

# The effect of domestication on plant evolution

L. W. D. VAN RAAMSDONK

Centre for Plant Breeding and Reproduction Research CPRO-DLO, PO Box 16,  
6700 AA Wageningen, The Netherlands

## SUMMARY

The processes of plant domestication and evolution are considered to have different objectives and are therefore treated as different. However, they are not independent. The dependence is discussed in terms of a contribution of the results of domestication to evolution and a contribution of knowledge about the included mechanisms. Reproductive isolation can be developed in the framework of domestication, and cultigens such as *Triticum aestivum*, *Solanum tuberosum*, *Coffea arabica* and *Vicia faba* are treated as species in the evolutionary sense. Newly obtained character combinations as a result of plant breeding can be transferred to natural populations by means of hybridization. Several methods for analysing the rate of gene flow are discussed. The study of the occurrence of horizontal gene transfer in nature is stimulated by the development of the technique of genetic modification in biotechnologic research. Presumed cases of transfer of genetic material between unrelated Angiosperms are based on phylogenetic inconsistencies between gene trees and species trees, although evidence on the vector involved in nature is not available.

**Key-words:** adaptation, barriers, horizontal gene transfer, introgression, reproductive isolation, speciation.

## INTRODUCTION

Domestication and evolution have common as well as differing aspects: the mechanisms involved are identical or at least comparable to a certain extent, whereas the objectives are supposed to be completely different (Van Raamsdonk 1993). Domestication can be defined as a process resulting in (i) characteristics profitable for man which generally reduce the fitness of plants in natural habitats, and (ii) a reduced or total incapacity to disseminate viable offspring. Statement (ii) is in fact a special case of the characteristics mentioned under (i). So, these crops survive thanks to special growing conditions and reproduction strategies imposed by man (cf. De Wet 1981; Harlan 1992; Van Raamsdonk 1993, 1995). Evolution is defined as the change through time of a group of organisms in order to reach better adaptation or higher fitness under local circumstances. Two types of evolutionary change have been recognized, i.e. anagenesis or adaptation and cladogenesis or speciation (Rensch 1959). Nowadays the concept of evolution is considered as a synthesis of a large range of different mechanisms which are known to function in nature. The accumulated changes resulting from the mechanisms at the micro-evolutionary level can be postulated to provide the best clarification for the observed pattern at the macro-evolutionary level.

The aim of this paper is to discuss the effect of domestication on the process of plant evolution, although comparison of the two processes will be addressed when appropriate. The phrase 'the effect on' includes two different levels of abstraction. One aspect of the effect on evolution is a presumed contribution of domestication in terms of new species (cladogenesis) and new variation (anagenesis), and the possibility of transfer of genetic material between plants subjected to either evolution or domestication. The other aspect of the effect of domestication on evolution is the increasing knowledge of specific mechanisms resulting from plant breeding studies. A comparison between evolution and domestication in terms of the mechanisms involved has been carried out by using a formal system of graphical representation (Van Raamsdonk 1993). The mechanisms included in the process of evolution can be divided in *variation-generating* mechanisms and *variation-regulating* mechanisms. New variation is primarily generated by mutations at the level of genes (point mutations, sequence differences), the level of chromosomes (deletions, additions, inversions, translocations) and the level of genomes (dysploidy, polyploidy, aneuploidy). Mutations will occur in plants independent from their background, i.e. at comparable frequencies under evolution and domestication. Transfer of mutated variants from a crop to a wild plant depends on the possibility of hybridization or horizontal gene transfer and these two mechanisms will be discussed. Mutation frequencies can range from 1 mutation per  $10^9$  alleles to 1 mutation per  $10^4$  alleles (Dobzhansky *et al.* 1977). Mutation induction by means of radiation (gene mutations), colchicine treatment (polyploidy) or other techniques is an important tool in plant breeding (Micke & Donini 1993).

When considering populations, new variation is generated inside the population by means of mutation in the broad sense or it is introduced from outside the population by means of introgression. The variation is regulated by mechanisms like selection and genetic drift. Besides the regulation of these so-called modifiers, containment of the impact of variation-generating mechanisms depends on reproductive isolation barriers (RIBs). These barriers can be active in every stage from the release of pollen grains via pollen tube growth, fertilization, embryo development and  $F_1$  plant growth to the establishment of an  $F_2$  population. The RIBs can be divided in external (outside the plant) and internal (inside the female parent) barriers, and the latter class can be subdivided in pre- and postzygotic barriers (large box in Fig. 1). Figure 1 will be used throughout this paper to illustrate certain aspects of the relation between evolution and domestication.

First, both cladogenesis and anagenesis will be discussed in the next two sections, whereafter two variation-generating mechanisms will be given attention, i.e. introgression and horizontal gene transfer. Mutations will not be treated extensively because they can occur in every plant individual without restriction due to RIBs (Fig. 1), no matter whether wild or domesticated plants are concerned.

## CLADOGENESIS IN THE FRAMEWORK OF DOMESTICATION

The splitting of a population in two separate ones, i.e. the formation of two independent evolutionary lineages is referred to as cladogenesis. The separation has to be achieved by the establishment of some type of reproductive isolation. The independent lineages are referred to as evolutionary species. A range of species definitions has been proposed in the past. The most important concepts have been reviewed by Stuessy (1990) and by Rieseberg & Brouillet (1994). In this paper the evolutionary species concept will be used,

which is a single lineage of ancestral-descendent populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate (definition taken from Wiley 1978). This definition comprises two main aspects, i.e. the isolation in time and space between different lineages, and the unique evolutionary role or niche. Both aspects as such are comparable to the concepts of the biological species and the ecological species, respectively. It has been argued that evolutionary forces are not fully applicable to cultigens, which are the resultants of domestication, since cultigens lack an evolutionary role in the strict sense and the tendencies of natural species and cultigens are different (Van Raamsdonk 1993; Hetterscheid & Brandenburg 1995). In order to discuss the span of the evolutionary species concept two requirements for the establishment and maintenance of an evolutionary species can be abstracted from the given definition. These are the existence of reproductive isolation and the possibility to fill an ecological niche. In order to discuss the process and resultant of domestication in an evolutionary framework, I will focus on both requirements separately.

The development of RIBs can take place in the course of a domestication process. Generally, polyploidy will result in reproductive isolation, mainly in internal barriers. Many polyploid crops are known: seven of the 20 economically most important crops are polyploid. This percentage of 35% is comparable to the fraction of polyploids in the naturally occurring flora of the Mediterranean area (Grant 1981), where a considerable part of crops originated (Zeven & De Wet 1982). Some of these crops were taken into cultivation after reaching the higher polyploid level, and reproductive isolation between polyploids and their diploid progenitors is then the result of the naturally occurring process of evolution. The occurrence of polyploidization in the framework of domestication can be decided on the basis of the absence of a wild progenitor at the same ploidy level or of the absence of closely related wild taxa possessing the same ploidy level. The first criterion in fact implies the second. The presence or absence of progenitors or wild relatives does not necessarily apply exclusively to the species level. Using these criteria, *Triticum aestivum* (bread wheat), *Solanum tuberosum* (potato), the polyploid cytotypes of *Musa acuminata* and its hybrids with *M. balbisiana* (banana), several auto- and allopolyploid species of *Dioscorea* (yams) and *Coffea arabica* (coffee) are the most important polyploid crops which reached the higher level of polyploidy in the course of their domestication process, a scenario which is described as the bread wheat domestication model (Van Raamsdonk 1995). RIBs can also result from breeding efforts on the diploid level either as side-effect or as breeding objective. In several crops a shift from allogamy to autogamy has been achieved, *Lycopersicon esculentum* (tomato) among them (Rick 1988). Unilateral incongruity (Hogenboom 1975) was found in crops, for instance in *Phaseolus* (Evans 1976), and reproductive isolation occurs between the cultigen *Vicia faba* and its wild relatives (Hanelt 1986).

Notwithstanding the recognition of RIBs, the question arises whether or not cladogenesis as an aspect of evolution can also be part of the process of domestication. With regard to the direction of domestication and of evolution these processes are completely incomparable. Domestication is directed by objectives set by man, whereas evolution is undirected, although this may be incorrect from a teleological point of view (Teilhard de Chardin 1955; Dobzhansky *et al.* 1977). A range of authors use a terminology which links the two processes of domestication and evolution. Examples are: 'evolution under domestication' (Pickersgill 1986; Hancock, 1992, p. 172); 'Modes of evolution in plants under domestication' (Zohary 1984); 'origin and evolution of

cultivated plants' (Pickersgill 1977); 'evolution of crops' (Simmonds 1979, p. 1; Harlan 1992, p. 90); 'evolution of crop plants'; (Simmonds 1976; Smartt & Simmonds 1995); 'evolution of cultigens' (Smartt 1990, p. 112); '[crop] plants have undergone dramatic coevolution with man as domesticates' (Small 1984). On the other hand, a different classification system of domesticated plants is proposed, since the classification of wild plants is based on evolutionary relationships while that of domesticated plants is not (Hetterscheid 1994; Hetterscheid & Brandenburg 1995). Nevertheless, the mechanisms involved in both processes appear to be identical to a certain extent (Van Raamsdonk 1993). Artificial selection can be treated as a special case of directional natural selection (Dobzhansky *et al.* 1977). So, cultigens such as *Triticum aestivum*, *Solanum tuberosum*, *Coffea arabica* and *Vicia faba* can be treated as species in the evolutionary sense since they pass the requirement of reproductive isolation, at least at the level as found in numerous wild species. The ecological part of the definition of an evolutionary species will be addressed in the next section.

## ANAGENESIS IN THE FRAMEWORK OF DOMESTICATION

Anagenesis is the gradual process of adaptation to the changing requirements of habitats in order to increase and optimize the fitness of the individuals involved. Adaptation in terms of states or better adaptedness is discussed by Knoll & Niklas (1987). The habitat of crop plants includes the requirements of man and discussion of anagenesis in the framework of domestication will start with aspects of human-oriented adaptations. It has been stated that anagenesis at the level of cultivars is excluded from the process of domestication because of the so-called DUS-concept, which means that a cultivar has to be distinct, uniform and stable in a genetic sense (Van Raamsdonk 1993). A specific cultivar cannot be adapted to new breeding objectives and a selected set of plants from a cultivar is simply designated a new cultivar (see also commentary in Hetterscheid & Brandenburg 1995). However, at the level of a cultigen anagenesis is clearly recognizable. Plants have been chosen from wild populations and were adapted to human needs by means of conscious or unconscious selection (Heiser 1988). The plant parts which are used by man vary from roots, stolons, stems, leaves, inflorescences to fruits. The distribution of the use of specific plant parts over the most important families to which crop plants belong is rather scattered (Hancock 1992). For instance, some of the most important crops eaten for their leaves belong to Chenopodiaceae (spinach), Cruciferae (cole crops), Compositae (endive and lettuce) and Liliaceae (leek). Similarly, crops with secondary thickening of their stem basis are found in Chenopodiaceae (beet), Cruciferae (turnip and rape), Umbelliferae (carrot) and Liliaceae (onion). Fruits in a variety of types of crops belonging to a range of families are adapted to human consumption. The type of fruit is subjected to natural divergence, since non-adaptive radiation resulted in general ground plans for families or other higher categories (Dobzhansky *et al.* 1977). So, berries for human use are found in families like Solanaceae, Rosaceae and Vitaceae, legumes in Leguminosae, pepos in Cucurbitaceae, achenes in Compositae, and grains in Gramineae. From the viewpoint of the families a more uniform situation can be observed. The two families with the most important crops are the Gramineae and Leguminosae. All the more important crops belonging to these two families except one are cultivated for their fruits. The only exception applies to *Saccharum* (sugar cane), which is cultivated for its stems. Taking these two families and the crops belonging to the Cucurbitaceae into consideration,

**Table 1.** List of crops belonging to three of the most important families with domesticated representatives. All listed crops except one (sugarcane) are cultivated for their fruits

Centre	Gramineae	Leguminosae	Cucurbitaceae
Middle East	Bread wheat, emmer, einkorn, barley, oat	Lentil, pea, faba bean, chickpea	Water melon
Africa	Rice, sorghum, pearl millet	Cowpea	Melon, bottle gourd
China	Rice, foxtail millet	Soybean	Melon, snake gourds
SE Asia	Rice, sugarcane	Pigeonpea, mung bean	Cucumber, sponge gourd
Mexico	Maize	Common bean, runner bean, tepary bean	Marrow, pumpkin, squash
South America	—	Common bean, Lima bean, ground nut	Pumpkin

remarkable parallelisms of domestication events can be traced at the family level. The number of recognized centres of domestication ranges from one (S. China; Carter 1977) or two (Middle East and Mexico; Blumler 1991) to six (Harlan 1971) or even 12 (Zhukovsky 1968). When following the designation of Harlan (1971), members of the three families are almost equally distributed over the centres of domestication (Table 1; Van Raamsdonk 1993; Smartt & Simmonds 1995). Another, striking example of parallel domestication is found in the genus *Dioscorea* (yams). The most important representatives are domesticated in Asia (*D. alata*), in Africa (*D. rotundata*) and America (*D. trifida*; Hahn 1995). These examples could indicate some sort of natural preadaptation of the considered crops which favoured them in the usefulness for mankind in several independent domestication centres.

The use of the term 'gradual' in the mentioned definition of anagenesis implies a continuous process of adaptation. Opposite to this theory of phyletic gradualism the theory of punctuated equilibria has been proposed (Eldredge & Gould 1972; Eldredge 1989). According to this theory, evolutionary change takes place rapidly in short periods of time and during the remaining (longer) periods of time the state of homeostasis prevails. In phyletic gradualism missing links in the fossil record are gaps which need to be filled, while according to punctuated equilibria intermediate forms are relatively rare. Both theories of anagenesis should be considered complementary rather than mutual exclusive (Rhodes 1987; von Vaupel-Klein 1994). Early remains of crop plants can often be distinguished from their immediate wild relatives by means of anatomical or histological structures in inflorescences which prevents seed dispersal. These characteristics are based on one or two genes in a number of cases (Hancock 1992; Ladizinsky 1979 for some legumes) and series of intermediate forms are then impossible to find. With regard to quantitative characters as objectives of plant breeding such as yield, a complete range between the extremes is present. For instance, in one specific backcross generation in *Zea mays* (maize), yield was based on 44 different QTLs (Stuber 1989). Monogenic, oligogenic or polygenic inheritance has been found for resistances against pests and diseases (Kofoet *et al.* 1990; Van der Beek *et al.* 1992, 1994; Maisonneuve *et al.* 1994) and for morphological characters (Kennard *et al.* 1994; Song *et al.* 1995; Bradshaw *et al.* 1995), and therefore, the existence of intermediate forms depends on the

genetic system involved. So, both theories of phyletic gradualism and punctuated equilibria can be applied to the adaptation of crops plants to the requirements of man.

In an ecological sense, in addition to human requirements, crop plants are adapted to the growing conditions of man-made habitats. These habitats can range from completely artificial (glasshouses) to only weak disturbance (production forests, roadsides). In any situation weeds may be found in these habitats. Weeds can be defined either according to unwantedness for man or to ecological preferences (Harlan 1992). They can be genetically related to a crop and originate after hybridization or escape, or just unrelated mimics (Barrett 1983). In the framework of the current discussion it is sufficient to focus on the capability of weeds to grow in man-made habitats as crops do, and on their ability to disperse their diaspores independently from man. Apparently man-made habitats provide unintentionally niches to two types of plants additional to crops, for which these habitats are specifically designed: (i) for weeds genetically related to crops, which is to be expected, and (ii) for unrelated weeds. The existence of the last category implies that man-made habitats provide niches in an ecological sense just as natural habitats do. It can be concluded that there is no principal difference between natural, disturbed or man-made habitats. The adaptation of crops to the latter category of habitats can be considered as a special form of anagenesis. It is of importance to consider whether the new traits or new combinations of characters can be transferred from domesticated to wild plants or vice versa.

## INTROGRESSION AND MIGRATION AS BRIDGES BETWEEN WILD AND DOMESTICATED PLANTS

Hybridization is an important mechanism in nature (Anderson 1949; Grant 1981; Small 1984; Abbott 1992), although its importance to plants is much greater than to animals (Dobzhansky *et al.* 1977). Stace (1975) estimated the extent of hybridization in the flora of the British Isles. He found successful hybridization in 55 plant families and a considerable amount of hybrids in 14 of them (Stace 1975). A total of 23 000 species combinations (excluding orchids) was estimated on a total amount of approximately 250 000 plant species (Van Damme 1992). Many specific situations have been studied; the case of *Iris* is a classical example (Nason *et al.* 1992).

Hybridization is a specific case of migration at and above the species level. When plant dispersal units migrate to a population of a closely related species, the impact of migration depends not exclusively on the migration rate, but also on the effectivity of the RIBs, which finally determines the level of successful hybridization and introgression (Abbott 1992). The importance of RIBs between species is expressed by the sizes of the arrows prior and after the RIB-box in Fig. 1: only in the case of fertile  $F_1$  plants can gene flow between two species occur, and a contribution to the next generation is indicated by the arrow in the lower right corner of Fig. 1. Notwithstanding the importance of RIBs, the mentioned estimated number of hybrid combinations (Van Damme 1992) equals about 9% of the number of vascular plants.

An attempt to calculate the level of gene flow during hybridization has been made by the development of the so-called crossability coefficient (Van Raamsdonk 1992). In this coefficient three subsequent stages are included, i.e. the production of seeds, the germination of seeds and the generative phase of the offspring. In each of these stages the result is scored. The coefficient is calculated by using a formula which is based on the three scores, and it ranges from zero (completely interfertile) to one

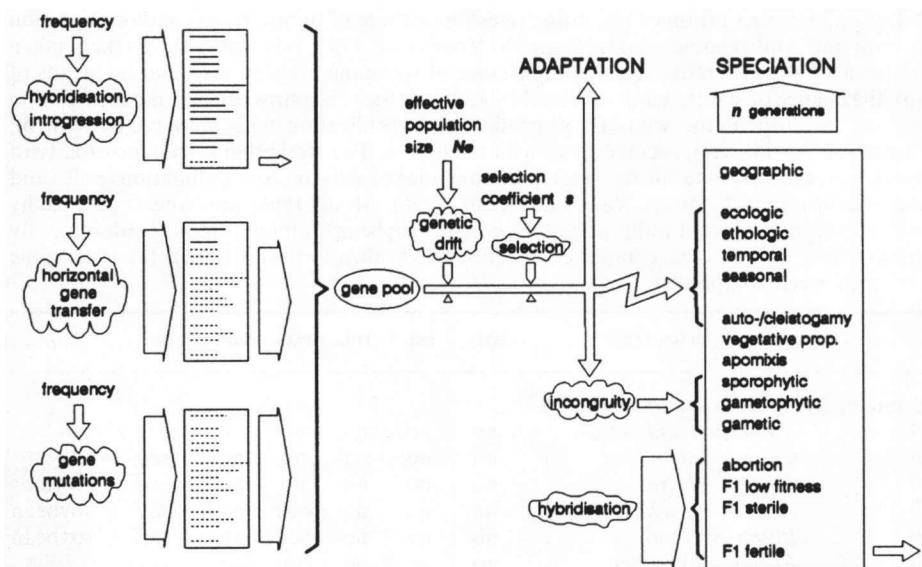


Fig. 1. Flow scheme of the three primary sources of variation with indication of filtering effect by reproductive isolation barriers, modification by drift and selection and final effect on adaptation and speciation. Meaning of symbols: cloud=process; arrow=causal relationship; zigzag arrow=stochastic relationship; valve=modifier; oval=gene pool.

(completely intersterile). The coefficient can be interpreted as a distance and dendrograms with crossability relationships have been calculated in several crop examples (Van Raamsdonk 1990, 1992, 1995; Van Raamsdonk *et al.* 1992, 1995; Van Raamsdonk & Sandbrink 1995). Crossability dendrograms appeared to be useful in molecular variation studies concerning nuclear (n) DNA as well as chloroplast (cp) DNA. In *Allium* subgenus *Rhizirideum* the phylogenetic distance based on nDNA between *A. cepa* (onion) and *A. roylei* is far greater than the distance based on cpDNA. The topology of the cpDNA tree appeared to be identical to the crossability dendrogram, and introgression of cytoplasm (chloroplast capture) was proposed as cause of the homology (Van Raamsdonk & Sandbrink 1995). This example of *Allium* indicates that the crossability coefficient can be useful in studies of introgression, but it is necessary to stress that the coefficient is designated as *crossability* coefficient, since only stages concerning the production of the first hybrid generation are involved. In order to use the same concept for an introgression coefficient, the formula should be extended to the next backcross generations, in the same way as the current crossability coefficient is an extension compared to the index used by Shore & Barrett (1985).

The rate of hybridization between domesticated plants and their wild relatives and of escape of domesticates has been estimated in the form of a so-called  $D_{pdf}$  code for 36 crop plants at the species level and for some genera (De Vries *et al.* 1992). The  $D_{pdf}$  code is designed for estimation of the risk of gene transfer from transgenic plants. It is a compilation of the chance of spontaneous gene dispersal by means of pollen (p), the chance of spontaneous dispersal by seed or other diaspores (d), and the distribution frequency of the crop in the wild (f). The higher the three values the higher the rate of hybridization and/or migration and, hence, the higher the risk of transgenic plant release. All possible combinations of values for p, d and f have been classified in

**Table 2.** List of 36 species arranged according to estimated rate of hybridization and/or migration between crop and wild relatives (taken from De Vries *et al.* 1992; pdf values in brackets taken from Frietema 1994), with indications of the chance of spontaneous gene dispersal by means of pollen (p), the chance of spontaneous dispersal by seed or other diaspores (d), and the distribution frequency of the crop in the wild (f), possibility of hybridization with wild relatives (hyb), establishment of hybrids (est), occurrence of wild relatives in The Netherlands (rel), possibility of escape (esc), possibility of naturalizing (nat), predominance of self- or cross-pollination (poll.) and crop domestication model (model: Van Raamsdonk 1995). Model types are 'wheat' (artificially polyploid crops), 'cotton' (naturally polyploid crops), 'soybean' (diploid crops, predominantly autogamous), 'c/w' (crop-weed complexes, extensive hybridization) and '(c/w)' (at least some aspects of crop-weed complexes)

pdf	Species name	hyb.	est.	rel.	esc.	nat.	poll.	model
<b>Limited rate of hybridization and migration</b>								
0 0 0	<i>Anthurium andreanum</i>	no	no	no	no	no		
0 1 0	<i>Cucumis melo</i>	no	no	no	no	no	self	
0 1 0	<i>Cucumis sativus</i>	no	no	no	no	no	self	cotton
0 1 0	<i>Phaseolus vulgaris</i>	no	no	no	occ	no	self	soybean
0 1 0	<i>Pisum sativum</i>	no	no	no	yes	no	self	soybean
0 1 0	<i>Rheum × hybridum</i>	no	no	no	occ	no	cross	
0 1 0	<i>Scorzonera hispanica</i>	no	no	no	occ	no		
0 1 0	<i>Secale cereale</i>	no	no	no	occ	no	cross	
0 1 1	<i>Lupinus luteus</i>	no	no	no	occ	no	cross	
0 2 1	<i>Lycopersicon esculentum</i>	no	no	no	yes	no	self*	(c/w)
1 1 0	<i>Allium cepa</i>	no	no	no	occ	no	cross	soybean
1 1 0	<i>Allium porrum</i>	?	no	dist	occ	no	cross	cotton
1 1 1	<i>Brassica oleracea</i>	yes	occ	yes	occ	no	cross	(c/w)
1 2 0	<i>Solanum tuberosum</i>	no	no	no	yes	occ	self	wheat
2 1 0	<i>Vicia faba</i>	no	no	no	occ	occ	self	soybean
<b>Medium rate of hybridization and migration</b>								
1 2 2	<i>Brassica napus</i>	occ	?	dist	yes	occ		
2 2 2	<i>Fragaria × ananassa</i>	occ	no	dist	yes	occ	cross	
3 1 2	<i>Avena sativa</i>	occ	occ	yes	occ	occ	self*	(c/w)
3 3 ?	<i>Cichorium endivia</i>	yes	?	yes	occ	?	self	
4 1 1	<i>Beta vulgaris</i>	yes	yes	yes	yes	no	cross	c/w
4 4 1	<i>Lilium bulbiferum</i>	occ	no	yes	occ	no		
4 4 1	<i>Narcissus pseudonarcissus</i>	occ	occ	yes	yes	yes		
4 4 1	<i>Tulipa sylvestris</i>	no	no	yes	occ	yes		
<b>High rate of hybridization and migration</b>								
3 4 ? (4 4 2)	<i>Lactuca sativa</i>	occ	rare	yes	occ	?	self	soybean
3 4 ?	<i>Raphanus sativus</i>	yes	yes	yes	yes	yes	cross	c/w
4 4 2	<i>Asparagus officinale</i>	yes	?	yes	occ	yes	cross	
4 4 2	<i>Cichorium intybus</i>	yes	?	yes	yes	yes	cross	
4 4 2	<i>Medicago sativa</i>	yes	yes	yes	yes	yes	cross	cotton
4 4 3	<i>Brassica rapa</i>	yes	?	yes	yes	occ	cross	(c/w)
4 4 3	<i>Daucus carota</i>	yes	yes	yes	occ	no	cross	c/w
4 4 3	<i>Trifolium repens</i>	yes	yes	yes	yes	?	cross	
5 4 3	<i>Agrostis capillaris</i>	yes	yes	yes	yes	yes	cross?	
5 4 3	<i>Agrostis stolonifera</i>	yes	yes	yes	yes	yes	cross?	
5 4 3	<i>Festuca pratensis</i>	yes	yes	yes	yes	yes	cross	c/w
5 4 3	<i>Lolium perenne</i>	yes	yes	yes	yes	yes	cross	c/w
5 4 3	<i>Poa pratensis</i>	occ	?	yes	yes	yes	cross	

\*Interfertility with related species.



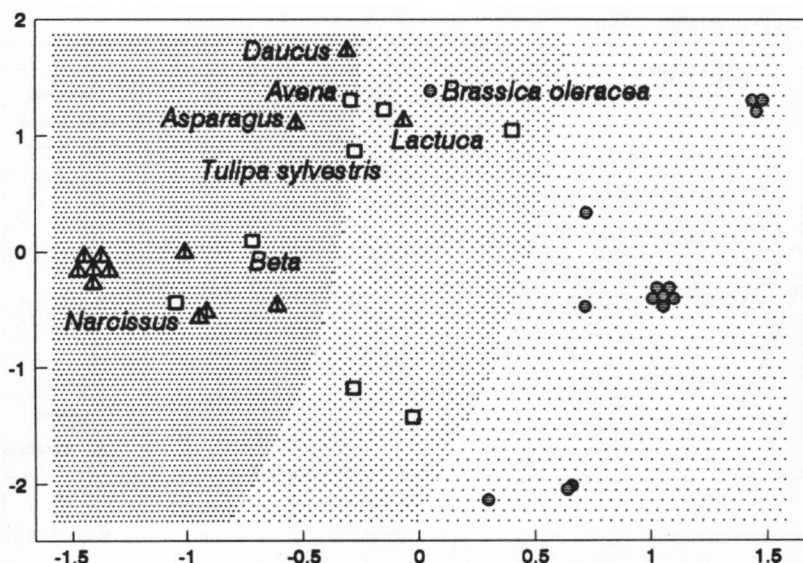


Fig. 2. Principal component plot based on four characters concerning the expectation of the rate of hybridization and migration of 36 crops in The Netherlands. The boundaries of the shaded areas resulted from the analysis. The sign of each crop is chosen according to the indication of De Vries *et al.* (1992). Meaning of indications: light shading+circles=limited rate; medium shading+squares=medium rate; dark shading+triangles=high rate.

three classes indicated as no, some and substantial ecological risk (De Vries *et al.* 1992; Table 2). In this paper these three classes will mainly be discussed in terms of limited, medium and high exchange rates. I have tabulated data on five additional parameters: possibility of hybridization (*hyb*), establishment of hybrids (*est*), occurrence of wild relatives in The Netherlands (*rel*), possibility of escape (*esc*), and possibility of naturalizing (*nat*). A major part of these data was collected by De Vries *et al.* (1992) for The Netherlands and further completed with data from some other sources (Keeler 1989; Raybould & Gray 1993). The total of eight parameters has been subjected to multivariate analysis using the program package IRIS (Van Raamsdonk 1988). The highest correlation was found between *hyb* and *est* (0.940). Other high correlations were found between *p* and *est* (0.891), *hyb* and *rel* (0.874), *p* and *f* (0.872), *d* and *f* (0.872), and *p* and *rel* (0.862). The parameters *p*, *d* and *f* were excluded prior to principal component analysis since the indication of exchange rate based on these three parameters will be used as an *a posteriori* overlay on the principal component plot. The parameter *hyb* is also excluded because of its high correlation with other parameters in order to avoid a too high level of redundancy in the dataset.

The resulting principal component plot is presented in Fig. 2. The x-axis represents 70.6% of the total variation. The possibility of hybridization appears to be more important in the presented distribution than the possibility of escape by means of seeds, as can be concluded from the factor loads, which is in concordance with literature studies (Ellstrand & Hoffman 1990). The classification of no (circles), some (squares) and substantial (triangles) exchange rate is generally well based on the used parameters *est*, *rel*, *esc* and *nat*. However, in detail some specific crops take aberrant positions in the plot. The estimation of exchange rate of De Vries *et al.* (1992) of crops like *Narcissus pseudonarcissus*, *Beta vulgaris*, *Avena sativa*, *Lactuca sativa* and *Brassica oleracea* should

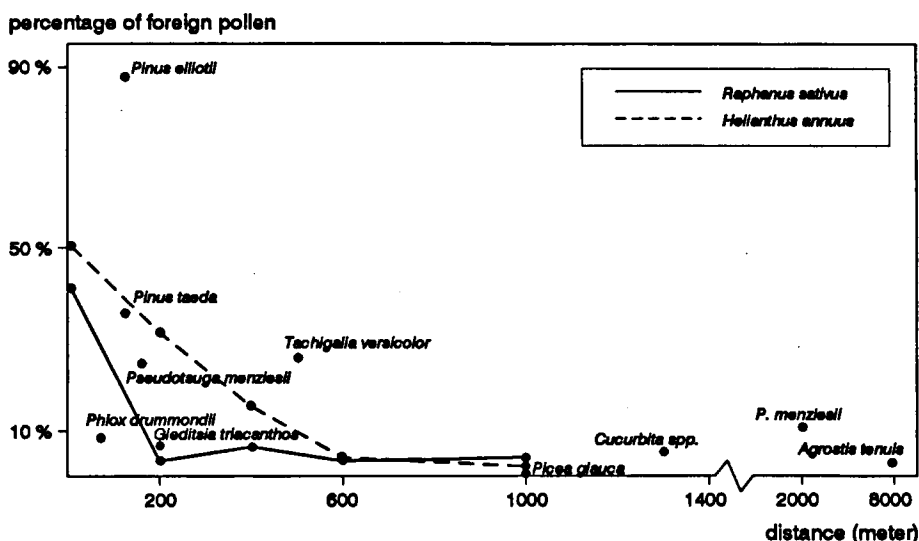


Fig. 3. Interpopulation mating rates estimated by paternity analysis by means of allozyme data of *Raphanus sativus* (Klinger *et al.* 1991) and *Helianthus annuus* (Arias & Rieseberg 1994) compared to data of other plant species (Ellstrand & Hoffman 1990).

be reconsidered. Gregorius & Steiner (1993) reached the same conclusion for *Narcissus pseudonarcissus* and *Lactuca sativa*. There is a strong correlation between estimated exchange rate and allogamy (Table 2). *Lactuca sativa* is the only autogamous crop classified with an estimated high exchange rate. Further study of this crop resulted in a higher  $D_{pdf}$  value due to the presumed conspecificity of *L. sativa* and its progenitor *L. serriola* (Frietema *et al.* 1994). This conspecificity is not supported by the results obtained by De Vries & Van Raamsdonk (1994; Van Raamsdonk & Van der Maesen 1996). The frequency of escape of *L. sativa* is still unknown. *Brassica oleracea* is considered to be not indigenous in The Netherlands (De Vries *et al.* 1992) but northern European races are assumed to have contributed to the present day crop (Hodgkin 1995). This assumption, and the span of the species concept used determine whether or not wild relatives and gene flow exist (Van Bothmer 1995). At least some aspects of crop/weed complexes can be recognized (Van Raamsdonk 1995).

Additional information from case studies is available for some other crops listed in Table 2. Considerable gene flow estimated from cpDNA variation patterns is reported in *Beta vulgaris* (Boudry *et al.* 1993) and in *Trifolium pratense* (Milligan 1991), which is a relative of *T. repens* possessing the same reproductive system. The gene flow in *Raphanus sativus* (Klinger *et al.* 1991; see also Gregorius & Steiner 1993) estimated by means of allozyme variation is considerable compared to other data (Ellstrand & Hoffman 1990; Arias & Rieseberg 1994; Fig. 3). Observable gene flow in *Agrostis capillaris* (under the synonym of *A. tenuis*) was found at a distance of 8000 m (Fig. 3). Hybrids between *Brassica napus* and *B. rapa* can be fertile to a large extent and gene flow from *B. napus* has been detected at a distance of 2000 m (Williamson 1993; Timmons *et al.* 1994). This information could provide an improved fundament to  $D_{pdf}$  codes for these crops.

There is also a certain indication that crops of which the domestication can be described according to the so-called Chilli Pepper model (crop/weed complexes; Van

Raamsdonk 1995; Van Raamsdonk & Van der Maesen 1996; Table 2) possess potential risk which is obviously due to the capability of these crops to contribute to hybrid swarms. Genetic exchange between domesticates and wild plants may play a greater role than estimated from the current data (Table 2), since these data represent the situation in The Netherlands. Crops without relatives in The Netherlands may be capable of hybridization and/or migration in their centre of origin. For example, *Helianthus annuus* (sunflower) was excluded in the Dutch study (De Vries *et al.* 1992) and was considered to have only minimal gene flow in an English study (Raybould & Gray 1993), while considerable gene flow was found in America (Rieseberg & Soltis 1991; Fig. 3). Studies concerning the possibility of genetic exchange should be based on globally collected data, as was also concluded by Bartsch *et al.* (1993) in the case of *Beta vulgaris*.

### THE OCCURRENCE OF HORIZONTAL GENE TRANSFER IN NATURE

Besides mutation, either on the gene, chromosome or genome level, and hybridization, a third mechanism can be recognized as a source of new variation within a population. Horizontal gene transfer is defined here as the transfer of genetic material from one species to another, sexually incompatible species by means of a vector, which does not belong to the nature of the organism. The term horizontal is used in contrast to vertical transfer, which is the sexual transfer of DNA from one generation to the next within the same species. The transfer of DNA from one eukaryotic to another eukaryotic species by a prokaryotic vector (bacterium) is a special situation covered by this definition. Transfer of prokaryotic DNA to an eukaryotic organism is excluded by using this definition, but most authors use a concept which includes all types of transfer except vertical. I use the given definition in this paper in order to be able to compare the occurrence in nature with genetic modification in laboratory experiments, called genetic modification.

Examples in the plant kingdom of characters presumed to be the product of horizontal transfer are rare. Of a list of nine documented cases of horizontal transfer (Syvanen 1994), six apply to prokaryotic–eukaryotic DNA transfer, two examples involve chloroplast–nucleus DNA transfer and one example concerns cytochrome *c*. This enzyme, as found in *Arabidopsis thaliana*, shows much more affinity at the molecular level to that of *Neurospora* than to those of other angiosperms (Kemmerer *et al.* 1991). The evidence for horizontal gene transfer is usually poor or conflicting (Prins & Zadoks 1994) or circumstantial by means of testing phylogenetic incongruencies between species trees and gene trees (Syvanen 1994). One of the nine cases of the list of Syvanen (1994) refers to Fe superoxide dismutase (Fe SOD) found in *Euglena gracilis* (Lengfelder & Elstner 1979), *Brassica rapa* (Salin & Bridges 1980), *Entamoeba histolytica* (Smith *et al.* 1992) and representatives of some other angiosperm families (Prins & Zadoks 1994). Fe SOD is assumed to be of prokaryotic origin (Salin & Bridges 1980; Syvanen 1994), but this assumption is based only on the erratic distribution of Fe SOD among plants. The assumption of several independent horizontal transfers is not likely (Prins & Zadoks 1994). A further example concerns the resistance gene for the bacteria *Pseudomonas syringae* f. sp. *tomato*, which has been found in the unrelated species *Lycopersicon esculentum* (Solanaceae; Keen *et al.* 1990) and in *Arabidopsis thaliana* (Cruciferae) and *Glycine max* (Leguminosae; Whalen *et al.* 1991). The matching of the resistance gene of these species and the avirulence gene of *P. syringae* is identical at the molecular level in all three species. The most likely explanation so far seems to be

horizontal gene transfer (Zadoks & De Wit 1992), although the plant species mentioned originate from Central America, Europe and eastern Asia, respectively, and it is to be expected that geographic isolation will prevent horizontal gene transfer. Examples of homology between transposable elements are also more frequent in animals than in plants. In the animal kingdom several cases of presumed horizontal gene transfer between species of *Drosophila* were documented, for instance the *P* transposable element (Daniels *et al.* 1990; Kidwell 1992). The transposase amino acid sequences of *hobo* in *Drosophila melanogaster*, *Ac* in *Zea mays* and *Tam3* in *Antirrhinum majus* show a higher similarity than may be concluded from the phylogenetic distances (Capy *et al.* 1994). On the other hand, the similarity between *Ac* or *Ac*-like transposons of *Zea mays* and *Pennisetum glaucum* (both Gramineae) is not higher than that between the *Adh1* genes of the same species (MacRae & Clegg 1992). Unexpected transposon similarities have also been found in strains of *Escherichia coli* (Lawrence *et al.* 1992). Retroviruses may play an important role as vector of horizontal transfer in nature (Capy *et al.* 1994). In all cases arguments for and against horizontal gene transfer are put forward (Capy *et al.* 1994; Cummings 1994). Other explanations of the detected similarities in spite of the low relationship between the carrying species may include loss of certain sequences by genetic drift, strong selective pressures, ancestral polymorphism, differences in evolution rate, treating orthologous genes as if they are paralogous, and convergence or parallel evolution (Capy *et al.* 1994; Syvanen 1994; Prins & Zadoks 1994). The first two mechanisms also modify the result of hybridization (Fig. 1). Ancestral polymorphism, also called phylogenetic sorting (see Doyle 1992) has to be investigated more fully in the presumed cases of horizontal gene transfer. It has been stated that cases of convergence may occur more often than previously assumed (Van Raamsdonk 1993). Direct proof of horizontal gene transfer between angiosperms should include evidence on the vector and on the specific transfer mechanism involved. Before accepting the scattered distribution of transposable elements as proven cases of horizontal gene transfer, the genetics of transposable elements have to be completely understood.

There are reasons why the effectivity of horizontal gene transfer in higher organisms should differ largely between plants and animals. This difference is caused by the presence of cell mobility, of a circulatory system, of an immunological system and of a germ line in animals (Klekowski 1988). The existence of uncontrolled growth of cancer cells after transformation can ruin the immunological system and cause death occasionally. The circulatory system can act as an effective vector for cancer cells. The transformed genotype will only be transferred to the next generation when the transformed cells belong to the specific germ line in animals. On the other hand, plants lack the special features as mentioned, although Prins & Zadoks (1994) recognized a germ line in plants. Tumour-like structures can develop in plant tissues, but cancer will not result due to the presence of permanent cell walls among other reasons (Klekowski 1988). Because of the lack of a germ line initiated early in the ontogenic development in higher plants (Wei & Mahowald 1994), a transformed cell may have a certain chance of being involved in gametogenesis and of contributing to the next generation (Prins & Zadoks 1994; generative HGT), or an even greater possibility of being involved in vegetatively propagated clones (Prins & Zadoks 1994; vegetative HGT).

The mechanism of horizontal gene transfer in the sense of the given strict definition has not yet been proved to take place in higher organisms, while it is a recognized phenomenon between prokaryotes (Levy & Miller 1989; Bergmans 1992; López-Pila & Scheler 1993; Van Raamsdonk 1993; Prins & Zadoks 1994). The *Ti*-plasmid of

**Table 3.** Transformation frequencies using *Agrobacterium tumefaciens*. The frequency denotes number of transgenic shoots per 100 inoculated transplants

Plant species, tissue	Frequency	Reference
Flax, hypocotyle	1.7–16.7	Dong <i>et al.</i> 1993
<i>Petunia</i> , shoot tips	11	Ulian <i>et al.</i> 1988
Cucumber, petiole, leaf segments	2–9	Sarmiento <i>et al.</i> 1992
Tomato, leaf discs	up to 100	Davis <i>et al.</i> 1991
Poplar, stems	up to 60	Leple <i>et al.</i> 1992

*Agrobacterium tumefaciens*, when incorporated in the genome of a host is considered not to be transferred to the next generation of this host in nature (Zadoks & De Wit 1992). Any attempt to discuss the impact of horizontal gene transfer on natural evolution has to be made indirectly. Data on frequency of successful transformation of leaf discs or cell cultures are available. The frequency of transformation using *A. tumefaciens* as vector ranges from 2 to 100% (Table 3). The rather high rates of horizontal DNA transfer under laboratory conditions resulted in the statement, that 'if a mechanism so potentially useful existed, nature would find a way to use it' (Syvanen 1994, p.238). There is some limitation of the impact that horizontal gene transfer may have on the structure of the gene pool (Fig. 1). It could be expected that exchange of DNA of physically isolated populations, either geographically (allopatry) and ecologically (allotopy), will be limited. The other RIBs are not effective, as is illustrated by the size of the arrows prior and after the RIB-box in Fig. 1.

## CONCLUSIONS

The occurrence of interspecific hybridization or cladogenesis in the framework of domestication depends on the span of the species concept. A narrow species concept results when discontinuities are all translated to differences between formal taxa (Stuessy 1990). On the other hand, in a situation where species include a considerable amount of variation the frequency of interspecific hybridization can be expected to be low. It can be concluded from the presented examples that acceptance of a moderate point of view on the span of species results in supposition of cladogenesis of cultigens at the specific level. Specific case studies on the relationship between domesticated and wild plants should also emphasize this aspect, as is illustrated by the examples given of *Lactuca sativa* and *Brassica oleracea*.

The restriction by RIBs of hybridization and introgression, and of horizontal gene transfer differs (Fig. 1). When not physically isolated, horizontal gene transfer is less restricted by RIBs, provided that an effective vector is available. Horizontal gene transfer may have a serious effect on phylogenetic results. Phylogenetic reconstruction is usually based on the distribution of derived states of the observed characters. The parsimony principle leads to a minimalization of the number of parallel occurrences of an apomorphic character state. Horizontal gene transfer will manifest itself as a special case of parallel evolution. The more characters are included in a phylogenetic analysis, the more cases of parallel evolution will be allowed. In small datasets, especially at the DNA level, parallel evolution and horizontal gene transfer may seriously bias the resulting phylogenetic tree. It is necessary to estimate the frequency and effect of

horizontal gene transfer in nature. Study of the mechanism and vector involved can be promoted by knowledge achieved in biotechnological experiments.

The contribution of domestication to plant evolution is twofold as stated; namely, a contribution in terms of actual material and in terms of knowledge. Plant material resulting from plant breeding efforts in particular cases can be considered species in an evolutionary sense. New character combinations can be transferred to natural populations by means of hybridization. New mechanisms are currently in development for the transfer of genetic material. The recent discussion and research regarding the occurrence of this mechanism in nature is promoted by the recent advancements in biotechnology. The difference between the mechanisms included in the processes of domestication and plant evolution increases by the development of new plant breeding techniques. However, when resultants and objectives are studied, the similarities between the processes are more prominent than the differences.

It can be concluded that the process of domestication has a recognizable effect on evolution and it is important to pay attention to new developments in modern plant breeding in the framework of evolutionary studies (Briggs & Walters 1984). Some sort of 'co-evolution' between studies on evolution and domestication could be mutually beneficial.

## ACKNOWLEDGEMENTS

I acknowledge with many thanks the constructive comments of Dr J. Jansen and Dr K. Puite (CPRO-DLO), Dr R. G. Van den Berg (Department of Plant Taxonomy, Wageningen Agricultural University) and Dr T. W. Prins (Department of Phytopathology, WAU).

## REFERENCES

- Abbott, R.J. (1992): Plant invasions, interspecific hybridization and the evolution of new plant taxa. *Trends Ecol. Evol.* 7: 401–405.
- Anderson, E. (1949): *Introgressive Hybridization*. John Wiley, New York.
- Arias, D.M. & Rieseberg, L.H. (1994): Gene flow between cultivated and wild sunflowers. *Theor. Appl. Gen.* 89: 655–660.
- Barrett, S.C.H. (1983): Crop mimicry in weeds. *Econ. Bot.* 37: 255–282.
- Bartsch, D., Sukopp, H. & Sukopp, U. (1993): Introduction of plants with special regard to cultigens running wild. In: Wöhrmann, K. & Tomiuk, J. (eds) *Transgenic Organisms, Risk Assessment of Deliberate Release*. 135–151. Birkhäuser Verlag, Basel.
- Bergmans, J.E.N. (1992): Horizontal gene transfer in micro-organisms: the role of plasmids and transposons. In: Weverling, J. & Hekstra, G.P. (eds) *Ecological Effects of Genetically Modified Organisms*. 93–100. Netherlands Ecological Society, Arnhem.
- Blumler, M.A. (1991): Modelling the origins of legume domestication and cultivation. *Econ. Bot.* 45: 243–250.
- Boudry, P., Mörchen, M., Saumitou-Laprade, P., Vernet, Ph. & Van Dijk, H. (1993): The origin and evolution of weed beets: consequences for the breeding and release of herbicide-resistant transgenic sugar beets. *Theor. Appl. Gen.* 87: 471–478.
- Bradshaw Jr., H.D., Wilbert, S.M., Otto, K.G. & Schemske, D.W. (1995): Genetic mapping of floral traits associated with reproductive isolation in monkeyflowers (*Mimulus*). *Nature* 376: 762–765.
- Briggs, D. & Walters, S.M. (1984): *Plant Variation and Evolution*, 2nd edn. Weidenfeld and Nicolson, London.
- Capy, P., Anxolabéhère, D. & Langin, Th. (1994): The strange phylogenies of transposable elements: are horizontal transfers the only explanation? *Tr. Genet.* 10: 7–12.
- Carter, G.F. (1977): A hypothesis suggesting a single origin of agriculture. In: Reed, C.A. (ed.) *Origins of Agriculture*. 89–133. Mouton Publ., The Hague.
- Cummings, M.P. (1994): Transmission patterns of eukaryotic transposable elements: arguments for and against horizontal transfer. *Trends Ecol. Evol.* 9: 141–145.

- Daniels, S.B., Peterson, K.R., Strausbaugh, L.D., Kidwell, M.G. & Chovnick, A. (1990): Evidence for horizontal transmission of the *P* transposable element between *Drosophila* species. *Genetics* **124**: 339–355.
- Davis, M.E., Lineberger, R.D. & Miller, A.R. (1991): Effects of tomato cultivar, leaf age, and bacterial strain on transformation by *Agrobacterium tumefaciens*. *Plant Cell, Tissue and Organ Culture* **24**: 115–121.
- De Vries, F.T., Van der Meijden, R. & Brandenburg, W.A. (1992): Botanical files: a study of the real chances for spontaneous gene flow from cultivated plants to the wild flora of the Netherlands. *Gorteria* (suppl. 1). Rijksherbarium/Hortus Botanicus, Leiden.
- De Vries, I.M. & Van Raamsdonk, L.W.D. (1994): Numerical morphological analysis of lettuce cultivars and species (*Lactuca* sect. *Lactuca*, Asteraceae). *Pl. Syst. Evol.* **193**: 125–141.
- De Wet, J.M.J. (1981): Species concepts and systematics of domesticated cereals. *Die Kulturpflanze* **29**: 177–198.
- Dobzhansky, Th., Ayala, F.J., Stebbins, G.L. & Valentine, J.W. (1977): *Evolution*. W.H. Freeman and Co., San Francisco.
- Dong, J.-Z. & McHughen, A. (1993): An improved procedure for production of transgenic flax plants using *Agrobacterium tumefaciens*. *Plant Science* **88**: 61–71.
- Doyle, J.J. (1992): Gene trees and species trees: molecular systematics as one-character taxonomy. *Syst. Bot.* **17**: 144–163.
- Eldredge, N. & Gould, S.J. (1972): Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf, T.J.M. (ed.) *Models in Paleobiology*. 82–115. W.H. Freeman and Co., San Francisco.
- Eldredge, N. (1989): *Macroevolutionary Dynamics—Species, Niches and Adaptive Peaks*. McGraw Hill, New York.
- Ellstrand, N.C. & Hoffman, C.A. (1990): Hybridization as an avenue of escape for engineered genes. Strategies for risk reduction. *Bioscience* **40**: 438–442.
- Evans, G.M. (1976): Rye, *Secale cereale*. In: Simmonds, N.W. (ed.) *Evolution of Crop Plants*. 108–111. Longman, London.
- Frietema de Vries, F.T., Van der Meijden, R. & Brandenburg, W.A. (1994): Botanical files on lettuce (*Lactuca sativa*): on the chance for gene flow between wild and cultivated lettuce (*Lactuca sativa* L. including *L. serriola* L., Compositae) and the generalized implications for risk-assessments on genetically modified plants. *Gorteria* (suppl. 2). Rijksherbarium/Hortus Botanicus, Leiden.
- Grant, V. (1981): *Plant Speciation*. Columbia University Press, New York.
- Gregorius, H.-R. & Steiner, W. (1993): Gene transfer in plants as a potential agent of introgression. In: Wöhrmann, K. & Tomiuk, J. (eds) *Transgenic Organisms, Risk Assessment of Deliberate Release*. 83–107. Birkhäuser Verlag, Basel.
- Hahn, S.K. (1995): Yams, *Dioscorea* spp. (Dioscoreaceae). In: Smartt, J. & Simmonds, N.W. (eds) *Evolution of Crop Plants*, 2nd edn. 112–120. Longman Scientific & Technical, Harlow.
- Hancock, J.F. (1992): *Plant Evolution and the Origin of Crop Species*. Prentice Hall, New Jersey.
- Hanelt, P. (1986): Pathways of domestication with regard to crop types. In: Barigozzi, C. (ed.) *The Origin and Domestication of Cultivated Plants*. 179–200. Elsevier, Amsterdam.
- Harlan, J.R. (1971): Agricultural origins: centers and noncenters. *Science* **174**: 468–474.
- Harlan, J.R. (1992): *Crops and Man*, 2nd edn. American Society of Agronomy, Crop Science Society of America, Madison, (WI).
- Heiser, C.B., Jr. (1988): Aspects of unconscious selection and the evolution of cultivated plants. *Euphytica* **37**: 77–81.
- Hettterscheid, W.L.A. (1994): The culton concept: recent developments in the systematics of cultivated plants. *Acta Bot. Neerl.* **43**: 78.
- Hettterscheid, W.L.A. & Brandenburg, W.A. (1995): Culton versus taxon: conceptual issues in cultivated plant systematics. *Taxon* **44**: 161–173.
- Hodgkin, T. (1995): Cabbages, kales etc., *Brassica oleracea* (Cruciferae). In: Smartt, J. & Simmonds, N.W. (eds) *Evolution of Crop Plants*, 2nd edn. 76–82. Longman Scientific & Technical, Harlow.
- Hogenboom, N.G. (1975): Incompatibility and incongruity: two different mechanisms of the non-functioning of intimate partner relationship. *Proc. Roy. Soc. London Series B* **188**: 361–375.
- Keeler, K.H. (1989): Can genetically engineered crops become weeds? *Bio/technology* **7**: 1134–1139.
- Keen, N.T. (1990): Gene-for-gene complementarity in plant-pathogen interactions. *Annual Rev. Gen.* **24**: 447–463.
- Kemmerer, E.C., Lei, M. & Wu, R. (1991): Structure and molecular evolutionary analysis of a plant cytochrome c gene: surprising implications for *Arabidopsis thaliana*. *J. Mol. Evol.* **32**: 227–237.
- Kennard, W.C., Slocum, M.K., Figdore, S.S. & Osborn, T.C. (1994): Genetic analysis of morphological variation in *Brassica oleracea* using molecular markers. *Theor. Appl. Genet.* **87**: 721–732.
- Kidwell, M.G. (1992): Horizontal gene transfer of P elements and other short inverted repeat transposons. *Genetica* **86**: 275–286.
- Klekowski, E.J. (1988): Mechanisms that maintain the genetic integrity of plants. In: Greuter, W. & Zimmer, B. (eds) *Proceedings of the XIV*

- International Botanical Congress*. 137–152. Koeltz, Königstein.
- Klinger, T., Elam, D.R. & Ellstrand, N.C. (1991): Radish as a model system for the study of engineered gene escape rates via crop-weed mating. *Cons. Biol.* 5: 531–535.
- Knoll, A.H. & Niklas, K.J. (1987): Adaptation, plant evolution, and the fossil records. *Review of Palaeobotany and Palynology* 50: 127–149.
- Kofoet, A., Kik, C., Wietsma, W.A. & De Vries, J.N. (1990): Inheritance of resistance to downy mildew (*Peronospora destructor* [Berk.] Casp.) from *Allium roylei* Stearn in the backcross *Allium cepa* L.  $\times$  (*A. roylei*  $\times$  *A. cepa*). *Plant Breeding* 105: 144–149.
- Ladizinsky, G. (1979): Seed dispersal in relation to the domestication of Middle East legumes. *Econ. Bot.* 33: 284–289.
- Lawrence, J.G., Ochman, H. & Hartl, D.L. (1992): The evolution of insertion sequences within enteric bacteria. *Genetics* 131: 9–20.
- Lengfelder, E. & Elstner, E.F. (1979): Cyanide insensitive iron superoxide dismutase in *Euglena gracilis*. Comparison of the reliability of different test systems for superoxide dismutases. *Z. Naturforsch* 34C: 374–380.
- Leple, J.C., Brasileiro, A.C.M., Michel, M.F., Delmotte, F. & Jouanin, L. (1992): Transgenic poplars: expression of chimeric genes using four different constructs. *Plant Cell Reports* 11: 137–141.
- Levy, S.B. & Miller, R.V. (eds) (1989): *Gene Transfer in the Environment*. McGraw-Hill Publishing Company, New York.
- López-Pila, J.M. & Scheler, C. (1993): Gene transfer from bacteria and heterologous viruses into cells of higher organisms. In: Wöhrmann, K. & Tomiuk, J. (eds) *Transgenic Organisms, Risk Assessment of Deliberate Release*. 65–52. Birkhäuser Verlag, Basel.
- MacRae, A.F. & Clegg, M.T. (1992): Evolution of *Ac* and *Ds1* elements in select grasses (poaceae). *Genetica* 86: 55–66.
- Maisonneuve, B., Bellec, Y., Anderson, P. & Michelmore, R.W. (1994): Rapid mapping of two genes for resistance to downy mildew from *Lactuca serriola* to existing clusters of resistance genes. *Theor. Appl. Genet.* 89: 96–104.
- Micke, A. & Donini, B. (1993): Induced mutations. In: Hayward, M., Bosemark, N. & Romagosa, I. (eds) *Plant Breeding: Principles and Prospects*. 52–62. Chapman and Hall, London.
- Milligan, B.G. (1991): Chloroplast DNA diversity within and among populations of *Trifolium pratense*. *Curr. Genet.* 19: 411–416.
- Nason, J.D., Ellstrand, N.C. & Arnold, M.L. (1992): Patterns of hybridization and introgression in populations of oaks, manzanitas and irises. *Am. J. Bot.* 79: 101–111.
- Pickersgill, B. (1977): Taxonomy and the origin and evolution of cultivated plants in the New World. *Nature* 268: 591–595.
- Pickersgill, B. (1986): Evolution of hierarchical variation patterns under domestication and their taxonomic treatment. In: Styles, B.T. (ed.) *Intraspecific Classification of Wild and Cultivated Plants*. 191–209. Clarendon Press, Oxford.
- Prins, T.W. & Zadoks, J.C. (1994): Horizontal gene transfer in plants, a biohazard? Outcome of a literature review. *Euphytica* 76: 133–138.
- Raybould, A.F. & Gray, A.J. (1993): Genetically modified crops and hybridization with wild relatives: a UK perspective. *J. Appl. Biol.* 30: 199–213.
- Rensch, B. (1959): *Evolution Above the Species Level*. Columbia University Press, New York.
- Rhodes, F.H.T. (1987): Darwinian gradualism and its limits: the development of Darwin's views on the rate and pattern of evolutionary change. *J. Hist. Biol.* 20: 139–157.
- Rick, C.M. (1988): Evolution of mating systems in cultivated plants. In: Gottlieb, L.D. & Jain, S.K. (eds) *Plant Evolutionary Biology*. 133–148. Chapman and Hall, London.
- Rieseberg, L.H. & Soltis, D.E. (1991): Phylogenetic consequences of cytoplasmic gene flow in plants. *Evol. Trends Pl.* 5: 65–84.
- Rieseberg, L.H. & Brouillet, L. (1994): Are many plant species paraphyletic? *Taxon* 43: 21–32.
- Salin, M.L. & Bridges, S.M. (1980): Isolation and characterization of iron-containing superoxide dismutase from an eukaryote, *Brassica campestris*. *Archives Biochem. Biophys.* 201: 369–474.
- Sarmiento, G.G., Alpert, K., Tang, F.A. & Punja, Z.K. (1992): Factors influencing *Agrobacterium tumefaciens* mediated transformation and expression of kanamycin resistance in pickling cucumber. *Plant Cell, Tissue and Organ Culture* 31: 185–193.
- Shore, J.S. & Barrett, S.C.H. (1985): Morphological differentiation and crossability among populations of the *Turnera ulmifolia* L. complex (Turneraceae). *Syst. Bot.* 10: 308–321.
- Simmonds, N.W. (ed.) (1976): *Evolution of Crop Plants*. Longman, London.
- Simmonds, N.W. (1979): *Principles of Crop Improvement*. Longman, London.
- Small, E. (1984): Hybridization in the domesticated weed-wild complex. In: Grant, W.F. (ed.) *Plant Biosystematics*. 195–210. Academic Press, Toronto.
- Smartt, J. (1990): *Grain Legumes: Evolution and Genetic Resources*. Cambridge University Press, Cambridge.



- Smartt, J. & Simmonds, N.W. (eds) (1995): *Evolution of Crop Plants*, 2nd edn. Longman Scientific & Technical, Harlow.
- Smith, M.W., Feng, D.F. & Doolittle, R.F. (1992): Evolution by acquisition: the case for horizontal gene transfers. *Trends Biochem. Sci.* **17**: 489–493.
- Song, K., Slocum, M.K. & Osborn, T.C. (1995): Molecular marker analysis of genes controlling morphological variation in *Brassica rapa* (syn. *campestris*). *Theor. Appl. Genet.* **90**: 1–10.
- Stace, C.A. (ed.) (1975): *Hybridization and the Flora of the British Isles*. Academic Press, London.
- Stuessy, T.F. (1990): *Plant Taxonomy*. Columbia University Press, New York.
- Stuber, C.W. (1989): Marker-based selection for quantitative traits. In: Röbbelen, G. (ed.) *Science for Plant Breeding*. Proceedings of the XII congress of EUCARPIA. 31–49. Paul Parey, Berlin.
- Syvanen, M. (1994): Horizontal gene transfer: evidence and possible consequences. *Annual Rev. Gen.* **28**: 237–261.
- Teilhard de Chardin, P. (1955): *Le Phénomène Humain*. SARL Editions du Seuil, Paris.
- Timmons, A.M., O'Brien, E.T., Charters, Y.M., Dubbels, S.J. & Wilkinson, M.J. (1994): Assessing the risk of wind pollination from transgenic fields of *Brassica napus* ssp. *oleifera*. *The Methodology of Plant Genetic Manipulation: Criteria for Decision Making*. Proceedings of the 1994 EUCARPIA conference. 11–14. September 1994.
- Ulian, E.C., Smith, R.H., Gould, J.H. & McKnight, T.D. (1988): Transformation of plants via the shoot apex. *In Vitro Cell. Devel. Biol.* **24**: 951–954.
- Van Damme, J.M.M. (1992): Hybridisation between wild and transgenic plants. In: Weverling, J. & Hekstra, G.P. (eds) *Ecological Effects of Genetically Modified Organisms*. 81–92. Netherlands Ecological Society, Arnhem.
- Van der Beek, J.G., Pet, G. & Lindhout, P. (1994): Resistance to powdery mildew (*Oidium lycopersicum*) in *Lycopersicon hirsutum* is controlled by an incompletely-dominant gene *Ol-1* on chromosome 6. *Theor. Appl. Genet.* **89**: 467–473.
- Van der Beek, J.G., Verkerk, R., Zabel, P. & Lindhout, P. (1992): Mapping strategy for resistance genes in tomato based on RFLPs between cultivars: *Cf9* (resistance of *Cladosporium fulvum*) on chromosome 1. *Theor. Appl. Genet.* **84**: 106–112.
- Van Raamsdonk, L.W.D. (1988): *IRIS: a program package for Information Regrouping to Identify Structures*. Release 3.1. CPRO-DLO, Wageningen.
- Van Raamsdonk, L.W.D. (1990): Biosystematics of cultivated plants and their wild relatives. In: Kawano, S. (ed.) *Biological Approaches and Evolutionary Trends in Plants*. 51–66. Academic Press, London.
- Van Raamsdonk, L.W.D. (1992): A crossability coefficient for the evaluation of crossing experiments. *Nord. J. Bot.* **12**: 177–182.
- Van Raamsdonk, L.W.D. (1993): Wild and cultivated plants: the parallelism between evolution and domestication. *Evol. Trends Pl.* **7**: 73–84.
- Van Raamsdonk, L.W.D. (1996): The cytological and genetical mechanisms of plant domestication exemplified by four crop models. *Botanical Review* **61** (in press).
- Van Raamsdonk, L.W.D., Eijk, J.P. & Eikelboom, W. (1995): The analysis of crossability between species of *Tulipa* subgenus *Tulipa*. *Bot. J. Linn. Soc.* **117**: 147–158.
- Van Raamsdonk, L.W.D. & Van der Maesen, L.J.G. (1996): Crop-weed complexes: the complex relationship between crop plants and their wild relatives. *Acta Bot. Neerl.* **45** (in press).
- Van Raamsdonk, L.W.D. & Sandbrink, J.M. (1995): Phylogenies inferred from morphological, nuclear DNA, chloroplasts DNA and crossability data in *Allium* section *Cepa* are not congruent due to different effects of introgression. *Acta Bot. Neerl.* **44**: 85.
- Van Raamsdonk, L.W.D., Wietsma, W.A. & De Vries, J.N. (1992): Crossing experiments in *Allium* section *Cepa*. *Bot. J. Linn. Soc.* **109**: 293–303.
- Von Bothmer, R., Gustafsson, M. & Snogerup, S. (1995): *Brassica* sect. *Brassica* (Brassicaceae). II. Inter- and intraspecific crosses with cultivars of *B. oleracea*. *Gen. Res. And Crop Evol.* **42**: 165–178.
- Von Vaupel-Klein, J.C. (1994): Punctuated equilibria and phyletic gradualism: even partners can be good friends. *Acta Biotheor.* **42**: 15–48.
- Wei, G. & Mahowald, A.P. (1994): The germline: familiar and newly uncovered properties. *Annual Rev. Gen.* **28**: 309–324.
- Whalen, M.C., Innes, R.W., Bent, A.F. & Staskawicz, B.J. (1991): Identification of *Pseudomonas syringae* pathogens of *Arabidopsis* and a bacterial locus determining avirulence on both *Arabidopsis* and soybean. *Plant Cell* **3**: 49–59.
- Wiley, E.O. (1978): The evolutionary species concept reconsidered. *Syst. Zool.* **27**: 17–26.
- Williamson, M. (1993): Risks from the release of GMOs: ecological and evolutionary considerations. *Evol. Trends Pl., Environment Update* **1**: 5–9.
- Zadoks, J.C. & De Wit, P.J.G.M. (1992): Invasiveness of plant pathogenic microorganisms. In: Weverling, J. & Hekstra, G.P. (eds) *Ecological Effects of Genetically Modified Organisms*. 45–49. Netherlands Ecological Society, Arnhem.

- Zeven, A.C. & De Wit, J.M.J. (1982): *Dictionary of Cultivated Plants and their Regions of Diversities*. PUDOC, Wageningen.
- Zhukovsky, P.M. (1968): New centres of origin and new gene centres of cultivated plants including specifically endemic microcentres of species closely allied to cultivated species. *Bot. Zhur.* 53: 430–460.
- Zohary, D. (1984): Modes of evolution in plants under domestication. In: Grant, W.F. (ed.) *Plant Biosystematics*. 579–586. Academic Press, Toronto.