Transgenic Maize and the Evolution of Landrace Diversity in Mexico. The Importance of Farmers' Behavior[1]

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The discovery of transgenic products in maize (*Zea mays*) landraces planted by small-scale Mexican farmers (Quist and Chapela, 2001, 2002; Christou, 2002; Editorial Note, 2002) raised questions about how the commercial introduction of transgenic maize varieties might affect the traditional agricultural systems of small-scale farmers. A key concern is whether their introduction will have a deleterious effect on the diversity of maize landraces that these farmers maintain.

Mexican agriculture, including maize production, has a bimodal structure (Bailey and Roberts, 1983; Nadal, 2000). On the one hand, a large number of small-scale farmers in rain-fed areas grow maize mainly for domestic consumption, though they may occasionally sell some surplus. On the other hand, a relatively small number of commercially oriented farmers practice large-scale maize production, mainly in irrigated areas, and their objectives and technological needs resemble those of their counterparts in the industrialized world. These large-scale farmers are the logical market for commercial transgenic maize varieties. Although small-scale farmers, who rarely purchase commercial seed, are an unlikely market for transgenic varieties, the introduction of transgenic maize varieties may nevertheless have important consequences for them. In this paper, we identify some of those consequences and explore their implications. Specifically, we examine how transgenes may diffuse in traditional agricultural systems, describe the mechanisms that encourage their diffusion, and discuss the implications for the loss of maize diversity and for biosafety risk assessment. Finally, we indicate how the issues surrounding the diffusion of transgenic varieties in Mexico's traditional systems may prove relevant in other countries and crop species.

An important concern in assessing the risk of growing a genetically modified crop in its center of domestication (i.e. where its wild relatives are present) is gene flow between the transgenic crop and its wild relatives. Even though data on this subject are limited, the potential impact of such gene flow has been under discussion for some time (Serratos et al., 1997; Blancas et al., 2002; Gepts and Papa, 2003). In this paper, we will focus on the less-explored issue of maize-to-maize gene flow, which plays an important role in the evolution of maize populations in Mexico (Louette et al., 1997; Perales et al., 2003a, 2003b) and other countries, such as Burkina Faso (Sanou et al., 1997).

TRADITIONAL AGRICULTURAL SYSTEMS AND MAIZE DIVERSITY

As a center of maize domestication and diversity (Sanchez et al., 2000; Piperno and Flannery, 2001; Matsuoka et al., 2002), Mexico can be considered one of the last reservoirs of maize genetic resources for humanity. About 6,000 years ago within the boundaries of present-day Mexico, farmers domesticated maize (Piperno and Flannery, 2001). Through constant divergent selection, they diversified the crop into many landraces (Fig. 1) and populations that met their cultural and agronomic needs (Hernandez, 1985; Pressoir and Berthaud, 2004). This diversity persists in today's traditional agricultural systems, which involve approximately 2 million households and cover around 6 million ha every year (Nadal, 2000).

In these systems, multiple maize populations coexist (Bellon and Brush, 1994). Most seed is saved from the previous harvest (Morris and López-Pereira, 1997), although some seed may also be acquired from other farmers or even commercial sources (Louette et al., 1997; Louette and Smale, 2000). Farmers may mix seed from different sources if they lack sufficient seed or if they wish to experiment with or expressly modify a maize population (Aguirre, 1999; Perales et al., 2003a). Farmers may incorporate improved varieties and expose them to their conditions and management, fostering their local adaptation, a process known as "creolization" (Bellon and Risopoulos, 2001). New alleles are introduced and, through recombination, incorporated into new genetic backgrounds. These practices and conditions are conducive to gene flow and the development of maize

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Figure 1. Mexican farmers have been growing commercial maize varieties (left) and landraces (right) side by side for more than 50 years. The farmers commonly incorporate genes from commercial varieties into their landraces, but this has not caused the disappearance of the landraces. Thus, farmer behavior needs to be taken into account when evaluating the effect of introducing transgenic maize into a traditional agricultural system that depends on landraces. Photo by CIMMYT.

populations with a long life that extends over many generations (Louette et al., 1997).

If transgenic varieties are introduced into these traditional systems, it is likely that they will be managed like local maize populations. Genes will be exchanged between transgenic varieties and local landraces through pollen flow between plants and by mixing seeds at several steps in the cropping process. This context departs strongly, in genetic and social terms, from the commercial setting for which transgenic varieties were developed and are marketed.

THE DYNAMICS OF TRANSGENES IN TRADITIONAL AGRICULTURAL SYSTEMS

Non-transgenic modern varieties have not been adopted widely in traditional agricultural systems (Morris and López-Pereira, 1999). If transgenic maize varieties are commercially introduced in Mexico, they probably will be incorporated into traditional systems in the form of creolized varieties. They will coexist with landraces in these systems, just like non-transgenic varieties have done (Bellon and Risopoulos, 2001). Therefore, the impacts of transgenic varieties on diversity may not differ from those observed with the incorporation of non-transgenic improved varieties into traditional systems, which, in most cases, has not led to a dramatic displacement of landraces (Bellon and Brush, 1994; Louette et al., 1997; Bellon et al., 2003a; Perales et al., 2003b).

Theoretically, in traditional systems, a continuous flow of genes from improved varieties to landraces could swamp local maize populations. Evidence to date suggests, however, that multiple populations of improved varieties, creolized varieties, and landraces will coexist, even in areas where improved maize has been widely planted for a long time, as long as traditional management practices persist (Bellon and Brush, 1994; Louette et al., 1997; Bellon et al., 2003; Perales et al., 2003b). Through a few crosses between a transgenic variety and local landraces, the transgene will diffuse into local landraces. Like any gene, the transgene will behave independently of the other genes in the transgenic variety, and its dynamics in local maize populations will depend on rates of selection and migration, which are regulated by natural factors and 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, farmers' actions may foster or hinder its diffusion.

The natural and human factors that control these processes may act antagonistically, making it difficult to foresee precisely how rapidly the transgene might diffuse to local maize populations and how widespread it might become within them. Nevertheless, we can foresee some situations that are rarely considered in risk assessment and management.

For example, the new transgene in the local population may cause the population to be better suited to the prevailing natural factors and human preferences (for example, a *Bacillus thuringiensis* transgene might improve insect resistance). Farmers who recognize the value of the new trait conferred by 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 that the transgene confers, however, is likely be only one among many others that farmers appreciate. Rather than reducing diversity, this process may result in the same amount of diversity as before, in terms of alleles and phenotypes, but with a transgenic component.

If biotechnology companies introduce transgenic varieties with different transgenes that were never meant to be in the same plant (and have not been tested together), gene flow could cause individual plants to harbor multiple transgenes (a phenomenon known as gene stacking; Hall et al., 2000). This even could include transgenes that should not enter the human food chain (a pharmaceutical protein and an enzyme used by the food industry, for example).

Yet another example involves varieties that are designed and produced with several transgenes, which may or may not be linked (Tran et al., 2003). The introduction of these varieties into traditional systems may cause the multiple transgenes to diffuse, although links between transgenes may be broken by recombination during diffusion.

Regardless of whether transgenes are linked, they will diffuse independently into local populations, according to their own dynamics. In most cases, the transgenes would not express a trait (because 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 (Fagard and Vaucheret, 2000), and the genetic backgrounds of transgenic varieties and local maize populations may be very different. The new genetic material in farmers' local populations can include active genes (which will be expressed to a greater or lesser extent, or not at all, depending on how they interact in the new background) and inactive genes and pieces of genes, which can remain in populations in a stable manner.

Although the probability of these events may be small (especially the likelihood that maize populations will absorb multiple transgenes that were never tested together and simultaneously express several traits), it is unknown and merits further research.

Another scenario that differs from commercial agriculture may occur if transgenes diffuse to landraces and society (or groups in society) regard the landraces as "contaminated." Regardless of whether the transgenes affect diversity (see the discussion in the next section), this value judgment will have a negative impact on landrace diversity. Because it may be difficult and costly to distinguish landraces with and without transgenes, all landraces might be considered "contaminated" and, therefore, devalued. Their diversity would be devalued as well. Careless use of the term "contamination," particularly if there is no evidence of harmful consequences associated with the presence of transgenes, would actually contribute to genetic erosion.

LIKELY IMPACTS OF TRANSGENES ON MAIZE DIVERSITY

It is unlikely that the presence of transgenes per se will automatically reduce the diversity of alleles in local maize populations or the morphological variants managed by small-scale farmers in Mexico. As mentioned, negative impacts on diversity are more likely to result from the perceptions and values associated with transgenes than from any biological impact. However, as our analysis suggests, 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 assessments and management protocols used to regulate transgenic varieties in industrialized countries. The processes that create diversity may also generate considerable uncertainty about the impacts of transgenes in farmers' fields and populations. We may see untested new combinations of transgenes, untested, and we may also see the separation of transgenes that are meant to work in combination.

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 (Maier, 2002)—procedures must be in place to ensure reversibility (i.e. the ability to return to the previous state in which local maize populations exist without transgenes).

The case of Starlink maize in the United States (Anonymous, 2003) showed that reversibility is possible under the regulatory framework and the agricultural and agro-industrial conditions of that country. Unfortunately, we know very little about the ability to manage the dynamics of transgenes once they enter traditional Mexican agricultural systems; hence, our knowledge of how to establish a reversible system is limited. How can we contain the spread of transgenes in a system that is based on the free flow of genes, particularly when this flow is a key component of the diversity observed in farmers' fields? Controlling and containing the diffusion and impacts of transgenes in these systems may require us to regulate or even stop the practices that generate or enhance diversity in the first place. It may not even be possible or feasible. Under these conditions, a reversible system may require interventions in the local seed systems that farmers rely upon to access landrace seed. Farmers may need more information and education about transgenic and non-transgenic varieties to understand how they differ from one another and the implications within their systems. Other research issues that need to be addressed include: an assessment of the rates of diffusion of transgenes in traditional systems, including their determinants; an assessment of the suitability of traits expressed by transgenes in traditional systems; the expression of transgenes in the genetic backgrounds of landraces; and an ex ante assessment of the probabilities that gene stacking may occur in landraces.

Diversity also may be threatened by the commercial introduction of transgenic varieties if the intellectual property rights associated with transgenes render some of farmers' traditional practices unacceptable or illegal, at least in principle. As mentioned earlier, these practices, which sustain and create diversity, include seed recycling, seed mixing, and creolization. For example, intellectual property regulations on transgenes may forbid their use by farmers who have not purchased seed of a transgenic variety and signed an agreement with the owners of the transgenes or their agents. Such regulations may be violated by farmers whose traditional practices favor the diffusion of transgenes—even unknowingly—into their populations. Clearly, these issues are beyond the scope of this paper, and farmers' liability would depend on the legislation and regulations applied to transgenes in Mexico, but these concerns merit careful consideration.

OTHER THREATS TO DIVERSITY

The alarm over the diffusion of transgenes into landraces has highlighted the importance of the conservation of maize diversity and concerns over its loss. Mexico is a center of diversity because small-scale farmers continue to plant (and, one could argue, create and maintain) multiple, distinct maize populations. The processes that threaten diversity 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.

If society values the maize diversity in Mexico's traditional agricultural systems 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 small-scale farmers' efforts to maintain that diversity. There are ways to support these efforts (Bellon, 2004), some of which have been tested in Mexico (Milpa Project, 1999; Chávez-Servia et al., 2002; Bellon et al., 2003b).

IMPLICATIONS FOR OTHER AREAS AND CROPS

Although the potential impacts of transgenes on diversity are particularly significant in the Mexican context, many of the issues addressed in this paper can apply to other countries and crop species, especially where farmers save seed and/or rely on other farmers to obtain it. Under these conditions, genetic migration and recombination will influence the genetic structure of crop populations, particularly landraces, regardless of whether they are grown in centers of domestication and/or diversity.

More than one-half of the maize area in non-temperate environments of the developing world was still planted to farmer-saved seed in the late 1990s (Morris, 2002), and maize landraces are grown throughout the world. In Latin America (excluding Argentina) and sub-Saharan Africa (excluding South Africa), about 60% of the maize area was planted to farmer-saved seed. Farmers maintain a great diversity of maize landraces in the Andean region (Brandolini, 1970; Taba, 1995), and even in sub-Saharan Africa, where maize was introduced only 500 years ago, numerous landraces have evolved under farmer management (McCann, 2001). In many of these areas, as in Mexico, commercial agriculture coexists with subsistence agriculture.

Although for most of these areas we lack the rich descriptions and understanding of farmers' practices that we have for Mexico, it is logical to hypothesize that some similar practices may exist. For example, Sanou et al. (1997) have shown that there are landraces in Burkina Faso (not as diverse as those in the Americas but still quite diverse) and that there is gene flow between improved varieties and landraces. Farmers' practices and local conditions (e.g. farmer selection, field type, and soil fertility) have an impact on the genetic structure of their maize populations. These conditions resemble those observed in Mexico's traditional agricultural systems, and it is not unreasonable to suggest that the issues identified in this paper are relevant for traditional maize systems in West Africa.

Although transgenic varieties of maize, soybeans (*Glycine max*), and cotton (*Gossypium hirsutum*) are the most common transgenic varieties currently available to farmers, in the near future they will have access to transgenic versions of other major food crops, including rice (*Oryza sativa*), bread wheat (*Triticum aestivum*), and potatoes (*Solanum tuberosum*). Maize is a cross-pollinating crop, rice and wheat are self-pollinating crops, and potatoes are generally clonally propagated, which means that genetic migration and recombination occur at a much lower rate in rice, wheat, and potatoes than in maize. Even so, many of the issues related to the diffusion of transgenes in local populations may still be quite relevant. Small-scale farmers in many parts of the developing world still plant landraces of rice, wheat, and potatoes, sometimes along with modern varieties. Many of these farmers save seed or planting stocks (e.g. potato tubers) and rely on informal seed systems.

About 29% of the rice area in Asia is still planted to landraces, though this aggregate figure may underestimate the area planted in particular countries (Hossain et al., 2003). Several case studies have shown that landraces and modern varieties coexist in the systems of small-scale farmers in different parts of Asia. These farmers select, save, and exchange seed (Bellon et al., 1997). There is evidence that rice varieties change under farmers' management (Tin et al., 2001). Although rice is a self-pollinating crop, some outcrossing may occur at relatively low rates, depending on the conditions of cultivation. Experiments in which different types of rice or rice and its wild relatives were planted together have shown that rice-rice and rice-wild relative hybrids are present in the progenies at low rates (Chen et al., 2004). In other experiments, gene flow has been found between transgenic and cultivated rice, also at very low rates (Messeguer et al., 2001).

Rice varieties collected in farmers' fields in parts of India and the Philippines have presented a combination of different genotypes (International Rice Research Institute [IRRI], 2000). When such combinations of varieties are present in farmers' fields, crosses (i.e. gene flow) and recombination will produce new genotypes. In Sierra Leone, where some farmers plant mixtures of two varieties belonging to two rice species, *O. sativa* and *Oryza glaberrima*, gene flow and recombination have resulted in natural hybrids between the two species (Jusu, 2000; Longley, 2000).

Given that farmers' practices in some traditional rice systems encourage gene flow between different types of rice, it is very likely that if these farmers plant transgenic rice, some gene flow to other varieties and species can be expected.

The data for wheat are more limited, but there is certainly evidence that landraces and improved varieties coexist in the systems of small-scale farmers in areas with a long history of wheat cultivation and that farmers save and select seed (Meng, 1997). Landraces of durum wheat are thought to be grown on about 40% of the durum wheat (*Triticum turgidum*) area in India and 80% in sub-Saharan Africa (Heisey et al., 2002). Clearly, the fact that landraces are planted points out to a certain reliance on informal seed systems.

Like rice, wheat is a self-pollinating crop. Although the rate of outcrossing is much lower in wheat than in maize (or other cross-pollinating crops), it can be greatly influenced by soil quality and other agroecological conditions (R. Trethowan, personal communication). The rice research described previously suggests that similar processes may occur in wheat, but research has been limited in wheat. Additional studies are needed to gain a better idea of the prospective dynamics of commercial transgenic wheat varieties in traditional systems.

Many of the factors analyzed here may even be relevant for a clonally propagated crop such as potato in traditional agricultural systems in its center of diversity. A study with Andean potatoes using isozymes and phenotypic characteristics showed considerable gene flow between cultivars of different morphological groups (Quiros et al., 1992). This gene flow is possible because traditional Andean farmers rely from time to time on botanical seed propagation to eliminate disease, rejuvenate their planting stocks, and create new cultivars, which leads to outcrossing between populations. Quiros et al. concluded that Andean potatoes form a large and plastic gene pool that is amplified and renewed by outcrossing and, in some cases, by human selection of desirable phenotypes. As in the case of wheat, additional research seems to be warranted, given that genetic migration and recombination may play a role in the evolution of genetic diversity in traditional potato systems.

CONCLUSIONS

The potential impacts of the commercial introduction of transgenic maize in Mexico should not be analyzed in biological terms alone. As we have seen, the analysis must take farmers' behavior and practices into account because they have a considerable influence on how transgenes may diffuse into local maize populations. Although the management practices and other conditions prevailing in Mexican farmers' traditional maize systems are maintained, the cultivation of transgenic varieties is not likely to reduce diversity in those systems. Even so, negative perceptions of transgenes and social and economic changes in traditional agricultural systems may have deleterious impacts on the diversity of maize landraces. The cultivation of transgenic maize varieties in traditional systems may also create situations that have not been considered in the biosafety risk assessments conducted in commercial agricultural systems in the industrialized world. These issues that have emerged for maize in Mexico are likely to be relevant to other countries and food crops, including rice, wheat, and potatoes, and they merit further study.

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