

# Gene Flow Between Crops and Their Wild Progenitors

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## INTRODUCTION

Gene flow occurs when there is migration of individuals (e.g., seeds) or gametes (e.g., pollen) between populations. Along with drift, selection, and mutation, it represents one of the main evolutionary forces causing changes in gene frequencies. The main effect of gene flow is the reduction of differentiation between populations accompanied by a parallel increase in differences between individuals within a population. The life history and demographic factors are also important in the determination of the effect of gene flow on the structure of genetic diversity (e.g., domestication bottleneck). Here we will briefly illustrate the current knowledge relative to the level, causes, and consequences of gene flow in the specific context of crops and their wild progenitors.

## IMPORTANCE OF GENE FLOW

Wild-to-domesticated gene flow has important implications in relation to the evolution of crop plants. After domestication, gene flow in the centers of origin can partially restore the low genetic diversity included in these first domesticated populations. For instance, the differentiation of domesticated barley from the Himalayas and India compared to the Near East germplasm is probably due to introgression from Asian populations of wild barley (*Hordeum vulgare* ssp. *spontaneum*) after domestication.<sup>[1]</sup> Gene flow still plays an important role as a source of new alleles for domesticated crops where traditional farming continues to be practiced.<sup>[2]</sup>

Besides this natural gene flow, we should also consider the human-driven gene flow from wild to domesticated populations due to modern plant breeding, whereby useful wild alleles are integrated into the domesticated crop species. Many sources of resistance to pathogens and parasites have been introduced from wild germplasm by breeders and, more recently, genes relating to quantitative traits, such as fruit size in tomato and grain yield in rice.<sup>[3]</sup> Gene flow from domesticated to wild populations is also an important issue relative to the release of transgenic

varieties because of the potential effect on the genetic diversity of the wild relatives and the possible production of new aggressive weeds.

## FACTORS AFFECTING GENE FLOW

Table 1 summarizes the various factors affecting gene flow. In order to exchange genes, individuals need first to be sexually compatible; in other words, gene flow occurs between populations of the same biological species, or between populations of closely related species (introgressive hybridization), among which hybrids are partially fertile and can yield fertile progeny. In most cases, crops and their wild progenitors belong to the same biological species.<sup>[4]</sup> However, in some cases domesticated crops and their progenitors belong to different biological species, in particular when domestication has involved polyploidization and/or interspecific hybridization, such as is seen for bread wheat (*Triticum aestivum* L.), a hexaploid originated by hybridization between a domesticated tetraploid and the wild diploid *Aegilops tauschii*. In these cases, even with the reproductive barrier due to the different ploidy level between the domesticated and wild progenitors, hybridization can still occur and can produce fertile progeny.

Gene flow between wild and domesticated populations is also limited by their phenology, geographic distribution, and spatial arrangement. Gene flow can occur if plant populations have overlapping flowering periods and are at a suitable distance, depending on the seed and pollen dispersal ability and the environmental factors such as wind, humidity, and biotic factors (pollinators and other animals favoring seed dispersal). Pollen and seed dispersal rates are strictly correlated with distance, such that dispersal rapidly decreases with distance to a very low value (e.g., within 50–200 meters), although a relatively low level of dispersal may occur even over very great distances (e.g., several kilometers). Evidence of gene flow between wild progenitors and domesticated crops has been documented for almost all crop species, including allogamous, autogamous, and vegetatively propagated



**Table 1** Factors related to gene flow between wild progenitors and domesticated crop populations

Factors	Key aspect(s)	General consequences
<i>Prezygotic</i>		
Reproductive barrier I	Pollen competition, sexual compatibility	Partial incompatibility will reduce gene flow. Pollen competition may reduce gene flow or increase it just in one direction.
Geographical distance	Pollen/seed dispersal ability	Gene flow occurring only within the center of origin of a crop or within the (sympatric) areas of distribution of wild populations
Phenology	Genotype x environment interaction	Gene flow occurring only if flowering period is overlapping in the areas of sympatry
Dispersal ability	Biotic and abiotic factors affecting dispersal/breeding and propagation system	Rate of gene flow higher in allogamous than autogamous or vegetative propagating species
Population size	Relative size of wild and domesticated populations	Different sizes of domesticated and wild populations may lead to one-way gene flow.
Weedy populations	Presence of uncultivated fields and disturbed areas. Weed control.	Gene flow will be limited by weed control and favored by the presence of disturbed or uncultivated fields.
<i>Postzygotic</i>		
Reproductive barrier II (Hybrid fertility)	Different ploidy, chromosomal mutation	Partial sterility will reduce gene flow.
Selection in wild populations	Level of differentiation between wild and domesticated/genetic control of the domestication syndrome	Selection will act only in the segregant progeny with a lower fitness of progeny homozygous for domesticated alleles (when wild alleles of the domestication syndrome are dominant).
Selection in domesticated populations	Farmers' conscious selection (e.g., seed)/agronomic practices/genetic control of the domestication syndrome	Selection will limit gene flow as a post-zygotic reproductive barrier by reducing the fitness of first generation hybrids (when domesticated alleles of the domestication syndrome are dominant).
Breeding system	Effective recombination (out-crossing and heterozygosity)	In allogamous species, introgression will be limited only for selected loci; in autogamous species, introgression will also be limited for loci linked to selected loci (hitchhiking).
Demography	Population size (bottleneck)	Reduced population size will increase hitchhiking and will extend the effect of selection following gene flow events.

species. One of the very few exceptions is the strict selfing species *Arachis hypogea*.<sup>[2,5]</sup> According to a theoretical model, the amount of gene flow needed to prevent the genetic isolation and differentiation of populations and their independent evolution has been shown to be relatively low, about one migrant per generation,<sup>[6]</sup> suggesting that even if the rate of dispersal and out-crossing is very variable among and even within species, gene flow is expected to be an important evolutionary force for most species.

Nevertheless, the reproductive and the propagation systems of domesticated crops represent crucial factors affecting the rate of gene flow between wild and domesticated populations. Clearly in an allogamous species the higher out-crossing rate results in a much higher frequency of domesticated-to-wild hybridizations than in an autogamous species. For vegetatively propa-

gated crops, such as fruit trees, gene flow from wild to domesticated populations will not occur unless farmers/breeders use sexual reproduction to obtain new cultivars. In contrast, gene flow will be very intensive in the opposite direction (domesticated to wild) leading to unilateral gene flow (one-way migration). One-way migration may also occur in sexually propagated species. For instance, in the common bean (*Phaseolus vulgaris* L.), the gene flow from the domesticated to the wild populations has been found to be about 3–4-times higher than that in the opposite direction.<sup>[7]</sup> In this case, one-way migration can be promoted by the presence of differences in population sizes between the wild and domesticated populations because the domesticated genes will gradually increase in the wild populations, while in the domesticated populations, the few immigrant genes will be diluted and hence have a very low effect on gene frequencies.

Farmers' fields usually contain a large number of individuals, while wild populations close to such fields will often be made up of a very small number of individuals. Consequently, hybridization events will be more frequent when wild plants are the maternal parent than when they are the paternal parent.

Farmers themselves can also affect the rate of gene flow from wild to domesticated crops. Indeed, in several cases traits related to the domestication syndrome are recessive, and, hence, first generation hybrids are usually more similar to the wild plants, and are thus easily detectable. For this reason farmers can discard first generation hybrids by choosing the seeds for the planting of the next generation, producing an effect analogous to that of a post-zygotic reproductive barrier. Gene flow is also limited by weed control and intensive cultivation (e.g., absence of uncultivated areas), which eliminate wild plants growing within and around the crop. It is likely that in the early ages of agriculture the opposite situation would have occurred, with the predominant direction of gene flow being from wild to domesticated populations because of the smaller crop populations and the lower differentiation between wild and domesticated forms.

In some cases, hybridization between wild and domesticated populations leads to the development of weedy populations<sup>[1,7]</sup> that can be found in farmers' fields or that can colonize other disturbed environments (i.e., field borders, abandoned fields, roadsides) and present intermediate characteristics between wild and domesticated forms.<sup>[4]</sup> These weedy forms can also originate as "escapes" from cultivation. In either case, their presence facilitates the exchange of genes between domesticated and wild populations.

## GENE FLOW AND SELECTION

In the previous paragraphs we have demonstrated that gene flow between wild progenitors and domesticated populations is a significant phenomenon in almost all crop species. However, wild progenitors and domesticated crops maintain their distinct phenotypes even in sympatry. This suggests that selection has a prominent role in limiting the introgression between the wild and domesticated forms. However, even if there is little direct evidence, selection is likely to vary greatly between the wild and the domesticated environments, as among the different genes involved in the control of the domestication syndrome, and among different crop species<sup>[8]</sup> and different agronomic systems. As previously indicated, for several key traits of the domestication syndrome, the wild alleles are dominant (i.e., shattering, dormancy, growth habit, photoperiodic sensitivity), and the first generation

hybrids are more similar to the wild than to the domesticated forms. Considering also that hybrids may show heterosis, the first generation hybrids will have a much higher reproductive success in the wild environment than in the domesticated environment, where farmers may easily eliminate them by selecting the seeds or because the progeny will not be included in the next harvest due to shattering or dormancy. Consequently, in the wild environment, selection against domesticated alleles will mainly occur in the segregating progeny following the  $F_1$  generation, thus favoring the introgression of genes from domesticated populations because of recombination. Both selection and asymmetric gene flow will favor the introgression from domesticated to wild populations rather than in the opposite direction; this may explain why in domesticated populations low levels of introgression from the wild progenitors are often seen,<sup>[1,7]</sup> even for allogamous species such as maize.<sup>[8]</sup>

Asymmetric gene flow and different types of selection can be considered as possible causes of the displacement of genetic diversity in the wild progenitor populations, as has been observed in cotton and rice,<sup>[5]</sup> and to a lesser extent in the common bean.<sup>[7]</sup> In addition to the target loci (i.e., genes for domestication traits), selection may affect the surrounding chromosome regions because of linkage (hitchhiking). Indeed, in allogamous species, which present a high level of heterozygosity, selection will affect (by elimination of the migrant alleles) only loci under selection because of recombination. In contrast, in autogamous species, selection will indirectly reduce the introgression for neutral loci linked to those under selection (hitchhiking). The extent of hitchhiking can be very low (a few hundred base pairs) in allogamous species such as maize,<sup>[9]</sup> but can also become very large (several cM) in autogamous species, because the reduction of the out-crossing rate drastically reduces the level of effective recombination. In addition, the extent of hitchhiking also varies according to the level of recombination in different parts of the genome, the demography of the population (e.g., the existence of bottlenecks in the evolution of the population versus the species as a whole), and other evolutionary factors such as selection.<sup>[10-12]</sup>

## CONCLUSION

Gene flow and introgression between domesticated crops and their wild progenitors occurs in most cases, although its intensity and effects are very variable in relation to any given species (of crop and its wild progenitor), its life history, the environment (space and time), genome location (in relation to domestication syndrome genes), the agro-ecosystem, and human activities. Knowledge of





this subject is currently growing rapidly because of the interest in evaluating the potential effects of transgene release into the environment and the role of wild progenitor genetic diversity in conservation and breeding.

**ARTICLES OF FURTHER INTEREST**

- Agriculture and Biodiversity*, p. 1
- Biosafety Approaches to Transgenic Crop Plant Gene Flow*, p. 150
- Biosafety Science: Overview of Plant Risk Issues*, p. 164
- Breeding: Incorporation of Exotic Germplasm*, p. 222
- Crop Domestication: Fate of Genetic Diversity*, p. 333
- Crop Improvement: Broadening the Genetic Base for*, p. 343
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- Molecular Evolution*, p. 748
- Molecular Technologies and Their Role Maintaining and Utilizing Genetic Resources*, p. 757
- Population Genetics*, p. 1042
- Quantitative Trait Locus Analyses of the Domestication Syndrome and Domestication Process*, p. 1069
- Transgenic Crop Plants in the Environment*, p. 1248

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