Gene Flow from Herbicide-Resistant Crops: It's Not Just for Transgenes

Carol A. Mallory-Smith* and Elena Sanchez Olguin

Department of Crop and Soil Science, Oregon State University, Corvallis, Oregon 97331, United States

ABSTRACT: Gene flow was raised as one of the first issues related to the development and release of genetically engineered (GE) crops. Gene flow has remained a topic of discussion for more than 20 years and is still used as an argument against the release of transgenic crops. With respect to herbicide-resistant crops, gene flow does not differ whether the herbicide resistance trait is introduced via genetic engineering or via conventional breeding techniques. Conventional breeding and genetic engineering techniques have been used to produce herbicide resistance in many of the same crop species. In addition, conventional breeding has been used to produce a broader range of herbicide-resistant crops than have been genetically engineered for herbicide resistance. Economic, political, and social concerns center on the breeding technique, but the results of gene flow for weed management are the same irrespective of breeding technique. This paper will focus on gene flow from nonGE herbicide-resistant crops in North America.

KEYWORDS: nonGE herbicide-resistant crops, gene flow, hybridization, transgenic, herbicide resistance

■ INTRODUCTION

Gene flow was one of the first and most frequent objections related to the release of genetically engineered (GE) crops and continues to be a recurring theme since the commercialization of transgenic crops including herbicide-resistant crops.[1-4] Questions and concerns related to transgene flow resulted in conferences, symposia, refereed and popular press articles, and books on the subject. Gene flow occurs naturally between crop cultivars and between crops and compatible relatives, occurs whether a gene is a transgene or not, and does not automatically result in a negative outcome.[5-7] Gene transfer from wild or weed species has been used for crop improvement, and there is continued selection for desirable traits that can be transferred among species. Many modern crops, including canola and wheat, are the result of gene flow and hybridization between species. The fact that it is easy to identify transgenes using quick tests or molecular markers has led to an overemphasis on the identification of the event rather than the impact of the gene.[8] Beyond measuring gene flow and identifying hybrids, it is important to determine if the gene will be retained over subsequent generations and introgressed and to determine the fitness of the hybrids and their offspring.

The continued debate about gene flow often ignores the actual consequences of gene movement, especially herbicide resistance genes. Because herbicide resistance does not impart a fitness advantage unless there is selection pressure from the specific herbicide to which it is resistant, there is little expectation that there would be an increase in a weed population due to the presence of a resistance gene. However, if the selection pressure is applied, the population would likely increase quickly and have the potential to spread. Depending on the site, the consequences could be significant. In most triazine-resistant weeds and canola, resistance results in decreased fitness.[9-12]

Although there has been documented movement of herbicide resistance transgenes, more than 15 years after the introduction of the transgenic crops, there have been no reports of negative environmental impacts from the movement of a herbicide-resistance trait via pollen to compatible weed species from commercial field production. The herbicide resistance transgene movement from crop to crop has raised either issues of market acceptance or issues for growers who must control the resistant volunteer crop or weed species. In addition, in North America, the most widely grown transgenic herbicide-resistant crops, soybean, corn, and cotton, do not have compatible weed species in the areas where they are grown.

Pollen flow is the basis for the unscientific and unsupported argument that the movement of a transgenic herbicide resistance trait to a weed species could result in a so-called "superweed" that could no longer be controlled.[13] The movement of a transgene or even two transgenes does not provide resistance to all herbicide classes. Having multiple forms of resistance in a weed species does make it more difficult and in many cases more expensive to manage, but weeds with multiple resistance have already evolved through natural selection. From a weed management standpoint, the fact that resistance is imparted by a transgene does not automatically make a weed more difficult to control than if the gene were from a conventionally bred crop or if it were selected by use of a particular herbicide. Once a weed population is resistant, an alternative control measure must be employed. Gene flow from GE herbicide-resistant crops has been extensively reviewed.[14-18] This paper will focus on gene flow from nonGE herbicide-resistant crops in North America.

There are many commercially available nonGE herbicide-resistant crops that were produced through conventional breeding techniques such as mutagenesis, cell culture, or crossing with a herbicide-resistant compatible relative. Triazine-resistant canola (*Brassica napus* L.), released in 1984, was the first widely grown herbicide-resistant crop.[19] The greatest number of

hectares and the greatest number of nonGE crops are imidazolinone-resistant (IR) and are sold under the trade name of Clearfield. Imidazolinone-resistant crops include canola, corn (*Zea mays* L.), lentils (*Lens culinaris* Medic), rice (*Oryza sativa* L.), sunflower (*Helianthus annuus* L.), and wheat (*Triticum aestivum* L.).[20−22] The specific herbicide that is sold with each resistant crop may vary. NonGE corn resistant to sethoxydim and sunflowers and soybean (*Glycine max* (L.) Merr.) with resistance to sulfonylurea herbicides also have been commercialized.[23] NonGE tall fescue (*Festuca arundinacea* Schreb.) and hard fescue (*Festuca longifolia* Thuill.) with resistance to glyphosate are being grown with more glyphosate-resistant grass species under development.[24] NonGE grain sorghum with resistance to either sulfonylurea or aryloxyphenoxy propionate herbicides is under development with expected release for the 2012 growing season (see ref 25; Thompson, personal communication). There have been other conventionally bred herbicide-resistant crops that were not commercialized. For example, IR cotton (*Gossypium hirsutum* L.) was produced through mutagenesis; sulfonylurea- and IR lettuce (*Lactuca sativa* L.) and diclofop-resistant Italian ryegrass (*Lolium multiflorum* Lam.) were produced by backcrossing the crop with resistant compatible weed species.[26−28]

■ GENE FLOW

Gene flow results in a change in gene frequency in one population due to movement of gametes, individuals, or groups of individuals from one population to another [29] and occurs both spatially and temporally. This is a broad definition that encompasses multiple means to move a gene in the environment. There are many opportunities for genes to be moved from one plant to another or from one site to another.

The potential for gene flow depends on the biology of the crop, especially pollination strategy; whether compatible species are present and receptive to the pollen; inheritance of the trait, which in most cases is controlled by a dominant or semidominant gene; how large and widespread the crop production area is; whether the crop is an annual or perennial; seed size and length of viability; and final use of the harvested seed. Production of feral populations, which maintain the gene in the environment, will increase the opportunity for gene flow to occur.

The concern for gene flow via pollen in crops that do not have compatible wild or weedy relatives is the movement of the trait to other cultivars of the crop. Outcrossing rates for different crops vary greatly from obligate outcrossing to extremely low rates of outcrossing. Even for crops that are considered to be self-pollinating, there is still a small percentage of outcrossing that occurs, and that rate may change with environmental conditions.[30−32] In the case of herbicide-resistant crops with compatible relatives that are weedy or naturalized, gene flow via pollen will produce hybrids that carry the resistance trait.

Most often in the literature, gene flow refers to movement via pollen; however, gene flow via seed is much more likely to occur in an agronomic situation.[17] In agricultural production, gene flow via seeds will become more important as the number of hectares planted continues to increase. Seeds are moved in the system from the time of purchase through the time of sale to and use by the final consumer. Whereas pollen has a very limited viability, hours to days, some seeds can remain viable for years, and whereas pollen must reach a compatible plant for gene flow to occur, a seed has only to reach a favorable environment for germination and plant establishment. Once established, it can become a pollen source or, if self-pollinating, produce seed, thus maintaining the gene in the environment. Seed admixture can occur with all crops and should be expected to happen.

Crops that are perennial and reproduce via seed and vegetative propagules have multiple avenues for gene flow. Vegetative propagules provide the advantage of establishing a clone that will maintain the transgene in the environment. Although vegetative propagules do not remain viable as long as seeds do, they do have a longer viability than pollen. Gene flow of herbicide resistance via vegetative propagules has not been adequately studied.

■ GENE FLOW CONSIDERATIONS BY CROP

Canola (*B. napus* L.). Two nonGE herbicide-resistant (triazine and imidazolinone) canola cultivars have been commercialized. Canola is a self-fertile and outcrossing annual species that can be either insect or wind pollinated. Outcrossing rates of up to 47% have been reported.[33] Canola is compatible with a number of related weed species that can produce hybrids to various degrees.[34] Canola readily hybridized with *Brassica rapa* L. but rarely crossed with *Raphanus raphanistrum* L., *Erucastrum gallicum* (Willd.) O. E. Schulz., or *Sinapis arvensis* L. Canola seed is small and easily dispersed. Feral canola populations frequently are found in sites with near proximity to agricultural activity including transportation routes.[35,36] Canola seed shatters during harvest, and seeds left in the field can produce volunteers in subsequent crops and can produce persistent soil seedbanks, which vary depending on the cultivar and the depth of burial.[37−39]

Triazine-resistant canola was released in 1984.[19] Triazine-resistant canola was produced by crossing the triazine-resistant weed species birdsrape mustard (*Brassica campestris* L.) with *B. napus* L.[40] The trait is maternally inherited, and thus gene flow via pollen movement is not a concern, but seed admixture can still occur. Because there is a fitness cost associated with triazine resistance, canola cultivars with other herbicide resistance traits are more commonly grown. Triazine-resistant canola is still grown in Australia but will likely be replaced by transgenic glyphosate-resistant canola, which has recently been approved there.

Imidazolinone-resistant canola is grown in the United States and Canada but less than the transgenic cultivars. Gene flow between transgenic and conventionally produced IR canola resulted in plants with resistance to three different herbicide classes, glyphosate, glufosinate, and imidazolinone.[41] Gene flow among canola cultivars resulted in seed stocks of nonherbicide-resistant seed containing the imidazolinone resistance trait.[42] The movement of herbicide resistance genes between canola cultivars or between canola and compatible relatives should be expected as long as the trait is carried in the pollen. Gene flow through seed movement has already been reported along highways and railways in Canada.[36]

Corn (*Z. mays* L.). Sethoxydim-resistant corn produced through tissue culture was commercialized but not widely grown.[43] Imidazolinone-resistant corn was initially developed to be planted in areas where there was carry-over of residual imidazolinone herbicides that would injure conventional corn. Corn is an annual, outcrossing species.[44] Corn has no compatible wild or weedy species in the United States or Canada, so the concern would be movement of the gene to another cultivar or as volunteers in the subsequent crop. Because corn is wind-pollinated, there is potential for cross-contamination of seed stocks.

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Under natural conditions pollen grains mostly fall within the adjacent rows.[45] Other studies indicated that nearly 98% of the pollen is dispersed within 25 m and <2% at 200 m or beyond.[46] Corn has a low level of seed shattering and limited seed dormancy and viability, which prevents feral populations or long-lived seedbanks so volunteers are expected to be problematic only in the year following production.[47] Corn seed is large, so it is not easily dispersed by natural means such as wind or water. Gene flow through admixture of resistant and susceptible seed is likely to occur because of the difficulty of keeping seed segregated in the supply chain of a crop that is as widely grown as corn,[48] especially if crops from herbicide-resistant varieties and -susceptible varieties are dried, cleaned, and stored in the same facilities. There are no specific reports for seed admixture between nonGE herbicide-resistant corn and conventional corn. However, seed admixture has been reported between *Bt* resistant corn and conventional corn[49] and between glyphosate-resistant corn and conventional corn.[50]

Lentil (*L. culinaris* Medik.). Imidazolinone-resistant lentils have been grown in Canada since 2008 and were introduced in the United States in 2010, with most of the production in North Dakota. Lentils are mainly self-pollinated with very low outcrossing. One study reported outcrossing rates between 0.01 and 0.08% measured over three years.[31] There are no compatible relatives of lentil in the United States or Canada, so gene flow would be to another cultivar via pollen or as a volunteer in subsequent crops via seed. Therefore, gene flow via pollen is of less concern than gene flow via seed movement.[31] Lentil seeds shatter during harvest and will volunteer in subsequent crops but can be controlled using herbicides with different modes of action (personal observation). Lentils have little seed dormancy and do not produce long-lived soil seedbanks.[51]

Rice (*O. sativa* L.). Imidazolinone-resistant rice was commercialized in 2002 and by 2010 was grown on more than 50% of the rice production hectares in the Mid-South. Rice is an annual, predominantly self-pollinating species with a reported maximum outcrossing rate of 0.7%.[30] Red rice, a conspecific weedy relative of rice, is one of the most difficult weeds to control in rice production because of its genetic relationship to rice. Hybridization rates between rice and red rice vary with rice cultivar. In one study, hybridization ranged from 1 to 7% for five cultivars but was 52% with a single cultivar.[52] Gene flow between two different imidazolinone-resistant rice cultivars and red rice was reported to be 0.008 and 0.003%, respectively. Gene flow from IR rice to red rice occurred in commercial rice fields in 2002 in Louisiana and in 2004 in Arkansas.[53,54] Reports vary on the soil seed life of red rice, but survival is longer than that of rice.[55] Dormancy of red rice ecotypes ranged from 63 to 97%, with most ecotypes having more than 80% dormancy at harvest.[56] The longer seed life and seed dormancy will maintain the resistance genes in the weed. Imidazolinone-resistant red rice populations will reduce the utility of growing the resistant rice because one of the biggest benefits of the technology was to control red rice.

Sorghum (*Sorghum bicolor* (L.) Moench ssp. *bicolor*). Grain sorghums with resistance to either sulfonylurea herbicides or quizalofop are being developed by DuPont Crop Protection in cooperation with Kansas State University Research Foundation, and the first cultivar with resistance to the sulfonylurea herbicides is expected to be released in 2012.[57,58] The cultivars will initially be released with a single resistance trait but in the future cultivars will likely have the traits stacked. The *Sorghum* genus is a complex group of crop and weed species with differing

levels of cross-compatibility. Sorghum is an annual species that is generally considered to be a self-pollinating, but outcrossing of 30% has been reported.[59] Sorghum is compatible with sudangrass (*S. bicolor* (L.) Moench ssp. *drummondii* (Nees ex Steud) de Wet & Harlan), shattercane (*S. bicolor* (L.) Moench ssp. *arundinaceum* (Desv.) de Wet & Harlan), and johnsongrass (*S. halpense* (L.) Pers.). Another compatible weed species, Columbus grass (*Sorghum almum* Parodi), occurs in the United States.[60] Sorghum and sudangrass are crossed to produce grain and forage varieties. Sudangrass also exists outside cultivation as a weed species. Shattercane is an annual weed species that was derived from wild and/or cultivated sorghum varieties. Shattercane is a noxious weed in at least six states. Shattercane seeds were reported to have 12% viability after being buried for 9 years.[61] Sorghum is one of the progenitors of johnsongrass, which is one of the world's 10 worst weeds[62] and is a noxious weed in 19 states.[60] A hybridization rate of 11% between sorghum and johnsongrass has been reported.[63] Johnsongrass is a self-incompatible, perennial that reproduces by seed and vegetatively by rhizomes. Johnsongrass seed has been reported to have 60–75% viability after 2.5 years in the soil.[64] No fitness differences were measured in hybrids between sorghum and johnsongrass versus either parent.[65] Hybrids between shattercane and johnsongrass are reported.

The gene that provides resistance to quizalofop originated in sudangrass and was transferred to grain sorghum.[58] The resistance gene to sulfonylurea herbicides was transferred from shattercane.[57] The inventors also reported resistance to imidazolinone herbicides. Gene flow via pollen and seed should be expected with the introduction of the resistant cultivars. In addition, resistance to both herbicides in weed populations should be expected to result from gene flow in a short time because there are already weed populations with resistance to the traits.[66−69] The complex hybridization of the *Sorghum* species will ensure that gene flow will occur. There will be crop-to-crop, crop-to-weed, and weed-to-weed species gene flow. The weedy traits of long seed viability and seed shattering in shattercane and johnsongrass will increase the potential of maintaining and moving the genes in the environment. Stewardship to prevent gene flow of these resistance traits will be impossible, and weed populations will quickly make the technology of little consequence.

Sunflower (*H. annuus* L.). Both IR and sulfonylurea-resistant sunflowers are grown commercially. The resistance genes were originally identified in a wild sunflower population in Kansas that been treated repeatedly with the imidazolinone herbicide imazethapyr. The genes that provide resistance to the two groups of herbicides were taken from the same population but from different plants.[70] Sunflower is an obligate outcrossing annual species.[5] Sunflower is compatible with its wild conspecific progenitor and with several other annual sunflower species.[71−73]

To determine if the resistance trait could be transferred to wild species under greenhouse and field conditions, the IR domestic sunflower was crossed with wild sunflower and with prairie sunflower.[74] Imidazolinone-resistant plants were produced with crosses of both species. The researchers concluded that there is a high potential for the spread of resistance and that the fertile hybrids could become a secondary pollen source. In a second study, the same researchers reported that the hybrids were as competitive as the domesticated sunflower; therefore, there would be no expectation that the gene would be lost over subsequent generations.[75] There are no reports of monitoring

gene flow via pollen from the resistant crop to wild sunflower populations. It is likely that gene flow via pollen is occurring but currently is not reported to be causing a weed management problem. Resistant volunteer sunflowers have been reported, but the volunteers can be controlled in the rotational crop, especially small grain crops, to which plant growth regulator herbicides can be applied (Howatt and Thompson, personal communications). Sunflowers with resistance to both sulfonylurea and imidazolinone herbicide classes have been investigated but are not being grown at this time.[76]

Tall Fescue (*F. arundinacea* Schreb.) and Hard Fescue (*F. longifolia* Thuill.). Glyphosate-resistant tall and hard fescues were produced through recurrent selection over multiple generations.[24] The level of resistance is low. The number of genes involved in the resistance and the segregation of the resistance trait were not reported; however, the trait is transferred via pollen.[77] Tall fescue and hard fescue are perennial, predominantly self-incompatible, wind-pollinated species.[78] Hybrids between tall fescue and other fescues have been reported but often have reduced fertility. Tall fescue also is compatible with perennial ryegrass (*Lolium perenne* L.) and Italian ryegrass and can produce fertile hybrids. Hybrids between tall fescue and the ryegrass species (× *Festulolium* Ascherson & Graebner) can backcross with either parent. Hard fescue is compatible with other fine fescue species in the *Festuca ovina* complex, such as slender creeping red fescue (*Festuca rubra* L. ssp. *litoralis* (GFW Meyer) Auquier) and chewings fescue (*F. ovina* L. ssp. *hirtula* (Hackel ex Travis) M. Wilkinson).[79,80] Hybrids of these crosses have various degrees of fertility. It is possible that gene flow will or has already moved the resistance trait among the compatible species, but the low level of resistance has not been reported under field conditions or perhaps there are multiple genes involved, so crossing with a susceptible plant could reduce the resistance level even further.

Other conventionally bred glyphosate-resistant turf grass species are under development. The taxonomy and cross-compatibility among grasses is very complex. Gene flow from perennial turf and forage grasses will likely be one of the most problematic that occurs. The plants survive for several years, and some produce vegetative propagules. Many species of grasses produce feral populations. Interspecific and intergeneric hybrids are reported for many grass complexes, but the compatibility between many species is unknown. It will be very difficult to predict the movement of a herbicide resistance gene via pollen, and movement via seed is probable, especially because the viable grass seed is an international commodity rather than a processed product.

Wheat (*T. aestivum* L.). Imidazolinone-resistant wheat is grown throughout the Pacific Northwest and the Great Plains, where jointed goatgrass (*Aegilops cylindrica* L.), a compatible species, is commonly associated with wheat production. The IR wheat provided the first selective control of jointed goatgrass in the wheat crop. Wheat is predominately self-pollinated, but reported outcrossing rates vary.[81−84] In one study, an outcrossing rate of nearly 7% was reported.[32] Movement of the resistance gene to nonresistant wheat has been documented under field conditions.[85] Wheat and jointed goatgrass hybridize and produce an F_1 that is male sterile but partially female fertile.[86] Subsequent backcrosses to either parent lead to increased fertility. Gene flow from IR wheat to jointed goatgrass was documented in commercial wheat fields in Oregon in 2008.[87] Hybrids and putative backcross plants produced by outcrossing of IR wheat with

jointed goatgrass were found frequently in field surveys conducted in 2009 and 2010 (personal observation). The occurrence of resistant backcross generations in the Pacific Northwest threatens the only selective chemical control for jointed goatgrass in wheat.

■ CONCLUSIONS

It is obvious that herbicide resistance genes move in the environment, and movement is not contingent on whether the gene is a transgene or not. It is time that research moved beyond identification of gene flow to documenting consequences of gene movement. The risk of gene flow needs to be based on the trait, the biology of the crop, and the occurrence of compatible relatives, not on the breeding technique. Conventional breeding and genetic engineering techniques have been used to produce herbicide resistance in many of the same crop species. Furthermore, conventional breeding has been used to produce herbicide resistance in some crop species that have not been genetically engineered, including lentils, sunflower, and sorghum. For at least three crops, triazine-resistant canola, imidazolinone- and sulfonylurea-resistant sunflower, and sulfonylurea-resistant sorghum, herbicide resistance genes were moved from a weed species to a crop species. Economic, political, and social concerns may center on the breeding technique, but the results of gene flow on weed management are the same irrespective of breeding technique.

■ AUTHOR INFORMATION

Corresponding Author
*E-mail Carol.Mallory-Smith@oregonstate.edu; phone (541) 737-5883; fax (541) 737-1589.

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