

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

Agriculture, Ecosystems and Environment xxx (2007) xxx–xxx

---

**Agriculture  
Ecosystems &  
Environment**


---

[www.elsevier.com/locate/agee](http://www.elsevier.com/locate/agee)

# Gene flow from transgenic maize to landraces in Mexico: An analysis

Kristin L. Mercer<sup>a,\*</sup>, Joel D. Wainwright<sup>b,1</sup><sup>a</sup> *Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, 300 Aronoff Laboratory, 318 West 12th Avenue, Columbus, OH 43210, United States*<sup>b</sup> *Department of Geography, The Ohio State University, 1169 Derby Hall, Columbus, OH 43210, United States*

Received 15 September 2006; received in revised form 27 April 2007; accepted 14 May 2007

---

## Abstract

A highly publicized study in 2001 reported that maize landraces in Oaxaca, Mexico were found to contain transgenes, yet not all follow-up research has detected transgenes in the same region. Continued testing for transgenes in Mexican maize, and calls for the removal of transgenes from landraces, have only fueled the debate about the dynamics of gene flow from transgenic maize to landraces in Mexico. This paper reviews these recent findings and discusses how evolution may be expected to alter the frequency of transgenes in crop populations over time. Further, it shows that calls for removing transgenes must be interpreted in light of two ecological complexities: (a) it may be impossible to purge a particular gene from a population and (b) scientists' ability to accurately determine the presence or absence of transgenes is limited by challenges related to sampling. The paper concludes by outlining two ways forward for removing transgenes from landraces.

© 2007 Elsevier B.V. All rights reserved.

*Keywords:* Maize; Mexico; Transgenic crops; Center of origin; Introgression

---

## 1. Introduction

The genetic diversity found in landraces (traditional, open-pollinated varieties) of major crops in centers of origin comprises one of the world's most important natural resources for future plant breeding efforts and global food security (Altieri et al., 1987). Conserving crop diversity with and through the very evolutionary processes that generate variability (Brush, 1989; IPGRI, 1993) leaves landraces open to change via gene flow and introgression. With the advent of genetically engineered crops, this openness to genetic change became a cause for concern among some conservationists.

Maize is arguably the world's most important food crop, with global production of ~700 million metric tons in 2005,

10% more than wheat and rice (FAOSTAT, 2006). Mexico, the center of origin of maize and the world's fourth largest maize producer (FAOSTAT, 2006) is home to 59 distinct races (Wellhausen et al., 1952; Sanchez et al., 2000). Landrace maize is still grown on >80% of Mexico's maize acreage (Aquino et al., 2001), largely by poor, indigenous farmers in Mexico's rural South and East (Mann, 2004). Many of these landraces are grown only in particular regions, often under low-input conditions. The cultural practices of Mexican farmers, such as seed sharing, mixing of seed, and farmer selection, influence the evolutionary processes acting on these populations (Bellon and Berthaud, 2006).

In 1996, 2 years after NAFTA led to sharp increases in US maize exports to Mexico, many US maize farmers began shifting to genetically modified (GM) maize, causing concern in Mexico about possible effects on local maize. In 1999, the Government of Mexico introduced a *de facto* moratorium on experimentation with and production of GM maize, but its importation (for consumption, not planting)

\* Corresponding author. Tel.: +1 614 292 8433; fax: +1 614 292 2030.

E-mail addresses: [mercercer.97@osu.edu](mailto:mercercer.97@osu.edu) (K.L. Mercer), [wainwright.11@osu.edu](mailto:wainwright.11@osu.edu) (J.D. Wainwright).<sup>1</sup> Tel.: +1 614 247 8746.

from the USA continued (CEC, 2004; González Aguirre and Aguilar Muñoz, 2006). In response, ~150 non-governmental organizations (or NGOs) called for a complete ban on the importation of GM maize in 2000; that same year, the Government signed the Cartagena Protocol on biosafety that mandates adherence to the precautionary principle while making regulatory decisions (González Aguirre and Aguilar Muñoz, 2006). So when Quist and Chapela (2001) published an article in *Nature* documenting the presence of transgenes in maize landraces in rural Oaxaca, their findings provoked demonstrations and recriminations. Quist and Chapela (2001, p. 542) claimed to find “a high level of gene flow from industrially produced maize towards populations of progenitor landraces”. Their results launched a vigorous debate and spurred several other studies. This paper reviews this body of recent research on transgenes in Mexican maize and their sampling protocols to consider their implications for the conservation of maize landraces. Before turning to the recent studies, a discussion of the dynamics of gene flow and introgression is warranted.

## 2. Transgene introgression in agricultural systems

Transgenes can move among crop populations in two ways: through *seed exchange* and/or *cross-pollination* among adjacent fields. These represent seed-mediated and pollen-mediated gene flow, respectively. Mexican farmers exchange seed to revitalize their populations or initiate new seed lots (Louette et al., 1997; Rice et al., 1998; Bellon and Risopoulos, 2001). They also occasionally plant seed from DICONSA (a Mexican state institution that distributes subsidized grain), which imported some maize from the USA prior to 2003 (SEDESOL, 2003). Transgenic seeds may have been inadvertently introduced by farmers in this way.

Cross-pollination among fields, or pollen-mediated gene flow, also results in the mixing of crop gene pools. Although most maize pollen does not move far (on the order of ~15 m; Louette, 1997), border plants receive pollen from adjacent fields (Ortiz Torres, 1993). Because maize fields in southern Mexico are typically small and irregularly shaped, they have comparatively large edges relative to their area and can be expected to produce hybrid seed resulting from cross-pollination between neighboring varieties. It is difficult to anticipate the degrees to which seed exchange and cross-pollination among fields act as sources of gene flow in a given population since results depend on field size and geography, as well as the local seed exchange practices.

If transgenes are introduced into a population via hybridization or seed-mediated gene flow, transgenes introgression into the landrace population depends primarily on two evolutionary forces: genetic drift and selection. The random process of drift can result in the loss or fixation of transgenes due to sampling effects, especially in smaller populations (Ellstrand and Elam, 1993). On the other hand,

the impact of selection on introgression will depend on how the transgene and other genes linked to it (physically or pleiotropically) influence plant survival, plant health, and pollen and seed production (i.e., lifetime fitness). If the survival, health, or yield of individual transgenic plants is compromised, seeds containing transgenes will be less likely to be selected by the farmer to plant the subsequent year's crop. If the transgene, and genes linked to it, reduce fitness, then transgenes should decline in frequency or be lost. By contrast, if these genes increase fitness, then the frequency of transgenes will increase over time, ultimately leading to adaptive introgression (Whitney et al., 2006). Transgenes encoding herbicide or insect resistance are not expected to increase fitness in the absence of the herbicide or insect pest, but may or may not confer a cost (Bergelson and Purrington, 1996; Snow et al., 1999, 2003). Also, the non-transgenic segments of the genetic background of a transgenic plant may have significant negative effects on fitness since transgenic maize is bred for the agroecological conditions of the US maize belt, which differ from southern Mexico.

## 3. Are there transgenes in Mexican maize landraces?

At least ten studies have been conducted since 2001 to test for the presence of transgenes in Mexico (see Table 1). The first was that of Quist and Chapela (2001), intended to establish a baseline for landrace genetics prior to the arrival of transgenes in rural Oaxaca (Ezcurra et al., 2001). The authors found that approximately 1% of kernels in all four landrace ears collected from two communities contained transgenes (see Table 1), though their small sample size reduces the strength of this conclusion. Although other claims made by the authors, such as the evidence of repeated introductions of transgenes into landrace genomes, were later discredited (Metz and Fütterer, 2002; Kaplinsky et al., 2002; see reply, Quist and Chapela, 2002), the primary claim of transgene presence was not.

These results inspired a string of studies conducted by diverse groups: the Mexican government; CIMMYT; farmers promoted by the ETC Group; ENHRUM; and independent Mexican and US scientists (see Table 1 for all studies and acronyms). These studies have each employed different seed sampling methods, with varying numbers of communities, fields, and ears sampled. Most focused their sampling in Oaxaca, where Quist and Chapela (2001) found transgenes, although the ETC Group and ENHRUM studies sampled in nine and 14 Mexican states, respectively. Only three of the studies have been published in academic journals; preliminary results from one study were published as a conference proceeding; and two were published on the web as reports. Results from most of the government studies are not published (see Table 1).

The available studies found transgenes, when present, at low or undetectable levels. Fully 95% of the 21 landrace maize fields sampled in Oaxaca and Puebla in 2001 by INE

Table 1  
Summary of the results of eight recent studies on the presence of transgenes in Mexican maize

Study author	Year maize collected	Published?	State and number communities sampled	Number landrace samples collected	Findings	Drawbacks
Quist and Chapela (2001)	2000	Yes	Oaxaca, 2	4	All 4 ears from landraces in Oaxaca had transgenic seeds. Transgenes thought to be at an approximate frequency of 0.01	Small sample size. Parts of paper disputed; eventually retracted by Nature
INE/SEMARNAT/CONABIO Ezcurra et al. (2002)	2000, 2001?	Conf	Oaxaca, 19 Puebla, 2	21	Of the 21 landraces populations sampled, 20 had 1–35% transgenic seeds	Possible false negatives. Subsequent unpublished findings show lower levels of transgenes
INIFAP/SAGARPA	?	No	Oaxaca, 12	162	Unknown	Unpublished: findings unknown
CBIOGEM/SAGARPA	2002	No	Oaxaca, 13–27	13–29	Unknown	Unpublished: findings unknown
CIMMYT (2002)	1997–1999	On-line	Germplasm bank and Oaxaca, 152	>300	No transgenic seeds detected at unknown level of precision	Unknown level of precision
ETC Group (2003a,b)	2002, 2003	On-line	9 states, 138	411	Found proteins produced by different herbicide and insect r resistance transgenes. 10–49% of samples were positive. Levels of transgenes within populations may range from 2 to 33%	Unknown level of precision. Results not presented clearly
Ortiz-García et al. (2005a,b,c)	2003, 2004	Yes	Oaxaca, 16	43, 81	No transgenic seeds detected; should have found them if they were at a frequency of 0.01–0.0001 in population	Sampling protocol disputed (see text)
ENHRUM/UNAM/ECOSUR	2002	Conf	14 states, ~84	530	Unknown	Not yet published
UNAM/ECOSUR	2002	No	Oaxaca, 2	30	Unknown	Not yet published
Serratos-Hernández et al., 2007	2003	Yes	Federal District, 4	42	~1% of plants were positive for transgenic proteins; positives found in ~8% of fields	Sampling better for transgene detection than for determining transgene frequency

CBIOGEM: Intersecretarial Commission Biosecurity and Genetically Modified Organisms; CIMMYT: International Center for Maize and Wheat Breeding; CONABIO: National Commission on Biodiversity; ECOSUR: College of the Southern Border; ENHRUM: The National Survey on Rural Mexican Households, College of Mexico; ETC Group: Action Group on Erosion, Technology and Concentration; INE: National Institute of Ecology; INIFAP: National Institute of Forestry and Agricultural Research; SAGARPA: Ministry of Agriculture, Livestock, and Rural Development; SEMARNAT: Ministry of Environment and Natural Resources; UNAM: National Autonomous University of Mexico; On-line: Reported in on-line brief; Conf: Reported at conference.

and SEMARNAT had variable, low levels of transgenes (1–35%; Ezcurra et al., 2001; see Table 1). False positives were possible and subsequent unpublished results appear to indicate lower levels of transgenes. CIMMYT (2002) tested their *ex situ* germplasm bank accessions from Oaxaca. These accessions, collected in 1997 and 1999, were found to be free of detectable levels of transgenes (see Table 1).

In an effort to broaden the geographical reach of the testing and to improve popular involvement in the research, in 2003 and 2004 several NGOs tested maize landraces from nine states using kits by Agdia (a USA-based testing-equipment company). After conducting tests “to determine the presence or absence of five types of proteins that are present in GM organisms”, they found “the presence of endotoxins through the DAS-ELISA technique”, indicating the presence of one of three transgenes in many of the communities sampled (ETC Group, 2003a, p. 4; see Table 1). They identified two insect resistance transgenes (Bt-Cry9C, i.e., ‘Starlink<sup>TM</sup>’, and Bt-Cry-1Ab/1Ac) and one herbicide resis-

tance transgene (CP4 EPSPS, or ‘Roundup ready<sup>TM</sup>’). Unfortunately, details on their methods and results are vague.

Ortiz-García et al. (2005a,b) sampled the Sierra de Juarez region of Oaxaca where Quist and Chapela (2001) found evidence of transgene presence in an effort to produce a more statistically rigorous analysis of the distribution and degree of transgene spread in local landraces. They sampled 4–5 ears from 1 to 5 fields within a total of 18 municipalities in 2003 and 2004, for a total of 153,746 seeds from 870 plants. Half of the ~306 seeds from each ear were sent to one laboratory for genetic analysis, and half went to another. They could not detect transgenes in their maize samples (see Table 1).

In their recent publication, Serratos-Hernández et al. (2007), sampled maize fields in the Mexican Federal District and used the ELISA technique to test for three transgenic proteins. Of the 42 fields sampled, they detected Cry1Ab/Ac in two fields and CP4 EPSPS in one, determining that transgenes were present.

#### 4. Potential for reduction of transgene frequency in landrace populations

In response to their unexpected results, Ortiz-García et al. note that common evolutionary forces – gene flow, drift, and selection – “may have prevented [transgenes] from persisting at detectable frequencies in the sampled seed” (Ortiz-García et al., 2005a, p. 12342). They argue that the amount of transgenic seed entering the region (i.e. gene flow) may have declined for two reasons: first, DICONSA ceased importing grain by 2003 (SEDESOL, 2003); second, increased GM awareness may have led farmers to avoid planting DICONSA seed. Moreover, Ortiz-García et al. (2005a) posit that repeated backcrossing of transgenic plants with non-transgenic plants may have considerably reduced the frequency of transgenes since the sampling by Quist and Chapela (2001). They also suggest that genes at low frequencies can be randomly lost due to genetic drift. Finally, if transgenic plants produce relatively fewer seeds or pollen, selection would act to reduce the frequency of transgenes in the landraces.

How can the different results from the published studies be squared? It is plausible that the variation could be explained by differences in methodology and sampling error. Yet it is also possible that these results could be accurate without contradiction. Between the sampling by Quist and Chapela in 2000 and that of Ortiz-García et al. in 2003 and 2004, a combination of the aforementioned evolutionary processes may have reduced the levels of transgenes to undetectable levels. Such rapid evolution is not unheard of (Reznick and Ghalambor, 2001), particularly where selection and population bottlenecks are extreme. Since the sampling for both studies was confined to one region (not considered a high-risk zone) where transgenic maize would not necessarily be expected (Cleveland et al., 2005), their results do not confirm the absence of transgenes in landraces in other parts of Oaxaca or Mexico. By contrast, the ETC Group may have sampled in higher-risk areas, suggesting that monitoring is needed beyond Oaxaca.

#### 5. Calls for ‘decontamination’

These scientific studies unfolded in the midst of a roiling political debate. The detection by Quist and Chapela (2001) and the ETC Group (2003a) of transgenes in Mexico’s maize landraces evoked strong responses from many farmers and NGOs, who demanded that the Mexican government and international regulatory bodies respond to transgenic ‘contamination’. The CEC was petitioned in 2002 by 21 indigenous groups (supported by more than 90 letters from NGOs) to organize a study on the “impacts of transgene introgression into landraces of maize in Mexico” (CEC, 2004, p. 6). The resulting CEC symposium in Oaxaca, March, 2004, saw hundreds of Oaxacan maize farmers enter the hall to present their demands—including the elimination

of GM maize from Mexico. Concurrently, another group of international NGOs published an open letter demanding the ‘decontamination’ of Mexican maize landraces. They argued that the Mexican government had “permitted the destruction of a resource that is critical for future global food security . . . It is urgent that a process of *decontamination* be undertaken” (ETC Group, 2003b, pp. 1–2, our italics, see also ETC Group, 2003c). Others soon made similar appeals.

In a subsequent paper, Bellon and Berthaud (2004, p. 885) discussed the consequences of full-scale introduction of transgenic maize into Mexico and introduced the concept of the reversibility of transgene introgression:

. . . if transgenic [maize] varieties are introduced on a large scale in Mexico . . . procedures must be in place to ensure reversibility (i.e., the ability to return to the previous state in which the local maize populations exist without transgenes).

In a second publication on the same theme, Bellon and Berthaud (2006) developed this concept further by contrasting the reversibility of transgene introgression to that of a product recall. When a drug is released on the market, for instance, a company may recall it if it is found to be unsafe. Yet, they note, “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” (Bellon and Berthaud, 2006, p. 11; see also Soleri et al., 2006a).

These statements by ETC group, CEC protesters, and Bellon and Berthaud beg the questions: what constitutes ‘decontamination’, and how could it be practiced? ‘Decontamination’ is a strong term, particularly when discussing introgression of novel DNA into a preexisting gene pool. However, breeders have long used ‘contamination’ as a relatively innocuous way to describe the presence of foreign DNA. The term ‘decontamination’ and calls for ‘reversibility’ could be interpreted as parallel appeals, by scientists and various political actors, for the removal of transgenes from landraces.

There are two problems with this call for ‘decontamination’. The first concerns the theoretical genetic possibility of reducing the frequency of a gene in a population to zero, either as a result of selection or drift. The concept of ‘decontamination’ implies that there is some ‘pure’, singular landrace population to return to, and yet landrace populations are diverse, heterogeneous, and evolving. Population genetic theory shows that, if transgenes act as dominant alleles, they would be lost if selected against. However, it is reasonable to expect neutral alleles or alleles that have a weak effect (positive or negative) on fitness to introgress into populations and remain as rare alleles at low levels. This may be especially common in a genetically diverse population like that of maize landraces where the effect of a given transgene on seed production and survival may differ for each plant, resulting in the maintenance a low level of transgenes in the population.

This leads to the second problem with the argument for decontamination, one concerning the scientific and statistical limits of detection, measurement, and sampling. The call for ‘decontamination’ presumes that it is possible to know and verify that such complete removal has occurred. Yet such conclusions must be based on analyses of a sample of the seeds produced, which are then tested, so that conclusions can be drawn about transgene frequencies. However, for rare alleles like transgenes, it is difficult to design experiments that provide a high level of certainty—especially for negative results (Andow, 2003; Cleveland et al., 2005). Theoretical work in conservation biology and crop genetic conservation have helped to develop sampling strategies to ensure a high probability of finding a rare allele in a population (Sjogren and Wyoni, 1994). However, a plant’s mating system, the population genetic structure, and the effective population size must be known to sample optimally (Vencovsky and Crossa, 1999, 2003).

These issues surrounding sampling protocol recently emerged in a response to Ortiz-García et al. (2005a) written by Cleveland et al. (2005). Their criticism centers on the sampling scheme employed, the joint interpretation of tests across locations, and the subsequent conclusions concerning the putative rarity of transgenes. More narrowly, they fault Ortiz-García et al. (2005a) for failing to take the effective population size of their sample into account when calculating the probabilities of failing to detect a transgene and therefore overestimating the precision of their sample. Cleveland et al. also claim that the practice of grouping data from multiple fields was problematic, since the genetic structure of the populations was not known. Therefore, they conclude that Ortiz-García et al. (2005a) should not have made any claims about the presence of transgenes in the region studied; rather, they should have been limited to making claims about *individual* locations.

The complexity of this debate lies in methodology. Ortiz-García et al. (2005c) originally analyzed their data using two different scales of analysis to calculate the probability of failing to detect transgenes in maize: first the *seed*, then the *ear*. The latter scale was even more conservative than that proposed by Cleveland et al. (2005). None of the new calculations suggested by Cleveland et al. (2005) would substantially change the conclusions of Ortiz-García et al. (2005a,c). Ortiz-García et al. (2005c) disagree that it is impossible to calculate a probability of *repeatedly* failing to detect transgenes across many fields. In a reanalysis of their data employing an even more conservative test than previously used, they find “the minimum detection level for transgenic seeds across localities is closer to one in one hundred (0.0077)” (Ortiz-García et al., 2005c, p. 5), rather than one in ten thousand. Therefore, transgenic seeds could have made up 1% of the total seeds in the population without having been detected under the most conservative assumptions.

This debate highlights the difficulty in defining a clear approach to identifying regions with maize landraces in need

of ‘decontamination’. Even with the research of Ortiz-García et al. (2005c), they still would not have been able to find a large group of transgenic seeds—between .01% and 1% of the seeds in the research area *could* have been transgenic without being found. The consensus emerging between Cleveland et al. (2005) and Ortiz-García et al. (2005c) is that studies should focus on testing fewer seeds from many ears and many fields, rather than emphasizing replication at the level of non-independent seeds from the same ear (Ortiz-García et al., 2006; Soleri et al., 2006b). Yet even with these changes, the amount of sampling and testing needed to bring the probability of *failing* to detect transgenes down to a reasonable level is high. And such an approach is more complex and expensive, particularly given the enormous scale of Mexico’s maize acreage. In effect, the debate could continue indefinitely because the acceptable level of ‘contamination’ cannot be determined. As Ortiz-García et al. (2005c, p. 6) note:

Because it is impossible to prove that transgenes are absent in a given region, discussions about the *consequences* of undetected transgenic plants should acknowledge that even extremely low frequencies could result in biological and/or socioeconomic effects, depending on the transgenes in question and how they are viewed by local farmers.

Herein lies the dilemma of the appeal for ‘decontamination’: farmers and conservationists may well desire precise answers that science cannot presently provide. In demanding the impossible, the call for ‘decontamination’ exposes this fundamental dilemma underlying the remediation of populations possessing transgenes.

## 6. Potential methods for transgene reduction

Nevertheless, scientists must articulate ways forward and paths to practices that may reduce or remove transgenes from landrace populations. Where there are maize landraces with transgenes in them, two strategies could be employed to decrease (albeit not eliminate) the frequency of transgenes in landrace populations. First, there could be a two-pronged effort to test landrace populations for the presence of transgenes (with methods used by farmers groups in Mexico) and to replace ‘contaminated’ stock with local, ‘non-contaminated’ landrace seed. This strategy would require a high level of organization and would work best if there were a dispersed effort that functioned at the local level that drew on existing social networks such as farmer’s organizations and local seed networks. However, the amount of testing required and the logistics of precisely identifying contaminated populations are major barriers to this strategy. Furthermore, if few populations are used as a seed source for many fields, this strategy has the potential to homogenize the landrace populations in a given area (Storfer, 1999). Finally, subsequent gene flow or germination of transgenic volunteers could always ‘recontaminate’ the population.

Second, it may be possible to harness natural evolutionary processes – selection, drift, and gene flow – to reduce the frequencies of transgenes in maize populations. For example, one might expect that transgenic maize bred for production in the US would not produce well in Oaxaca, especially if cultivated with the low nutrients and high weed pressure conditions not well-tolerated by modern varieties (Bellon, 1991). Such conditions might induce the reduction of transgenes because problematic ‘genetic baggage’ linked to transgenes would prevent transgenic plants from growing well and flowering (but see Soleri et al., 2006a). Further, the normal practice of selecting few (~140) ears from 40,000 plants per hectare to plant the following season’s crop (Cleveland et al., 2005) could produce such an extreme bottleneck that low frequency transgenes would be easily lost by chance (i.e., drift). As we have seen, Ortiz-García et al. (2005a) mention such factors could have been involved in decreasing the presence of transgenes in maize fields in the Sierra de Juárez region of Oaxaca between the Quist and Chapela sampling of 2000 and their sampling in 2003 and 2004. Alternatively, gene flow could be manipulated to reduce transgene frequency by selective use of detasseling of corn plants along the edges of populations thought to contain transgenes or by adding seed from non-transgenic populations into populations potentially containing transgenes.

## 7. Conclusion

Although the debates over GM agriculture are far from over, they are shifting to a new terrain where the prevailing question is not *whether* states should allow GM agriculture, but *how best* to regulate its effects. In this light, difficulties of detecting and reducing transgene introgression underscore the importance of strategies and practices that may prevent transgene introgression from occurring in the first place. The importance of the recommendations outlined by the trilateral CEC Secretariat report (CEC, 2004) on the effects of transgenic maize in Mexico deserve reiteration. This commission of scientists argued that the moratorium on planting transgenic maize in Mexico should be extended and strengthened by “minimizing the import of living transgenic maize grain from countries that grow transgenic maize commercially . . . by milling transgenic grain at the point of entry” (CEC, 2004, p. 27). They also called for further interdisciplinary research on the effects of transgenic introgression on maize evolution. Research into the ways that evolutionary processes (e.g. natural selection) and farmer practices (i.e. aspects of seed management and farming) could be exploited to reduce the frequencies of transgenes that find their way into landrace populations is urgently needed. Such research should attempt to discern mechanisms for removing transgenes from populations—practices that could be used by farmers to decrease the likelihood of transgene introgression. The growing prominence of GM agriculture and the narrowing of the debate to

ecological questions creates new research opportunities and responsibilities for agroecologists. Agroecologists are especially well-positioned to play important roles in teams that study, monitor, and regulate the potentially negative economic and ecological effects of GM agriculture.

## Acknowledgements

K.L.M. thanks the International Institute for Education, COMEXUS, and a Fulbright-García Robles grant for funding her research in Mexico in 2005. J.D.W. conducted research for this paper as a Killam Fellow in the Department of Geography at the University of British Columbia. We thank three anonymous reviewers for their comments on previous versions of the ms. Our paper also benefited from conversations with L. Campbell, K. McSweeney, A. Snow, and especially H. Perales. We are solely responsible for errors.

## References

- Altieri, M., Anderson, K., Merrick, L., 1987. Peasant agriculture and the conservation of crop and wild plant resources. *Conserv. Biol.* 1, 49–58.
- Andow, D.A., 2003. Editorial: Negative and positive data, statistical power, and confidence intervals. *Environ. Biosaf. Res.* 2, 75–80.
- Aquino, P., Carrión, F., Calvo, R., Flores, D., 2001. Selected maize statistics. In: Pingali, P. (Ed.), *CIMMYT 1999–2000 World Maize Facts and Trends: Meeting World Maize Needs: Technological Opportunities and Priorities for the Public Sector*. CIMMYT, Mexico, D.F., pp. 45–57.
- Bellon, M., 1991. The ethnoecology of maize variety management: a case study from Mexico. *Hum. Ecol.* 19, 389–418.
- Bellon, M., Berthaud, J., 2004. Transgenic maize and the evolution of landrace diversity in Mexico: the importance of farmers’ behavior. *Plant Physiol.* 134, 883–888.
- Bellon, M., Berthaud, J., 2006. Traditional Mexican agricultural systems and the potential impacts of transgenic varieties on maize diversity. *Agric. Hum. Val.* 23, 3–14.
- Bellon, M., Risopoulos, J., 2001. Small-scale farmers expand the benefits of improved maize germplasm: a case study from Chiapas, Mexico. *World Devel.* 29, 799–811.
- Bergelson, J., Purrington, C.B., 1996. Surveying patterns in the cost of resistance in plants. *Am. Nat.* 148, 536–558.
- Brush, S., 1989. Rethinking crop genetic resource conservation. *Conserv. Biol.* 3, 19–29.
- CEC (Commission for Environmental Cooperation), 2004. *Maize and Biodiversity: The Effects of Transgenic Maize in Mexico*. CEC, Montréal, Canada.
- CIMMYT (Centro Internacional de Mejoramiento de Maíz y Trigo), 2002. *Los últimos escrutinios de maíz criollo en México no revelan la presencia del promotor relacionado con los transgenes*. CIMMYT, Mexico, D.F.
- Cleveland, D.A., Soleri, D., Aragon Cuevas, F., Crossa, J., Gepts, P., 2005. Detecting (trans)gene flow to landraces in centers of crop origin: lessons from the case of maize in Mexico. *Environ. Biosaf. Res.* 4, 197–208.
- Ellstrand, N.C., Elam, D.R., 1993. Population genetic consequences of small population size: implications for plant conservation. *Ann. Rev. Ecol. Syst.* 24, 217–242.
- ETC Group (Action Group on Erosion, Technology and Concentration), 2003a. *Contamination of Bt Genetically Modified Maize in Mexico Much Worse Than Feared*. ETC Group, Mexico City, Mexico [www.etc-group.org](http://www.etc-group.org).

- ETC Group (Action Group on Erosion, Technology and Concentration), 2003b. Open Letter from International Civil Society Organizations on Transgenic Contamination in the Centers of Origin and Diversity. ETC Group, Mexico City, Mexico [www.etcgroup.org](http://www.etcgroup.org).
- ETC Group (Action Group on Erosion, Technology and Concentration), 2003c. Maize Rage in Mexico: GM Maize Contamination in Mexico—2 Years Later. ETC Group, Mexico City, Mexico [www.etcgroup.org](http://www.etcgroup.org).
- Ezcurra, E., Ortiz, S., Soberón Mainero, J., 2001. Evidence of gene flow from transgenic maize to local varieties in Mexico. In: LMOs and the Environment: Proceedings of an International Conference, OECD, Durham, North Carolina, pp. 289–295.
- FAOSTAT, 2006. <http://faostat.fao.org> (accessed June 16, 2006).
- González Aguirre, R.L., Aguilar Muñoz, E.J., 2006. Bioseguridad y actores sociales. In: Presentation at the 2006 Latin American Studies Association Conference, San Juan, Puerto Rico.
- IPGRI (International Plant Genetic Resources Institute), 1993. Diversity for Development: The Strategy of the International Plant Genetic Resources Institution. International Plant Genetic Resources Institution, Rome.
- Kaplinsky, N., Braun, D., Lisch, D., Hay, A., Hake, S., Freeling, M., 2002. Maize transgene results in Mexico are artifacts. *Nature* 416, 601.
- Louette, D., 1997. Seed exchange among farmers and gene flow among maize varieties in traditional agricultural systems. In: Serratos, J.A., Wilcox, M.C., Castillo González, F. (Eds.), *Gene Flow Among Maize Landraces, Improved Maize Varieties, and Teosinte: Implications for Transgenic Maize*. CIMMYT, Mexico, D.F., pp. 56–66.
- Louette, D., Charrier, A., Berthaud, J., 1997. In situ conservation of maize in Mexico: genetic diversity and maize seed management in a traditional community. *Econ. Bot.* 51, 20–38.
- Mann, C., 2004. Diversity on the Farm: How Traditional Crops Around the World Help to Feed Us All, and Why We Should Reward the People Who Grow Them. University of Massachusetts, Amherst, MA <http://www.peri.umass.edu/fileadmin/pdf/Mann.pdf> (article accessed on March 3, 2007).
- Metz, M., Fütterer, J., 2002. Suspect evidence of transgenic contamination. *Nature* 416, 600–601.
- Ortiz-García, S., Ezcurra, E., Schoel, B., Acevedo, F., Soberón, J., Snow, A.A., 2005a. Absence of detectable transgenes in local landraces of maize in Oaxaca, Mexico (2003–2004). *Proc. Natl. Acad. Sci. U.S.A.* 102, 12338–12343.
- Ortiz-García, S., Ezcurra, E., Schoel, B., Acevedo, F., Soberón, J., Snow, A.A., 2005b. Correction. *Proc. Natl. Acad. Sci. U.S.A.* 102, 18242.
- Ortiz-García, S., Ezcurra, E., Schoel, B., Acevedo, F., Soberón, J., Snow, A.A., 2005c. Reply to Cleveland et al.'s critique of 'Absence of detectable transgenes in local landraces of maize in Oaxaca, Mexico (2003–2004)' *Environ. Biosaf. Res.* 4, 209–215.
- Ortiz-García, S., Ezcurra, E., Schoel, B., Acevedo, F., Soberón, J., Snow, A.A., 2006. Transgenic maize in Mexico. *Bioscience* 56, 709.
- Ortiz Torres, E., 1993. Aislamiento y dispersión de polen en la producción semilla de maíz. MS Thesis. College of Postgraduates, Montecillo, México, 81 pp.
- Quist, D., Chapela, I., 2001. Transgenic DNA introgressed into traditional maize landraces in Oaxaca, Mexico. *Nature* 414, 541–543.
- Quist, D., Chapela, I., 2002. Quist and Chapela reply. *Nature* 416, 602.
- Reznick, D.N., Ghalambor, C.K., 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* 112/113, 183–198.
- Rice, E., Smale, M., Blanco, J.L., 1998. Farmers' use of improved seed selection practices in Mexican maize: evidence and issues from the Sierra de Santa Marta. *World Devel.* 26, 1625–1640.
- Sanchez, G.J.J., Goodman, M.M., Stuber, C.W., 2000. Isozymatic and morphological diversity in the races of maize of Mexico. *Econ. Bot.* 54, 43–59.
- SEDESOL (Secretaría de Desarrollo Social), 2003. Apoya SEDESOL al campo Mexicano; ni un solo grano de maíz comprado al exterior este año. [http://www.sedesol.gob.mx/prensa/comunicados/c\\_074\\_2003.htm](http://www.sedesol.gob.mx/prensa/comunicados/c_074_2003.htm) (accessed June 15, 2006).
- Serratos-Hernández, J.A., Gómez-Olivares, J.L., Salinas-Arreortua, N., Buendía-Rodríguez, E., Islas-Gutiérrez, F., de-Ita, A., 2007. Transgenic proteins in maize in the soil conservation area of Federal District, Mexico. *Front. Ecol. Environ.* 5, 247–252.
- Sjogren, P., Wyoni, P.I., 1994. Conservation genetics and detection of rare alleles in finite populations. *Conserv. Biol.* 8, 267.
- Snow, A.A., Andersen, B., Jorgensen, R.B., 1999. Costs of transgenic herbicide resistance introgressed from *Brassica napus* into weedy *B. rapa*. *Mol. Ecol.* 8, 605–615.
- Snow, A.A., Pilsen, D., Rieseberg, L.H., Paulsen, M.J., Pleskac, N., Reagon, M.R., Wolf, D.E., Selbo, S.M., 2003. A *Bt* transgene reduces herbivory and enhances fecundity in wild sunflowers. *Ecol. Appl.* 13, 279–286.
- Soleri, D., Cleveland, D., Aragón Cuevas, F., 2006a. Transgenic crops and crop varietal diversity: the case of maize in Mexico. *Bioscience* 56, 503–513.
- Soleri, D., Cleveland, D., Aragón Cuevas, F., 2006b. Response from Soleri and colleagues. *Bioscience* 56, 709–710.
- Storfer, A., 1999. Gene flow and endangered species translocations: a topic revisited. *Biol. Cons.* 87, 173–180.
- Vencovsky, R., Crossa, J., 1999. Variance effective population size under mixed self and random mating with applications to genetic conservation of species. *Crop Sci.* 39, 1282–1294.
- Vencovsky, R., Crossa, J., 2003. Measurements of representativeness used in genetic resources conservation and plant breeding. *Crop Sci.* 43, 1912–1921.
- Wellhausen, E., Roberts, J., Roberts, L.M., Hernández, E., 1952. *Races of Maize in Mexico: Their Origin, Characteristics, and Distribution*. Harvard University Press, Cambridge, MA.
- Whitney, K.D., Randell, R.A., Rieseberg, L.H., 2006. Adaptive introgression of herbivore resistance traits in weedy sunflower *Helianthus annuus*. *Am. Nat.* 167, 794–807.