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Some Corny Ideas About Gene Flow and Biodiversity

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Mother Nature has been taking a beating. Her products are receiving a bum rap. Carbon dioxide, the gas that plants need to make sugars and that nearly all organisms respire, has been decried as a pollutant amidst fears that it is the principal cause of global warming. The latest hit against Mother Nature's ways came in the *USA Today* headline "Gene-altered DNA may be 'polluting' corn" (Manning 2001). Behind the headline was a tale from the science weekly, *Nature*, about genetically engineered snippets of DNA that were found in native varieties of corn grown in Mexico. The DNA was claimed to have flowed into the native corn varieties (or landraces) via pollen from U.S. corn hybrids that contained a gene from the insect pathogen, *Bacillus thuringiensis* (Bt). The gene was inserted into the genome of the U.S. corn hybrids using the techniques of biotechnology so that the plants would produce a protein that is selectively toxic to specific insect pests, namely the European corn borer and the corn earworm. Such plants can be called biotechnology derived (i.e., BD plants or crops) to distinguish them from plants bred conventionally by laborious crossing and selection of desirable traits over many years.

The DNA in question was called a pollutant because it shouldn't have been in the Mexican corn. Bt-corn, as the genetically modified commodity is called, is not allowed into Mexico. Perhaps some farmers who wanted to grow more food and make some money made a mistake out of



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ignorance. Apparently not, according to the newspaper-quoted author of the report that appeared in *Nature* (**Quist and Chapela 2001**). The principal investigator from the University of California-Berkeley (UCB) warned, “The probability is high that diversity is going to be crowded out by these genetic bullies.” Furthermore, the UCB investigator stated categorically that plants with the Bt toxin have “been shown to have potentially very bad effects on insects and the microbes in the soil.”

Stimulated by the *Nature* paper, environmental advocacy groups (EAGs) issued yet another proclamation for a total ban on all BD crops. No one wants to see biodiversity destroyed and soil fertility ruined by “crop pollution.” A spokesperson for the Union of Concerned Scientists (UCS) summed up another belief among the EAGs when he said, “We should not be going forward on an experiment when we have no idea of the parameters” (**Manning 2001**).

If carbon dioxide and DNA are considered pollutants, could it be that Mother Nature is meaner than we think? Are we threatening biodiversity and soil health by our complete lack of knowledge of what the heck we are doing? Or are the reports and hand wringing over the UCB investigators’ letter to *Nature* magazine just one more mischaracterization of what is really going on? What do we really know about the parameters related to biodiversity of corn in its native homeland and the possible impact of BD corn?

Gene Sleuths

First, exactly what was reported in the letter to *Nature* (**Quist and Chapela 2001**)? Samples of corn from an isolated region near Oaxaca, Mexico, were collected and analyzed for genetic markers that would indicate the presence of transgenic DNA. Transgenic DNA in this case would be any DNA that is not naturally present in the corn genome but comes from other plant or bacteria species. Specifically, the UCB scientists were looking for either a Bt toxin gene (i.e., a whole gene that codes for a protein known as Cry1Ab) or a snippet of DNA called the cauliflower mosaic virus 35S promoter (CaMV 35S). The CaMV 35S sequence could also come from Roundup Ready corn, a variety that is modified to resist the herbicide glyphosate. CaMV 35S DNA does not code for a protein but rather functions to help BD plants transcribe Bt genes into messenger RNA for eventual translation into proteins. Corn plants don’t normally have genes for Cry1Ab nor DNA for CaMV 35S unless they are introduced by biotechnological methods.

In essence, the UCB scientists were testing the hypothesis that pollen from illegally planted Bt corn had fertilized native Mexican landraces. A landrace is still *Zea mays*, the name for all corn, but it has been developed in Mexico and adapted to its specific climatic conditions.

The UCB scientists did not say why they suspected that illegal corn hybrids were brought into the country nor did they explain their reason for choosing particular corn samples to test. Nevertheless, the researchers tackled the corn samples with a technique called PCR (polymerase chain reaction) that enables detection of very tiny amounts of DNA by synthesizing many strands from only a single strand (for a lucid explanation of PCR techniques see

http://www.accessexcellence.org/AB/IE/PCR_Xeroxing_DNA.html). In other words, one copy of a gene or DNA sequence in one corn seed out of hundreds can be amplified into over a billion copies to identify a DNA sequence that may be derived from genetic engineering.

The UCB scientists concluded they found evidence of CaMV 35S in five of seven landrace corn samples. The conclusion of BD DNA “contamination” was solely based on the use of two consecutive PCRs to detect a piece of the CaMV 35S promoter DNA. In other words, so little CaMV 35S was present in the native landraces that two amplification cycles were required to detect it.

Based on many generations of crossing descendants of the original Bt corn plants, the gene construct containing CaMV 35S is known to be stable. However, the UCB scientists used a technique called inverse PCR to indicate that the CaMV 35S DNA introgressed into the native landrace genome at multiple regions and also broke into smaller fragments. If this random insertion of the promoter DNA or its pieces all over the genome did happen, then it is possible that normal development of the seed could be disrupted. The UCB scientists also reported that one corn sample tested positive for the Bt Cry1Ab toxin gene, but the *Nature* article did not provide the DNA evidence to prove that the Bt gene was actually present let alone functional.

Considering that small farmers in Mexico select their seed for desirable traits and then replant it (**Louette 1997**), the UCB scientists implied that the presence of BD DNA threatened the integrity and sustainability of the Mexican corn landraces. Moreover, the UCB scientists stated their concern for “future genetics of the global food system” in the presence of the widespread planting of BD crops. Yet, those concerns did not motivate the UCB team to plant the “rogue” seeds to determine whether the Bt character or the CaMV 35S were stable introgressions and whether the seed was even viable. Such experiments seem a necessary first step to even begin answering the bigger concerns of impacts on biodiversity.

The UCB scientists gained more than just the admiring attention of the media and environmental groups. Their failure to take the next logical step and redo the tests on the next generation of plants from the rogue seed before publication brought the critical attention of molecular biologists from numerous academic and government institutions.

The Gene is Out of the Bottle

Within days after the release of the UCB report, CIMMYT (International Maize and Wheat Improvement Center), a public research foundation whose mission is preservation of maize biodiversity and crop improvement, released a press release of their foundation’s own results in a search for biotechnology-derived DNA introgressions (**CIMMYT 2001**). None of the forty-three Oaxacan landraces in CIMMYT’s gene bank or a new collection of forty-two different varieties had detectable levels of CaMV 35S promoter.

The editorial board of the journal *Transgenic Research* issued an essay critiquing the UCB report (**Christou 2002**). Furthermore, two critical letters that were published in *Nature*

uncovered profound shortcomings in the methods and interpretations by the UCB researchers (Kaplinsky et al. 2002; Metz and Futterer 2002). In short, major flaws were found upon critical examination of the experimental design and techniques. PCR tests alone are subject to artifacts (i.e., false positives) and must be confirmed by additional types of molecular tests commonly exercised to confirm PCR results (for a pictorial explanation of the technique see <http://www.accessexcellence.org/AB/GG/southBlotg.html>). The critics recommended that all claims of introgressed BD DNA should also be supported by growing out the F1 hybrid (i.e., planting the rogue seeds, which are actually the progeny, or F1 generation, that grows into the next generation of plants) and re-doing the molecular tests along with examining obvious effects on plant morphology. *Nature* allowed the UCB researchers to answer their critics in a rebuttal that included additional data not included in the original report. *Nature's* editors encouraged readers to make up their own mind about the “truth.”

The controversy over “DNA pollution” grew as environmental advocacy groups banded together to issue a joint statement denouncing industry-paid, biotechnology proponents in academia and government for personally attacking the integrity of the UCB scientists. In response, a statement was put together with signatures from scientists all over the world stating that critique of research methods are not ad hominem attacks and that science could only progress by constant skeptical inquiry and correction. (**The Joint Statement 2002**) (As a skeptic, I admit I signed the latter statement).

Such controversy is the stuff movies are made of. Well, at least newspaper headlines. The press was still having a field day months after the story broke. Witness the March 20, 2002 headline and leader in the *Christian Science Monitor*: “**Calling Poirot: bizarre case of cross-border 'super corn'**. Scientists claim genetically modified grain from US invades Mexico, threatening purity of birthplace of corn” (**Belsie 2002**).

The Genes Flow In and the Genes Flow Out

The lead sentence of the *Christian Science Monitor* headline encapsulates a common misconception about plants, namely that their genome is somehow fixed (i.e., pure). Plants, unlike animals, are immobile and must rely on dispersal of pollen through physical (e.g., wind) and biological (e.g., bees) processes. Without the gene flow that occurs from dispersed pollen, plant populations are likely to go through a genetic bottleneck from too much inbreeding and consequently suffer reduced genetic diversity and possible fitness (**Mayr 1971**). Indeed, farmers in Mexico have noted reduced productivity after growing local varieties (i.e., landraces) for numerous generations in the same field without the benefit of significant pollination from other varieties (**Gonzalez and Goodman 1997**). Thus, wind- and insect-pollinated plants are naturally “promiscuous,” and it is for their own good.

Frankly speaking, the idea that Mexican landraces are “pure” is absurd. Let’s set the record straight. With few exceptions, modern food crops are not ancient inviolate species. In essence, they are human-directed inventions of genetic manipulation by educated trial and error coupled with intense selection pressure. Without human intervention our crops would not be here for our

use, whether they are U.S.-improved cultivars or Mexican landraces. The very fact that genes could be easily exchanged between our food crops and their ancestors has allowed continuous improvement in agronomic traits. Such an exchange of genes between unlike populations of the same or related species is called hybridization, and it's perfectly natural, especially in plants (**Mayr 1970**).

Somehow the myth was started that introgression of "foreign" genes into native landraces of corn would reduce biodiversity. Ironically, Mexican farmers have long been exchanging seeds from local varieties with each other to improve productivity (and genetic diversity) of their corn (**Louette 1997**). The difference between Mexican and U.S. seed corn production practices boils down to open pollination vs. hybridization. In the United States, inbred seed lines (i.e., corn varieties that are allowed to pollinate only themselves) are crossed each year to produce superior performing (and more genetically diverse) hybrids. U.S. farmers pay a premium for hybrid corn bought every year from seed companies. Hybrid corn has a certified genetic makeup, and it consistently yields well under the environmental conditions in which it was developed. In Mexico, farmers grow their own seed from varieties that are open-pollinated. In other words, they grow varieties that are subject to cross-pollination (i.e., gene flow) from similar varieties or non-local varieties.

Indeed, studies of grower practices in Mexico show that there are many different distinct varieties of corn grown in fields in close proximity to one another. In the region of Cuzalapa on the western Pacific coast of Mexico, twenty-six distinct varieties were grown in a 24,000-hectare watershed containing 1000 hectares of corn (**Louette 1997**). Fifty-three percent of the corn in the watershed was produced from an individual farmer's own seed planted in previous years. The rest of the corn was produced from seed exchanged with other farmers in the same watershed (36%) or from seed outside the region (11%). One of the non-local varieties was identified as an improved cultivar of hybrid corn from the United States.

Because Mexican farmers make no attempt to segregate different varieties, plenty of cross-pollination has been occurring (estimated at 38% probability for outcrossing in the Cuzalapa region) (**Louette 1997**). About one-third of local corn varieties may already have introgressed genes from non-local and improved varieties (**Gonzalez and Goodman 1997**). Consequently, a continuum of morphological traits and genetic characteristics exists among all the major local varieties (**Louette 1997**). In other words, within a region abrupt shifts from one morphological trait to another were absent. Seeds in a given field were not necessarily all one color (white, blue, or yellow); rather, mixtures were present (a.k.a. heterozygosity). Yet, despite the tremendous amount of gene flow from non-local to locally adapted and selected cultivars, the varieties survived intact as recognizable entities.

So what is the problem with biodiversity should a gene derived from biotechnology-based breeding outcross to a local landrace variety? Given that a plethora of genes are moving among distinct local varieties and non-local varieties all the time without loss of biodiversity, the answer seems to be "nothing is wrong" other than some people are hung up about the process of

breeding rather than the results. I maintain that the real focus of concern should be the ecological effects of gene flow in the context of the local habitat, not the origin of the DNA.

Teosinte: The Great Granddaddy of All Corn

For a head start on answers to the question of ecological effects of gene flow, we can learn a lot by close examination of the relationship between modern corn and teosinte, a grass recognized as the feral progenitor species of corn that grows in Mexico and some Central American countries (**Benz 2001**). At one time, teosinte was classified as a separate species, *Zea mexicana*, but modern genetic analysis indicates it is more likely a subspecies, *Zea mays* subsp. *parviglumis*. Thus, if gene flow and introgression were going to have any ecologically significant effects, it would have already happened to teosinte in regions where modern corn and the wild grass are growing near one another.

The stinging critique of the UCB study by the editorial board of *Transgenic Research* began its argument by stating a long known reality: wind pollination would inevitably lead to gene flow between domesticated crop varieties and their wild ancestors when grown in close proximity to each other (**Christou 2002**). Indeed, studies on travel distances of corn pollen (e.g., Table 1) show that the potential for gene flow between corn and teosinte is very high whether the plants are growing together in the same field, the teosinte is growing along the borders of the cornfield, or the teosinte is growing in dense patches outside of the cornfield. In both Europe and the United States, recommended distances for separation of hybrid seed-cornfields are 200 m. Corn pollen can be detected at distances greater than 800 m from a field (**Eastham and Sweet 2002**).

Despite the tremendous potential for gene flow between modern corn and teosinte, the literature about the origin of maize and likelihood of introgressions with teosinte suggest a great deal of uncertainty about whether introgressions are even occurring in the direction of cultivated corn to the teosintes (**Doebley 1984; Kato Y. 1997**), or whether such introgressions can become fixed without selection pressure (**Martinez-Soriano and Leal-Klevezas 2000**). For example, if a trait conferring insect resistance in a landrace introgressed into teosinte, that trait would not be important unless the particular pests were also feeding on teosinte and more importantly, were also major mortality factors limiting spread of the plant. Similarly, if herbicide tolerance introgressed into a wild relative, the gene would not be important unless herbicides were used in the areas where the plants are growing.

Flower Power

The big difference between teosinte and corn is in the flower (inflorescence) and seed morphology (**Wilkes 1997**) (Figure 1). Teosinte has multiple branching inflorescences that only produce two seed rows after fertilization. Modern corn generally produces one large inflorescence but has multiple rows of seeds. Teosinte produces a seed covered in a very hard coat called a glume that is not digestible by animals. The glume of modern corn has been

reduced to that white stuff that sticks in your teeth when you take a bite out of sweet corn. Finally, teosinte seeds easily break off the inflorescence and can disperse themselves. Corn seeds do not break off the cob and are incapable of self-dispersal. Given the differences in morphology between teosinte and corn, hybrids should be easy to spot. Indeed, hybrids of corn and teosinte have been found in the field, as well as produced by artificial pollination techniques, but the seeds either do not germinate or the F1 (initial) generation is not very fit (**Kermicle 1997**). The inability of corn to disperse its own seed also limits its ability to escape from fields and invade teosinte habitat.

The striking evolutionary divergence in inflorescence morphology of domesticated maize and teosintes exists to this day, suggesting genetic isolation after the initial characteristics of consumable corn were fixed despite the known gene flow between the subspecies. Recent research shows that a gene called *tb1* largely controls the difference in inflorescence morphology. The key to understanding why teosinte and corn remain morphologically distinct and teosinte is able to retain its diversity may lie in the function of *tb1*. Like many genes, *tb1* has a region that actually codes for a protein (the transcribed region) and a region that is not transcribed but acts like a controller over the transcribed region (the regulatory region). The regulatory region functions as a switching area to turn on and off transcription of DNA to messenger RNA. The transcribed regions of *tb1* in both cultivated maize and teosinte have maintained their polymorphic character (i.e., their genetic variability or diversity still exists). The non-transcribed regulatory region of *tb1* in modern corn, however, has only 3% of the genetic variation found in teosinte (**Wang et al. 1999**). Thus, both corn and teosinte maintain their separate diversity in inflorescence character, which is coded for on the transcribed region of *tb1*, and only the control mechanism of modern corn has been altered over time with loss of its original genetic diversity.

Given the fact that at minimum several hundred years of artificial selection were required to fix the changes in the regulatory region of *tb1*, it is difficult to support a hypothesis that a transgene coding for a pest resistance character would all of a sudden change biological diversity in teosinte or native landraces in the absence of intense selection pressure. Indeed, after thousands of years of cultivation of different varieties of corn in the presence of teosinte, teosinte still retains diverse forms but none of them look (or act) like modern corn.

Biodiversity Redux

One of the arguments about the “problem” of BD plants grown near wild relatives is that a transgene could flow to its feral ancestor. The resulting hybrid would acquire a fitness that could elevate it to the status of super weed, crowding out its unfortunate ancestor. The problem with this hypothesis is its focus on the derivation of the gene rather than on the biology of the plants. Crop hybridization with wild relatives has long been known, and in some isolated cases there has been increased weediness of the hybrids (**Ellstrand 2001**). But the highlighted examples of potential problems involve conventionally bred plants and presumably introgression of numerous genes. We can test whether a new trait (e.g., insect resistance or herbicide tolerance) due to a known single gene will increase fitness. For example, field research from the U.K. has

shown that, over a period of ten years, herbicide-resistant corn did not survive well outside of the agricultural field and never took on the characteristics of a weed (**Crawley et al. 2001**). In recognition of possible advantages in fitness or acquisition of weedy characteristics in introduced plant species, the U.S. regulatory system requires consideration of such events for BD crops (**NRC 2002**).

Concerns about gene flow and biodiversity need to focus on specific crop species and ecological situations on a case-by-case basis. If one is concerned about loss of teosinte, or even Mexican landraces, whenever BD corn is introduced into Mexico, then the following question should be considered: if hybridization between crops with enhanced traits and feral relatives is so rampant and so likely to reduce biodiversity, why has teosinte remained distinct with its known diversity of subspecies? After all, distinct landraces of *Zea mays* have been grown near teosinte for many hundreds of years. Such deductive reasoning suggests no effect on biodiversity for corn-teosinte interactions, but does not absolve responsibilities for careful testing under field conditions.

A corollary question is: Why have crops with superior qualities for insect (and/or herbicide tolerance) not become weeds after ten years of testing (**Crawley 2001**)? Part of the answer is lack of appropriate selection pressure, if indeed the hybrids are stable plants. Also, some crop plants themselves are probably not fit enough or lack characteristics to take on the habits of weeds. For example, corn seeds do not disperse and therefore are not likely to become invasive.

On the other hand, certain characters, such as ability to survive drought or salty soils, might impart different selective advantages (**Crawley 2001**). In that case, those situations should be studied, but the problem is independent of how the characters were bred into the crop. The National Research Council (NRC), the research arm of the National Academy of Sciences, emphasizes that how crops are bred, whether by laborious hand selection and crossings over many years, or quickly by the techniques of molecular biology, is irrelevant to assessing ecological risk (NRC 2000, 2002). The characters produced by the techniques should be the focus of discussion, and they should be assessed in the relevant environments where the crops will be produced.

If we really care about biodiversity, then we should pay attention to efficiency of land use and environmental benefits of crop improvement. Obtaining more yield per acre of land with reduced inputs of pesticides should make more land available for conservation. This goal seems attainable in Mexico where research suggests that all the gene flow over the last half-century between local landraces and non-local varieties, including improved hybrids, has increased per-acre yields (**Gonzalez and Goodman 1997**) (Table 2).

The problem with biodiversity does not lie with how crops are bred. Rather, it lies with land management. A statement from the executive summary of a meeting concerning the impacts of modern corn on prospects for survival of teosinte sums up our misplaced concerns about transgenic corn cultivars.

“Changes in land use — especially increased grazing and urbanization — are the principal threats to teosinte. In recent decades there has been a drastic reduction in teosinte populations and the danger of extinction is real. In fact, transgenic maize may be considered a marginal threat, compared with the effects of urban growth” (Serratos et al. 1997).

Ironically, if teosinte did adapt with a few more weedy characteristics, it would probably fare better as its habitat is reduced in scope. But based on past experience, that doesn't seem likely to happen.

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Table 1. Deposition of pollen (as a percentage falling into each density category) on milkweeds as a function of distance from the edge of a cornfield (modified from **Pleasants et al. 2001**). Note that few pollen grains are deposited beyond 5 m, although a single pollen grain may travel for over 800 m (**Eastham and Sweet 2002**). Most of the pollen leaving a field is blocked by the first several rows in a field. Thus, successful pollination between crop varieties would depend on distance of separation between fields and density of pollen flow. In corn, one pollen grain would have to land on the tip of the female flower (called a silk) for successful fertilization and production of one embryo (seed) on a cob that would normally have hundreds of seeds.

Pollen Density (grains/cm ²)	Inside Field	Distance from Edge of Cornfield (meters)			
		0	1	2	4-5
0 - 100	52.7	83.3	90.0	97.4	99.6
100 - 200	17.0	9.3	6.2	2.4	0.4
200 - 300	10.1	3.3	2.2	0.0	
300 - 400	7.2	1.7	0.6	0.2	
400 - 500	4.1	0.8	0.2		
600 - 700	2.1	0.2	0.1		
700 - 800	0.9	0.2	0.1		
800 - 900	0.9	0.3	0.1		
900 - 1000	0.2	0.1	0.0		

Table 2. Comparison of yields of different landraces collected approximately 30 years apart in Mexico and in Medellin, Columbia. The data are based on Gonzalez and Goodman (1997), who summarized the research from two independent studies. Seeds collected years ago were stored in germplasm seed banks using practices to ensure the viability of the seed. Periodically the seed is grown out and a new generation of seeds is obtained. Caution should be used in interpreting the data because differences in yield could be due to physiological effects from the age of the seed or it could be due to enhanced vigor associated with hybridization of local landraces with new varieties. Nevertheless, the data suggest that gene flow among landraces has the capability of improving productivity and thus can increase land use efficiency as measured by yield per hectare.

Geographic Origin (Collection Time)	Number of Entries	Yield (tons/hectare)	Days to Flowering
Puebla (old)	21	1.8	83
Puebla (new)	110	2.3	81
Mexico (old)	40	1.4	79
Mexico (new)	92	2.1	80
Tlaxcala (old)	4	1.1	76
Tlaxcala (new)	66	2.0	76
Medellin, Columbia (old)	10	2.3	No data
Medellin, Columbia (new)	10	3.16	No data

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Figure 1. Evolution in morphology of *Zea mays* from ancestral teosinte (left) to modern corn (right). The middle figure shows possible hybrids of teosinte and corn landraces.



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