintaining seed from their own stocks, Mexican farmers commonly acquire seed from other farmers or sources within or outside the community. For example, *Zapalote chico*, a tropical maize race found at sea level, has been introduced from the Isthmus of Tehuantepec into communities of the Central Valleys of Oaxaca, 200 km away and at 1,800 masl (meters above sea level). Seed flow among farmers may account for almost half of all seed planted (Louette et al., 1997).

There are several reasons for seed flows. Farmers lose seed to pests, diseases, drought, frost, and other problems. Farmers also like to experiment and will plant small quantities of foreign seed to assess performance under various conditions and management. They may also plant small areas because of socioeconomic constraints or because they want to harvest only a small amount of a particular landrace. If those crops fail, farmers easily find themselves without seed (Aguirre Gómez, 1999; Louette et al., 1997). Seed flows are also encouraged by the common belief that seed must be changed regularly to maintain productivity, enabling farmers to “sow the same maize type but from new seed” (Louette et al., 1997: 31–32). As Louette et al. report, seed renewal is quite variable in time and quantity.

Seed flows are important for understanding the dynamics of diversity in a given location because they are the basis for incorporating new populations and obtaining seed of populations that have been lost but are desirable. They may be an important mechanism for the migration of genes (Louette et al., 1997).

Mixing seed of different origins

It is not uncommon for farmers to obtain seed from other farmers or commercial sources to plant alongside their

own, either because they lack sufficient seed or expressly wish to modify a maize population (Aguirre Gómez, 1999; Perales et al., 2003b). Farmers may do this every two to three years, usually to improve a population. The modification may involve combining desirable characteristics of a foreign population with one's own, or it may be done to counter the loss of vigor in a population. Because of inbreeding, a population starts to express deleterious mutations after being planted for many consecutive seasons. Many farmers say that the seed "gets tired" ("*se cansa*") and that they must add seed from a foreign population to it. For example, when landraces collected in the Central Valleys of Oaxaca were self-pollinated,⁷ a high frequency of deleterious mutations was detected. An influx of foreign genes may enhance heterozygosity and prevent such mutations from being expressed, a phenomenon that has been called "genetic rescue" (Keller and Waller, 2002).

Creolization

Strictly speaking, the adoption of improved maize varieties⁸ has been limited in Mexico, but there is increasing evidence that through their breeding practices small-scale subsistence farmers have incorporated improved varieties into their farming systems. By exposing improved varieties to their conditions and management, continually selecting seed of these varieties for replanting, and in some cases promoting their

hybridization with landraces either by design or accident, farmers produce "creolized" varieties (Bellon and Risopoulous, 2001). Creolized varieties are appreciated because they combine the advantages of improved varieties and landraces.

It should be pointed out, however, that the process of creolization is not restricted to improved varieties, but also is applied to "foreign" maize populations that are of interest to farmers, including landraces from other regions. After a few planting seasons – sometimes as few as two – the "foreign" maize population that has proven successful under local farmers' conditions may be referred to as a "criollo" or local landrace. There are cases, for example, where farmers refer to populations they grow as "Hibrido Blanco" or "Hibrido Criollo" (white hybrid or local hybrid), which are considered as local landraces though farmers may recognize as well that originally these maize populations were introduced as improved varieties.

Table 1 illustrates the practices and management conditions of Mexican farmers that are conducive to gene flow. These practices help to explain why maize diversity in farmers' fields is not static but dynamic. Gene flow and farmer selection are the basis of this diversity, and gene flow may counter endogamy in maize populations planted over small areas. Gene flow can occur over long distances with very diverse materials, and even though some may not be appropriate for environments where they are introduced, they may constitute a source of new alleles for local populations.

Table 1. Examples of farmers' practices and management conditions.

	Vicente Guerrero, Chiapas ^a	Central Valleys, Oaxaca ^a	Southeastern, Guanajuato ^a	Coast of Oaxaca, ^b	La Frailesca, Chiapas ^b
Year	1997	1997	1996	2001	2001
Number of households	98	240	160	163	162
Number of communities	1	6	21	6	6
Varieties/household					
Average	2.4	1.5	2.0	1.3	1.5
Min–max	1–5	1–5	1–4	1–3	1–5
Fields/household					
Average	2.6	3.4	2.2	1.1	2
Min–max	1–7	1–9	1–6	1–3	1–5
Field size (ha)					
Average	3.4	0.92	4.22	2.2	3.1
Min–max	0.05–13	0.062–6	0.5–26	0.25–16	0.01–20
Households who recycled seed (%)	92.9	96.3	nd	65.6	43.5
Households who mixed seed (%)	7.1	30.4	49.3	6.7	5.0
Households who planted seed from outside (%)	43.9	19.6	39.8	35.0	56.5
Households who gave seed to others (%)	36.7	37.5	nd	29.4	12.4
Same community (of those who gave seed)	50.0	97.8	nd	91.7	85.0
Outside community (of those who gave seed)	61.1	13.3	nd	8.3	15.0

Sources: ^aBellon and Berthaud (2002).

^bCIMMYT Unpublished data.

nd=no data.

The genetics of farmers' management of local maize populations and their implications for transgene dynamics

By recycling seed, farmers give their maize populations a long life that extends over many generations and has specific genetic consequences, especially for the presence of transgenes in local maize populations. At the same time, there are opportunities for genes to migrate between populations. When a migrant reaches a new population, it will introduce new alleles, and through recombination,⁹ these new alleles will be incorporated into new genetic backgrounds.¹⁰

Recombination

In long-lived populations, recombination plays a role in each generation. Through recombination, genes belonging to a specific variety can migrate into a new genetic background – that of the local population. In addition, when several (exotic) varieties are successively introduced, genes from these varieties may also be established in a new genetic background – that of the local population and even in the same plant.

Linked genes may eventually break their linkage.¹¹ The frequency with which such linkages are broken depends on the strength of the linkage and the number of generations involved. If a trait requires the expression of several linked genes, its expression may disappear after the genes are introduced into a local population because its elements (the alleles of the genes) will not remain together in all of the plants in a population.

Drift, migration, and selection

According to population genetics theory and case studies (in sunflower, for example, see Whitton et al. 1997), when a selectively neutral gene is introduced into a population, it will remain in the population at the same frequency as when it was first introduced. Two forces can cause its frequency to vary from generation to generation: genetic drift (chance effects due to small population size and the randomness of meiotic segregation) and migration. Drift generally applies only to small populations and is independent of selection. Migration among populations (“gene flow”) will tend to homogenize their allele frequencies. A study in sunflower showed that a large proportion (31%–38%) of alleles from the cultivated varieties was introduced into adjacent wild populations over several years of gene flow (Linder et al., 1998). When genes are not neutral – in other words, when they have a positive or negative selective effect – selection will drive changes in the frequencies of these genes. The more favorable the gene (allele), the more rapid its frequency increases in a population. The

importance of human selection – not just natural selection – in the process of crop evolution should be emphasized

Transgenes in local populations

If transgenic varieties are introduced commercially into these systems, it is likely that they will be managed like the local maize populations and that creolization will take place. Genes will be exchanged between transgenic varieties and local landraces through pollen flow between plants as well as by mixing seeds at several steps in the cropping process.

Transgenes should behave like any other genes, subject to the genetic rules that operate in these long-lived populations. Drift, migration, selection, and recombination will play their roles. Transgenes can enter local populations in the agroecosystem in multiple ways. Several transgenes can reach the same population and be present in the same plant. This process is known as “gene stacking.” Gene stacking has been observed in canola in Canada, where three herbicide resistance genes from three different varieties cultivated for several years on the same farm accumulated in the same plant (Hall et al., 2000). Gene stacking may occur much more easily and widely as increasing numbers of transgenes are released over time.

In the very near future, transgenic traits could result from the expression of several linked transgenes acting simultaneously in the same plant. As noted, through recombination, these linkages could break. The different genes could become independent, and local populations could carry transgenes without expressing transgenic traits. The expression of a gene depends on the genetic background in which it exists. Transgenes expressed in one genetic background may have their expression modified and even silenced in another background (Fagard and Vaucheret, 2000). The genetic backgrounds of transgenic varieties and local maize populations may be very different, so traditional Mexican maize farming systems may have local transgenic populations in which transgenes are expressed to a greater or lesser extent, or not at all.

Potential impacts of transgenes on maize diversity

The presence of transgenes in Mexico, the extent of their presence, and the mechanisms by which they may have entered into some maize landraces are still debated. Regardless of the results of this debate, probably a more significant issue is the likely impact of transgenes on maize diversity if transgenic varieties were introduced at a commercial scale. Without trying to be exhaustive, we examined three potential models of the diffusion of transgenes and their implications for a potentially

deleterious impact on maize diversity: (1) the invasive species model, (2) the gene flow model, and (3) the human values-perception model. These models incorporate the special characteristics of Mexico's traditional agricultural systems. The first two models are grounded on biological phenomena, while the third is based on human values and perceptions.

The invasive species model

Throughout history people have introduced (accidentally in some cases, deliberately in others) many foreign organisms into "new" ecosystems, in numerous cases leading to the extinction of native wild species and consequently a loss of diversity (Sakaj et al., 2001). In Mexico's traditional agricultural systems, transgenic varieties can be seen as invaders that will displace and eventually eliminate local landraces, leading to a loss of biological and genetic diversity. This view is similar to the conventional model of crop genetic erosion, in which farmers increasingly specialize and replace diverse sets of landraces with a few high-yielding modern varieties that provide them with higher incomes. While there is no question that this process has occurred in many parts of the world, particularly the industrialized world and more commercial agricultural areas of the developing world, it has been far from universal.

In certain regions of Mexico, maize landraces are being lost to modern varieties, especially hybrids, and some races are difficult to find (Sanchez et al., 2000). Throughout Mexico, however, modern varieties account for only 20% of the area planted to maize, despite the availability of modern varieties for the last 40 years (Morris and Lopez-Pereira, 1999). To plant 80% of Mexico's maize area, farmers still rely on their own seed or that of their family, neighbors, or friends. Maize is still subject to the traditional management practices and conditions described above. In these systems, improved varieties have not completely displaced local landraces. Instead, as we have observed, improved varieties have been and continue to be planted alongside landraces (Bellon and Risopoulos, 2001). Once they are incorporated into the system, farmers manage them like their local landraces and creolization occurs. This process favors the diffusion of genes from new varieties into local landraces rather than the complete substitution of one by the other.

For this model to be valid, the introduced transgenic varieties would have to be greatly superior to the local landraces in terms of the many traits that farmers value, convincing farmers to abandon their landraces – something that has not occurred with non-transgenic improved varieties. Transgenic varieties would have to be widely available to small-scale farmers through a seed distribution system able to provide large quantities of

seed. These farmers, who are usually relatively poor, would have to be willing to pay premium prices for seed of these varieties. These conditions are very unlikely to occur in the near future, and the analogy between the introduction of transgenic varieties and an invasive species is not appropriate. The invasive species model would be valid for the introduction of a foreign organism into the wild and subject mainly to natural selection. However, transgenes are not organisms, they are genes, and agricultural systems are not wild, they are human-driven systems in which human selection plays a more important role than natural selection. It is much more likely that the incorporation of transgenic varieties in traditional agricultural systems would lead to their creolization as well as the diffusion of transgenes into other local maize populations. What would be the consequences of this gene flow between transgenic varieties and local landraces?

The gene flow model

To evaluate how gene flow from transgenic varieties might affect the diversity of local landraces, it is useful to distinguish between (1) the introduction of a modern (transgenic) variety and (2) the introduction of a transgene (made possible by the introduction of a transgenic variety) into a traditional agricultural system.

Introducing a new variety

In Mexico's traditional systems, farmers maintain local landraces and creolized varieties at the same time, and since farmers may also continue to introduce improved varieties into their agroecosystems, these three types of maize may coexist. For example, in 2001 in six communities of the Frailesca region of Chiapas, a commercial maize production area with a long history of introduction and use of improved germplasm, only 24.8% of the area was planted to hybrids, while the rest was planted to recycled seed of either improved varieties (53.2%) or landraces (22%) (Bellon et al., 2003b). A collection of 53 maize samples from the region showed that 54.7% were landraces with no discernable influence of improved characteristics in them.¹² If transgenic varieties were introduced into these systems, after a few generations under farmers' management, they would probably become creolized transgenic varieties. Based on what we know about creolized varieties, the most likely scenario is that creolized transgenic and non-transgenic varieties will coexist with landraces, as the latter currently do. The impacts of transgenic varieties on diversity, therefore, may not differ from what we have observed with the incorporation of non-transgenic improved varieties into these systems.

It is possible, however, to envision at least two scenarios in which improved varieties (transgenic or not)

may affect the genetic diversity of local landraces. The first situation would occur when a continuous, large inflow of seed of modern varieties causes a large area to be planted to these varieties season after season and only a small area to be sown to local landraces. The large, continuous flow of genes from the improved varieties to the local landraces would swamp the local maize populations. This process has been observed in nature when a locally rare species loses its genetic integrity and becomes assimilated into a common species following repeated rounds of hybridization and introgression (Ellstrand et al., 1999). Although this process may have occurred where landraces were almost entirely displaced by improved varieties in commercial farming areas, the evidence to date suggests that, even in areas where improved maize has been widely planted for a long time, as long as the management practices we described earlier are present, the maize populations have not become a large, undifferentiated, “creolized” or “improved” maize population. Instead we see multiple populations, some of them improved varieties, others creolized, and still others landraces.

The second situation would occur if hybridization between the introduced transgenic varieties and local landraces leads to outbreeding depression, in which progenies of these hybridizations are very inferior to their parents. Outbreeding depression occurs when the progenitors are very different genetically. This phenomenon has been frequently observed for hybridization between species (Ellstrand et al., 1999), but is not very common within species.

Introducing a new gene (or several new genes)

Through a few crosses between a transgenic variety and local landraces, the transgene will diffuse from the former to the latter. In the diffusion process, the transgene, like any other gene, will behave independently of the other genes of the transgenic varieties. The dynamics of transgene diffusion will depend on two factors: the rate of selection and the rate of migration. In turn, these rates are regulated not only by natural factors but by human management. Depending on whether the transgene is expressed, and, if it is expressed, whether farmers perceive its phenotypic expression as beneficial, deleterious, or neutral, their actions may foster or hinder its diffusion.

The natural and human factors that control the diffusion and presence of a transgene may act antagonistically, making it difficult to foresee how rapidly the transgene might diffuse and how widespread it might be within local populations. But some situations can be foreseen which are rarely considered in risk assessment and management. One is that the transgene may cause the population with the transgene to have higher fitness – not

only in terms of natural factors, but also in terms of human preferences (for example, a Bt transgene might improve insect resistance). Farmers realizing the value of the transgene will favor its diffusion to the landraces that they value by mixing seed of the transgenic variety with seed from their landraces. The advantage a transgene confers, however, is likely to be only one among many other factors that farmers appreciate. Rather than having less diversity, this process may result in the same amount of diversity as before, in terms of alleles and phenotypes, but with a transgenic component. A portion of the diversity present may be transgenic, but all the morphological variants and diverse alleles present before will still be there. An alternative possibility is that the introduction of a transgene into landraces could confer some new perceived advantage and farmers decide to plant the first transgenic landraces available without bothering to go through the process of diffusion and creolization, hence leading to the abandonment of their other landraces. This would lead to some loss of diversity.

In the future, if varieties with new and different transgenes make their way into farmers’ fields (e.g., Maier, 2002), gene flow and recombination could cause the same plants to harbor transgenes that were never intended to be together and act simultaneously. Another possibility is that varieties are designed and produced with several transgenes, which may or may not be linked (e.g., Tran et al., 2003). The introduction of these varieties into these systems may lead to the diffusion of multiple transgenes. Links between transgenes may be broken by recombination during diffusion. Whether the transgenes were linked or not, however, they would diffuse independently, according to their own dynamics. In most cases, these transgenes would not express a trait (as parts may be missing) and would remain unnoticed, but in other cases they would express it. The expression of a gene depends on the genetic background in which it exists, which in the case of transgenic varieties and local maize populations may be very different. The new genetic material in farmers’ populations may include the following: (1) active genes which may be expressed to a greater or lesser extent or not at all depending on their interaction with the new backgrounds in which they may be incorporated; (2) inactive genes; and (3) pieces of genes, which can remain in these populations in a stable manner. While the probability of these events may be small, it is unknown and merits further research.

This model would probably operate if transgenic varieties were available in Mexico at the same level as other improved maize varieties. Commercial areas where transgenic varieties are available may be a sufficient prerequisite for these varieties and their transgenes to diffuse to other agroecosystems. Small-scale farmers may not have to buy transgenic varieties directly but still have

access to seed from them, particularly through the same informal seed systems that they use to obtain seed of non-transgenic improved varieties.

The human values-perception model

If transgenes diffuse to landraces, and society (or groups in society) regard transgenes as “bad” and the landraces as “contaminated,” then regardless of whether the transgenes affect diversity, this value judgment will have a negative impact on landraces and their diversity.

The perceived value of landraces with transgenes would diminish. Since distinguishing between landraces with and without transgenes may be difficult and costly, all landraces may be considered “contaminated” (guilty by association). In that case, all landraces and their diversity may be devalued. The careless use of the term “contamination,” particularly if there is no evidence of harmful consequences associated with the presence of transgenes, can actually contribute to genetic erosion.

The perception that landraces are contaminated by transgenes may be triggered in three situations. Landraces may be considered contaminated simply because people (accurately or inaccurately) think they contain transgenes, regardless of what the specific transgenes may be or whether they express a trait. Second, landraces may be considered contaminated if unwanted transgenes are present – not because they are transgenes per se, but because they have not been approved to reach farmers’ fields or because they have traits that could be hazardous in the food chain, such as antibodies, specific fatty acids, or vaccines. Third, landraces may be considered contaminated if the same plants or populations in farmers’ fields have (or are perceived to have) combinations of transgenes that have not been subject to biosafety assessments because they have accumulated from varieties of many different origins. It is difficult to imagine how to eliminate all of this accumulated genetic material without eliminating the landraces themselves. This last situation could be particularly detrimental to landraces, which may end up being perceived as a sort of genetic junkyard, regardless of whether they actually have multiple transgenes or whether these transgenes are expressed.

There are also perception models that look at the introgression of transgenes into landraces as positive. One positive view is that the introgression of transgenes into landraces may increase rather than decrease diversity, since a new gene or genes (the transgenes) would be incorporated into the maize genome, hence introgression could be actually “good” for diversity. Clearly, this view is simplistic, because the positive or negative value for diversity of the incorporation of transgenes into landraces would depend, as argued in the previous models,

on the expression or lack of expression of the transgene, the interaction of the transgene with the new genetic background of the landraces where it introgresses, and the interaction of the novel trait that the transgene codes for if expressed with the environment. From a traditional farmer perspective it is also possible to envision a positive view on the introgression if a transgene codes for a trait that is perceived to be useful, so that traditional farmers may foster its diffusion. This is not farfetched at all, as the press recently reported that cotton farmers in Gujarat, India, are cross-fertilizing transgenic cotton with local cotton varieties that are perceived as more suited to the local climate to generate their own version of transgenic cotton (Gosh, 2003), a form of creolization.

Discussion

By developing the models presented above, we hope to contribute to a more focused discussion of the potential impacts of transgenes on diversity in traditional farming systems in a center of crop diversity and domestication.

It is unlikely that the introduction of transgenes, just because they are transgenes, will automatically reduce the diversity of alleles in local maize populations or the morphological variants managed by small-scale farmers in Mexico if the management practices and conditions prevalent in these systems are maintained. Most likely, any negative impacts on diversity probably will be related more to perceptions and values about transgenes than to any biological impact they may have. Our analysis suggests, however, that the processes that maintain diversity in traditional agricultural systems – gene flow and farmer selection – may not only foster the diffusion of transgenes to other maize populations, but may create situations that have never been considered in the biosafety risk assessment and management protocols that regulate transgenic varieties in industrialized countries. We may see new combinations of transgenes that have never been tested, and we may also see the separation of transgenes that are meant to work in combination. The processes that create diversity may also create a great degree of uncertainty about the impacts of transgenes once they are in farmers’ fields and populations. Diversity can evolve in many different ways.

Given this uncertainty, if transgenic varieties are introduced on a large scale into Mexico – particularly if they include multiple transgenes or transgenes that are not meant to enter the food chain, such as antibodies, fatty acids, or vaccines – procedures must be in place to insure reversibility (i.e., the ability to return to the previous state, in which local maize populations exist without transgenes). Reversibility is an important consideration in the pharmaceutical industry. Drugs are subject to rigorous testing and clinical trials over a long

period, but they may present unexpected detrimental effects once they are on the market and used more widely. If negative effects are detected, it is possible to recall the drug and contain its negative impact. With respect to transgenic maize, one example of reversibility has already occurred with the commercial variety Starlink in the United States. This variety contains the *Cry9C* transgene that was approved only for animal feed, but was introduced into the human food chain (Anonymous, 2003). All maize produced from this variety was recalled to eliminate it from the human food chain. The recall was successful but expensive. Clearly, under the regulatory framework and the agricultural and agro-industrial conditions of the U.S., reversibility is possible.

Unfortunately we know very little about our ability to manage the dynamics of transgenes once they enter Mexican traditional agricultural systems and hence about how to establish a reversible system. It may not be feasible to contain the spread of transgenes in a system based on practices that foster the free flow of genes, particularly when this flow is a key component of the diversity observed in farmers' fields. Under these conditions, a reversible system may require interventions in the local seed systems farmers rely on to access landrace seed, as well as more information for, and education of, farmers with respect to transgenic and non-transgenic varieties.

Clearly, vigorous research is needed to develop a system to monitor and understand the choices that must be made if transgenes are to be introduced on a large scale in Mexico. The research issues identified here are (1) an assessment of the rates of diffusion of transgenes, including their determinants and particularly the fitness conferred by traits coded by transgenes under the conditions of traditional systems; (2) the expression of transgenes in the genetic backgrounds of landraces; and (3) estimating the probabilities that gene stacking may occur and be expressed in landraces if varieties with multiple transgenes are introduced. Such research must draw on expertise from different disciplines to understand how farmers' behavior and management interact with biological processes. Many of the issues raised here may be relevant not only for Mexico, but also to other agricultural systems throughout the world where small-scale farmers have similar management practices.

Concern over the diffusion of transgenes into landraces has highlighted the importance of Mexico as a center of maize diversity, the role that small-scale farmers play in maintaining it, and the threats to this diversity. Mexico is a center of diversity because small-scale farmers continue to plant (and, one could argue, create and maintain) multiple, distinct maize populations. Their interests and practices sustain maize diversity. If farmers are not interested in maize production or abandon their traditional management practices, maize diversity as we

know it will disappear. The processes that threaten diversity, therefore, are more complex than the "simple" replacement of landraces by modern varieties, and they go beyond the potential impacts of transgenes in local agroecosystems. These processes include the abandonment of maize cultivation altogether as farmers migrate or shift to other crops, the aging of the farming population, and the lack of interest in agriculture among young people, particularly if they are better educated. Rather than growing maize for profit, many farmers grow it to ensure household food security, as part of an economic safety net, and/or to obtain appreciated varieties that cannot easily be bought in the market. Farmers' ability to grow a diversity of landraces may diminish due to the increasing direct and indirect costs of obtaining seed (Bellon, 2004), although studies have shown that there are ways to support their efforts (Bellon et al., 2003a; Chávez-Servia et al., 2002; Milpa Project, 1999; Smith et al., 2001). If society values this diversity and is committed to its conservation – as the great concern over the impact of transgenes on maize diversity suggests – it should be willing to invest in supporting small-scale farmers' efforts to maintain it.

Another question that our analysis raises is how the owners of the transgenes may react to diffusion they cannot control. The companies that develop transgenes invest considerably in their development. They want to control and profit from their use. Under the management practices of Mexican farmers, transgenes may diffuse in a way that may be difficult for anybody to control. Would transgenes – which can be patented under the current Mexican Law of Industrial Property – make some of farmers' traditional practices that are allowed under the current Mexican Federal Law for the Protection of Plant Varieties (based on UPOV 1978) such as seed recycling, mixing, and creolization, illegal? The interaction and precedence between these two laws would determine the legality or illegality of farmers' traditional practices in relation to transgenic maize varieties.¹³

Conclusions

An analysis of the potential for the diffusion of transgenes and their likely impacts on maize diversity has to take into account farmers' behavior and practices and cannot be cast only in biological terms. It is unlikely that the cultivation of transgenic varieties may lead to a loss of maize diversity if the management practices and conditions prevalent in traditional agricultural systems are maintained, but it may also lead to situations that have not been considered in the industrialized world. Society's negative perceptions of transgenes, however, may have deleterious impacts on landrace diversity. Research is needed to develop a system to monitor and

understand the choices that must be made if transgenes are to be introduced on a commercial scale in Mexico.

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Notes

1. The views expressed in this publication are the sole responsibility of the authors and do not necessarily reflect views or policies of the institutions with which the authors are affiliated.
2. Throughout this paper we refer to different types of maize populations. We use the term “maize population” as a generic term for any group of plants under management by breeders or farmers (similar to the concept of population in population genetics). “Landrace” refers to a locally grown maize population that has been the result of farmer selection and management over many generations. An “improved variety” is a maize population that has been scientifically bred and conforms to the International Union for the Protection of New Varieties of Plants (UPOV) criteria of being distinct, uniform, and stable. Improved maize varieties may be hybrids or open-pollinated improved varieties. A “creolized” variety is an improved variety that has been under farmer management for several generations.
3. By “traditional” we do not mean that farmers in these systems do not change or innovate (they do); we mean that they maintain the traditional germplasm management practices described here.
4. A gene is a DNA sequence, coding for a protein which can interact in a biochemical pathway or control the expression of other genes. Genes are assembled along chromosomes. The number of chromosomes is fixed in a species. Each individual receives a set of chromosomes from each parent during fertilization. Alleles are different versions of a gene. In each individual plant, there are two alleles for each gene, transmitted by the male and female parent. In many cases, the expression of a trait requires the coordinated expression of several genes. The genotype is the set of genes (and their various alleles) of a plant. The phenotype of a plant is what we observe – its visible characteristics. The phenotype is the result of the expression of the genes modulated by the interaction with the external environment.
5. These traits include culinary characteristics, which depend on the specific use of the maize in food preparations; fodder production and quality; characteristics of the husk, which may also be used for special food preparations; and ease of dehusking and shelling, important traits when these actions have to be done manually.
6. It is difficult to know exactly how many farmers follow the practices that characterize traditional agricultural systems in Mexico. It is estimated that there are between 2.5 and 3 million maize producers (De Janvry et al., 1997; Nadal, 2000). Approximately 50% produce maize exclusively for domestic use (Nadal, 2000). The remainder grows maize for domestic use and sells any surplus or produces maize only for sale (a minority). Hence an estimate of about two million producers is realistic. The area planted with saved seed in Mexico is approximately 80% (Morris and Lopez-Pereira, 1999), assuming that this area stays more or less constant. Approximately 7.3 million hectares were planted to maize during the rainy season of 2002 (SAGARPA, 2003), suggesting that an area of roughly 5.8 million hectares was planted to farmer-saved seed.
7. Maize is an open-pollinated species, which means that when maize plants reproduce, the pollen that fertilizes a given seed most likely comes from a different plant. Naturally the fraction of pollen that fertilizes a seed from the same plant is very small. For experimental purposes, one can manipulate the pollination process so that this fraction reaches or comes close to 100%. This allows the expression of deleterious mutations that may be present in the genome but “hidden” from being expressed because of heterozygosity (the presence of two different alleles – or versions of a gene – in one locus).
8. There are two types of improved maize varieties: hybrids and open-pollinated varieties (OPVs). For simplicity a hybrid can be defined as the result of the combination of two inbred lines, while improved OPVs are populations that have been subject to selection by breeders for a very specific set of traits. If seed from a hybrid is replanted it will not be as productive as the original seed. Therefore, seed has to be purchased every season to maintain high productivity. On the other hand, seed from an OPV can be replanted without major drops in yield usually up to three years; hence, seed can be purchased once every three years. In terms of creolization, farmers do not distinguish between the two types of improved varieties for this process.
9. Recombination is the process by which alleles are exchanged between homologous chromosomes during sexual reproduction. Recombination creates new combinations of alleles at different loci along the chromosome.
10. The genome of a plant comprises tens of thousands of genes. The “genetic background” refers to all of the genes in the recipient plant. When an allele or a gene is moved from one plant to another through crossing and selection, the expression of the allele or gene that has moved can be modified considerably through interaction with these genes.
11. Linkage refers to the probability that alleles of two genes, located closely on a chromosome, pass together to the next generation. Independent genes are genes situated on different chromosomes or far enough apart on the same chromosome to enable their alleles to be inherited independently (linkage=0).

12. This is based on a racial characterization made by Dr. Juan Manuel Hernández Casillas, an expert maize taxonomist and head of the INIFAP gene bank using the criteria for this racial characterization from Wellhausen et al., (1952) (CIMMYT unpublished data).
13. As signatory of the Cartagena Protocol on Biosafety, Mexico has drafted a Biosafety Law for Genetically Modified Organisms, currently being discussed in the Mexican Congress. This law once approved will also have a bearing on the legality or illegality of farmers' traditional practices in relation to transgenic maize varieties.

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Address for correspondence: Mauricio R. Bellon, IPGRI, Via dei Tre Denari 472/a, 00057 Maccarese, Rome, Italy
Phone: +39-0661181; Fax: +39-0661979661;
E-mail: m.bellon@cgiar.org