



Review

Gene flow of transgenic seed-expressed traits: Biosafety considerations

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ABSTRACT

There are a few instances where seed-expressed traits may pose a biosafety risk, depending on the species, the trait, and where it is cultivated. The fewest ecological risks of pollen flow are posed to the natural environment, as there are few crops growing in or near pristine environments that have interbreeding relatives, or bear traits that could disrupt ecological balances. Some seed-expressed traits might pose an agro-ecological risk if introgressed into related weeds. Only pharmaceutical or industrial seed-expressed traits are likely to introgress into other varieties of a crop at regulatory red flag levels due to zero tolerance at the most sensitive levels of detection when grown at normal separation distances. Other traits would be below regulatory thresholds if required separations distances are met. Two of the three transgenic containment methods described (plastome transformation, attenuated viruses) are unlikely to work with seed-expressed traits. Transgenic mitigation could be used where the seed-expressed trait is linked with a trait that is positive or neutral to a crop but deleterious to its wild or weedy relative. Typical mitigation traits are dwarfing, no seed shattering, and lack of secondary dormancy. There are special mitigator genes, such as transgenically dominant sugary endosperm that might be appropriate for pharmaceutical traits. Biosafety gene flow protection mechanisms are also needed to prevent wild type poisonous seed crops (e.g. castor and *Jatropha*) from introgressing toxin genes into seeds of varieties where these toxins have been transgenically eliminated.

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Contents

1. Introduction	630
2. Transgene flow to the wild	631
3. Transgene flow from crop to related weeds	631
4. Transgene flow to other varieties of the crop	631
5. Dealing with transgene flow	632
5.1. Containing gene flow	632
5.2. Mitigation of transgene flow	632
5.2.1. The special case of mitigating transgenes encoding pharmaceuticals in seeds	632
6. Protecting biotech crops from gene flow from the wild	633
7. Concluding remarks	633
Acknowledgement	633
References	633

1. Introduction

Many seed-expressed traits have been described in this issue. From the standpoint of biosafety one must determine if there could be undesirable effects should these traits be expressed elsewhere due to gene flow. Too many discussions end at answering whether genes will flow; but here we will also discuss strategies

to preclude gene flow and mitigate its effects, should it be undesirable.

There has been much discussion of low level contamination of one bulk export crop with unregistered transgenes from another crop; e.g. recent USA soybean exports to Europe that contained unregistered (in Europe) novel Bt traits from maize. Though often bulked with gene flow ("gene contamination") it is obvious to the biologist but not the popular press that maize genes do not end up in soybean seeds; minute but PCR detectable amounts of maize leaf dust were found at orders of magnitude lower thresholds than the amounts of rodent feces, insect parts, and dirt allowable in the

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same bulk shipments. This review will deal only with genetic gene flow via pollen.

Some activists against biotechnology often decry the possibilities of gene flow to the wild and predict dire ecological consequences. When pressed for examples of where this is possible, specific answers are not forthcoming except usually to give examples of gene flow to weeds. It is surprising but typical that most ecologists dealing with gene flow issues do not differentiate between undisturbed ecosystems where wild species grow, and agroecosystems where weeds are rampant, or ruderal, human disturbed ecosystems (e.g. roadsides), which often have a different evolutionarily adapted flora, e.g. [1–3]. These ecologists differentiate only crop or wild, ignoring a vast literature that weedy is not wild [4]. There are very few places where crops are cultivated close enough to wild relatives to allow significant gene flow [5], but proximity easily allows gene flow between crop and related weeds. The same botanical species can have wild, weedy and crop genotypes. There is far more evidence of destructive gene flow from the wild to crops than vice versa; e.g. bolting (premature flowering) genes from wild maritime beet to sugar beets [6]. There are many more cases of undesirable gene flow from crop-related weeds to crops than wild to crops [7].

Thus in dealing with ecological and regulatory issues of transgene flow one must ask three questions; “to whom?” “can it?” and “so what?”. “To whom?” includes other varieties, weed, to wild species; “can it?” refers to geographical barriers (e.g. distance) and genetic barriers to crossing; and “so what” refers to whether the movement of a gene will have any ecological significance. For example, some accessions of *Aegilops peregrina* contained a bit of non-coding wheat DNA, most did not, and there seemed to be no significance other than its being there [8]. Thus, interspecific “diagonal” gene flow can occur between related species that do not have the same chromosome numbers and have homoeologous (different but similar) chromosomes, but not homologous (identical) chromosomes. If there is a real gene flow problem, it is then valid to ask the next question: “how gene flow be dealt with to alleviate the problem?”. There are no needs to solve phantom problems that do not exist.

2. Transgene flow to the wild

Some crops do grow sufficiently near their progenitors to interbreed. For example, rice *Oryza sativa* can cross with botanically conspecific wild annual *Oryza nivara* and perennial *Oryza rufipogon* (the taxonomists gave each form a separate name despite free intercrossing) [9]. Typically highly distinct hybrid swarms form at the boundary between crop and wild, but are rather discretely delineated from the wild. Are there seed-expressed traits that might change that?

Assuming the more typical unlikely case of a transgenic crop being sufficiently related to a wild species to form viable hybrids, and being close enough to it for viable pollen to reach the wild species, what seed-expressed traits might be of significance? Any trait that reduces reproductive fitness would quickly disappear, as there would always be far more wild pollen in a wild habitat than crop pollen, a parameter ignored in a grossly illogical, counter-Darwinian model that suggested that crop genes could swamp the wild [1]. Only traits that are neutral or confer fitness advantages might persist in a crop-wild hybrid, if they could get there. Of the seed traits discussed elsewhere in this issue, uniform germination and non-shattering are unfit and would not persist in competition with the wild type. Wild relatives of crops typically have a better nutritional balance than the crop seeds; our ancestors bred for high yield, and resistance to herbivores, resulting in less and unbalanced protein, to “convince” the herbivores that the nearby wild grains were better [10]. Thus, such traits are already in the wild. Industrial

and pharmaceutical product traits would probably be neutral from an ecological point of view, but movement of their genes into the wild is undesirable from a regulatory point of view. Thus, only such traits as longevity, stress tolerances, anti-herbivory would provide the wild relative with a fitness advantage that might modify its balance position in an ecological pecking order. That is, if the wild relative does not already possess these traits, as many do.

3. Transgene flow from crop to related weeds

Unlike wild species, weeds within a crop field are often bathed in crop pollen. Detractors of transgenic technologies often warn of superweeds, reminding the listener/reader that horizontal gene flow is common in nature, and thus superweeds could be common. Horizontal gene flow is common among bacteria but such promiscuity is exceedingly rare among higher eukaryotic organisms as well as between eukaryotic organisms and bacteria or viruses in evolutionary time, and virtually non-existent in a human time scale. Thus we can exclude gene flow from crops to totally unrelated weeds or wild species.

There are though many instances where crops can cross vertically with conspecific weedy forms, as well as “diagonally” with related, interbreeding weeds where there are some incomplete barriers to crossing. Many of these are highly pernicious feral weedy forms of the crop such as sorghum’s con-specific shattercane [11], weedy rice [9,12], weedy sunflowers [3], and bolting weedy beets [6,13]. Wheat has a intercrossing weedy relative *Aegilops cylindrica* [14], oilseed rape (canola) has *Brassica rapa* [15], sorghum has weedy *Sorghum halepense* [11], etc. The situation with sorghum is so problematic that in African sorghum monoculture there can be a gradient from weedy morphotypes to domesticated morphotypes [16]. Maize has no weedy relatives in most of the world; it can interbreed with weedy forms of teosinte in Mexico and is unlikely to cross with wild forms further away.

Crop traits such as transgenic herbicide, disease, insect and drought-resistance could provide a distinct advantage to the weed. Herbicide resistance would render the weed back to being impossible to control [5], should the gene introgress into the weed. Not many seed-only expressed traits could be of advantage to a related weed in an agroecosystem, and the likelihood diminishes as we go to wild species. Post-harvest disease and herbivore resistance especially could result in the weed becoming a much larger proportion of the weed seed bank, if the weed seeds are not eaten or do not rot in the soil. While there may be no ecological advantage to industrial or pharmacological traits in weeds, regulators will clearly not want to see such traits remaining in the weeds; they later could cross back into related conventional crops from such weeds.

Indeed, as discussed in Section 5.2, there are natural seed traits resulting from human domestication that one might like see flow into weeds, as the weeds would no longer be weedy (non-shattering, no secondary dormancy). These traits are typically recessive, so they would not be expressed in hybrids between crops and weeds. It is a different matter if they are transgenic, where they are dominant.

4. Transgene flow to other varieties of the crop

Pollen can and does flow from one variety to another nearby [17–19]. The distance can be great [18], but the frequency of such pollination mostly drops off exponentially with distance, except for a very small proportion that due to wind eddies, etc., does not follow the rules. Thus, if there is a threshold of allowable transgenic material in an adjacent crop, separation distances of a few meters are usually sufficient to preclude above threshold flow. It is unlikely that there can be ecological significance to such gene flow, only

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