Gene flow between crops and related taxa — some case studies

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Abstract

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Gene flow is understood here as the movement of genes among sympatric or neighbouring populations of crops and related taxa or the introduction of genes from related taxa into the recipient genepool of a crop, i.e. it describes the processes also known as introgression.
We must differ between artificial or induced and spontaneously occuring gene flow.
Artificial or human-caused gene flow has a rather long history in plant breeding and applied genetics and is documented by the efforts to use wild or weedy relatives of crops as donors of economically important characters. The successful breeding e.g. of disease resistant cultivars in many crop species by the transfer of resistance genes from wild taxa are well-known examples. The spontaneous occurence of gene flow between crops and relatives however is a poorly understood phenomenon and has been described only anecdotically in most cases.
There were gene flow processes between wild taxa and crops in the past which led to obvious evolutionary changes, e.g. to the formation of new species (hexaploid wheats). Actual gene flow between crops and relatives can be detected only by careful field studies.
In general such gene flow is a rare event and can happen only in crops if their primary genepools includes related taxa and if crop and relatives are more or less sympatric. In Europe the possibility of gene flow between crops and relatives is greatly restricted, because European crops are mostly exotic plants from other regions of the world which lack relatives in the European flora.
Some examples of gene flow occuring on different taxonomic levels had been described in some detail for carrot, beet, alfalfa, rice, foxtail millet and *Chenopodium* and the importance of ethnobotanical observations for the understanding of gene flow processes is underlined.

Gene flow will be defined for our purpose in a somewhat restricted sense and will be understood as the exchange of genes between sympatric or neighbouring populations of crops and related taxa or as the introduction of genes from related taxa into the recipient genepool of a crop or vice versa. Such processes also known as introgression.

We must differentiate between artificial or induced and spontaneous gene flow:

Artificial gene flow

This introduction by humans of foreign genes into the genepool of a crop is a process which has been applied by plant breeders and applied geneticists for almost 100 years. By this method desirable characters not present in the crop itself are transferred to the crop's genepool. Such breeding programmes focus mainly on traits like resistance against biotic and abiotic environmental factors and on improvement of quality of the crop in a broad sense. Many resistant or improved cultivars had been selected by these means and the use of wild relatives in plant breeding is well documented (Harlan 1976, Watson 1970, Ladizinsky 1989). Two almost classical examples may illustrate this approach: *Aegilops* species had been successfully used as donors of disease resistance characters. Leaf rust resistance from *A. umbellulata* and yellow rust resistance from *A. comosa* were transferred to *Triticum aestivum* with the help of cross breeding and complicated chromosome manipulations (Sears 1956, Riley & al. 1968). The high soluble solids content (mainly sugars) of a small wild Peruvian tomato, *Lycopersicon chmielewskii*, has been used for the breeding of new tomato cultivars with an increased dry matter content (2% more than the standards) by means of species hybridization and repeated backcrosses and subsequent pedigree selection. An increased dry matter content is highly appreciated by the food industry (Rick 1974, Iltis 1988). Thus artificial gene flow implies very often a considerable economic success!

At least some of these induced gene flow processes, e.g. between *Aegilops* and *Triticum* species, have been reported as naturally occuring events also, and the prevention of these evolutionary processes during the isolated *ex situ* reproduction of genebank accessions is one of the main arguments in favour of *in situ* conservation of plant genetic resources (Vellvé 1993). Artificial gene flow will become much more important in the future, because the new molecular techniques will allow the use of a much broader range of gene donors than formerly possisble.

Spontaneous gene flow

Gene flow can happen spontaneously only when crop cultivation and the distribution of its relatives are more or less sympatric or at least overlapping locally, and if they are cross-compatible and produce at least somewhat fertile offspring. This means that gene flow will occur mainly within the primary genepool of a crop species according to the classification of Harlan & de Wet (1971). Crops in which domestication resulted in true speciation and strong reproductive isolation (like *Vicia faba, Allium cepa*), cannot be involved in gene flow processes.

There are prehistorical gene flow events which led after subsequent chromosome doubling to the evolution of new amphiploid crop species. I may mention only the well-known examples of the hexaploid common wheat, *Triticum aestivum* (its D genome came from the SW Asiatic *Aegilops tauschii,* whereas its A and B genomes were provided by the tetraploid wheats), and the amphiploid *Brassica* species, e.g. the Ethiopian cultigen *B. carinata*, which combines the B genome of *B. nigra* ($n = 8$) and the C genome from the cultivated *B. oleracea* ($n = 9$).

Actual gene flow – although expected to be a rather widespread phenomenon – is still a poorly understood and badly documented process. It can be detected only by careful field studies and genetical and biochemical analyses. There are few representative studies (mainly for non-European examples) and mostly gene flow had been described anecdotically, in many cases not substantiated by unambiguous data (see also Doebley 1989).

In Europe the possibilities for gene flow between crops and wild relatives is rather restricted. Especially the more important cultivated crops in Europe are alien plants geographically widely isolated from their relatives (maize, potato, tomato, cucumber, cucurbits, spinach, beans) or come into contact with wild relatives in very restricted geographical areas, e.g. the *Brassica* crops, barley, rye, wheat, grape vine, or beet. A rather broad sympatric occurence of crops and relatives is true for some forage grasses and legumes, forest trees and some fruit trees or shrubs.

Recently the gene flow problem became a topic of public interest because of the supposed risk with the cultivation of transgenic crop plants to contaminate the wild flora with undesirable genes through gene flow to the wild relatives (Kapteijns 1993, Wöhrmann & Tomiuk 1993, Sukopp & Sukopp 1994, Brandt 1995).

Gene flow can occur at different taxonomic levels. For the sake of convenience the following types can be distinguished: intraspecific, interspecific and intergeneric. We must be aware however that this grouping may be very much influenced by the taxonomic concept applied by the researchers. The extent of gene flow is governed by the breeding systems of the partners involved, the availability of pollinating agents, the planting design of the crop, the distribution pattern of the partners, the distance between them and their population sizes (Levin & Kerster 1974, Klinger & al. 1992). Even for the same partners it depends strongly on local conditions. The same is true for the direction of gene flow, which can go to and from the crop or in both ways.

The selection of the following examples of gene flow is somewhat biased by personal preferences and by the attempt to concentrate on European plants. Other genera like *Cucurbita, Helianthus, Gossypium, Phaseolus, Pennisetum* or *Sorghum*, that are also relevant to this topic have had to be omitted.

Infraspecific gene flow

Daucus carota

The carrot is a very variable species, distributed in Europe, N. Africa and W. Asia, and introduced into other continents; it is represented by a dozen intergrading (and grouped into two complexes) subspecies, one of which is the strictly biennial cultivated subsp. *sativus* (Heywood 1968, Small 1984), others are true wild or weedy taxa and all of them are obviously interfertile. Crossings can easily happen when the cultivated carrot is grown for seed production and it is reported from Canada that the production of uncontaminated seeds of subsp. *sativus* is very difficult because of the frequent occu rence of the introduced weedy subsp. *carota* (Small 1984). Likewise in Europe, where bolters, i.e. single flowering individuals in the vegetable stands of the crop, are considered as products of gene flow from the widespread subsp. *carota*. Wijnheijmer & al. (1989) described the morphological intermediate position of these bolters between the cultivated crop and the wild subspecies in the Netherlands, and demonstrated gene flow in both directions by the analysis of the descendants of plants of both subspecies which have grown close together to avoid such cross-pollination, frequent mowings of road verges and ditch sides is nowadays requested officially in the vicinity of seed fields of carrots in the Netherlands.

Beta vulgaris

A similar situation has been reported for the beet. The noxious annual, early-flowering beets are widely distributed over parts of Britain, Ireland, Belgium, France and Spain. They are interfertile with cultivated beets, vital pollen can be transported up to 1000 m (Kapteijns 1993, Boudry & al. 1993). In northern France these weedy beets proved to be the products of accidental pollinations of cultivated beets (mainly sugar beets) grown for seed production, by adventitious wild beets, which occur rather frequently in the southern seed-producing areas. Hybrid seeds are then transported together with the true beet seeds to the sugar beet producing regions and contaminate these fields (Boudry & al. 1993). An increased salt tolerance of these bolter seedlings, which was described by Evans & Weir (1981) may indicate however that at least sometimes the bolting plants could have been the results of gene flow between coastal wild populations of *Beta vulgaris* subsp. *maritima* and cultivated plants of the species.

Oryza sativa

For many years spontaneous hybrids between cultivated rice and weedy form of *O. sativa* (and of other wild *Oryza* species) had been reported, mainly from S. and S.E. Asia. Weedy rices are often mimicking the cultivated plants and make weeding difficult. To overcome this, cultivars had been bred with red leaves to distinguishthem from the weed plants. Afterwards red-leaved weeds appeared and had been interpreted as products of gene flow between the crop and the weed (Harlan 1982). It is however also possible, that they were selected from the original weed population and that their spread was brought about by the high selective advantage that these crop colour mimics had. But the phenomenon of gene flow in rice has been studied very thoroughly in the USA by Langevin & al. (1990). They used a red weed variant introduced from India to North America long ago, which infests most of the rice fields in the Southern US. Seeds of this weed were collected in fields of 6 different cultivars growing under uniform conditions (with replicate fields), were grown in the next year and studied thoroughly for morphological characters and electrophoretically in regard to several enzyme systems. Hybrids could be detected among the offspring of the weed plants from all cultivars, but with varying frequencies from 1 % to more than 50 % by means of morphological markers and the enzyme heterozygosity (interlocus heterodimers). Most of the hybrids had been F1 plants. However, among the weed/cultivar hybrids from 'Nortai' obviously backcross offsprings dominated, which could explain the high percentage of these hybrids and the morphological convergence which they showed to the crop parent, whereas all other hybrids are significantly different from both parents. Backcrossing are favoured in fields of 'Nortai', because this late-flowering variety has a similar flowering period as the hybrids, which is however delayed in comparison to the true weed rice and to the other cultivars. This means that only in late-flowering cultivars grown in the United States the formation of long-lasting hybrid populations, hybrid swarms and extensive introgression is possible (both of weed genes into the crop and of crop genes into the weed).

Humulus lupulus

The wild hop has a holarctic distribution and is classified into several allopatric varieties, occuring in Europe, E. Asia, W., E. and Midwest North America respectively. Gene flow from the local wild forms into the cultivars had been reported in the USA and Japan by the analysis of micromorphological characters of the female cone and historical data of hop cultivation in these countries (Small 1984). Also in Germany hop growers suspect that deterioration of their plantations is caused by the local wild variety. In the neighbourhood of the plantings male wild plants are regularly eradicated.

Helianthus annuus

The possibility of an infraspecific crop-weed gene flow was experimentally studied for the sunflower. Arias & Rieseberg (1994) analyzed by means of a similar design as later reported for *Raphanus* (Klinger & al. 1992) frequencies of gene flow from a cultivar to wild races of *Helianthus annuus*, using an isozyme allele, homozygous in the cultivar, as marker. Gene flow frequencies ranged from 0 to 0.60 and a total amount of 10 % of hybrids could be detected in the analyzed progenies. This study also showed that the distance of the wild plants from the cultivated fields, and the spatial arrangement of the wild susbpopulations greatly affected the amount of gene flow.

Phaseolus vulgaris

Recent field explorations (Beebe & al., in press) revealed the existence of large crop-weed complexes in the common kidney bean with genetic exchange between local cultivars, weedy types and wild forms in Peru and Colombia. Stabilized non-segregating weedy genotypes with crop characters, as well as still segregating populations indicate recurrent crossing. In other words, such gene flow processes are still occuring and happened in the past, too. the importance of such complexes for conservation and breeding should not be underestimated.

Gene flow between European sympatric conspecific wild and crop plants, in grasses (*Poa, Festuca, Dactylis, Lolium* spp.) or forage legumes (*Trifolium pratense, T. repens, Lotus corniculatus, Lupinus* spp. etc.) with a less distinct crop/relative differentiation are still more candidates for gene flow processes; but, to my knowledge, this has never been analyzed in detail.

Interspecific gene flow

Medicago sativa alliance

This is a very complex, taxonomically controversely classified group with diploid and tetraploid taxa. The earliest forage domesticate, *M. sativa* in the strict sense, is a tetraploid taxon. Hybridization and hybrid swarms between the crop and wild relatives, mainly *M. falcata*, as well as between several wild taxa of the complex, have been frequently reported. Some of the more or less stabilized hybrid populations have been given species names by Russian authors (e.g. *M. polychroa, M. hemicycla*). In Europe the *falcata* ×

sativa hybrids are widespread and at least the F_1 hybrids can easily to be recognized by their dirty-greenish flower colour. Hybrid populations are established however also rather distantly from the parent populations and have apparently a selective advantage on sandy soils with an open, more or less disturbed vegetation. Such rather stable stands can be observed in Germany near the Baltic sea. They are also described from Ireland and S. England in similar habitats (Stace 1975). Small (1981, 1984) showed that most of the Turkish ruderal populations of alfalfa represent such hybridization products also. By backcrossing contamination of the cultivated alfalfa can occur and breeders especially are of the opinion that all cultivars of alfalfa outside of its presumed centre of origin in the Near and Middle East contain genes of the wild taxa of the complex, which had been also deliberately introduced into the crop through breeding programs. The controversial data on the fertility of the *falcata* x *sativa*-hybrids may be explained by the contribution of diploid as well as of tetraploid *falcata* strains, the latter are more widespread in northern parts of Europe.

Raphanus sativus group

Several examples of gene flow between crop and wild plants are known in the *Cruciferae*. Those from the genus *Brassica* are considered elsewhere in this volume in more detail. Another case is the self-incompatible, freely crossable pair of species *R. sativus* and *R. raphanistrum*, the latter a widespread weed on soils with a low pH. Bolters in radish cultivation, yellow-flowering plants in fields of fodder radish (convar. *oleifer*), and white-coloured flowers of *R. raphanistrum* (at least in Northern areas of its distribution) had been interpreted as products of such mutual gene flow. In California, introgressed *R. sativus* developed aggressive weed populations (Panetsos & Baker 1968).Recently; the effect of different distances between the wild and the cultivated cross-partner and of the population size of the wild one was analyzed in detail (Klinger & al. 1992). Only by careful consideration of both parameters the actual introgression rate will be understandable.

Setaria italica group

Gene flow maybe important even in more or less strictly autogamous plant species, as analysed in detail for the foxtail millet and its wild progenitor *S. viridis* (also sometimes subordinated as subsp. *viridis* to *S. italica*). Natural outcrossingwithin these two taxa occur at between 0 % and 2.2 % (if different panicles are bagged together up to 4.0 %) and interspecific hybridizations occur partly in the same order of magnitude, but was different according to the distances of the partners and the design of the experimental plots (Bougry & al. 1993). Nevertheless offtypes observed regularly in fields of cultivated foxtail in France – their seeds having been grown for the analysis of the offsprings – proved to be of hybrid origin from crosses between *S. italica* and *S. viridis*; they segregate for one or all of the selected differential characters and according to the segregation ratios could be interpreted as F_2 or F_3 plants. The RFLP pattern of their cpDNA revealed that in most cases *S. viridis* was the female parent, only once was the crop species the female parent of the hybrid. Most susceptable for gene flow contamination are obviously late flowering cultivars of *S. italica*, because the reproductive productivity of the strongly tillering *S. viridis* increases with the season. Stabilisation of the gene flow introgressants led obviously in the past to the evolution of the more vigorous weedy subspecies *S. viridis* subsp. *pycnocoma (S. viridis* var. *major)*, with which the offtypes and their offsprings had been identified (Bougry & al. 1993).

Hordeum vulgare sensu lato

There is a rich literature which documents the gene flow between barley and its wild ancestor *H. spontaneum* (mostly included within *H. vulgare* as subsp. *spontaneum*) (Zohary 1964, Harlan 1976, Hammer & al. 1985, von Bothmer & al. 1990) and which had led even to morphologically striking introgressants, formerly described as species *(H. agriocrithon, H. lagunculiforme)*. Within Europe wild barley is reported only from Crete, thus gene flow can not have any major impact on the barleys in Europe.

The same situation is true for other crops from the New World. There gene flow between teosinte and corn (Doebley 1990), between the Peruvian wild tomato *Lycopersicon pimpinellifolium* and *L. esculentum* (Rick & al. 1974), between wild and cultivated cucurbits (Decker & Wilson 1987, WILSON 1990, Wilson & al. 1994) and between wild and cultivated cotton taxa (Brubaker & al. 1993) had been studied in detail.

To these we should add the following example from N. America which has been recently analysed:

Chenopodium quinoa group

This South American grain chenopod is in its home countries accompanied by a weedy subspecies *milleanum* and putative crop/weed hybrids can frequently be found, but they cannot directly identified in progeny tests, because of the absence of molecular differentiations (Wilson & Manhart 1993). The problem of gene flow had been studied in Washington state, where quinoa cultivations is practised. Another closely related weed species from the same subsection *Cellulata (C. berlandieri)* is widely distributed and occurs as weed in these quinoa fields. Seeds of *C. berlandieri* had been collected at several other places in Washington and within the quinoa stands; the progenies were analyzed in regard to morphology, enzyme spectra, and pollen fertility. Hybridity could be documented with one insignificant exception only among the progenies of weeds associated with the quinoa cultivation: 32.8 % of 262 offspring tested carried an LAP 1m allele which is fixed to *C. quinoa*, were morphologically intermediates and had a low pollen fertility. This high percentage of gene flow from the crop to the weedy relative could be explained (1) by the population structure of the parents (large pure stands of the crop, single individuals of the weed with the same flowering time) which produced a disproportional pollen load to pollinate the weed and (2) by the facultative outcrossing breeding system of *C. berlandieri*. This example can be used as a model for what happens in South America where the same population structure can be observed for quinoa and its weedy companions and where crop/weed hybridization and backcrosses could result in more or less continuous variation between the crop and theweed taxa (Wilson & Manhart 1993). Presumably the same processes are responsible for the variation pattern of other crop/weed complexes, too.

Intergeneric gene flow

Also in the case of this type of gene flow we have to noteonce more the lack of thoroughly worked out cases. Reports on intergeneric gene flow refer hitherto mainly to members of the grass family.

Triticum and related genera

Hybridization between wheat and *Aegilops* species has been observed several times. Zohary (1971) noted spontaneous hybrids between durum and also soft wheat and *Aegilops tauschii*, the D genome donor, from Iran, and similar reports can be found in the Russian literature. Other species can be involved too, in Italy there occurs seldom the hybrid between *Aegilops geniculata* and *Tr. aestivum* (× *Aegilotriticum triticoides*), more frequently distributed is the generic hybrid *Haynaldoticum sardoum*, i.e. *Dasypyrum villosum* × *Triticum durum*, with localities on the Italian islands, in South Italy and the Tuscany (Pignatti 1982). Nothing is known about the natural reproduction of the hybrids and if a gene flow can be postulated by backcrossing.

Festuca spp. and *Lolium* spp.

Hybrid progenies of species of these genera are named × *Festulolium.* They have been reported from several European countries, e.g. from England, France, Germany etc. Mostly the hybrids occured near cultivation of one of the parents (Stace 1975) so that one can assume that crop/wild species crosses took place. Differences in the cross-compatibility of the parental species, male or female sterility of the hybrids and their perennial growth offer the possibility to gene flow between the forage crop and sympatric wild taxa from the other genus, but this had never been analyzed in detail. *Festuca pratensis* × *Lolium perenne* (less often *L. multiflorum*) seems to be the most frequently occuring hybrid. There are also recently released fodder grass cultivars in Germany, belonging to the hybrid genus × *Festulolium.*

Ethnobotany, fruit trees and gene flow

Introgressions between wild and cultivated fruit trees, especially among the temperate genera, have been frequently reported. Zohary & Hopf (1993) summarized such data and draw the attention to the fact that regular grafting of cultivars to spontaneously growing individuals of wild relatives — as it is done in the Near East — enhances gene flow between fruit crops and relatives. It should be emphasized that close cooperation between ethnobotanists and crop evolutionists can contribute distinctly to a better understanding of some crop/wild relative relations. I may mention a few data from our own experience, mainly from Georgia: grafting apple cultivar scions on wild growing trees of *Malus orientalis* is an old tradition especially in the province of Racha in Georgia and will be undertaken by farmers, after a child is born to them. Wild trees of *Prunus cerasifera* or other fruit trees are spared from clearings and cuttings in the neighbourhood of settlements and thus come into close contact with planted fruit trees of the same genus. At least in former decades some primitive local races of vine had been cultivated which had retained the dioecious condition characteristic of the wild *V. sylvestris*. Only female plants were grown and for pollination flowering twigs of male *V. sylvestris* had been collected from neighbouring wild localities and deposited among the female plants (Ramishvili, pers. comm.). Gene flow however must have been extremely rare by this method because only in very rare cases was propagation of vines by seed practised. The reverse direction of gene flow may happen sometimes and perhaps the occurence of light-coloured berries of *V. sylvestris* in Dagestan could be explained by this manner (Pirmagomedov 1982). Often wild plants of fruit trees or of wild relatives are transplanted into the orchards in Georgia, are then growing side by side with cultivars and gene flow becomes unavoidable. Hammer (pers. comm.) observed in Calabria that along their regular routes shepherds used to graft pear cultivars on the wild individuals of *Pyrus amygdaliformis* and thus confirmed for Italy the custom described already by Zohary (1971). These and other ethnobotanical data may help to understand some observations in regard to distribution, taxonomy, hybridisation and introgression of fruit crops and relatives which had otherwise remained rather mysterious.

Concluding remarks

It has been shown that even in Europe where many crops do not have any wild relatives, gene flow between crops and their closely related wild taxa occurs not infrequently. The study of gene flow processes is important for solving practical problems (release of transgenic plants, *in situ* conservation, contamination of crops) as well as theoretical problems (crop and weed evolution, phylogeny and differentiation of crop-weed complexes). Especially for Europe there is still a serious lack of detailed analyses of such gene flow events, although their results had been observed many times and material for such research is easily available. The idea that in Europe also, unrestricted gene flow between crops and their wild relatives can contribute to the further evolution of the crop species and the transfer of desirable traits into the crop remains to be proved. It could be expected in cases where the crop occurs sympatrically with large spontaneous populations of the same species, and where breeding system and life span of the partners favour gene flow processes, e.g. in forage grasses or legumes (like *Trifolium, Medicago*). Gene flow can have detrimental effects to the crop only in seed crops and especially for seed production (e.g. *Daucus, Beta* etc). Gene flow in the reverse direction may adapt the weed better to human-made habitats (e.g. *Oryza, Setaria* etc). In general there is agreement among evolutionists that for the sessile higher plants gene flow between populations of the same species as well as between different ones is 'too restricted to have any significant effect beyond the local population' (Grant 1985). That has been questioned and may be not fully true especially for the crops and their relatives, because human interference may broaden these effects to a larger scale, simply by transporting contaminated seed or plant material by humans.

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