Methods for Risk Assessment of Transgenic plants
IV. Biodiversity and Biotechnology
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Vertical gene flow

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1. Introductory remarks

By comparing potential and actual risks in both fields we need a clear view of the similarities and differences. Raamsdonk 1993 has given a scheme of gene flow, whether natural or influenced by human activity. It clearly shows that most pathways of gene flow are both natural and also strongly influenced by agriculture and breeding. But there is one notable exception: Transformation is something quite new. It is now possible to jump over the limits of species, genera and even families and orders in a much easier way. Let's not forget that there is something universal about the sequences used for transformation and often lay persons are puzzled by expressions like "a fish gene" for instance. They have not the knowledge how to judge the novelty of such transformation. But this statement also counts for the experts: Position effects and pleiotropic effects after transformation have to be considered in all cases, this is why we need to think about new risk assessment methods for genetic engineering. But we should always be aware of the fact that classical breeding is also dealing with the introduction of genes to a crop plant. The big difference is that these genes introduced in classical breeding are always belonging to some relatively close parents, transformation is always done in the relatively narrow environment of interbreeding species groups. But again we have to consider all cases in classical breeding, where single gene mutations or the change of only a small number of genes has dramatically changed morphology, growth and yield of a crop, especially in the case of maize and wheat. Considering the possible escape of transgenes to wild relatives there are parallels between classical breeding and genetic engineering regarding the processes of vertical gene flow, but the results may be different in the case of a possible escape of a novel transgene having new ecological potential.

2. Outcrossing on neighbouring natural area: gene transfer and cross-hybridisation

Genetic engineering is obviously different and more powerful than traditional breeding. The question is whether this difference and power translate into greater, more serious risks, or whether the risks are different from those of traditionally bred products. At this early stage in the use of the technology, it is impossible to answer this question with certainty.

Gene escape depends on many ecological and agronomical factors: whether or not the crop is allowed to flower; how far its pollen travels, success of fertilisation, extent of seed dispersal, seed survival and so on. Even if a gene does escape, its future may be bleak if it handicaps its new host (Young 1989).

The probability of successful pollination depends on a great number of interrelated factors, such as: level of pollen production of (transgenic) plant, rate of self- and cross-fertilisation of receptor plant, rate of dispersion of donor pollen, properties of pollinating agents, spatial distance between pollen donor and wild recipient population, local density of recipient population, difference in phenology between crop and wild population.

But there are more barriers to hybridization:

Families with economically important crops often show low hybridization barriers. Simmonds (1976) gives an overview of the history of major and minor crop plants. It appears that hybridization was a common technique in the breeding history of 31 out of 39 families, and in 70 out of 90 genera, i.e. 75-80 percent of the cases.

Adaptative traits acquired under domestication usually have no selective value in natural habitats, and sustainable genetic introgression from domestic plants to wild relatives is rare. Gene exchange is more known in the other direction, from wild relatives to crops (Newmann 1990).

There are more barriers to hybridization (Hadley and Openshaw,1980)

a) External barriers such as spacial, ecological, phenological, mechanical and pollination ecological isolation phenomena.

b) Internal barriers such as prevention of fertilisation, hybrid weakness or inviability, hybrid sterility, hybrid breakdown in the F2 generation.

c) There are also barriers to pollen dissemination: Pollen viability, pollen sedimentation, distance of receiving plants, separation of anthers and stigmas by various contrivances.

Sexual reproduction occurs among crops, weeds, and wild plants within the distance that pollination can occur and where the plants are sexually compatible. Because pollen transfer is mediated primarily by wind and insects, the distance within which pollination can occur is affected by wind turbulence, speed and direction and/or the flying range of insects (Regal, 1982). Another factor is the longevity of the pollen itself. Generally, pollen is viable only a short time ; that is, it is capable of fertilising eggs only within a time period of minutes, hours or days after being produced.

Of particular importance is the aerial transport of pollen grains. With plants that are pollinated by insects, one approach is to follow the pollinator. Insect such as honeybees and bumblebees are often loyal to a particular variety of flower for a given period of time. Moreover, they prefer short trips between blooms, visiting several flowers on a single plant perhaps, and then flying to a near neighbour, a few meters away at most. Yet because bees do not deposit all the pollen from one plant to the next, genes tend to travel further than appearances suggest (genes travelled twice that distance between two stops of bees) (Young 1989). With plants that are pollinated by wind, most pollen is deposited near to home, but a small amount travels much farther (Young 1989). It should also taken into account that indigenous pollinatior insects often are better adapted to local variation in climate than honey bees (Boyle-Makowski et al. 1985.)

3. Do transgenes have an influence in hybridizing dynamics of crops ?

Theoretically, genetic modification may affect hybrid formation either by changing frequency with which it occurs, or by altering the range of species with which the crop is sexually compatible. Increasingly the evidence suggests that modification has little or no impact on either factor with the present day transgenes released in the fields. In general, plant fertility is maintained after the genetic modification, although there are instances where a particular transformation protocol has produced sterile plants. For example, transgenic maize regenerated from protoplasts is sterile if the protoplasts are transformed by electroporation (Rhodes et al. 1988), but fertile if transformed by polyethylene glycol (Omirulleh et al. 1993). Fertility problems in transgenic plants may therefore be due to particular combinations within the transformation protocol and starting material rather than due to the transformation in itself. It is unlikely that totally sterile transgenics would be of interest as they are unsuitable for breeding purposes. It may be assumed, therefore, that commercial transgenic crop varieties will show similar fertility as non-transgenics. One exception is the crop modified for male sterility. These crops are useful to plant breeders.

One of the most important factors of hybridisation is the movement of the fertile pollen to a receptive stigma. Clearly, pollen production in the crop and the stigma-ripening in the wild relative must be concurrent. If the phenology of a transgenic crop is different from the un-modified form, then the potential for hybridisation will be modified. Several genetic modifications have produced alterations in flower development, but these tend to be changes in structure, leading to morphologically abnormal flowers (Mizukami and Ma 1992 ; Mandel et al. 1992) rather than the production of normal flowers with different flowering periods. These experiments were done with genes known to be involved in flower development or promoters only activated in floral tissue. Up to now, transformation does not seem to alter flowering period. However, as flowering period is a multigenic trait there is a possibility that a transgene may integrate into and disrupt the expression of a gene involved in flowering-period determination. Assuming simultaneous flowering, the extent of pollen transport will determine the potential for crop pollen to land on the stigma of a wild relative. Pollen flow, in most cases, describes a highly leptokurtic distribution from the source plant, with most grain moving less than 2 m in herbaceous plant (Levin and Kerster, 1974). Recent work confirms this for transgenic pollen (Tynan et al. 1989; Umbeck et al. 1991; Morris et al. in press). However, it is misleading to conclude from these data that hybridisation between crops and wild relatives can only occur over short distances. Even in case a hybridisation over long distances takes place only rarely, it may produce a new, viable founder population.

Pollination is a major determinant factor for the hybridisation rate, but the types of hybrids are determined by interspecific incompatibility mechanisms. The genetics of these mechanisms are still not clear. Unless interspecific incompatibility is controlled by one or a small number of genes, the transformation process is unlikely to alter the cross-compatibility of the plants following transformation. Transformation of a self-compatible species with an S-allele involved in self-incompatibility mechanisms has been achieved, but the transgenic plants became self-compatible (Toriyama et al. 1991). Introduction of an incompatibility system into self compatible species will be useful to plant breeders, but it is not clear whether self incompatibility is involved in interspecific incompatibility, and, consequently, such modifications can be expected to have little effect on interspecific hybridisation.

Another important question is whether or not the relation between pollinators and plants will be modified by transformation. First the new proteins synthesized by the transgenic plant should be toxic for bees. The non-toxicity of the chitinase has been proved (Pham-Delègue et al. 1992). Could the character of a transgenic plant modify the activity of the insect ? The same group demonstrated that the foraging time was shorter on a transgenic plant than on a non-transgenic one. However, Pham-Delègue et al. concluded that transgenic oilseed rape has no negative effects on foraging bees under controlled conditions. They need to repeat the experiment in the field (Grallien et al., 1995). Similarly, Paul et al. (1991) found that there are no differences in the range of animals and the frequency of visits between modified and non-modified tobacco plants.

Insects like bees are attracted by light of a wave length between 300 nm and 650 nm (Dumas 1984). This includes part of the ultraviolet light but excludes the long-waved red light. A change in the flower colour could disturb the attractiveness of the flower for the insects and change cross-pollination rate for insect-pollinated plants.

On the other hand, genetic engineering may be favourable to the hybridisation process. Studies regarding alfalfa *(Medicago sativa)* treated by a pesticide (dimethoate) clearly demonstrated that this pesticide is found in the pollen and the nectar at a very low level but even at a low level this pesticide is toxic for the bees (Dumas 1984). This has an effect on the entomophilous pollination. Plants resistant to diseases will not be treated with pesticides, so that the efficiency of pollination for entomophilous plants could be enhanced.

4. The assessment of a potential risk regarding field release of transgenic crops: Introduction to gene flow indices

As a result of discussions in the symposium at Louverain, we propose gene flow indices after the idea of some Dutch authors ([Frietema] De Vries et al. 1992, Frietema De Vries 1996). We are giving here an adapted version in order to spur discussion on an European level. We think it is desirable to establish a European classification system as proposed by Frietema De Vries (1996), where some of our proposals have been adopted. It is not possible to arbitrate the crops and their wild relatives on one and the same level all over Europe: Classification work has to be done on a regional scale taking into account local environmental conditions, species and transgenes. This regional scale has been proposed by Frietema De Vries (1996), following the well known subdivisions of Meusel.

Here we deal only with the three first codes, but we feel strongly the necessity of a fourth code for the future: We need to assess also the effect of the inserted transgene itself. For this Dg code we need experimental approaches on all levels from a strict containment over small scale field releases to the large scale releases over long periods. For the time being there remains only the possibility of a rough estimate of how transgenes will have side effects in the long run, some comments are built in provisionally in code Dp (vertical gene flow). The authors are well aware of the pragmatic view they take, which is blurring the logic of the three codes already defined.

These codes are presented here in order to open debate on feasibility and organisation of such codes for future risk assessment:. The codes can serve as a first routh estimate, before going into more detail for a risk assessment based on field monitoring and experimental approach, where judged necessary.

5. Dpdf-codes, adapted to Swiss and European needs as a whole

a) Classification of the codes of dispersal of pollen (Dp)

Dispersal of pollen and hybridization potential, including a differentiation of possible negative ecological effects of the inserted gene itself. Categories 0 (lowest risk) to 5 (highest risk) and U (unknown)

Category Dp 0:

No chance for hybridization because there are no wild relatives growing in Switzerland. No ecological effects when the cultivated plants come into flower.

Monitored field releases possible, no containment experiments and no field experiments necessary.

Category Dp 1:

No chance for hybridization with wild relatives because it is experimentally proven that wild species of the same genus in Switzerland are not compatible with the cultivated plant: (artificial pollination methods and/or embryo rescue are necessary to produce hybrids).

No ecological effects when cultivated plants come into flower. Monitored field releases possible without containment. However, experiments should be carried out, to test there are no negative effects on the host / predator system in case of transgenes introducing new resistance and/or competition effects.

Category Dp 2:

No chance for hybridization with wild relatives because there is no record of spontaneously formed hybrids of the cultivated plant with wild species of the same genus in Switzerland.

However, hybridization is possible under experimental conditions and progeny is fertile without any artificial help. Chances of gene flow by hybridization is small due to various outcrossing barriers (competition, biogeographical or ecological incompatibility), but under special local or artificial conditions in agricultural systems still to be considered as possible rare events.

a) In certain species groups there is a small chance of getting new transgenic hybrids, but no invasions are to be expected.

b) In other species groups there is a small chance of getting new transgenic weeds which tend to be aggressive and will possibly cause invasions under unfavourable conditions.

Category Dp 3:

Natural hybridization occurs only occasionally, backcrosses have not been observed up to now. Local situations have to be studied carefully in risk assessment of field experiments. Species to species, region by region and step by step approach required.

a) In certain species groups and under unfavourable circumstances gene flow by pollen transfer will occur, but new transgenic hybrids do not tend to be invasive.

b) In other species groups and under unfavourable circumstances gene flow by pollen transfer can influence ecosystems negatively: Local invasions of new transgenic weeds will occur.

Category Dp 4:

Chance for natural hybridization is medium; backcrosses have been observed, successful outcrossing occurs fairly often. Natural fertile hybrids are sometimes observed, small hybrid populations can be detected in nature. Species to species, region by region and step by step approach required.

a) Transgenic hybrids will have no ecological effects on the flora of the Switzerland, since the new hybrid is only capable to invade small ecological niches, and therefore does not demonstrate any disturbing invasiveness, since the inserted gene itself did not show negative ecological effects in long term monitoring experiments. Experiments should also be carried through proving that there are no negative effects on the host / predator system.

b) Transgenic hybrids will have ecological effects on the flora of the Switzerland, since the new weed is capable to invade ecological niches, and therefore is potentially demonstrating invasiveness. There may also be negative effects (e.g. more competitive, more allelopathic) caused by the inserted gene itself.

Category Dp 5:

Chance for natural hybridization is high; vertical gene flow occurs often, hybrids are fertile and backcross frequently. Hybrid populations are often found in nature. Species to species, region by region and step by step approach required.

a) Transgenic weeds will have no ecological effects on the flora of Switzerland, nevertheless the new weed is capable to invade important ecological niches and it will act as a new weed (which should by all means be avoided!), but the inserted gene itself does not show negative ecological effects.

b) Transgenic weeds will have negative ecological effects on the flora of Switzerland since it is capable of invading many ecological niches as a major new weed and/or since the inserted gene itself may have characters demonstrating negative ecological effects.

Category Dp U:

Data too scanty or lacking at all, no evaluation possible.

b) Classification of the codes for the dispersal of diaspores (Dd)

Category Dd 0:

No chance for dispersal of diaspores to the wild: Seeds are sterile or otherwise deficient, they have lost reproductive function. No ecological effects are expected from fruiting of the cultivated plants.

Category Dd 1:

Dd to the wild occurs only occasionally and under very favourable conditions, plants usually survive only for one season (advena), they are not adapted for survival in our climate. No ecological effects are to be expected regarding the Swiss ecosystem.

Category Dd 2:

Chance for dispersal of diaspores to the wild is small, but under favourable and exceptional conditions possible. Further research on population dynamics seems necessary. For risk assessment the standing of the plants in the Swiss ecosystem can be of importance.

Category Dd 3:

Chance for dispersal of diaspores (by spontaneous vegetative reproduction) is real; fruiting of the cultivated plant is essentially undesirable and will normally be suppressed by various methods. Further research on population dynamics is necessary. For risk assessment the standing of the plants in the Swiss ecosystem can be of importance.

Category Dd 4:

Chance for dispersal of diaspores to the wild real. Fruiting of the cultivated plant occurs normally during cultivation. Ecological effects can be expected from fruiting of the cultivated plant. For risk assessment the standing of the plants in the Swiss ecosystem will be of importance.

Category Dd 5:

Dispersal of diaspores to the wild will be the rule. Fruiting occurs very frequently and also extremely abundant. Ecological effects can be expected from fruiting of cultivated plant. For risk assessment the standing of the plants in the Swiss ecosystem will be of importance.

Category Dd U:

Data too scanty or lacking at all, no evaluation possible.

c) Classification of the codes for Df (frequency of distribution)

Category Df 0:

No plants of this species or of a wild relative, no feral populations found in nature; no ecological effects are expected from the introduction of the cultivated transgenic plant.

Category Df 1:

Plants of this species or of wild relatives are extremely rare in the wild and have their stable place in the Swiss ecosystem in specific associations. No feral populations are found in Switzerland. Chances for hybridising with the wild or feral populations are negligible. Locations to grow transgenic plants should be appropriately chosen in order to avoid hybridisation and any ecological effect.

Category Df 2:

Plants of this species or of wild relatives are rare, but occur sporadically, distribution difficult to predict and essentially uncontrollable. Feral populations may exist in certain regions. Chances for hybridising with wild populations are scanty but unpredictable. Ecological effects from the introduction of the cultivated plant may be expected, but in most cases on a local scale only.

Locations to grow transgenic plants should be appropriately chosen in order to avoid hybridisation and any ecological effect.

Category Df 3:

Plants of this species or of wild relatives are not very common in the wild and have their stable place in Swiss ecosystem. Feral populations are known from Switzerland, but not frequent. Chances of hybridising with the wild populations exist but are small. Some ecological effect from the introduction of the cultivated plant may be expected under unfavourable conditions when cultivated plants and wild relatives are not sufficiently separated. Locations to grow transgenic plants should be carefully chosen in order to avoid hybridisation and any ecological effect.

Category Df 4:

Plants of this species and their wild relatives are not frequent but well distributed over the whole Swiss plateau, chances for hybridising with wild populations are considerable, but under very favourable conditions it can still be safely prevented. Feral populations are known and distributed over an important part of Switzerland. Locations to grow transgenic plants should be carefully chosen in order to avoid hybridisation and any ecological effect. Detailed biogeographical studies are necessary to reach this goal.

Category Df 5:

Plants of this species and their wild relatives are common and well distributed over the whole Swiss plateau, chances for hybridising with wild populations must be expected and cannot be prevented in field experiments. Feral populations are frequent and distributed over the whole Switzerland. In exceptional cases locations to grow transgenic plants can still be carefully chosen in order to avoid hybridisation and any ecological effect. Detailed biogeographical studies are necessary to reach this goal

Category Df U:

Data too scanty or lacking at all, no evaluation possible.

6. Vertical gene flow classification by combination of the three codes

The goal of this study was to develop a convenient classification of gene dispersal probability from transgenic crop to the wild flora, adapted for Switzerland. After an evaluation of the three single factors (see above, dispersal codes), the combination of these codes enables us to estimate impact on the wild flora. Five categories of risk probability have been developed:

After an evaluation of the three single factors, their combination enables us to estimate the impact of a transgenic species on the environment. Six categories of risk probability have been developed:

1. No effect

No related species or no compatible related species of the crop are known in Switzerland. Field releases of species belonging to this category are possible without any containment or short term monitoring.

Certain transgenes have to be tested in medium term field experiments regarding their secondary effects on ecosystems: Sustainable resistance must be achieved. To reach this goal a long term monitoring is required.

2. Minimal effects

No records of spontaneous hybridization between the crop and the wild relatives are known in Switzerland. Field releases are possible after a thorough clarification of the biogeographical situation. Short term monitoring in confinements should be done prior to large scale field releases.

Certain transgenes have to be tested in medium term field experiments regarding their secondary effects on ecosystems (pest and insect resistance genes).

3. Low but local effects

Gene flow occurs towards wild or feral species existing also outside agricultural environment and control. Release experiments should first be done in confinements and afterwards in small scale releases closely monitored.

This statement is restricted to transgenes not causing enhanced competitiveness outside agricultural environment, such as herbicide tolerance. Any other transgenes should be carefully tested in confinements.

4. Substantial but local effects

Gene flow is high and substantial, but still locally controllable.

Field releases could be done within strict confinements. A case by case analysis including the potential effects of the transgene is required before any field releases are done.

Long term monitoring of field releases under strict biological or geographical confinement conditions is necessary in order to study competitiveness of the transgenic crop. Risky transgenes have to be avoided.

5. Substantial and wide-spread effects

Gene flow is high, substantial, and widespread and will not be controllable by any means.

No field releases of species belonging to this fifth category are possible.

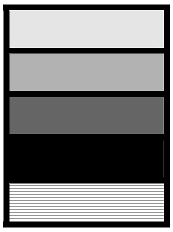
Medium term monitoring under strict confinement conditions is necessary in order to find out about competitiveness of the transgenic varieties.Experiments with less risky crop varieties (e.g. with male sterility) having the same favourable effect desired.

Unknown (one of the three indices is unknown)

More studies are needed before any field releases are done.

Table 1: Risk categories for some crops important to Switzerland

		Dp code					
Df code	Dd code	0	1	2	3	4	5
0	0						
	1	Tomato					
	2	Tobacc					
	3						
	4						
	5						
1	0						
	1						
	2		Beet				
	3						
	4						
	5						
2	0						
	1						
	2				Endive		
	3						
	4				Turnip		
	5						Lettuce
3	0						
	1						
	2				Cabbag		
	3				Radish		
	4						
	5				Rape		
4	0	Maize					
	1			Barley			
	2			Wheat		Carrot	
	3			Rye	Chicory		
	4						
	5						
5	0						
	1	Potato					
	2						
	3		Clovers				
	4						**Alfa**
	5						**Gra**



No effect
Minimal effect
Low but local effect
Substantial but local effect
Substantial and wide-spread effect

7. Conclusions

Besides direct measurement of transgene flow to wild relatives we need a system which builds on decades old experience. This is why we think that the most reliable data do not stem from short term field experiments of outcrossing schemes, which are always dependent on meteorological conditions and regional characteristics. This decades old data material is obtainable in herbaria, which always contain a rich material on hybrids, collected by specialized taxonomists. Taxonomists have a very sharp eye for unusual morphology of hybrids within large populations, and usually, hybrid specimens are over-represented in well assorted big herbaria, with collectors items gathered over centuries. Morphometrics add to the precision of hybrid recognition in herbaria, allow or statistically sound data sets and give a fairly well documented picture on hybrid processes out in the field, which is at least as valuable a data set compared to lab, garden and short term field experiments. Our Dutch-Swiss method of recognizing hybrids with other means than experimental ones needs to be enhanced in the view of biogeography. It would be necessary to regionalize the Dp codes in Europe, since the biogeography of the wild relatives for many crops vary considerably.

9. Literature

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