

- Endemic*, a domesticate occupying a well defined geographic region which is a center of origin and center of variation as well.
- Semiendemic*, a center of diversity may be discernible with some diffusion of the domesticate out of that range.
- Monocentric*, a discernible center of origin which is also a center of diversity, but with wide distribution of the domesticate, a model which is applied to plantation crops such as coffee, cacao and oil palm.
- Oligocentric*, domesticates with a wide distribution, with two or more discernible centers of diversity. This model is applied to most seed crops such as wheat, barley, maize, pea, lentil and lima bean.
- Noncentric*, domesticates with ample distribution but no clear center of diversity, a model which can be applied to sorghum, American beans and bottle gourd.

These patterns of distribution, based mainly on spatial distribution of diversity, come close to Vavilov's centers of origin based on geographic distribution of diversity.

### 1.9 CONCLUSIONS

During most of his time on earth man has lived as a hunter-gatherer, and began to produce his food only in the last 10 000 years. The most likely reason for this transition was food crises resulting from human populations expanding beyond the carrying capacity of the habitats where they lived. Continuous planting-harvest cycles of wild plants created selection pressure which had not occurred previously and encouraged the emergence of domesticated types in seed crops. Some horticulture plants apparently were selected in the wild and brought to the horticulturalist garden, but the reasons for selecting specific wild plants for cultivation are not always clear. Under cultivation domesticated plants have continued to evolve and have further diverged from their wild progenitors.

The wild progenitors of the major crop plants have been identified, through comparative studies of morphology, cytology, and variation in biochemical and molecular markers; breeding experiments have always been the crucial test. Crop plants comprise a tiny portion of the world flora and belong to a small number of families. Domestication of these plants was restricted to particular geographical areas which are regarded as centers of origin.

## Increasing diversity under domestication

In any group of plants and animals evolution is the history of changes in genetic diversity. These changes are the result of subtle interactions between internal factors such as mutations, and external factors, mostly natural selection. The basic biological unit which is the subject of evolutionary process is the breeding population, i.e. a group of individuals which are bound by breeding relationships. At any given point in space and time genetic diversity is an outcome of three different, and sometimes conflicting, forces: factors and mechanisms acting toward greater diversity; factors decreasing diversity; and mechanisms to maintain existing diversity. The effect of these forces in shaping plant and animal evolution has been studied in detail in natural populations and they are also effective under domestication. The difference between the two is that in the latter, man has become an important element affecting trends and rates. To learn more about the nature of evolution under domestication it would be useful to examine the relative importance of each of the various forces and their effect.

Increasing diversity is achieved through mutations, recombination, immigration and introgression. Mutation is the only means by which novel alleles can be formed and is an essential element in evolution. Recombination is the process by which gene combinations are formed, and immigration and introgression are means by which diversity of a local population can be enriched by contributions from other populations of the same species or from other species.

### 2.1 MUTATIONS AND THEIR EFFECT

Mutations occur as a result of changes in the DNA sequence of the gene and are referred to as gene mutations or point mutations. The change may involve substitution of a nucleotide in the coding region of the gene or inversion of the order of nucleotides, which may result in encoding of a different amino acid in the polypeptide chain, compared with the

original polypeptide. Another possible change is an addition or deletion of a nucleotide in the coding area which may cause a change in the reading frame and subsequent production of a totally different protein.

In addition to gene mutations, chromosome mutations may occur as well. They are primarily a result of chromosome breakage and reunion in new forms. Chromosome mutations may affect single genes when the breakage occurs in the coding zone, or by translocating genes into or close to a heterochromatin region where they become inactive. Chromosome mutations include deletions and duplications of small segments, and translocations and inversions as a result of rearrangements. These rearrangements modify the linkage groups of the involved chromosomes. Chromosome doubling of a diploid plant results in polyploidy, which is also regarded as a chromosome mutation. New mutants, either gene or chromosome, are usually maladapted and inferior to the common gene, or chromosome arrangement, the wild type as it is often called. This is why the role of mutation as a source of genetic diversity is sometimes underestimated. It seems, however, that some of the mutations are adaptively neutral. The enormous diversity in molecular genes and specifically in non-coding DNA segments are thought to result from adaptive neutrality and stochastic events.

Mutations, either of genes or chromosomes, are rare and estimating the rate of their occurrence is laborious and expensive. These rates vary between organisms and specific genes in the ranges of  $1 \times 10^{-4}$  and  $1 \times 10^{-6}$  per gamete per generation, or even lower. In barley, Kahler, Allard and Miller (1984) estimated mutations in the electrophoretic mobility of five enzymes to be lower than  $3 \times 10^{-6}$ .

Adaptive inferiority and low formation rate are the two major features of mutations which must be borne in mind in assessing their effect on evolution under domestication. Most, if not all, the characteristics of cultivated plants are negatively selected in the wild and rarely have been established there. This is particularly obvious in traits such as lack of seed dispersal mechanism, quick germination and low level of alkaloids in fruits and seeds. Some of these characteristics are controlled by a single or a small number of genes (Table 2.1) and are likely to be formed in wild populations but immediately eliminated by natural selection. There is no reason to believe that cultivation, particularly in the early stages, was an element which could increase the mutation rate in these genes.

The mutation rate of genes controlling characteristics which have been altered by domestication is unknown. If, however, the ranges found in other genes apply here too, it is unlikely that man selected these mutants as soon as they were formed to create the new domesticated population. At least in the early stages of domestication, characteristics associated with seed dispersal mechanisms apparently had been favored unconsciously in the agricultural practices used by farmers, and only

Table 2.1 Genetics of traits associated with domestication

Crops and traits	Characters	No. of genes	References
<i>Seed retention</i>			
Barley, <i>Hordeum spontaneum</i>	tough rachis	2, recessive at either locus	Hockett & Nilan 1985
Chickpea, <i>Cicer arietinum</i>	pod indehiscence	1, recessive	Kazan <i>et al.</i> 1993
Cowpea, <i>Vigna unguiculata</i>	pod indehiscence	1, recessive	Rawal 1975
Indian rice, <i>Zizania palustris</i>	seed non-shattering	2, complementary dominants	Elliot & Perlinger 1977
Lentil, <i>Lens culinaris</i>	pod indehiscence	1, recessive	Ladizinsky 1979b
Lupinus, <i>Lupinus luteus</i>	pod indehiscence	1, recessive	Sengbusch & Zimmerman 1937
<i>L. angustifolius</i>	pod indehiscence	1, recessive	
<i>L. digitatus</i>	spikelet retention	1, recessive	Gladston 1967
Oats, <i>Avena sativa</i>	spikelet retention	1, dominant	Marshall <i>et al.</i> 1992
<i>A. strigosa</i>	floret retention	2, recessive	Jones 1940
Pea, <i>Pisum sativum</i>	pod indehiscence	1, recessive	Waines 1975
Pearl millet, <i>Pennisetum glaucum</i>	spikelet retention	3, recessive	Bliquez & Lecomte 1969
Rice, <i>Oryza sativa</i>	seed non-shattering	2, recessive	Nagao 1951
Sorghum, <i>Sorghum bicolor</i>	seed non-shattering	2, recessive	Karper & Quinby 1947
Soybean, <i>Glycine max</i>	pod indehiscence	1-2, additive	Tsuchiya 1987
Wheat, <i>Triticum monococcum</i>	tough rachis	2, recessive	Sharma & Waines 1980
<i>Change of spikelet and awn structure</i>			
Barley, <i>H. vulgare</i>	awnlessness	1, dominant	Hockett & Nilan 1985
	smooth awn	2, recessive	
	hooded awn	1, dominant	
	6-rowed spike	1, recessive	
Oat, <i>A. sativa</i>	awnlessness	1, recessive	Marshall <i>et al.</i> 1992
Rice, <i>O. sativa</i>	awnlessness	1, recessive	Nagao 1951

Table 2.1 Continued

Crops and traits	Characters	No. of genes	References
<i>Growth habit</i>			
Oat, <i>A. sativa</i>	dwarfism	1-2, dominant or recessive	Marshall <i>et al.</i> 1992
Pea, <i>Pisum sativum</i>	dwarfism	1, recessive	Marx 1985
Rice, <i>O. sativa</i>	dwarfism	1, recessive	Nagao 1951
Soybean, <i>G. max</i>	determinant growth	1, recessive	Bernard 1972
<i>Fruit characteristics</i>			
Almond, <i>Amygdalus communis</i>	sweet kernel	1, dominant	Heppner 1923, 1926
Bottle gourd, <i>Lagynaria vulgaris</i>	sweet fruit	1, recessive	Pathak & Singh 1950
Fig, <i>Ficus carica</i>	parthenocarpy	1, heterozygous	Storey 1975
Grapes, <i>Vitis vinifera</i>	seedlessness	2, recessive	Spiegel-Roy <i>et al.</i> 1990
Watermelon, <i>Citrullus lanatus</i>	sweet fruit	1, recessive	Navot <i>et al.</i> 1990
	red flesh	1, recessive	Navot <i>et al.</i> 1990
<i>Seed characteristics</i>			
Blue lupin, <i>Lupinus angustifolius</i>	soft seededness	1, recessive	Forbes & Wells 1968
Lentil, <i>L. culinaris</i>	soft seededness	1, dominant	Ladizinsky 1985a
<i>Breeding system</i>			
Grapes, <i>V. vinifera</i>	hermaphroditism	1, a three allele series	Olmo 1976
Banana, <i>M. acuminata</i>	parthenocarpy	at least 3 complementary dominant genes	Simmonds 1976
Fig, <i>F. carica</i>	parthenocarpy	1, heterozygous	Storey 1975

later, when these traits reached greater proportions, did they become noticeable and deliberately selected for. On the other hand, quick germination in legumes apparently was favored before cultivation, as argued in section 1.6.1. Similarly, it is likely that low alkaloid potato, sweet watermelon and sweet almond were selected prior to cultivation.

Seed retention in seed crops is usually controlled by a small number of genes. In wheat and barley the domesticated type is recessive, but in the common oat it is dominant (Table 2.1). In legumes, almost invariably, pod indehiscence is controlled by a single recessive gene. This behavior is a clear example of Darwin's parallel variation, and Vavilov's homologous series in crop plants.

Seed retention in maize presents one of the most radical morphological changes that has occurred under domestication. The morphological differences between maize and teosinte, particularly the ear structure, were thought to have evolved gradually by the accumulation of about five mutations (Beadle, 1980). Gradual transition from teosinte to maize, however, cannot be supported by archaeological evidence, because teosinte has not been recovered in archaeological settlements and the oldest maize remains are maize, albeit much smaller than modern maize, and not a transient form. To account for the profound morphological differences between maize and teosinte, yet reconcile with the archaeological evidence, Iltis (1983) proposed a radical theory of sexual transmutation. In *Zea*, flowers are characterized by relic bisexuality and can switch to either direction as a result of environmental conditions. Both in maize and teosinte hormone distribution along the stem determines the male zone at the top and the female zone below, under a certain threshold. According to Iltis, maize ear originated from a tassel which was transformed into female inflorescence following drastic shortening of the teosinte lateral branches, placing the tassel in the female hormone zone. The sexual transmutation theory is intriguing, not only because it elegantly settles morphological and archaeological peculiarities of maize, but also because it provides an example of evolution by jumps or punctuated equilibrium (Eldridge and Gould, 1972). The sexual transmutation theory also implies that man selected this 'helpful monster' as soon as it occurred, because it had completely lost its seed dispersal mechanism. It is hard to believe that just by chance such a rare 'monster' was picked up by man and immediately cultivated. Probably, as a result of unique environmental and climatic conditions, which helped to upset the hormone gradient, these 'monsters' were common enough to be noticed and used by man and subsequently were cultivated.

Some of the mutations occurring under domestication have reduced the function of certain organs or caused elimination of structures which became redundant in the new environment. On the other hand, they restored the function of other structures which declined and became redundant in the wild. Seeds of wild wheat, barley and oat are tightly

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covered by shafts. This tight packing became looser under domestication and free threshing, or naked grain types were selected.

In grasses, awns are an important element of the seed dispersal mechanism since they help to direct the seed into the soil and ensure quick burial. Under domestication, where seed dispersal is done by man, awns not only have become redundant, but they are a nuisance in threshing. Awnless types were selected in wheat, rice and oat, and in barley types with modified awns were selected. All these are products of single mutations (Table 2.1).

Each node of the wild barley's spike contains three spikelets but only the middle one is fertile. The lateral spikelets are either completely sterile or staminate. As a result, the spike is made of two rows of seeds. This characteristic is not unique to barley, but is typical of the entire genus *Hordeum*. Under domestication, however, a single mutation restored fertility of the lateral spikelets giving rise to the six-rowed barley.

Most of the mutations selected under domestication had an obvious advantage and were beneficial to the farmer. For some other mutations this advantage is not so clear, at least on first sight; seed and flower color are among them. Seed coat color varies tremendously in the phaseolus beans. The white color type is confined only to the cultivated bean. Levels of tannin are much higher in black and red beans compared with white ones. The tannin interacts with proteinases to decrease digestibility (Elias, Fernandez and Bressini, 1977), hence the possible advantage of the white seeded types. Flower color in chickpea can be pink, blue or white and is controlled by three genes, the white being the universal recessive (Muehlbauer and Singh, 1987). Under cultivation the white flower has no obvious advantage over pink or blue, and it can be argued that it was randomly fixed, or deliberately selected as an attraction. It appears, however, that flower color in chickpea is linked to testae color which may be associated with quick germination, cooking characteristics, or both. The association between flower color and seed color was observed in pea by Mendel in his famous breeding experiments.

Confusing, however, is the variation in epicotyl color in many lentil and chickpea varieties. Epicotyl color in the chickpea and lentil wild progenitors is purple red, but green epicotyls are common in many land races and advanced varieties of these pulses. It is difficult to imagine that green epicotyl types were purposely selected by man, but linkage relationships with other characteristics of agronomic value, or pleiotropic effects of the epicotyl color have not yet been documented.

In polyploid crop plants mutations might cause gene silencing. The genome of the tetraploid wheat (AABB,  $2n=28$ ) had been extracted from the hexaploid wheat (AABBDD,  $2n=42$ ) by the backcrossing technique (Kerber, 1964). The reconstituted tetraploid did not resemble any of currently described varieties. The plants were dwarf, lacked vigor and were partially or completely sterile, despite normal chromosome pairing

at meiosis. It has been suggested that many duplicated genes of the tetraploid genome which are active and essential in the tetraploid wheats were lost or mutated in the hexaploids. Gene silencing by mutation should not be confused with epistatic effects. In the reconstructed tetraploid wheat some proteins were detected which have not been observed in the hexaploid progenitor, indicating suppression of the tetraploid protein production by genes of the D genome (Galili and Feldman, 1984). In oats, a diploid sector emerged in a hexaploid plant derived from a cross between the common oat ( $2n=42$ ) and a wild tetraploid ( $2n=28$ ) species. Chromosome pairing in this sector was nearly normal but its development had not progressed beyond the boot stage (Ladizinsky and Fainstein, 1978). Again, the diploid genome apparently lost some important genes controlling development toward maturity. In tobacco, chlorophyll production is governed by two genes, *Ws1* and *Ws2*, and they were assigned to chromosomes G and T, respectively. Both genes were functioning in 25 tobacco varieties, in one, only the *Ws1* gene was operating, and in another eight varieties the chlorophyll production was attained only by the *Ws2* gene (Clausen and Cameron, 1950). When two genes control the same function the loss of one of them is tolerable, and the silenced locus may either be lost or may acquire a new function.

The list of characters involved in domestication in Table 2.1 shows that the vast majority of them are controlled by single recessive genes. Other characters selected at more advanced stages of domestication are also essentially recessive. This has been taken by Lester (1989) to suggest that domesticated types are not advanced forms, but genetically incapacitated because they lack some functions which have emerged by natural selection in their wild relatives. The domesticated characters are not novel in the sense that they resulted from new, previously non-existent enzymes or biosynthetic pathway. More likely, they resulted from malfunctioning or deformation of certain enzymes. While some of the recessive characters of crops behave as null, there is still very little evidence to relate characters of the domesticate to any specific biosynthetic process; the few, however, are suggestive. The wrinkled seed type of pea is recessive (*rr*). In the round seed type (*RR*, *Rr*) two isoforms of the starch branching enzyme are present in the mature embryos, but only one of them in the wrinkled type embryos (Smith, 1988). Lester's arguments can be extended further to suggest that parallel variation among botanically related crops (homologous series in Vavilov's term) resulted not from random mutation, but from the same defect in a common synthetic pathway.

### 2.1.1 Mutations in quantitative traits

Traits which are governed by single genes are by far fewer than those governed by many genes. Furthermore, expression of characters

controlled by major genes often show a background effect suggesting the involvement of minor genes (modifiers) as well. Pod indehiscence is governed by a single gene in many legume crops, but occasionally in crosses of pod-dehiscent × pod-indehiscent types, some F<sub>2</sub> individuals which may be classified as indehiscent under normal conditions, show some degree of pod dehiscence at higher temperatures or following over-drying. The degree of so-called instable indehiscence may vary between different cross combinations and different environmental conditions.

A great proportion of characteristics separating a cultigen from its wild progenitor are of a quantitative nature and controlled by many genes (polygenes). Mutations in these genes played a role in crop evolution after the initial domestication had been achieved by mutations in the key major genes. They have widened the morphological and physiological gap between the crop and its wild progenitor and their accumulation usually represents the second phase of domestication. Mutations in traits controlled by several genes had conspicuous effects in traits of plant organs used by man, i.e. plant habit and adaptability. Most dramatic is the increase of plant parts, gigantism, according to some authors (Schwanitz, 1966; Hawkes, 1983; Smartt, 1990). The Brassicas exhibit remarkable changes in bud and leaf shape and size, and stem and root structure. Mutations in these characters emerged and were selected for independently in two species in different geographical areas and produced different crop types (Table 2.2).

The swollen stem (so-called bulb) of kohlrabi is determined by three multiple factors of which two are major and one is a minor, or modifying factor (Pease, 1926). Yarnell (1956) cited Malinowski who could not find any well developed 'bulb' in F<sub>2</sub> plants of cabbage × kohlrabi

**Table 2.2** Crop types and their geographic origin in the Brassicas

Species*	Organ used	Crop type	Geographical region
<i>Brassica oleracea</i>	leaves	kale	Europe
	buds	cabbage	Europe
		Brussels sprouts	Europe
		stems kohlrabi	Europe
		flowers broccoli	Europe
		Chinese broccoli	E. Asia
		cauliflower	Europe
<i>B. campestris</i>	leaves	pak choi	E. Asia
	buds	Chinese cabbage	E. Asia
		turnip	E. Asia
	roots		Europe
	flowers	pak choi variant	E. Asia
		broccoletto	Europe

\* adapted from Crisp 1989

hybrids, indicating the involvement of more than three genes. Pease (1925) suggested that two genes are controlling the heart formation of cabbage. Hearting takes place when the two genes are homozygous recessive, n<sub>1</sub>n<sub>1</sub>, n<sub>2</sub>n<sub>2</sub>; no hearting occurs when at least three dominant alleles are present, and intermediate hearting in other allelic combinations. The number of genes involved seems to be higher, at least three, because only about 1% of the cabbage × kale F<sub>2</sub> 6302 plants showed the cabbage heart (Kristofferson, 1924). The development of heads in leaf axils in Brussels sprouts seems to be controlled by several genes since this character showed continuous variation in cabbage × Brussels sprouts F<sub>2</sub> populations (Kristofferson, 1924).

Another character exhibiting a considerable departure from the wild type, and gigantism, is seed size, particularly among pulses (Table 2.3). In some crop plants such as lentil and chickpea there is a continuum from the wild to the cultivated types, but in others, like common beans, there is often a gap in seed weight and size between the two. Furthermore, within the crops variation in seed size and weight is so immense that it has been used for intraspecific classification. In lentil, small seeded types are classified as subsp. *microsperma* and large seeded types as subsp. *macrosperma*. Small, medium and large seeded types of broad bean are known as vars *paucijuga*, *equina* and *major*, respectively. Crosses between small and large seeded types in lentil indicated polygenic inheritance (Abbo, Ladizinsky and Weeden, 1992). Differences between small wild and large cultivated seeded types in length, width, height and weight are controlled by at least ten genetic factors in common bean (Motto, Soressi and Salamini, 1978), and at least eight genetic factors in chickpea (Niknejad, Khosh-Khui and Ghorashy, 1971).

Variation in adaptability of crop plants is apparently established in two main stages: in the beginning the accumulation of genes conferring adaptability to the cultivated field, and at a more advanced stage the acquisition of adaptability to different soil types and response to day length and air temperature, following migration to other geographical

**Table 2.3** Ranges of 100 seed weight (g) of several pulses and their wild progenitors

Crop	Wild	Cultivated	Reference
Broad bean		13–238	Cubero 1973
Chickpea	2.5–12.5*	1–75	Cubero 1987
Groundnuts	2–5	up to 100	Smartt 1990
Lentil	0.65–2.9*	1.5–8.5	Solh and Erskin 1980
Lima beans	6.9–13.8	31.7–193.2	Mackie 1943
Soybean	about 2.9	3.8–43.2	Hymowitz and Newell 1980
Tepary bean	1.7–2.2	3.5–21.5	Pratt and Nabhan 1981

\* unpublished data

regions or altitudes. These responses are particularly noticeable in soybeans. Soybean cultivars of the USA have been assigned to 13 maturity groups according to their yield performance in different latitudes (Figure 2.1) which represents their day-length sensitivity. Of the 560 wild soybean accessions in the USA collection 528 originated from latitudes comparable to maturity groups II–VII, suggesting that diversity in cultivars growing in other latitudes has emerged under cultivation. Day-length response in soybean is governed by four genes,  $E_1$ – $E_4$ , but only the  $E_4$  allele is day-length insensitive (Palmer and Kilen, 1987).

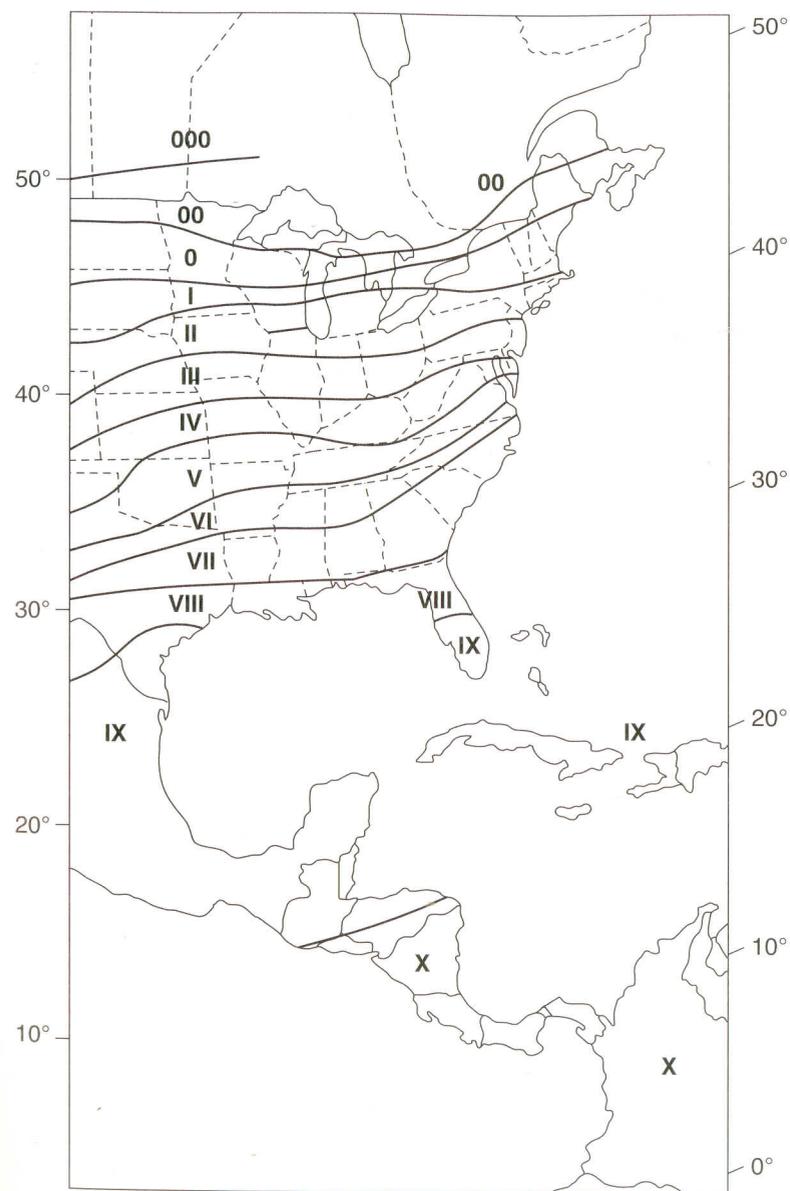
### 2.1.2 Chromosome mutations

#### (a) Chromosomal rearrangements

Apart from rare terminal deletions, all chromosome mutations require at least two chromosome breakages, either in the same chromosome (inversion), or in two non-homologous chromosomes (reciprocal translocations). Chromosome rearrangements entail change of linkage groups and may cause silencing or triggering of particular genes as a result of their removal to new sites. Diversity caused by chromosomal rearrangements is significant because of its bearing on sterility of individuals which are heterozygous to these rearrangements, and as a mechanism in speciation. The rearrangements are para and pericentric inversions, Robertsonian and reciprocal translocations.

In paracentric inversions a part of a chromosome arm is rearranged in a reverse order. In the heterozygous state the normal and the inverted chromosomes form a loop at the pachytene and crossing over inside the loop causes the formation of an anaphase bridge and about 50% gamete lethality (Figure 2.2). In pericentric inversion the inverted segment contains the centromere. Pachytene in individuals heterozygous to pericentric inversion also shows a characteristic loop. Crossing over in the loop would not result in an anaphase bridge but would cause about the same sterility as in paracentric inversion (Figure 2.3). Because all products of crossing over in the inverted segments are aborted (except rare two strand double crossing over) the linkage group of the inverted segment remains intact.

Robertsonian translocations are rearrangements in which two telocentrics mingle to form one metacentric chromosome (Figure 2.4). This involves the loss of one centromere and a small chromosome segment. The result is a reduction in chromosome number, though without change in the number of chromosome arms. Robertsonian translocations are the main mechanism by which aneuploid series are formed within species and may lead to the formation of new species. The different arrangement of the chromosome arms cause some sterility in crosses between members with different chromosome numbers.



**Figure 2.1** Maturity groups in soybean cultivars relative to the area in which they grow commercially. Reproduced from Fehr, W.R. 1989. Soybean, in *Oil Plants of the World* (eds G. Röbbelen, R.K. Downey and A. Ashri), p. 295, McGraw-Hill, New York.

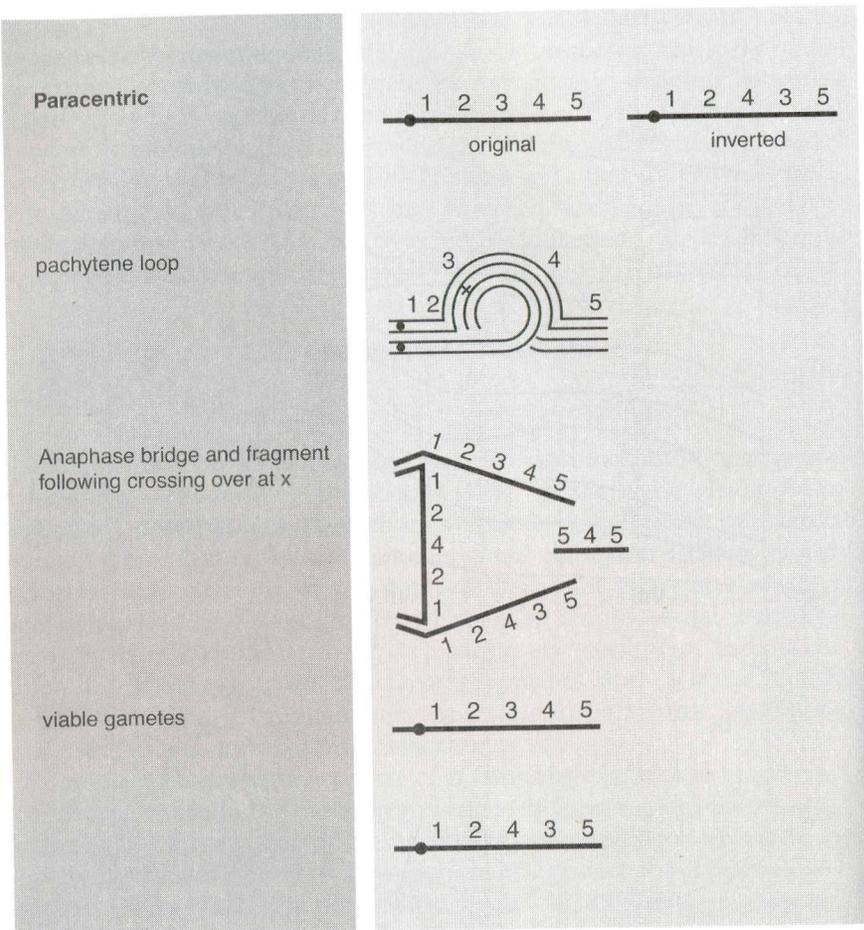


Figure 2.2 Cytogenetic consequences of paracentric inversion.

In reciprocal translocations segments are exchanged between non-homologous chromosomes (Figure 2.5). In individuals heterozygous to reciprocal translocation the two pairs of chromosomes involved in the rearrangement form a cross-shaped configuration of four at pachytene, and quadrivalent at metaphase I. The mode of the quadrivalent segregation at anaphase I determines the fertility of these individuals. Only one type, alternate, or zig-zag, would produce viable gametes (Figure 2.5).

Chromosome rearrangements occur naturally at low frequencies, but they may be more common in polyploid organisms than in diploid species. There is no reason to believe that this low rate has been changed under domestication or cultivation. Any kind of chromosome mutation in crop plants is likely to originate from chromosome polymorphism in the wild progenitor, or from a mutation occurring after domestication.

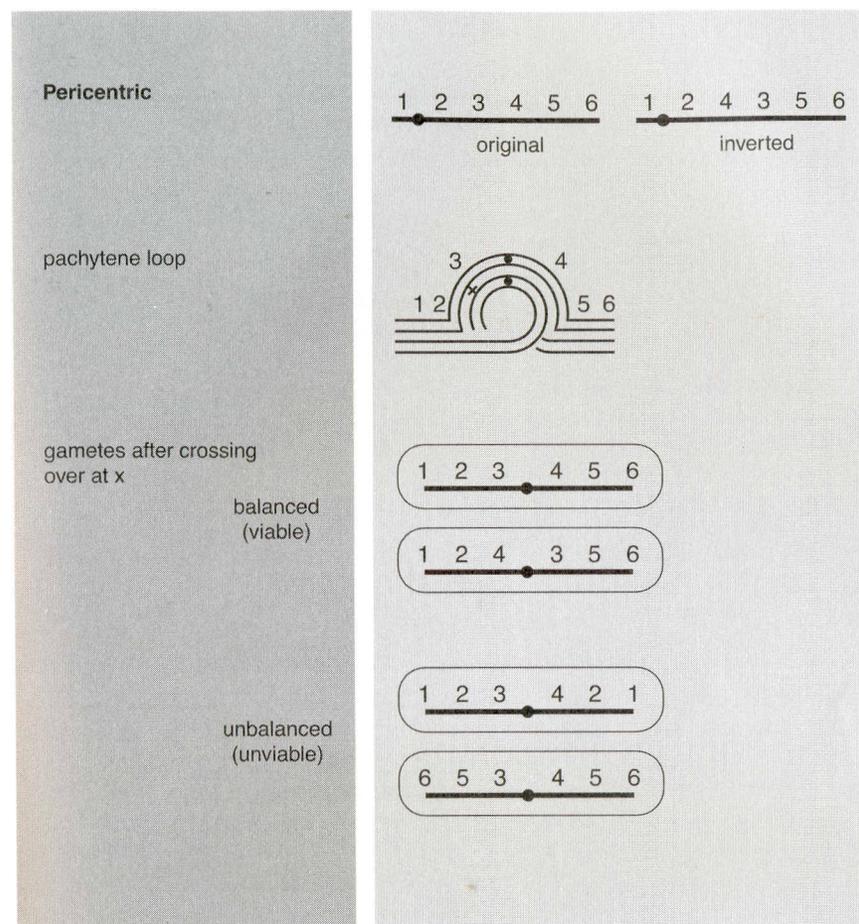


Figure 2.3 Cytogenetic consequences of pericentric inversion.

In the *Capsicum annuum-chinense-frutescens* complex of the chili pepper, domesticated forms of *C. annuum* and *C. chinense* differ from each other by one chromosomal interchange. Wild *C. annuum* contains two chromosomal races: one is identical to that of the domesticated *C. annuum*, and the second race has a chromosome arrangement similar to that of cultivated *C. chinense* (Pickersgill, 1971, 1989).

The occurrence of paracentric inversion and a reciprocal translocation after domestication in an Ethiopian chickpea line (Ladizinsky and Adler, 1976a) has already been mentioned (section 1.4.2). Furthermore, two pairs of satellited chromosomes have been observed in the karyotype of the chickpea wild progenitor *C. reticulatum*. Some cultivated chickpea lines also have two pairs of satellited chromosomes, whereas others have only one pair. This may be interpreted as silencing of one of the rDNA

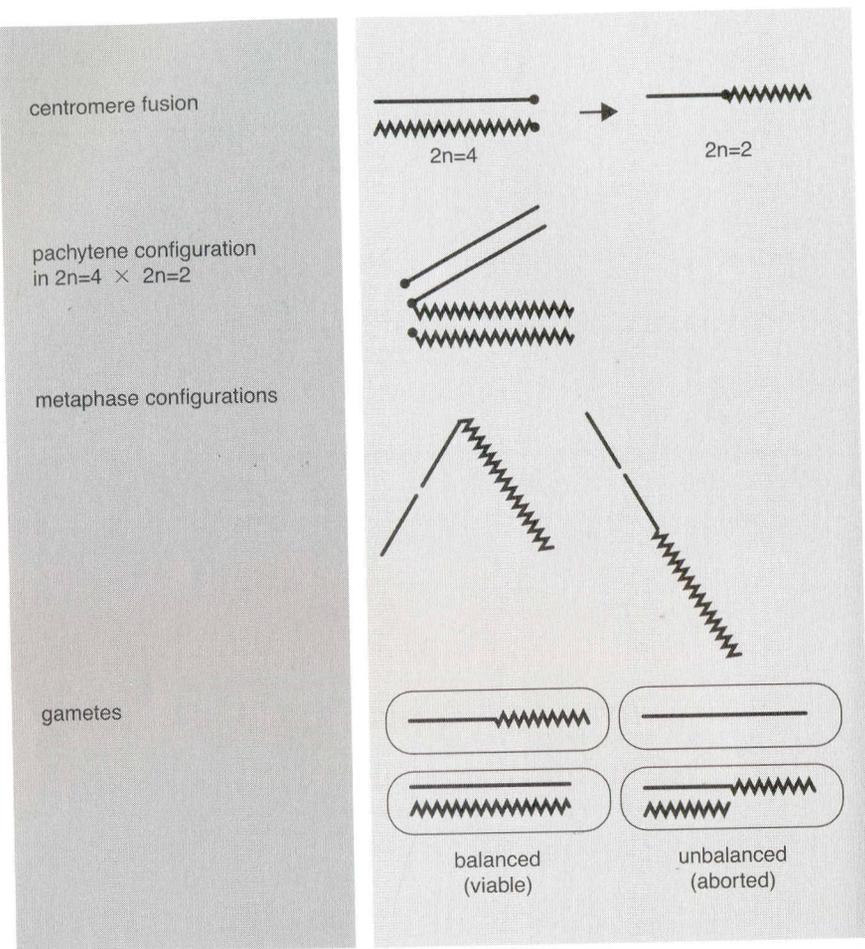


Figure 2.4 Cytogenetic consequences of Robertsonian translocation.

sites, or translocation of the satellite to another chromosome. *In situ* hybridization experiments with an rDNA probe in chickpea lines with only a single pair of satellited chromosomes indicated that the latter is the case because three hybridization sites were observed: one at the secondary constriction area of the satellited chromosomes, another one at the telomere of the second largest chromosome, the one possessing secondary constriction and satellite in lines having two pairs, and a third very faint one in other chromosome (Abbo *et al.*, 1994).

### 2.1.3 Polyploidy

Doubling the entire chromosomal set has much less drastic effect on the individual than chromosomal rearrangement, and instantaneously

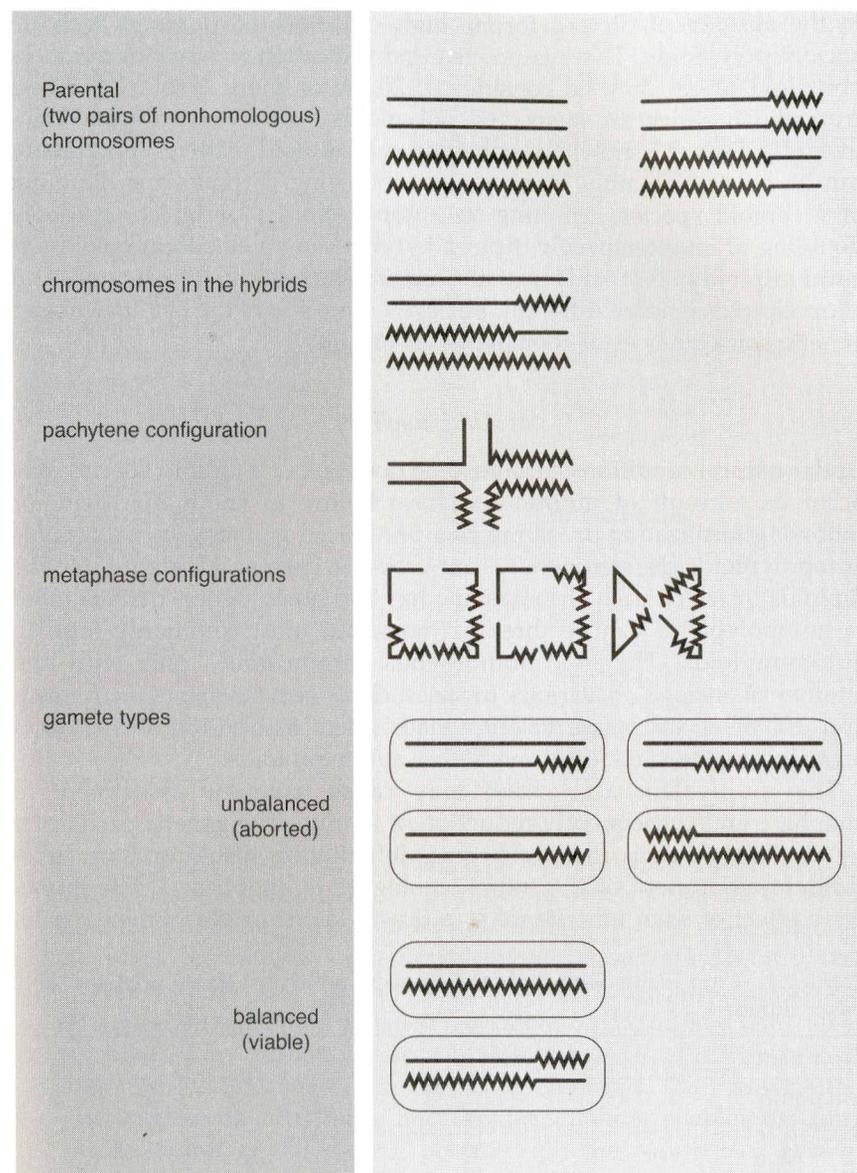


Figure 2.5 Cytogenetic consequences of reciprocal translocation.

creates new biological species (section 4.3.1) with a reproductive isolation from other diploid individuals which is far more effective than chromosomal rearrangement. Occurrence of polyploidy in crop plants is evident in closely related species differing from one another by euploid chromosome numbers, suggesting the occurrence of a polyploid series.

In the absence of diploid forms, high chromosome numbers indicate ancient polyploidy. There is no clear-cut indication at what  $2n$  numbers polyploid origin may be considered; 20, 30 or more. Table 2.4 shows crop plants which are suspected polyploids but have no diploid relatives and Table 2.5 shows those having such diploid relatives. Polyploidy can be obtained mainly in two ways: following chromosome doubling of a diploid species, resulting in autopolyploidy, or by chromosome doubling of an interspecific diploid hybrid, known as allopolyploidy or amphidiploidy. Not only are the circumstances by which auto and allopolyploids emerge different, but even more so are the cytological and genetic consequences of their mode of origin.

(a) Autopolyploidy

Under natural conditions chromosome doubling of a diploid species may occur as a result of mitotic anaphase failure in shoot meristem, or following fertilization involving two unreduced gametes. In wild plants autopolyploidy is confined to out-crossing, perennial plants. Unlike diploids in which each chromosome has two homologues, their number in autopolyploids can be three or more, but most commonly four, in autotetraploids. The four homologous chromosomes pair with one another at meiosis in various forms such as two bivalents, a trivalent and univalent and quadrivalent. Quadrivalent association at meiosis is regarded as the cytological marker of autotetraploids.

The multivalent association may cause irregular assortment at anaphase and consequently reduction of fertility. The genetic peculiarity of autotetraploids is their tetrasomic inheritance, resulting from independent assortment of the four homologues at anaphase I. The immediate effect of such inheritance is a drastic reduction of homozygosity.

**Table 2.4** Crop plants with high chromosome number with no relatives with lower numbers

Crop plant	$2n$
Amaranth	32, 34
Apple	34
Cassava	36
Cucurbitas	40
Okra	72, 144
Pear	34
Pineapple	50
Pistachio	30
Soybean	40
Sunflower	34
Sweet potato	60, 90
Tea	30
Yam	30-80

**Table 2.5** Crop plants with evident polyploid origin

Crop plant	$2n$	Kind of polyploidy
Alfalfa, <i>Medicago sativa</i>	32	Autotetraploid
Banana, <i>Mussa acuminata</i>	33, 44	Autotriploid, autotetraploid
Brown mustard, <i>Brassica juncea</i>	36	Allotetraploid
Chinese chives, <i>Allium tuberosum</i>	32	?
Coffee, <i>Coffea arabica</i>	44	?
Cotton, <i>Gossypium hirsutum</i>	52	Allotetraploid
Ethiopian mustard, <i>Brassica carinata</i>	34	Allotetraploid
Groundnut, <i>Arachis hypogea</i>	40	Allotetraploid
Leek, <i>Allium ampeloprasum</i>	32	?
Millet, <i>Elusine coracana</i>	36	Allotetraploid?
Oat, <i>Avena sativa</i>	42	Allohexaploid
European plum, <i>Prunus domestica</i>	48	Allohexaploid?
Potato, <i>Solanum tuberosum</i>	48	Autotetraploid
Quinoa, <i>Chenopodium quinoa</i>	36	?
Rakkoy, <i>Allium chinense</i>	32	?
Rape, <i>Brassica napus</i>	38	Allotetraploid
Sugercane, <i>Sacharrum</i> ssp.	40-122	?
Strawberry, <i>Fragaria ananassa</i>	56	Autooctaploid
Sweet potato, <i>Ipomoea batata</i>	40	?
Tobacco, <i>Nicotiana tabacum</i>	48	Allotetraploid
Wheat, <i>Triticum turgidum</i>	28	Allotetraploid
<i>T. aestivum</i>	42	Allohexaploid
White clover, <i>Trifolium repens</i>	32	Autotetraploid?
Yam, <i>Discorea alata</i>	30-80	Autopolyploids
<i>D. rotundata</i>	40-80	Autopolyploids?

While in a panmictic diploid population in which two alleles are equally present, 50% of the individuals are assumed to be homozygous, a similar situation in autotetraploids would result with only little more than 5% homozygous. Furthermore, heterozygosity in autotetraploids is potentially more variable than in the diploids. While only one heterozygote combination can be formed between two alleles in the diploid (Aa), three can be formed in autotetraploid (AAAa, AAaa, Aaaa) (Figure 2.6). Autopolyploidy occurs in out-crossed perennials. The association between tetrasomic inheritance and cross-pollination enables the foremost exploitation of the genetic potential by the coexistence of four alleles per locus. The drawback is lower fertility resulting from meiotic irregularities, but this is compensated by the perennial growth habit, for which a high seed set is not as critical as in annuals.

Only a few wild autopolyploids gave rise to domesticate derivatives, such as strawberry, possibly some yam species, and alfalfa and orchard-grass among the forages (Table 2.5). Under cultivation autopolyploidy had been a major step in the evolution of potato and banana. Spontaneous autotetraploid sectors have appeared in several crop plants and may be favored by farmers and horticulturalists. Such autotetraploids were

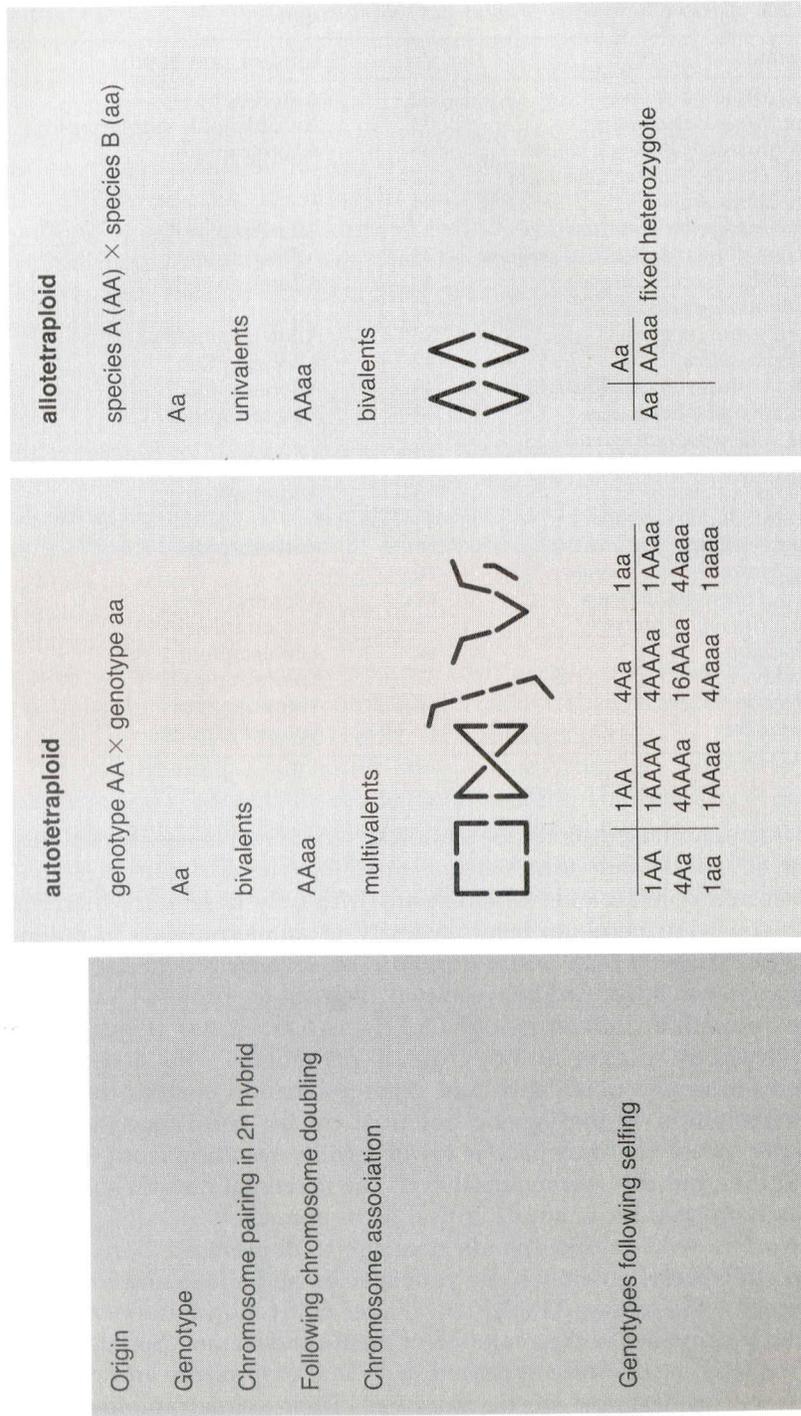


Figure 2.6 Cytogenetic consequences of polyploidy.

selected in a number of fruit trees long before their chromosome number were confirmed cytologically. Among others are grapes, apples, pears, cherries, citrus, pineapple and tea. Autopolyploidy may increase the size of vegetative parts and fruits, but usually reduces fertility; therefore, spontaneous autopolyploidy has been exploited more in vegetatively propagated plants or those in which the vegetative parts are utilized.

The discovery that colchicine, an alkaloid occurring in corms and seeds of the autumn crocus, *Colchicum autumnale*, is capable of arresting spindle formation at cell division and thereby doubling the chromosome number (Dustin, Havas and Lits, 1937), has provoked numerous attempts to create new autopolyploid varieties in many crop plants (Blackslee and Avery, 1937). Relative success has been achieved in crops which are vegetatively propagated, or that are grown for their vegetative parts and as ornamentals. In sugarbeet, autotetraploid lines have been inferior to diploids in their sugar yield. Triploids produced by crossing a male sterile diploid with an autotetraploid have a sugar yield almost as good as the diploid varieties, but have been advantageous because of a monogerm which has been incorporated in them and drastically reduced the need for singling (Hornsey, 1975). A monogerm plant bears a single flower at each inflorescence node instead of a cluster of flowers which fuse during fruit and seed maturation resulting in a multigerm situation. Production of similar triploid varieties is now rapidly expanding in watermelon because these varieties are practically seedless. Artificially induced polyploidy is popular in flower breeding because of its effect on the enlargement of various plant parts, and occasionally longer flowering period.

Production of autopolyploid varieties has been much less successful in seed crops. The raw autotetraploids showed no better performance than the diploid varieties, and were inferior in seed set because of partial sterility. Some autotetraploid rye became more successful following hybridization between different lines which enabled the manifestation of their heterotic potential (Müntzing, 1951).

Another aspect of artificial chromosome doubling in crop plants is the potential for creation of self-fertile types from self-incompatible diploids. Particularly in gametic self-incompatibility, doubling chromosome number of a self-incompatible diploid restores self-fertility. All the cultivated diploid potatoes are self-incompatible, but all the natural tetraploids are self-fertile. Similarly in rye the diploid is self-incompatible, but the autotetraploid self-fertile.

#### (b) Allopolyploidy

Chromosome doubling of a sterile diploid hybrid has four main cytogenetic and evolutionary consequences: it may immediately restore fertility because each chromosome is now represented by two homologues which

can pair and segregate as in a diploid; the genomes of the diploid species remain separate in the same nucleus resulting in disomic inheritance; since the chromosomes of the two genomes are kept apart, the allotetraploid turns out to be a permanent hybrid for a great part of its genome; and the raw allotetraploid becomes, at once, isolated from its diploid progenitors (Figure 2.6).

Some crop plants derived from natural allopolyploids, such as tetraploid wheat and common oat, and several others have been spontaneously formed under cultivation (section 4.3.2). Chromosome doubling of several artificial interspecific hybrids produced a number of raw allopolyploids which have been used mainly in breeding programs. One of these, the wheat × rye hybrid (triticale), has gained some economic importance.

#### 2.1.4 Induced mutations

The discovery that the rate at which a single gene mutates can be increased by ionizing radiation and by mutagenic chemicals has accelerated the production of new mutants in many crop plants in the second half of this century. The effect of x-rays as a mutagen was realized by Muller in 1927 (Muller, 1956) in his mutation experiments in *Drosophila*. Similar experiments with plants were disappointing because most of the mutants were inferior to the cultivar from which they were derived, or even lethal. As a source of genetic variation, and a branch in plant breeding, mutations became more effective after 1960 when chemical mutagens were introduced. Theoretically, mutation breeding offers the possibility of introducing new diversity into existing varieties without upsetting the entire genome, as may happen when diversity is introduced by hybridization. Another possible advantage of mutation breeding is to create diversity in traits which only recently have become a target of breeding efforts and have never been selected for in land races. It is also unlikely that these traits will be available in the wild gene pool because, almost as a rule, these characteristics, if occurring spontaneously, are negatively selected for in the wild.

Plant parts which have been exposed to mutational treatment include seed, leaf blade, leaf rachis, leaf petioles, nodal stems, stem cuttings, tubers, dormant rhizomes and pollen. As a result of mutational treatments variation has been reported in almost any characteristic of economic value. The number of varieties which are a direct result of mutation breeding is rapidly increasing. According to Mücke, Donini and Maluszynski (1990) over 1000 cultivars have been the product of induced mutations: 567 in seed propagated crops; 40 in fruit plants; 29 in other vegetatively propagated crops; and 409 in ornamental plants. The contribution of mutation breeding is even higher if one considers also cultivars which resulted from crosses involving mutant plants. It is less clear, however, how many of these reported cultivars have gained popularity

among farmers and are superior to varieties derived from classical breeding. Some mutation-induced varieties definitely have been far superior. The cultivar 'Pallas', selected from 'Bonus' following x-ray treatment, has been sown on about 40% of the barley acreage in Denmark (Sigurbjörnsson, 1983). The peppermint production in the USA, threatened by verticillium wilt, was rescued by several new varieties selected from the susceptible variety following irradiation treatment. In ornamental plants mutation-induced cultivars have provided a large number of forms with new flower and leaf colors and patterns, and different shapes and size. By 1981, 263 radiation-induced cultivars of 22 ornamental plants were commercialized. It has been estimated that about 40% of the chrysanthemum cultivars grown in the Netherlands are the product of induced mutations (Konzak, 1984).

While induced mutations are an important source of new genetic diversity which may mark a new step in crop plant evolution, the difficulty with this new approach should not be underestimated. Specific change cannot be created at will. Even induced mutations are produced randomly and at a low rate. Therefore, the usefulness of mutation breeding depends, primarily, on selection and detection methods. In classical mutation breeding a large number of treated plants, and mostly their progenies, have to be raised in order to detect the desirable mutant. It could be that with the improvement of cell culture techniques, including haploid cells, selection and regeneration methods, mutagenesis induced in cell cultures might save a great part of the expense of growing a large number of plants following mutagenic treatment.

## 2.2 HYBRIDIZATION

The term hybridization is used in diverse situations of gene transfer. Aside from the recent development in somatic hybridization, hybridization is achieved by the sexual process, starting with the germination of pollen of one plant on the stigma of another plant. In crop plant evolution, hybridization manifests itself at three different levels: hybridization within and between populations of the crop; hybridization between the crop plant and its wild progenitor; and hybridization between the crop plant and more distant relatives, wild and cultivated. At each level the significance of hybridization in enhancing genetic variation depends upon the breeding system of the crop plant.

### 2.2.1 Pollination and breeding systems

Like wild plants, crops exhibit a wide range of breeding behavior from strict self-pollination to obligatory cross-pollination with a wide variation between the two extremes (Table 2.6).

**Table 2.6** Breeding system of selected crop plants

<i>Predominantly selfers</i>	<i>Predominantly outcrossers</i>	<i>Obligatory outcrossers</i>
apricot	alfalfa	almond <sup>s</sup>
barley	avocado	apple <sup>s</sup> (most cultivars)
chickpea	beet	asparagus <sup>d</sup>
citrus	broad bean	cabbages <sup>s</sup>
coffee	carrot	cocoa <sup>s</sup>
common bean	cashew	cherry <sup>s</sup>
cotton	cucumber	clover <sup>s</sup>
cowpea	fig	date palm <sup>d</sup>
eggplant	guava	hemp <sup>d</sup>
finger millet	maize	grapes <sup>d</sup> (in the wild)
flax	mango	papaya <sup>d</sup>
groundnut	melon	pistachio <sup>d</sup>
lentil	olive	pear <sup>s</sup> (most cultivars)
lettuce	onion	European plum <sup>s</sup> (most cultivars)
lima bean	pearl millet	radish <sup>s</sup>
mungbean	pecan	rape <sup>s</sup>
oats	persimmon	rye <sup>s</sup>
pea	pigeon pea	strawberry <sup>d</sup>
peach	sorghum	sunflower <sup>s</sup>
pepper	walnut	turnip <sup>s</sup>
rice	watermelon	
safflower		
sesame		
tomato		
wheat		

s = self-incompatible, d = dioecious

In selfers, anthesis usually takes place before flowering, but any delay in pollen discharge, because of environmental or genetic reasons, may allow some cross-pollination ranging from fractions of a percent, up to several percent. Cross-fertilization (allogamy) may be guaranteed by sex chromosomes as in hops, in some monoecious plants where staminate and pistillate flowers are separated, and in dioecious plants consisting of androecious and gynoecious individuals. In hermaphrodites, obligatory cross-fertilization may be maintained by self-incompatibility, or by mechanisms enhancing cross-pollination or inhibiting self-pollination. In others, outcrossing generally prevails but some degree of selfing is tolerated. Although the breeding behavior of a particular crop plant is quite uniform, some geographic and genetic variation may occur. In the broad bean, for example, outcrossing is the rule, some cultivars are even self-incompatible, but some cultivars, particularly from Afghanistan, are highly selfers. The breeding system of crop plants dictates their genetic structure. Outbreeders are, as a rule, highly heterozygous and in each generation genetic combinations are formed and dismantled because of

crossing over and random chromosome assortment. Inbreeders, on the other hand, are highly homozygous and the genetic diversity of the population is maintained and manifested by a mixture of pure lines. Novel diversity may be generated by mutations or rare outcrossing.

### 2.2.2 Hybridization within the cultigen

Obligatory cross-fertilization results in high levels of heterozygosity. This is usually the case in other cross-pollinating plants. Each generation, gene combinations break down and are recreated. Homozygosity and specific gene combinations can be fixed due to natural selection, assortative mating and drift, particularly in small populations. Under cultivation specific gene combinations can be maintained by human selection. Maize races grown by the Indians in Mexico maintain their identity even when they grow in the same area or even in the same field (Wellhausen, Fuentes and Hernandez Coroz, 1957; Wilkes, 1977). This may be achieved in part by selecting specific plants for the next year's planting, but also by preferential hybridization. In mixed planting of white flint and yellow sweet maize varieties, intercrossing was 35.8–46.7%. Selection for six years of types similar to the original lines in the same interplanting design, reduced cross-pollination between them to 3.4–4.9% (Paterniani, 1969).

Natural cross-hybridization plays a smaller role in the handling of diversity in selfers. In cultivation this may be true for horticulture plants growing in small plots, but in field crops cross-pollination as low as 1% may have considerable impact. It means that in a field of one hectare where 2–3 million plants are growing, 20 000–30 000 are natural hybrids. In heterogeneous crop populations even that amount of cross-fertilization can be a major source of new variation.

The greater role of hybridization in crop plant evolution started when man began applying artificial crossing to combine characteristics occurring in different lines. Employment of cross-pollination by man is a reflection of his understanding of sexuality in plants.

Date palm is a wind pollinated dioecious plant with male and female inflorescences occurring on different individuals. Under artificial pollination, pollen produced by one male tree is sufficient to pollinate about 100 female trees, but about 10 trees under natural conditions. In modern date palm growing, pollen is collected from the male trees and female trees are pollinated artificially. This procedure has two main advantages: it reduces the number of unproductive trees in the date-palm orchard, and it allows employment of specific male trees as pollen donors. In date palm, pollen could affect fruit size, color and ripening time, known as *Metaxenia*, and male trees differ from one another in these respects. Artificial cross-pollination in date palm is mentioned in the cuneiform texts of Ur, Mesopotamia about 2300 BC (Oudejans, 1969). Another indication of date palm hand pollination in ancient times comes from

bas-reliefs in Ashurnasirpal palace at Nimrud, ninth century BC, deposited in the British Museum, which contain many date palm trees. In one of the exhibited bas-reliefs, the king is seen in a ceremonial act standing in front of a date palm tree and a priest behind him carries a staminate inflorescence, and what might be a pollen basket.

The notion that sex in plants could be the same in principle as in the animal kingdom apparently did not extend beyond the date palm or, if it did, it had no agricultural impact and probably was lost during the following millennia. Written records indicate that it was rediscovered in the 17th century (Roberts, 1929) by Rudolph Jakob Camerer, a Professor of Natural Philosophy at the University of Tübingen, better known under the Latinized name of Camerarius. He appears to be the first botanist to discover by actual experimentation that pollen is indispensable to fertilization, and that pollen-producing flowers or plants are, therefore, male and seed-bearing plants are female.

Thomas Andrew Knight (1759–1838), in England, was apparently the first in modern times to apply hybridization for raising new varieties of fruit trees and vegetables. His main crossing work was carried out with currants, grapes, apples, pears and peaches. Of specific interest are his experiments with peas. The pea lines he employed, and his results, were similar to those used by Mendel nearly 50 years later. Knight did not bother himself with numbers and proportions of different types in the segregating generations of his hybrids and thus could not formulate his results in the form of laws of inheritance as Mendel did.

Contemporary with Knight, John Goss also did some hybridization experiments with peas. He mentioned the behavior in which the characteristic of only one of the parents prevails in the hybrid, now known as dominance, but, as in Knight's case, he did not count the number of offspring of each class in the segregating generation and could not observe regularity which can be formulated as genetic laws.

William Herbert, also an Englishman, born in 1778, was interested mainly in hybridization experiments with ornamental plants. Besides genetic and physiological conclusions which he drew from his experiments, his idea on the species concept is of interest. On interspecific crosses which he performed he stated 'the production of a fertile intermixture designates the common origin of the two parent species'.

More or less at the same time, in France, Augustin Sageret initiated crosses among the cucurbites. In hybrids between muskmelon and cantaloupe he described the morphology of the hybrids he obtained and introduced the term dominance to express the appearance of characters of one parent in the hybrid but not of the other.

In his letter on hybridization to the Paris Academy of Science in 1863, Charles Naudin (1815–1888) confirmed earlier observations on the nature of artificial hybrids and generalized the uniformity of the  $F_1$  and the reappearance of the parental characteristics in  $F_2$ . He also indicated that

some characteristics in the hybrids are intermediate of the parents, while others express only one of them.

Throughout the first part of the 19th century hybridization was practised by horticulturalists and botanists in England, France and Germany. All this could not escape Mendel's mind when he launched his experiments with the pea. Gregor Johann Mendel (1822–1884) conducted his breeding experiments for eight years (1857–1865) while a priest in the monastery of St. Thomas in Brunn, Bohemia. Throughout his experiments he kept records on the morphology of each of the hybrids he produced and of its descendants. This finally enabled him to establish the law of segregation in mono- and dihybrids. In 1865 Mendel presented his results at the meeting of the Natural Society of Brunn. In discussing his results and those of earlier workers he indicated the methodology which should be followed in the experiments: proper care should be given to distinction between generations; identification of genotypes; studying the ratio exhibited by their progeny (Mendel, 1965).

Mendel's discovery passed unnoticed by the scientific circles of Europe and was overlooked until 1900. It was brought to light more or less at the same time but independently by de Vries in The Netherlands, Correns in Germany and Tschermak in Austria.

### 2.2.3 Hybridization between crop plants and their wild progenitors

From the genetic point of view a cultigen and its wild progenitors are conspecific and the affinities between them are as between any two cultivars. They may spontaneously hybridize with one another when grown side by side, throughout the natural distributional range of the wild form. Such spontaneous hybridization may lead to infiltration of wild genes to the cultivated germplasm and vice versa. Such gene flow between populations adapted to different environments was termed introgressive hybridization by Anderson (1949), or in short, introgression. Introgression is more likely to occur in cross-pollinating crops, but has also repeatedly been observed among selfers. The consequences of these hybridizations depend largely upon the direction of the cross. The seed parent determines whether the cultivated or the wild populations would be affected.

#### (a) The wild form as a seed parent

This is apparently the most common cross direction. It occurs in places where the wild progenitor grows adjacent to the field. At such points of contact the crop plant grows in much denser stands than the wild form and produces much more pollen which is an important factor, particularly in wind pollinated plants. Hybrid seeds produced on the wild type would germinate and grow in the wild habitat and any

characteristic of the cultigen which reduces adaptability in that habitat would be already eliminated in the  $F_1$  hybrids or in their derivatives. This may include quick germination, lack of seed dispersal mechanism, lack of protecting organs such as shells, hairs and other parts of the dispersal apparatus. Other characteristics of the cultigen, such as flower color, may readily be established in the wild population. Parallel variation in the cultigen and the wild progenitor at a specific site is not necessarily a proof of gene flow, particularly in primitive agriculture in which the crop and the wild type originated from the same stock and have been exposed to similar natural selection pressure. In maize some authors (Mangelsdorf and Reeves, 1938; Wilkes, 1977; Bird, 1978) considered large seed size and a red and hairy leaf sheath in teosinte as an indication of introgression from maize, while Doebley (1984) argued that these are genuine teosinte traits evolving in response to local environments.

Gene flow from the cultigen to the wild can reliably be detected when the former possesses characteristics which are absent in the wild population. In six-rowed barley all three spikelets in a spike node are fertile. This characteristic is absent not only in the barley's wild progenitor, but in the entire genus *Hordeum*. Hybrid swarms between six-rowed barley and *H. spontaneum* are recognized by disarticulating six-rowed types among the two-rowed wild barley, commonly called agriocrithon. It is believed that the agriocrithon types would last one or a few generations following hybridization since they are not adapted to wild habitats. Nevertheless, several agriocrithon populations have been detected throughout the state of Israel, some of them in places where barley has not been a crop for the last 25 years. They are all restricted to disturbed habitats such as edges of fields and roadsides and may extend from several square meters up to strips of more than one kilometer.

Gene flow from a crop plant to its wild progenitor is particularly effective when it helps the latter to mimic the crop. Wild rice has been a serious weed in rice fields in India. The purple-leaved variety was introduced to allow the farmers to weed out the spontaneous green-leaved wild rice. But within about 20 years the purple-leaf gene had been introduced to the wild rice to such an extent that weeding was no longer a safe practice for eliminating wild rice.

Additional examples of gene flow from crop plants to their wild progenitor are listed in Table 2.7.

(b) *The crop plant as seed parent*

Some gene flow from the wild to the cultivated population apparently also occurs whenever the two grow side by side, but it must be far less significant than crossing in the other direction. Beside the usual barriers to hybridization between the two, such as gaps in flowering

Table 2.7 Indications of gene flow from crop plants to their wild progenitors

Crop	Transferred traits	References
Alfalfa	Flower color	Small 1984
Barley	Fertile lateral spikelets	See text
Maize	Luxuriant growth, wide leaf	Wilkes 1977
	MMV tolerance	Brewbaker 1979
Rice	Purple leaf	Dave 1943
Sunflower	Yellow inflorescence disc	Heiser 1965
Sugar beet	monogerm, CMS	Hornsey & Arnold 1979, Boudry <i>et al.</i> 1993

time, selection by man is paramount. Nevertheless, a significant number of hybrid seeds between the two can be produced in some cases. In rice fields in Florida where weed red rice occurs, the percentage of hybrid seeds detected in the cultigen varies considerably, 1–52%, in different varieties (Langevin, Clay and Grace, 1990). Introduction of cytoplasmic male sterility (Owen 1945) and monogerm, i.e. formation of only one, possibly two, flowers in the flower cluster (Savitsky, 1954) were major steps towards production of monogerm hybrid varieties in sugarbeet. These two characteristics soon appeared in weed beet (Hornsey and Arnold, 1979). It has been shown lately (Boudry *et al.*, 1993) that these weeds contain the chloroplast and mitochondrial DNA of the cytoplasmic male sterile sugarbeet which is routinely used in sugarbeet seed production. So, although sugarbeet was the seed parent, gene flow has been from the cultivated to the weed population.

Human selection in the field and natural selection outside the field are the two components of disruptive selection which maintain the crop plant and its wild progenitor as two distinct populations. Human selection might be applied at any stage of the plant growth. Cultivated amaranths have mostly pale seeds, compared with black seeds of wild amaranths. Black seed color is dominant and black seeds are regarded as hybrid with wild amaranths and rejected for planting by farmers (Sauer, 1967). Spontaneous cross-pollination between cultivated and wild carrot across the Mediterranean region, Europe and Canada produces an annual white carrot, instead of the biennial orange type, which is immediately rejected (Small, 1978; Brandenburg, 1981). Hybrids between the cultigen and its wild progenitor in sorghum may occur over a vast area in Africa. They are recognized by their narrower leaves and uprooted at seedling stage (Doggett and Majisu, 1968). Similarly, maize  $\times$  teosinte hybrids are recognized by their leaf shape and uprooted before flowering. Some, however, are left either intentionally or because they have been overlooked and the process of gene flow may be initiated. Farmers both in Africa and Mexico know that after three years (generations) these hybrids may produce seeds of acceptable quality but they

do not encourage such a gene flow. Even if gene trickling from the wild to the crop does occur, it is difficult to trace and it is almost impossible to determine whether parallel variation in the two is a result of recent gene flow or is typical of the crop which has been selected as a geographical race. Wilkes (1977) believes that short, thick rachilla and upcurved indurated glumes in some maize land races in Mexico originated from teosinte germplasm. Obviously gene flow from the wild would be tolerated as long as it does not upset traits of economic importance. It may improve tolerance to biotic and abiotic stresses to which both the crop and its wild progenitor are exposed, but any trait of the wild plant which reduces the domesticate standard would be immediately rejected by the cultivator. Thus, it is unlikely that major traits associated with the domesticate syndrome would be introduced by introgression from the wild progenitor. While it has been proposed that injection of teosinte germplasm to maize helped in maintaining better performance and hybrid vigor, it has been claimed that the large kernel race of maize could not be developed in the teosinte growing zone because of gene flow (Galinat, 1974). Wild progenitors might possess diversity in traits of a quantitative nature such as seed size, in lentil (Abbo, Ladizinsky and Weeden, 1992), oil content, in wild hexaploid oat *Avena sterilis* (Frey, Hammond and Lawrence, 1975) and even grain yield, in oat (Helsel and Frey, 1978), but there is no evidence that variation in such traits has been introduced to the cultigen via natural introgression.

The issue of introgression in maize has also been approached by isozyme electrophoresis (Doebley, Goodman and Stuber, 1987). Unlike some morphological and physiological characteristics, isozyme variation is not expected to be affected by human selection, as long as it is not linked to genes of economic importance. Variation in a specific enzymic gene in the crop and its wild progenitor may show one of the following patterns: similar allelic frequencies in both, which could be a result of multiple domestications, or massive introgression after domestication; allelic frequency high in one but low in the other: when an allele is more widespread in the wild population it might indicate independent evolution or barriers to introgression; and lastly, an allele is present only in one of them, wild or cultivated: this could be interpreted as genetic drift, independent evolution, and most important, selection against the allele in the environment where it is absent. Isozyme diversity was similar between maize and teosinte in some areas, but differences were found between areas. In higher elevations, frequencies of *Eupl-14* and *Glul-8* were 0.3 in teosinte and only 0.01 in maize. If this is a sign of introgression as suggested by Doebley, Goodman and Stuber (1987), and these alleles are selectively neutral, one would expect that their occurrence in the domesticated population would be much higher, because maize and teosinte have hybridized freely and grown side by side for thousands of years. An alternative explanation is that these alleles are either not

selectively neutral or that they are linked to other characteristics of teosinte which are negatively selected in cultivation.

Adaptation to the environment of the cultivated field is a characteristic of crop plants which via hybridization could be transferred to their wild forms and a simple means by which weed types have formed. Some believe that because of their weedy characteristics weedy species were pre-adapted to domestication (Hawkes, 1969). While this is probably true for plants like oat, in other crop-weed pairs, weedy forms could have been developed through gene flow from the cultigen to its wild progenitor, or by back-mutation (Harlan, 1976a). This is apparently the case with the wild barley, *H. spontaneum* which grows both in primary and man-made habitats in the Middle East. In the latter habitats the populations are much denser and occasionally they infest wheat fields to a degree that one may wonder if these are wheat or barley fields. The weed forms also occur outside the natural distributional range of the wild barley where they could originate from back-mutation. Habitat differentiation can hardly be distinguished between teosinte and maize. The former grows almost exclusively in man-made habitats and rarely in sites where it seems to occupy natural habitats, but these are not too distant from maize fields. The near absence of teosinte in primary habitats and its outstanding weedy nature should not be overlooked in any comprehensive view of maize-teosinte relations, and could be taken as another argument for considering teosinte as a derived rather than a genuine wild form (Wilkes, 1989).

#### 2.2.4 Directed introgression between crop plants and their wild progenitors

Identification of the wild progenitors of many crop plants and realization of their close genetic affinities have made them a potential source of genetic variation for the breeder. To a large extent they have been explored for useful characteristics, mainly for biotic and abiotic stresses but for other characteristics of economic value as well (Kalloo, 1992). Transferring characteristics from the wild to the cultivated background is generally rather simple because neither crossability nor recombination barriers occur between them. The only inconvenience is the need of several backcrosses to get rid of the undesirable traits of the wild parent. Deliberate introduction of genes from wild progenitors is now being employed in almost all major crop plants (Harlan, 1976a; Stalker, 1980; Goodman *et al.*, 1987).

#### 2.2.5 Introgression from more distantly related species

Natural introgression of genes to a crop plant from more distantly related species is even less likely to occur because of crossability barriers, hybrid

inviability or hybrid sterility which are typical of interspecific hybridization. However, this has been employed to various degrees of success by plant breeders. The rationale of searching more distantly related species for traits of economic importance is that because of reproductive isolation, the gene pools of the crop and the wild relative have evolved independently and the latter may possess characteristics lacking in the cultigen and also in its wild progenitor. As an example, protein content in the seeds of the tetraploid oats *A. magna* and *A. murphyi* is about 30% higher than in the cultivated oat or its wild progenitor.

Successful introgression to cultivars from distantly related species, wild or cultivated, depends upon:

1. Cross-compatibility
2. Production of hybrid seeds
3. Normal development of the F<sub>1</sub> hybrids
4. Certain amount of seed production on these hybrids either naturally or by back-crossing
5. No hybrid breakdown in the segregating generations.

According to Harlan and de Wet (1971) terminology, species which possess these reproductive characteristics are regarded as members of the secondary gene pool of the crop (section 4.1.2). Breeders have successfully transferred traits of agronomic value from these wild relatives to cultivars (Table 2.8), but barriers to introgression may rest at any of these phases and sometimes in a combination of them. They are part of the reproductive isolation between species. More details on reproductive barriers are given in Chapter 4, but some which are associated with introgression are mentioned here.

## 2.3 BARRIERS TO INTROGRESSION

### 2.3.1 Cross-incompatibility

A prerequisite for any gene transfer between a crop plant and members of its secondary gene pool is cross-compatibility. This includes all the subtle pollen-pistil relationships which in the end allow pollen grains of an alien species to germinate and the pollen tube to penetrate the stigma. It includes further all the factors affecting normal growth of the pollen tube through the stylar tissue, entering the ovary and ending in successful fertilization (Heslop-Harrison and Heslop-Harrison, 1986). Collectively, they represent a prezygotic reproductive barrier and under natural conditions any one of them or combinations of them are effective means of reproductive isolation.

In some crop plants crosses with members of the secondary gene pool can be made only unilaterally. When this is due to pollen-pistil

**Table 2.8** A short list of characteristics introgressed to crop plants from species of their secondary gene pool

Crop	Characteristic	Donor	Reference
<i>Abelmoschus esculentus</i>	Yellow vein mosaic virus resistance	<i>A. maniot</i>	Jambhale 1986
<i>Beta vulgaris</i>	Nematode resistance	<i>B. procumbence</i>	Savitsky 1975
<i>Brassica napus</i>	Plasmodiophora resistance	<i>B. campestris</i>	Gowers 1982
<i>B. napus</i>	Plasmodiophora resistance	<i>B. oleracea</i>	Yamagishi <i>et al.</i> 1980
<i>B. napus</i>	Black-leg resistance	<i>B. juncea</i>	Roy 1984
<i>B. oleracea</i>	Cytoplasmic male sterility	<i>Raphanus sativus</i>	Paulman & Robbelen 1988
<i>B. oleracea</i>	Cytoplasmic male sterility	<i>Raphanus sativus</i>	McCollum 1988
<i>B. oleracea</i>	Plasmodiophora resistance	<i>B. napus</i>	Chiang & Crete 1983
<i>C. moschata</i>	Bushy growth habit	<i>C. pepo</i>	Rhodes 1959
<i>Gossypium barbadense</i>	Black-arm resistance	<i>G. herbaceum</i>	Knight 1963
<i>G. hirsutum</i>	Jassids resistance	<i>G. arboreum</i>	Khush and Brar 1991
<i>G. hirsutum</i>	Glanded plant, glandless seed	<i>G. sturtianum</i>	Altman <i>et al.</i> 1987
<i>G. hirsutum</i>	Lint length and strength	<i>G. thurberi</i>	Kerr, in Kalloo 1992
<i>Heliantus annuus</i>	Downy mildew	<i>H. tuberosus</i>	in: Kalloo 1992
<i>H. annuus</i>	High linolenic acid	<i>H. decapetalus</i>	in: Kalloo 1992
<i>H. annuus</i>	Powdery mildew resistance	<i>H. debilis</i>	Jan & Chandler 1985
<i>H. annuus</i>	Male sterility	<i>H. tuberosus</i>	in: Kalloo 1992
<i>H. annuus</i>	Restorer genes	<i>H. agrophyllus</i>	in: Kalloo 1992
<i>Lactuca sativa</i>	Leaf aphids resistance	<i>L. virosa</i>	Khush and Brar 1991
<i>L. sativa</i>	Mildew resistance	<i>L. serriola</i>	Jagger and Whitaker 1940
<i>Lycopersicon esculentum</i>	Soluble solid content	<i>L. chmielewskii</i>	Rick 1974
<i>L. esculentum</i>	Brown root rot and cyst nematode resistance	<i>L. hirsutum</i>	in: Kalloo 1992
<i>L. esculentum</i>	TLCV resistance	<i>L. hirsutum</i>	Kaloo and Banerjee 1990
<i>L. esculentum</i>	Early blight resistance	<i>L. hirsutum</i>	in: Kalloo 1992
<i>L. esculentum</i>	Resistance to arthropods	<i>L. hirsutum</i>	Khush and Brar 1991
<i>L. esculentum</i>	Male sterility	<i>L. parviflorum</i>	Kesicki 1980
<i>L. esculentum</i>	TMV resistance	<i>L. peruvianum</i>	Alexandr 1963

Table 2.8 Continued

Crop	Characteristic	Donor	Reference
<i>Nicotiana tabacum</i>	TMV resistance	<i>N. glutinosa</i>	Holmes 1938
<i>N. tabacum</i>	Resistance to wild fire disease	<i>N. longiflora</i>	in: Kalloo 1992
<i>N. tabacum</i>	Black mold resistance	<i>N. debneyi</i>	in: Kalloo 1992
<i>N. tabacum</i>	Powdery mildew resistance	<i>N. goodspeedii</i>	in: Kalloo 1992
<i>S. tuberosum</i>	Virus X resistance	<i>S. acuale</i>	Ross 1986
<i>S. tuberosum</i>	Potato beetle resistance	<i>S. chacoense</i>	Ross 1986
<i>S. tuberosum</i>	Late blight resistance	<i>S. demissum</i>	Ross 1986
<i>S. tuberosum</i>	Virus Y resistance	<i>S. stoloniferum</i>	Ross 1986
<i>Triticum aestivum</i>	Leaf rust	<i>Aegilops squarrosa</i>	Kerber & Dyck 1969
	Stem rust	<i>Triticum monococcum</i>	Kerber & Dyck 1973
	Leaf, stem and stripe rust	<i>Agropyron intermedium</i>	Wienhues 1966
	Yellow rust	<i>Ae. comosa</i>	Riley <i>et al.</i> 1968
	Greenbug toxicity	<i>Ae. squarrosa</i>	Joppa <i>et al.</i> 1980

compatibility two patterns can be distinguished. The first one may be observed in crosses involving self-incompatible (SI) and self-compatible (SC) species. Crosses are usually successful when the SI species is the pollen parent. Rarely, SC species also exhibit unilateral cross relations, only as pollen donor, but this is typical of species which only recently acquired their self-compatibility. SI is common in the genus *Solanum*, but *S. pennellii* is SC and it is thought to be of a relatively recent origin. Crosses of this species with tomato have been successful only when it was used as the male parent. It has been suggested (Pandey, 1981) that unilateral crosses are another expression of the S gene of SI species, preventing the introduction of SC alleles which might upset the genetic structure of the species. SI species are highly heterozygous and contain a considerable number of deleterious genes when in a homozygous condition.

The second type of unilateral cross occurs either between SI species, or between SI and SC species when the latter serves as the male parent. This is thought to be unrelated to the mechanism of self-incompatibility in SI plants, but an independent evolution of cross-incompatibility; it was termed incongruity by Hogenboom (1972).

Only limited information is available on the genetics of unilateral incompatibility (UI) in interspecific hybridization. This genetic nature may be revealed when variation in the response to interspecific hybridization occurs in the parental species. In wheat × rye cross the pollen tubes are arrested between the base of the style and the upper part of the embryo sac (Jalani and Moss, 1980, 1981). Hybrid seeds were obtained only when rye was the pollen parent, but seed set largely depended on the wheat genotype. Crosses with some cultivars yielded up to 50% seeds while others not more than 5%. This difference appeared to be controlled by two genes, *kr1* and *kr2* (Lein 1943) located on chromosomes 5A and 5B (Riley and Chapman 1967). These two genes also affect seed set in crosses involving wheat with *Hordeum bulbosum* (Snape *et al.*, 1979).

Among crop plants UI following interspecific hybrids was reported in *Brassica*, *Capsicum*, *Linum*, *Lycopersicon*, *Nicotiana*, *Phaseolus* and *Solanum*, and in intergeneric crosses *Triticum* × *Secale* and *Cajanus* × *Alyosia* and *Cajanus* × *Rhynchosia* (Ladizinsky, 1992).

Another type of unilateral hybridization results from failure of embryo development and early abortion. It is rather common in crosses involving species with different ploidy level, but even occurs in crosses between species sharing the same chromosome number. The diploid wheats *T. boeoticum* and *T. urartu* are cross-compatible only when the latter is the female parent. In the other cross direction the 10-day-old embryos collapse (Johnson and Dahaliwal, 1976). The common unilateral direction in interspecific crosses involving species with different ploidy has led to the assumption that a certain genetic ratio must be maintained in

the endosperm for normal embryo development. The endosperm is a triploid tissue possessing two maternal and a single paternal genomes. This ratio is more likely to be upset when the parent of the lower ploidy parent is the female, but it is not always the case. In oats, for example, crosses between diploids and some tetraploids are obtainable only when the diploids are the female parent, but with another tetraploid species, seeds are obtained in both cross directions. In crosses between hexaploid and tetraploid species, hybrid seeds can be obtained only when the hexaploids are the female parent, as in the case of crosses involving *Avena magna* and *A. murphyi*, or either as male or female parent in crosses with *A. barbata* (Table 2.9). Crosses between diploids and hexaploid species are difficult to obtain, and if so, only when the hexaploids are the male parent. Besides the general feature of interploidy crosses some accessions are likely to behave differently than expected. Many attempts to cross *A. barbata* with the hexaploids have failed, but Nishiyama and Yabuno (1978) reported success, indicating genetic variation in cross-compatibility (Table 2.9).

Normally, the pollen tube delivers two sperm nuclei to the embryo sac; one fertilizes the egg, producing the diploid zygotic nucleus, while the other one fuses with the two polar nuclei of the embryo sac to produce a triploid primary endosperm nucleus. In wide crosses this course of double fertilization may be disturbed as in a wheat × maize intergeneric cross where of the 100 attempted crosses 80 yielded embryos but not endosperm, eight only endosperm and double fertilization occurred in the rest. Similar irregularity of double fertilization was observed also in wheat × sorghum and barley × maize intergeneric crosses (Laurie and Bennett, 1988).

### 2.3.2 Postzygotic barriers

Even if a zygote is being formed following interspecific crosses, barriers to introgression may occur at various stages of hybrid development. These may include all stages of embryo development, seed maturation

**Table 2.9** Successful cross-direction of interspecific hybridization in *Avena* involving species of different ploidy

(2x) × (4x)	(4x) × (2x)	(6x) × (4x)
<i>A. strigosa</i> × <i>A. magna</i>	<i>A. barbata</i> × <i>A. strigosa</i>	<i>A. sativa</i> × <i>A. magna</i>
<i>A. strigosa</i> × <i>A. murphyi</i>	<i>A. barbata</i> × <i>A. longiglumis</i>	<i>A. sativa</i> × <i>A. murphyi</i>
<i>A. longiglumis</i> × <i>A. magna</i>		<i>A. sativa</i> × <i>A. barbata</i> <sup>R</sup>
<i>A. longiglumis</i> × <i>A. barbata</i>		
<i>A. prostrata</i> × <i>A. magna</i>		
<i>A. prostrata</i> × <i>A. murphyi</i>		

R = reciprocal

and germination, and normal growth of the hybrid plants. Incompatibilities at these stages have been regarded as developmental mechanisms (Stebbins, 1958) or post-zygotic incompatibility (Sedgley and Griffin, 1989). Other factors affecting introgression are associated with the fertility of the interspecific hybrids and of their descendants, and were named segregational mechanisms (Stebbins, 1958).

#### (a) Chromosome elimination

In crosses of cultivated barley or wheat with the wild barley *Hordeum bulbosum*, the entire chromosome complement of the wild barley is eliminated. It starts in the first mitotic divisions of the zygote (Kasha and Rao, 1970; Barclay, 1975), and may be completed five days after fertilization (Bennett, Finch and Barclay, 1976). The embryos continue to grow but they are haploids containing the genome of the cultivated barley. In another interspecific *Hordeum* hybrid, *H. vulgare* × *H. murinum*, the chromosomes of both species were eliminated but in different tissues. The *H. murinum* chromosomes were lost in the embryo, while those of *H. vulgare* in the endosperm (Finch and Bennett, 1983). Through chromosome elimination, haploid wheats were obtained also in wheat × sorghum, and wheat × maize crosses. Haploid formation following interspecific crosses is occasionally interpreted as parthenogenesis. It is likely that some of these haploids are the result of elimination of a complete chromosome set.

Chromosome elimination is a strong reproductive barrier, but for the breeder it may serve as a useful tool. One of the major obstacles for rapid progress in breeding programs is the selection of homozygous lines after initial intervarietal crosses, which may last a few years. Haploids resulting from interspecific crosses may shorten this period significantly. In the case of wheat, F<sub>1</sub> hybrids are crossed to either *H. bulbosum*, sorghum or maize, resulting in wheat haploid formation. Each of the haploids is expected to present different genetic combination and can be stabilized following chromosome doubling by colchicine treatment.

#### (b) Hybrid embryo abortion

Abnormal development of hybrid embryos in interspecific crosses is a major obstacle to introgression (Ladizinsky, 1992; Pickersgill, 1993). Abortion may take place in different stages of the embryo development and for various reasons. In *Pisum sativum* × *Vicia faba* cross embryos remained six days near the micropylar end, while parental embryos of the same age were located in the cavity center (Gritton and Wierzbicka, 1975). More common, however, is abortion resulting from embryo and endosperm disintegration which may occur a few days after fertilization

up to more advanced stages when root and shoot primordia have already been formed. The disintegration has been documented by many anatomical studies and the common conclusion is that it begins with the endosperm tissue. Yet, in many instances the disintegration starts almost simultaneously both in the embryo and the endosperm.

As with pistil-pollen interaction where instances of unilateral compatibility have been recorded, hybrid embryo abortion may occur in both cross directions or only in one of them. In the genus *Lens* hybrid abortion occurs in *L. culinaris* × *L. ervoides* and *L. culinaris* × *L. nigricans* crosses and in both cross directions. In *Phaseolus*, on the other hand, the cross between *Ph. vulgaris* and *Ph. coccineus* is successful when the latter is the male parent, but not in the reciprocal cross direction because of embryo abortion.

Unilateral hybrid embryo abortion is common in interspecific hybrids involving species of different ploidy levels. Usually but not exclusively, hybrid embryo abortion occurs when the parent with lower chromosome number is used as the female (Table 2.9).

When the hybrid embryo breakdown occurs at advanced stages of embryo development, usually after reaching the heart stage, the embryos can be rescued by planting them in appropriate artificial medium. Hybrid embryo culture has been attempted in many interspecific crosses involving crop plants (Table 2.10). Successful hybrid embryo rescue may depend upon the specific parents of the interspecific hybrid. Embryos of the *Lens culinaris* × *L. ervoides* hybrid were successfully rescued by embryo culture when the latter parent was of Mediterranean origin, but not so with an Ethiopian accession.

Successful culturing of interspecific hybrid embryos depends primarily upon the stage at which the breakdown occurs. It is extremely difficult to rescue embryos earlier than the heart stage, because of either specific nutritional-hormonal requirements, or more basic problems associated with insufficient differentiation at early stages.

### (c) Seedling lethality

Other obstacles of a developmental nature are those associated with hybrid seed germination and seedling development. Abnormalities during seed germination are not uncommon in interspecific crosses. Low germination rates or complete failure are usually associated with abnormal shoots and roots. When germination is normal, albinism or insufficient chlorophyll production are usually terminal. Albino seedlings may grow for several days until exhausting all their nutrients. Rearing albino interspecific hybrids to maturity is extremely difficult, but can be done only with partial albinos, or in cases when a green sector is developing in the hybrid. Albino seedlings of interspecific hybrids are a common isolation mechanism among the legumes. In the

**Table 2.10** Wide crosses in crop plants obtained by embryo culture from otherwise incompatible parents

Crops and crosses	Reference
<b>Abelmoschus</b>	
<i>Abelmoschus esculentus</i> × <i>A. manihot</i>	Patil (1966)
<i>A. esculentus</i> × <i>A. moschatus</i>	Gadwal <i>et al.</i> (1968)
<b>Allium</b>	
<i>Allium cepa</i> × <i>A. altaicum</i>	Yureva and Titova (1984)
<i>A. cepa</i> × <i>A. fistulosum</i>	Gonzalez and Ford-Lloyd (1987)
<i>A. cepa</i> × <i>A. nunanans</i>	Yureva and Titova (1984)
<i>A. cepa</i> × <i>A. schoenoprasum</i>	Yureva and Titova (1984)
<i>A. cepa</i> × <i>A. vavilovi</i>	Yuerva and Titova (1984)
<b>Arachis</b>	
<i>Arachis hypogea</i> × <i>A. glabrata</i>	Sastri and Moss (1982)
<i>A. hypogea</i> × <i>A. villosa</i>	Bajaj <i>et al.</i> (1982)
<b>Avena</b>	
<i>Avena sativa</i> × <i>A. canariensis</i>	Rajhathy and Thomas (1974)
<i>A. sativa</i> × <i>A. clauda</i>	Rajhathy and Thomas (1974)
<i>A. sativa</i> × <i>A. longiglumis</i>	Rajhathy and Thomas (1974)
<i>A. sativa</i> × <i>A. prostrata</i>	Rajhathy and Thomas (1974)
<i>A. sativa</i> × <i>A. strigosa</i>	Rajhathy and Thomas (1974)
<i>A. sativa</i> × <i>A. macrostachya</i>	Leggett (1985)
<b>Brassica (turnip)</b>	
<i>Brassica campestris</i> × <i>B. nigra</i>	Matsuzawa (1983)
<i>B. campestris</i> × <i>B. oleracea</i>	Matsuzawa (1978); Inomata (1978)
<i>B. oleracea</i> × <i>B. campestris</i>	Harberd (1969)
<b>Brassica (cabbage)</b>	
<i>Brassica oleracea</i> × <i>B. campestris</i>	Harberd (1969)
<i>B. napus</i> × <i>B. oleracea</i>	Ayotte <i>et al.</i> (1987); Quazi (1988)
<b>Brassica (rape)</b>	
<i>Brassica napus</i> × <i>B. oleracea</i>	Ayotte <i>et al.</i> (1987); Quazi (1988)
<i>B. napus</i> × <i>B. juncea</i>	Bajaj <i>et al.</i> (1986)
<b>Gossypium</b>	
<i>Gossypium arboreum</i> × <i>G. harknessii</i>	Stewart (1981)
<i>G. arboreum</i> × <i>G. longicalyx</i>	Stewart (1981)
<i>G. arboreum</i> × <i>G. mostelium</i>	Stewart (1981)
<i>G. arboreum</i> × <i>G. somalense</i>	Stewart (1981)
<i>G. arboreum</i> × <i>G. stocksii</i>	Gill and Bajaj (1984)
<i>G. herbaceum</i> × <i>G. amurianum</i>	Gill and Bajaj (1984)
<i>G. herbaceum</i> × <i>G. harknessii</i>	Gill and Bajaj (1984)
<i>G. herbaceum</i> × <i>G. longicalyx</i>	Gill and Bajaj (1984)
<i>G. herbaceum</i> × <i>G. somalense</i>	Gill and Bajaj (1984)
<i>G. herbaceum</i> × <i>G. stocksii</i>	Gill and Bajaj (1984)
<i>G. barbadense</i> × <i>G. australe</i>	Stewart (1981)
<i>G. hirsutum</i> × <i>G. arboreum</i>	Thengane <i>et al.</i> (1986)
<i>G. hirsutum</i> × <i>G. bickii</i>	Stewart (1981)
<b>Hordeum</b>	
<i>Hordeum brachyantherum</i> × <i>H. vulgare</i>	Morison <i>et al.</i> (1959)
<i>H. depressum</i> × <i>H. vulgare</i>	Morrison <i>et al.</i> (1959)
<i>H. vulgare</i> × <i>H. bulbosum</i>	Davies (1960)
<i>H. vulgare</i> × <i>S. cereale</i>	Shumny <i>et al.</i> (1981)
<i>H. vulgare</i> × <i>T. aestivum</i>	Shumny <i>et al.</i> (1981)
<i>H. vulgare</i> × <i>T. timofeevii</i>	Shumny <i>et al.</i> (1981)
<b>Lens</b>	
<i>Lens ervoides</i> × <i>L. culinaris</i>	Cohen <i>et al.</i> (1984)

Table 2.10 Continued

Crops and crosses	Reference
<b>Soyabean</b>	
<i>Glycine max</i> × <i>G. tomentella</i>	Newell and Hymowitz (1982)
<i>G. max</i> × <i>G. clandestina</i>	Singh <i>et al.</i> (1987)
( <i>G. tomentella</i> × <i>G. canescens</i> ) × <i>G. max</i>	Broue <i>et al.</i> (1982)
<b>Medicago</b>	
<i>Medicago sativa</i> × <i>M. rupestris</i>	McCoy (1985)
<b>Nicotiana</b>	
<i>Nicotiana rustica</i> × <i>N. tabacum</i>	Reed and Collins (1978)
<i>N. rustica</i> × <i>N. glutinosa</i>	Reed and Collins (1978)
<i>N. stockonii</i> × <i>N. tabacum</i>	Reed and Collins (1978)
<b>Ornithopus</b>	
<i>Ornithopus sativus</i> × <i>O. compressus</i>	Williams and de Lautour (1980)
<i>O. pinnatus</i> × <i>O. sativus</i>	Williams and de Lautour (1980)
<b>Oryza</b>	
<i>Oryza sativa</i> × <i>minuta</i>	Nakajima and Morishima (1958)
<b>Phaseolus and Vigna</b>	
<i>Phaseolus actifolius</i> × <i>P. vulgaris</i>	C.V. Thomas and Waines (1984)
<i>P. coccineus</i> × <i>P. vulgaris</i>	Shii <i>et al.</i> (1982)
<i>P. vulgaris</i> × <i>P. acutifolius</i>	Mok <i>et al.</i> (1978)
<i>P. vulgaris</i> × <i>P. lunatus</i>	Mok <i>et al.</i> (1978)
<i>P. vulgaris</i> × <i>P. ritensis</i>	Braak and Kooistra (1975)
<i>Vigna angularis</i> × <i>V. umbellata</i>	Chen <i>et al.</i> (1983)
<i>V. mungo</i> × <i>V. radiata</i>	Gosal and Bajaj (1983)
<i>V. radiata</i> × <i>V. angularis</i>	Chen <i>et al.</i> (1983)
<i>V. umbellata</i> × <i>V. angularis</i>	Chen <i>et al.</i> (1983)
<b>Raphanus</b>	
<i>Raphanus sativus</i> × <i>Brassica nigra</i>	Matsuzawa and Sarashima (1984)
<b>Secale</b>	
<i>Hordeum bulbosum</i> × <i>Secale cereale</i>	Wojciechowska (1982)
<i>H. depressum</i> × <i>S. cereale</i>	Morrison <i>et al.</i> (1959)
<i>H. geniculatum</i> × <i>S. cereale</i>	Shumny <i>et al.</i> (1981)
<i>H. jubatum</i> × <i>S. cereale</i>	Brink <i>et al.</i> (1944)
<b>Trifolium</b>	
<i>Trifolium ambigum</i> × <i>T. hybridum</i>	Williams and de Lautour (1980)
<i>T. ambigum</i> × <i>T. repens</i>	Williams and de Lautour (1980)
<i>T. pretense</i> × <i>T. sarosienae</i>	Phillips <i>et al.</i> (1982)
<i>T. repens</i> × <i>T. isthmocarpum</i>	Rupert and Evans (1980)
<i>T. repens</i> × <i>T. nigricans</i>	A.M. Evans (1962)
<i>T. repens</i> × <i>T. uniflorum</i>	Williams and de Lautour (1980)
<b>Triticum</b>	
<i>Aegilops squarrosa</i> × <i>Triticum boeoticum</i>	Gill <i>et al.</i> (1981)
<i>Ae. squarrosa</i> × <i>T. aestivum</i>	Gill and Raupp (1987)
<i>T. aestivum</i> × <i>Agropyron distichum</i>	Pienaar (1980, 1981)
<i>T. aestivum</i> × <i>A. intermedium</i>	Sharma and Gill (1983a)
<i>T. aestivum</i> × <i>A. junceum</i>	Sharma and Gill (1983a)
<i>T. aestivum</i> × <i>A. scribeum</i>	Sharma and Gill (1983a)
<i>T. aestivum</i> × <i>A. yezoense</i>	Sharma and Gill (1983a)
<i>T. aestivum</i> × <i>Hordeum bulbosum</i>	Inagaki and Snape (1982)
<i>T. aestivum</i> × <i>Secale cereale</i>	Oettler (1983)
<i>T. durum</i> × <i>S. cereale</i>	Oettler (1983)
<i>T. turgidum</i> × <i>A. distichum</i>	Pienaar (1980, 1981)

Source: Ladizinsky, G. 1992. Crossability relations. In: Distant Hybridization of Crop Plants. G. Kallou and J.B. Chowdhury eds. Springer Verlag, Berlin pp. 15-31. With permission.

*Vicia narbonensis* group complete or partial seedling albinism is typical of many interspecific combinations (Ladizinsky, 1975b). It is also common among the wild relatives of chickpea and of fenugreek.

Lethality of normal-looking seedlings was reported in the *Crepis tectorum* × *C. capillaris* hybrid, which appeared to be controlled by a single gene (Hollingshead, 1930). The developmental sterility may be expressed at even later stages of hybrid developments. The *Lagenaria siceraria* × *L. spherica* hybrid develops normally but it is sterile because pistillate flowers abort at early stages of development (Whitaker, 1971).

#### (d) Meiotic irregularities and hybrid sterility

Irregular chromosome pairing at early meiotic stages and uneven segregation at meiosis are the main causes of sterility in interspecific crosses. However, in some cases complete sterility occurs despite seemingly normal chromosome pairing and regular meiosis. Hybrids between the cultivated *Salvia sclarea* and what was believed to be a wild chemotype from northern Israel had seemingly normal meiosis with regular formation of bivalents and number of chiasmata similar to that observed in the parental lines, but they were self-sterile and did not set any seed even following massive backcrossing to the parents (Elnir *et al.*, 1992). The reason for the observed sterility can be genetic or cytogenetic. Genetic factors may cause sterility in various stages of pollen and ovular development and may persist whenever the hybrid combination is maintained. Cytogenetic sterility may result from small chromosomal differences among the parental species, particularly in segments free of crossing-over, and therefore do not cause meiotic irregularities (such as multivalents and anaphase bridges). While numerically, chromosome segregation would appear normal, the daughter cells are likely to contain chromosomes of different parents and hence unbalanced genetic content. Some loci would be presented in duplicates, others will be missing altogether. By doubling the chromosome number of such hybrids chromosomes would be able to pair with their true homologues and to produce genetically balanced and fertile gametes. Chromosome doubling, however, would not restore fertility when hybrid sterility is of a genetic nature.

Many interspecific hybrids are characterized by irregular chromosome pairing at meiosis causing reduced fertility. This irregularity may result from lack of homology between the parental chromosomes, which in extreme cases may cause asynapsis and considerable reduction of genetic recombination. Another common type of irregularity is the occurrence of multivalents resulting from chromosome repatterning. The mode of the multivalent segregation at anaphase may cause genetically unbalanced and inviable gametes. Usually there is a negative correlation between the number of chromosomal rearrangement differences between the parental species and the fertility of their hybrids.

Unbalanced gametes seem to be tolerated more in the megaspores rather than in microspores, and in some self-sterile interspecific hybrids with complete pollen infertility a few seeds may be set following backcross to either parent. This limited seed set may occur in nature when the interspecific hybrids grow among the parental species. The backcross progeny are likely to resemble the recurrent parent but may exhibit some characteristics of the other parental species. Fertility is usually restored to a degree that these backcross progeny are at least partially self-fertile, and full fertility may be achieved in another one or two generations.

(e)  $F_2$  breakdown

Another expression of segregational barriers is lethality and sub-lethality among interspecific hybrid progeny which may operate at different stages of plant development. In *Gossypium* (Hutchinson, Silo and Stephanes, 1947), among *G. hirsutum* var. *punctatum* × *G. tomentosum*  $F_2$  110 sown seeds, germination and seedling development were as follows:

Seeds with small embryos that failed to germinate:	7
Seeds with apparently normal embryos that failed to germinate:	36
Seedlings that failed to expand the cotyledons:	9
Seedlings died within three weeks:	22
Unthrifty seedlings at three weeks old:	16
Strong seedlings at three weeks old:	20

The many obstacles to introgression from species of the secondary gene pool to a crop plant indicate that under natural conditions they apparently have not been a source of variation for the crop. A crop plant may be isolated from its wild relatives by a single reproductive barrier, but it is not uncommon that the isolation is reinforced by a battery of barriers making the introgression unlikely if not impossible. In the genus *Lens* this is the case between two morphologically akin species *L. odemensis* and *L. nigricans*, they are cross-incompatible because of early hybrid embryo abortion, rare hybrid seeds or embryos raised through embryo culture are albino, and a green sector developed on an albino plant gave rise to normal but sterile plants because of serious meiotic irregularities. Plant geneticists and breeders, nevertheless, have employed the variation of the secondary gene pool and have intensified introgression under controlled experiments. Many interspecific hybrids are being raised by manipulating chromosome numbers of the species involved to obtain successful combinations, with the aid of hormone application to increase the number of hybrid seeds, via embryo culture techniques to rescue embryos which otherwise abort, and extensive backcrossing of the sterile or semisterile interspecific hybrids. Some characteristics of the secondary gene pool which have been artificially introgressed to their cultivated relative are listed in Table 2.8.

## 2.4 CROP DIFFUSION

Since antiquity crop movement has been a reflection of human migration and contacts. People carried their crop plants whenever they moved into new territories and crop products have been important commodities since early trading. Currently the most important crops are distributed worldwide and their main production areas sometimes are far away from their place of origin. Caufield (1982) estimated that 98% of the USA crop production is based on species that originated outside its borders. In historical times, plant migration and introduction are evident by written documents, and in pre-historic times they are suggested by plant remains in archaeological sites outside the distribution range of the wild progenitor. Acceptance and establishment of introduced crop plants in new territories depend upon biological as well as cultural elements. Pre-adaptation to the local ecosystem or immediate selection of a better adapted genotype are essential for any further experiments with the introduced plant. Poor adaptability probably has been a major barrier for crop movement from tropical to temperate zones and vice versa. The first barley introduction by the Spanish to Spain failed because of poor adaptability. The first potato introduction to Europe was around 1570. For about 200 years it was kept as a garden plant of little economic value until a long day type became available, either as an introduction from south America, or out of local selection.

Cultural elements involving the acceptance of an introduced plant are complex and may vary from plant to plant and from region to region. Acceptance may be rather quick when the plant bears some analogy to existing crops and can supplement them. Wheat and barley introduction to highlands Ethiopia must have been a major supplement to the only native cereal tef, *Eragrostis abyssinica*. They are easier to grow and more productive, but nevertheless, tef has remained the noble cereal. Another Ethiopian example of an important introduction is the chili pepper, *Capsicum annuum*, by the Portuguese in the 16th century when they came to salvage the Christian Ethiopian from Moslem invaders. One of the reasons for the rapid acceptance of the chili pepper has been its effect on stomach worms which are common in Ethiopia as a result of the habit of eating raw meat. Various herbs, including flowers of the tree *Hagenia abyssinica* have been used as remedy but only with partial success.

For completely different reasons potato became the staple food in Ireland during the 17th century (Salaman, 1949). On the top of the misery of the Irish people at that time, the political and economic decisions to turn arable land to pasture had resulted in further growing poverty and food shortages among peasants. Potato which started spreading at that time provided sufficient food from small plots to peasants and industry workers alike.

The maize growing in the western Pyrenees is another example of socio-economic change as a result of plant introduction (Gómez-Ibáñez, 1975). Maize was introduced to the western Pyrenees around 1570–75, but spread slowly. One of the reasons was the traditional triennial seed rotation based on winter wheat, spring cereal, barley or millet, in the second year and the third year fallow. Replacing the spring crop by maize apparently was too risky for a society living on the edge of subsistence as in the western Pyrenees. Nevertheless, maize had been tested in kitchen gardens where it had proven successful. When sown by broadcasting it yielded better than wheat, and in spaced rows three times as much. It then became apparent that spring sowing of maize gave the soil enough time to rest and the third fallow year became redundant. The shift to biennial seed rotation again doubled the yield potential of the land. The shift to maize also made a great contribution to the Pyrenees animal husbandry. The surpluses of maize enabled the people to cope with the declining pasture land which had been replaced by stabling.

Establishment of an introduced crop plant may involve adoption of new agricultural practices and technology. The traditional Middle Eastern crops are sown in the autumn, grow in the rainy winter and mature in late spring or early summer. Growing the summer crops sesame and sorghum introduced from India required spring planting and use of residual moisture.

Introduction of a new crop plant may result in crop replacement. This undoubtedly has occurred many times throughout the history of agriculture and probably will continue as long as agriculture becomes more sophisticated and competitive, as in the case of flax. From ancient times flax was the major vegetal source of textile fibers in western Asia. During the last century it has been replaced by tetraploid cotton of the New World. Flax is still grown on a limited scale but mostly as an oil crop.

Crop migration in prehistoric times in the Old World is concluded from the occurrence of crop plant remains in ancient sites located outside a crop's place of origin. The scenario of crop movement is still patchy and liable to modification as new evidence emerges, but the general pattern is quite clear. Crop plant movement started shortly after domestication, first spread to neighboring regions and later to more distant localities. Some crops became cosmopolitan, others remained local.

Barley and wheat were domesticated in west Asia before the 6th millennium BC. By the 6th millennium they had already reached northern India (Jarrige and Meadow, 1980). Pea and lentil, also of west Asiatic origin, domesticated at about the same time as barley and wheat, arrived in India only by the 4th millennium bp. Chickpea, also a west Asiatic legume, was evident in India only between 2500 and 2200 bp (Vishnu-Mittre, 1977). The Middle East was not the only source of crop plants to the Indian subcontinent. Sorghum, of African origin, was

present and had become a staple in India by about 3700 bp. The Harapan culture of the north-northwestern Indian subcontinent (6220–5540 bp) heavily depended upon exotic food plants originating from western Asia and Africa.

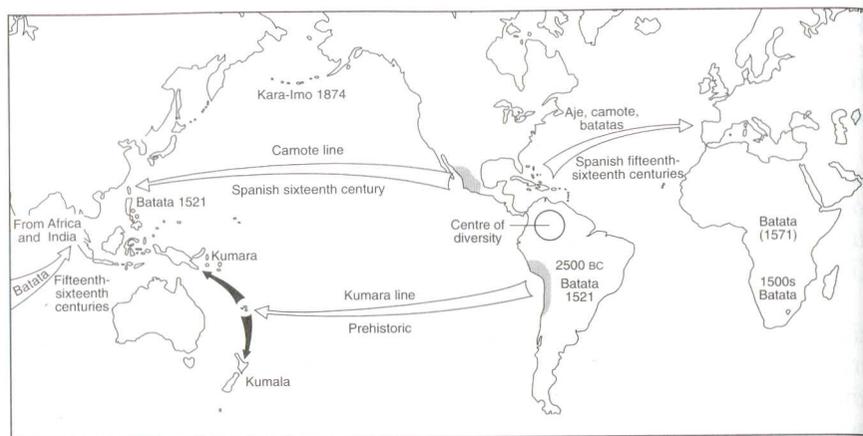
Barley and wheat migration to the Far East had been slower and the migration route is not certain, though undoubtedly terrestrial. Barley is mentioned in the 'Book of Poetry' (Shin-Ching), a compilation of poems from 3000–2500 bp. Wheat seems to have arrived later, in 2200–2100 bp (Keng, 1977).

To the west barley had progressed along certain routes and at a relatively steady pace. By the 8th millennium bp it arrived in the Balkans; in Italy, southern and eastern France, eastern Spain and Germany during the 7th millennium, and during the 6th millennium bp it arrived in southern Sweden and Britain (Zohary and Hopf, 1988). Crop migration from the Far East to west Asia and Europe had been slow and relatively late. Perhaps the most outstanding contribution is peach, a native plant of China (Hesse, 1975) which arrived at Iran during the 22nd or 21st century bp along the silk road (Laufer, 1919).

The more or less similar rate at which wheat, barley, pea and lentil moved from their place of origin in the Middle East to Europe suggests that they formed an integrated complex which had been a key element in the spread of agriculture in Europe.

Plant exchange between the Old and the New Worlds has been confined, almost exclusively, to the post-Columbian era. A few doubtful examples of pre-Columbian plant movements between the East and West are the bottle gourd, *Lagenaria siceraria*, sweet potato, *Ipomoea batatas* and the diploid cotton *Gossypium herbaceum*.

The bottle gourd is an African plant, but has been identified in ancient sites in Mexico from the 12th millennium bp. Since there is no evidence of such an early contact between the Old and the New World civilizations, sea crossing by flotation has been suggested. However, assuming such an incredible dispersal also must take into account that the bottle gourd plant had naturalized in America to a degree that man had appreciated its usefulness. The bottle gourd is nevertheless not a wild plant in America. Migration of sweet potato is not free of complications either. While most of the sweet potato spread took place in post-Columbian times, it has repeatedly been claimed that the Polynesian stock derived from south America in pre-Columbian times (Bohac, Duke and Austin, 1995) (Figure 2.7). The sensational voyage of the Kon-Tiki from Peru to Polynesia on sea currents in 1947 was a major validation of the idea of pre-Columbian contacts between America and Polynesia, and so the possible introduction of sweet potato along this route. While it is difficult to substantiate morphological similarity between sweet potatoes of these two regions, there is a piece of circumstantial archaeological evidence which might support ancient introduction (Yen, 1974, and



**Figure 2.7** The theoretical spread of sweet potato from its origin in South America. Reproduced with permission from Bohac, J. R., Dukes, P. D. and Austin, D. F. 1995. Sweet potato. In: *Evolution of Crop Plants* (eds J. Smartt and N.W. Simmonds), p. 60, Blackwell Science, Oxford.

personal communication). The origin of American cotton is obscure in the sense that one of its diploid progenitors is an African species which had to be introduced somehow to the Americas to enable hybridization with the other diploid progenitor. This issue is discussed further in section 4.4.1.

### 2.4.1 Crop migration and diversity

Besides its effect on human economy and agricultural practices, crop migration has profound evolutionary consequences. The emergence of new variations may be a result of:

1. Selection of new mutants which are more adapted to the new environment
2. Hybridization between genotypes previously isolated, as a result of several introductions from different areas of the crop origin
3. Hybridization with wild relatives which are absent in the crop's center of origin.

Under new environmental conditions novel variation may emerge and in several crops it resulted in the development of secondary centers of variation. Ethiopia became an important center of variation of the Middle Eastern crops wheat, barley, pea, chickpea lentil and broad bean. Similarly, the Far East became a secondary center of variation of barley and oats. The origin of muskmelon, *Cucumis melo*, is uncertain, some suggest Africa, others India where the wild form *Cucumis callosus*

is native and is fully interfertile with the cultivated muskmelon (Parthasarathy and Sambandam, 1980). India is only one center of muskmelon variation, others being the Middle East, including Iran, Central Asia and China. Those are likely to be secondary. The rate at which new variation is being accumulated in the new territory may be fast indeed. Coffee, *Coffea arabica*, a native plant in the Ethiopian highlands, was introduced to Brazil in 1780. Since then 30 spontaneous mutations have been selected and utilized there (Purseglove, 1972). The accumulated variation may create geographical races as in rice. From its center of diversity in north east India, Bangladesh, and a zone stretching across Burma, Thailand, Laos, Vietnam and southern China, rice migrated to adjoining areas and formed three main geographical races: the temperate race in the Yellow river valley of China, Korea and Japan; the tropical race in India, eastern China and south east Asia; and the tall large bold grain race in Indochina and the Philippines (Chang, 1995).

Spread across latitude may result in different day length response. For example, lentil is a long day plant in its main growing area in south west Asia and the Mediterranean region, but is day length insensitive in Ethiopia. Different day length sensitivity is even more distinctive in soybean where every latitude in USA and Canada has its own set of cultivars (Figure 2.1).

When the response to photoperiod conditions is controlled by a single gene, a better adapted population of the crop may be selected in a relatively short time. This kind of control has been reported in several crops. Many lettuce cultivars bolt under long day conditions, but some are day neutral. Bolting is controlled by a single gene with day neutral bolting being recessive (Robinson *et al.*, 1983).

Pea normally flowers under a long day photoperiod. The ability to respond to this photoperiod depends on the joint presence of the dominant genes *Sn* and *Dne* which together confer a long day habit. The genotypes *Sn dne*, *sn Dne* and *sn dne* are essentially day-length neutral (King and Murfet, 1985). The control is even more complex because several other genes interact with *Sn* and *Dne* in the expression of the photoperiod response (Arumingtyas and Murfet, 1994).

Sorghum normally flowers and matures under a short day photoperiod. When grown under a long day photoperiod, maturity is delayed. Time to maturity in sorghum is controlled by four genes which become effective under long day conditions. The longest time to maturity is obtained with dominant alleles in each of the four genes, and the shortest with a dominant allele in only one of these loci (Quinby, 1967).

The establishment of wheat in Europe was possible by selection of material with specific requirements for flowering time. The characters involved were vernalization sensitivity, photoperiod sensitivity, and earliness *per se* (Worland, 1996). The majority of the European wheats are vernalization sensitive winter cultivars, sown in autumn and

flowering when day length and temperature increase in the spring. The vernalization sensitivity prevents early flowering in autumn as a result of an occasional hot spell. The vernalization insensitive cultivars are common in southern Spain and Portugal where winter temperatures are mild and the summers are hot and dry. Vernalization insensitivity is also essential in the European spring wheat. In Spain and Portugal vernalization insensitivity is combined with photoperiod insensitivity and allows flowering under relatively short days of late winter and filling of grains before the onset of the hot dry period.

When several introductions were made to the same area, types which previously were isolated geographically and genetically distinct could inter-cross to create new gene combinations. Multiple introduction, particularly at historical times, is evident from written documents. Another indication may be provided by molecular markers such as seed proteins, isozymes and DNA markers. The common bean *Phaseolus vulgaris* was domesticated in central America and the Andean region of south America. The wild progenitor and land races from these two centers differ by the electrophoretic pattern of the phaseolin seed protein. In Central America the S type is predominant with a few other types, mainly M, while in South America the T type is predominant (Gepts *et al.*, 1986), and the C type in Colombia (Gepts and Bliss, 1986). Land races in Central America show mainly the S type and those of Andean South America the T type with S, T and C in Colombia, suggesting that Colombia had been a place of contact between the two main centers. Bean cultivars in Mexico and southern US are mostly of the S phaseolin type, conforming to Central American origin, while occurrence of S, T and C phaseolin types in the northern USA and Canada indicates introductions from both centers of origin (Gepts *et al.*, 1988). Also in Africa phaseolus beans possess the three main phaseolin types, indicating direct or indirect introductions from the two centers (Gepts and Bliss, 1988).

In the new territory, the introduced plant may hybridize with wild relatives which are endemic to the region. Cassava, *Manihot esculanta*, is believed to have been introduced by the Portuguese to the delta of the Congo river and Guinea during the last part of the 16th century. The tree *Manihot glaziovii* is a native plant of that region and hybridizes with the bushy cultivated cassava. Hybrid swarms exhibit morphological intergradations and their isozyme profile is intermediate between the two species (Lefèvre and Charrier, 1993). Cassava in tropical Africa is severely infected by cassava mosaic disease, a disease which has not been reported from Latin America where the genus *Manihot* is indigenous. *Manihot glaziovii* is resistant to the mosaic disease and could be used as a resistance source for cassava.

Early grapevine introductions to the USA by European settlers failed because they were ill-adapted to the climatic conditions and susceptible to local pests and diseases. Viticulture became more successful following

selection of local wild species, probably as a result of hybridization with the introduced cultivars of *Vitis vinifera*. The variety Alexander which became popular at the beginning of the 19th century was selected from *V. labrusca* probably with *V. vinifera* in its parentage. The variety Concord emerged in a similar way. Artificial hybridizations by amateur horticulturalists between local *Vitis* species and *V. vinifera* yielded a large number of varieties. In a list of 65 old grape varieties in the USA and Canada, 47 had *V. vinifera* in their parentage (Snyder, 1937).

Wider adaptation following hybridization with wild relatives in new territories enabled the expansion of the blue-flowered alfalfa, *Medicago sativa*. This important forage crop evolved in the Turkey-Iran region, spread to the Mediterranean countries but could not survive the cold winter of central Europe. Natural crosses with the yellow-flowered *M. falcata*, an indigenous wild species of the region, have resulted in a number of varieties combining the growth characteristics of the blue-flowered and the winter hardiness of the yellow-flowered alfalfa. This winter hardiness was insufficient when the European varieties were introduced to the northern midwest of the USA and most plants could not survive the winter. Seed collected from a few survivors produced much better winter hardy types which gave rise to varieties which could grow in that area as well.

## 2.5 MANIPULATING GENETIC VARIATION BY BREEDING

The beginning of hybridization experiments with crop plants, about 200 years ago, marked a new era in plant improvement. Until that time conscious selection was the only means by which new and better types could be developed. It is not the intention here to review the history and achievement of plant breeding in the last two centuries, but to pinpoint its impact on the genetic makeup of many crop plants. Breeding has affected crop evolution in two basic ways: assembling genetic variation existing in separate cultivars or land races in one cultivar, and exploiting heterotic effects.

### 2.5.1 New gene combinations

The aim of plant breeding has always been the improvement of existing cultivars by adding to them variations of economic importance found in other less distinguished lines, or elite types from distinguished cultivars. The artificial new gene combinations resulted in improved characters such as yield, better pest and disease tolerance and wider adaptation. Specific characters also have been introduced from alien species or following mutagenesis. Besides improving characters controlled by single or a small number of genes, significant progress has

been obtained with characters of a quantitative nature, affected by several genes (polygenes). The effect of an individual gene in this case is small and its impact may be influenced by the environment, and genotype  $\times$  environment interactions may play an important part in the performance of specific genotypes. Despite the subtle nature of polygenes, breeding resulted in significant improvement of plant characters of a quantitative nature such as vegetative characters, total yield and yield components. Advances in plant breeding became possible by contributions from other scientific fields such as cytogenetics, mutation breeding, quantitative and population genetics, pathology, entomology and chemistry.

### 2.5.2 Utilization of heterotic effects

Aside from creating new gene combinations by breeding, a major development of plant breeding has been the discovery and utilization of heterosis, or hybrid vigor, in several crops, maize in particular. Heterosis is defined as vigor of the  $F_1$  hybrid over the mean of its parents, or the mean of the better parent. Heterosis may be observed in vegetative and yield characters, disease and insect resistance or biochemical compounds. Although the economic impact of heterosis has been tremendous, its genetic basis has not been satisfactorily explained, despite many attempts to do so (Crow, 1952; Stuber, 1994). Two hypotheses have been suggested to explain hybrid vigor: the dominance hypothesis, which correlates between recessiveness and detrimental effects, namely, that the dominant allele is always superior to the recessive allele, and the vigor stems from buffering the deleterious effect of the recessive factors by the dominant allele; and the overdominance hypothesis, according to which heterozygosity *per se* causes vigor.

The deleterious effect of recessive factors is well demonstrated by inbreeding depression of cross-pollinating crops, and may partially support the dominance theory. On the other hand, it is difficult to explain how a hybrid between two inbred lines could greatly exceed in fitness and yield the equilibrium population from which these inbreds were selected. Furthermore, the dominance theory can not account for heterosis in self-pollinating species.

The overdominance hypothesis assumes a kind of gene action known to be rare, but even if a small number of genes are involved in heterosis they must also affect the population variance. Obviously, neither hypothesis alone can explain heterosis, and for specific genes one or both may be applicable, in addition to epistatic (Otsuka, Elberhart and Russell, 1972; Stuber, Williams and Moll, 1973) and complementary effects (Gibson and Schertz, 1977).

Hybrid varieties are common now in many field and horticulture crops and are among the factors enabling higher production and better food

and feed supply to the growing world population. Apart from their superiority over non-hybrid cultivars, seed companies invest more in their production because they have much better control of their profit compared with non-hybrid cultivars.

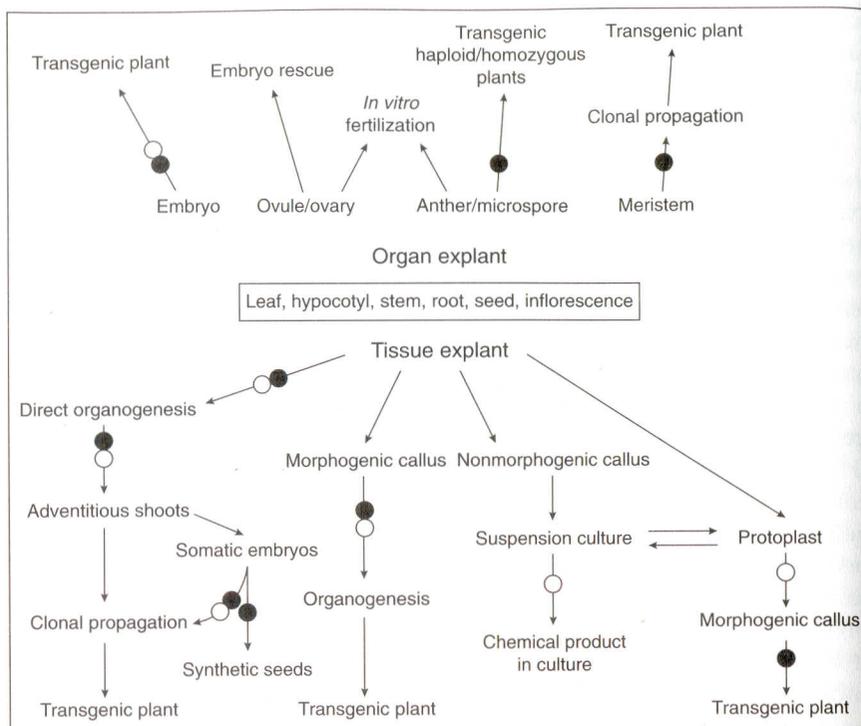
Plant breeding has produced a large number of high yielding cultivars with better adaptation than most land races. Unlike land races, bred cultivars are highly uniform, particularly for morphological characters and those associated with performance. Naturally, in many crops outstanding cultivars have been grown over large areas replacing the less productive varieties. The immediate consequence has been reduction of variation in many crop gene pools. Particularly because of disease and pest resistance, genetic homogeneity and a narrow genetic base for a crop are potentially hazardous because they may encourage the emergence of more virulent disease biotypes and the spread of epidemics (Harlan, 1972). To avoid this, Browning *et al.* (1979) have introduced the concept of multiline cultivar, a cultivar which is composed of several genotypes each resistant to different biotypes of the disease, but all are nearly isogenic in their agronomic characters. By its genetic composition a multiline cultivar is closer to the wild population, which normally possesses a number of resistant genes, than to a uniform bred cultivar. It may be infected to a certain degree by the disease, but is much better protected from it and to large extent prevents epidemics.

## 2.6 DEVELOPING NEW VARIATION BY TRANSGENESIS

While breeding can manipulate genetic variation through hybridization, molecular techniques provide the opportunities of exploiting, through production of transgenic plants, variation of alien species which cannot exchange genes with the cultigen by sexual means. Molecular techniques also may be instrumental in altering the mode of action of key genes and metabolism of the cultigen by genetic engineering. The field of genetic transformation and genetic engineering in crop plants is developing rapidly; some of the prospects and limitations are discussed here.

During the last two decades methods of genetic transformation have been established (Figure 2.8), a number of transgenic plants have been produced and the list is rapidly growing. Successful transgenesis requires:

1. Isolation of the relevant gene from a donor species
2. A receptive crop plant which is amenable to tissue culture techniques, i.e. plant cells can grow *in vitro* and regenerate to plant
3. An efficient method for DNA delivery
4. An effective selection method to detect transformed cells
5. Adequate expression of the inserted DNA in the new environment



**Figure 2.8** Plant tissue culture and transformation. Various techniques of plant tissue culture are indicated. Steps at which transformation can be carried out by *Agrobacterium* (open circle) and particle bombardment (filled circles) are indicated. From Waldan, R. and Wingender, R. 1995. Gene transfer and regeneration techniques. *Tibtech*. 13:3224–331.

6. Concerted action with the genome of the receptive plant with no deleterious effects on other characters.

Gene cloning exploits one or more of the four characteristics that defines genes: they have a primary structure (sequence); they occupy a particular site within the genome; they encode an RNA with a particular expression pattern, and most of them have a function. The most widely used methods for isolating genes based on their function involve protein purification or complementation of mutant phenotypes. The difficulty of isolating many desirable genes is that their product is not known, or can not be purified in sufficient quantities to permit sequencing or the preparation of antibodies (Gibson and Somerville, 1993).

Delivery of the foreign DNA into plant cells is routinely done *in vitro* by *Agrobacterium tumefaciens* as a vector in dicotyledonous plants because it requires minimal exposure of cells to tissue culture conditions and

gives high frequencies of transformation. Cereals are outside the natural host range of *Agrobacterium* and this kind of transformation is ineffective for them. Direct delivery can be done in protoplasts or by bombardment of cells with DNA. Protoplasts are ideal cells for DNA delivery because the removal of the cell wall eliminates a major barrier. The commonly used procedure for direct DNA delivery into plant protoplasts involves treatment with polyethylene glycol (PEG) to alter plasma membrane properties by causing reversible permeability that enables exogenous macromolecules to enter the cytoplasm. In bombardment-mediated transformation DNA coated microprojectiles are forcefully injected into cells by gun powder discharge or pressurized helium gas. This last method seems particularly suitable for cereals (Vasil, 1994).

When a transgene integrates into the genome of the receptive plant, it may or may not be expressed. Silencing of the alien gene may occur at the transcriptional or post-transcriptional level. The numerous examples of gene silencing in transgenic plants have indicated the complexity and the requirements for the expression of transgenes and may be a major obstacle for transgenesis (Meyer, 1995). Although many transgenic crop plants have been produced in the last few years, only a small number of them entered field tests, and even fewer passed one. Besides the novelty and expression of a foreign gene, a transgenic cultivar may be accepted by farmers if it also complies with the rigorous requirements of adaptation, yield and quality. In addition, it has to be accepted by the consumer which sometimes can be a problem. Also, products of transgenic plants must be safe with no or minimum risk to the environment. Herbicide tolerant transgenic plants are available now in many crop plants. They tolerate the herbicide throughout their life while the weeds do not, and treatment of the transgenic plants with the herbicide can be made at any required moment. The risk here is twofold: extensive use of the same herbicide for a long time in many different crops may hasten the appearance of tolerant weeds; and the herbicide tolerant gene may introgress into a wild or weed wild relative of the transgenic crop. Lately, Mikkelsen, Andersen and Jørgesen (1996) have demonstrated the introgression of the BASTA tolerant gene from a transgenic oilseed rape, *Brassica napus* genome AACC,  $2n=28$ , to a weed form of its diploid relative *Brassica campestris*, genome AA,  $2n=20$ . The interspecific hybrids were only partially sterile and following a back-cross to their parents produced an average of more than 450 seeds per plant. A second back-cross to *B. campestris* of phenotypically *B. campestris* derivatives, produced 42% BASTA tolerant fertile *B. campestris* plants.

While the appropriate frame of utilizing transgenic plants must be approved and enforced, it is beyond doubt that transgenesis offers breeders a new powerful tool to exploit variation which previously was inaccessible, or that has been produced by genetic engineering. The scope of this new technology seems so vast that it is difficult to envisage the

future spectrum of changes in individual plants. Transgenesis also offers new opportunities for better understanding of plant development and metabolism. With the creation and utilization of transgenic cultivars it will be necessary to re-examine some of the basic concepts of evolution and biology, the species concept being one of them.

## 2.7 CONCLUSIONS

Sources of variation in crop evolution are the same as in organic evolution. Selection by man of characters with low selective value in the wild marks the beginning of plant domestication. The major characters differentiating the crop and its wild progenitor are controlled by single genes. Many other characters of secondary importance are also controlled by single genes while other genes show quantitative inheritance. The spread of crops to new territories exposed them to selection pressures which are absent in the nuclear domestication area, and consequently selection of individuals with better adaptation to the new ecological conditions was possible.

Increasing variation via natural hybridization between the crop and its wild relatives had greater effects on the wild species than the crop. In a few cases, however, establishment of the crop in new territory became possible only following hybridization with wild relatives adapted to the local conditions. Artificial hybridization in crop plants started about 200 years ago. It has enabled the assembling in one plant of characters existing individually in several land races and cultivars. The discovery and utilization of heterosis is a direct outcome of hybridization experiments, and hybrid varieties are common now in many crop and ornamental plants.

Production of novel variation has been achieved by mutagenesis, and transgenesis is the very latest phase of increasing variation in crop plants through gene manipulation by biotechnological methods. The origin of the new characters is from reconstructing the crop's genes, or from other species which are naturally reproductively isolated from the crop.

# The course of reducing and maintaining genetic diversity under domestication

Reducing genetic diversity under domestication is another aspect of favoring characters which are better adapted to cultivation. The elimination of genetic variation was automatic rather than by human selection, and random events in the form of genetic drift. Maintaining genetic variation in individual crop plants resulted from the habit of traditional farmers of growing several types of the same crop either in the same field, or in different plots. Another major source is geographical variation.

## 3.1 SELECTION

Natural selection alters gene frequency in wild populations through differential fertility and survival of various genotypes. In some cases natural selection is a purifying process eliminating undesirable recombinants, newly formed mutants or other genotypes which drastically deviate from the standard make-up of the species, such as dominant or recessive lethal mutations. In most cases, however, natural selection is expressed by differential contribution of the various genotypes to the next generation, and it is a statistical rather than deterministic process. The number of adult offspring produced by any genotype is obviously determined by a large number of factors related to somatic as well as reproductive success and is known as Darwinian fitness, or simply fitness. Fitness of a given genotype is not an absolute value but a relative one. It is always proportional to the genotype with the greatest contribution to the next generation and can never exceed 1. The selection coefficient against specific genotype ( $S$ ) is  $1 - \text{fitness}$ . Because it is so subtle, measuring the actual effect of natural selection is difficult indeed. This is the reason why so many mathematical models have been produced in attempts to gain a better insight into this complex process.

Most of these models deal with hypothetical situations and hypothetical populations in which genotypes differ from one another by a single, two or not more than three genes. It is, however, important to bear in mind that in reality individuals differ from one another by a large number of genes and even if they share specific genes, their performance may depend upon interaction with other genes.

Rough estimates of natural selection can be obtained by measuring genotype frequency in two consecutive generations, or more. The change in the relative frequency of each genotypes is an indication of its fitness (Table 3.1).

Natural selection may affect gene frequency in three main ways:

1. Stabilizing and narrowing the variation through eliminating types.
2. Favouring genotypes with characteristics which are either above or below the population mean, known as directional selection.
3. Dividing the population into sub-populations by favouring contrasting genotypes, known as disruptive selection.

### 3.1.1 Natural selection in crop evolution

Although human selection has played an important role in the evolution of crop plants, the effect of natural selection should not be underestimated. Crop plants are subjected to the same biotic and abiotic pressures as their neighboring wild relatives. Climatic conditions may be major factors of stabilizing selection in crop plants by eliminating genotypes with inappropriate photoperiodic responses, or when they are maladapted to temperature and moisture conditions. Similarly, types will be selected against if they cannot cope with soil conditions such as texture, presence of various substances and the prevailing pH. The plants are vulnerable to new races of pathogens and insects and are in constant competition with other genotypes of the same crop and weeds. It is safe to say that in crop plants any characteristic which is not of immediate interest to the cultivator, or affected by his activity, is subjected to natural selection. Other characters may be affected by interactions between natural and human selection. As long as the crop plant is grown in the same geographical area as its wild progenitor, natural selection might

**Table 3.1** Measuring selection coefficient following one cycle of reproduction

Genotype	AA	Aa	aa
Frequency I	0.25	0.50	0.25
Frequency II	0.35	0.45	0.20
Fitness	1.40	0.90	0.80
Relative fitness	1	0.64	0.57
Selection coefficient	0	0.36	0.43

have similar effects on both. Introducing the crop plant to other regions exposes it to new selection pressures which may result in the emergence of geographic variation. This is apparently the case with the resistance to the barley yellow dwarf virus (BYDV) disease in the Ethiopian highlands barley. Resistance sources to BYDV are practically absent in barley collections, wild and cultivated, but were detected in about 80% of the cultivated barley accessions from highlands Ethiopia. Variation in day length response among cultivars of maize, soybean and other crops is also an outcome of natural selection and could emerge only after the crop has been moved outside its place of origin.

### 3.1.2 Human selection

Human selection is the strongest element of evolution under domestication. It is manifested through the introduction of new genotypes and new setting of ecological complexes. In principle, human activity can be regarded as another factor, besides many others, or a unique case, of natural selection. Yet, the distinction is justified because in many instances the evolutionary outcome of human activity contradicts the pattern of evolution favored by natural selection. As a result, two different systems exist side by side and may even interact or contradict each other. Human effects on plant evolution may result from directional selection through agricultural practices which have encouraged the emergence of new genotypes, and later stabilizing selection to maintain the domesticated population. By disruptive selection, different parts of the same plant often have been modified to provide different crops and products, as in the cabbages (section 2.1.1). It is not always easy to elaborate about how directional selection operates. Obviously, it must include intentional human involvement, but also unintentional acts as well. Distinction between these two processes which occurred thousands of years ago is not possible, but seemingly intentional selection could be possible when the characteristic to be selected became widespread enough following unintentional selection.

#### (a) Unintentional selection

This includes selection of plant types as a result of agricultural practices starting with cultivation. It has also been termed automatic selection (Harlan, 1975) and unconscious selection (Heiser, 1988). The evolution of the domesticate syndrome in seed crops discussed in Chapter 1 is an example of unconscious selection derived from harvest-planting cycles. The characteristics which are of concern here are seed retention and quick germination. Other characteristics are those associated with growing in greater density than in the wild and creating fierce competition among members of the same crop. It has been suggested (Harlan,

de Wet and Price, 1973) that this encouraged bigger seeds which could support rapid seedling growth. While larger seed is typical of many seed crops it can not always be related to unconscious selection in conjunction with rapid seedling growth. Seeds of wild wheat *Triticum dicoccoides* are as large or even larger than those of many *T. turgidum* cultivars. In lentil, seed size of many land races is virtually the same as in the wild progenitor. Archaeological records suggest that larger seed types evolved several millennia after lentil had become a crop (Zohary and Hopf, 1988). Erect growth habit and tallness are also an obvious outcome of growing plants in dense stands, as a result of competition for light between members of the same crop and also with weeds. Most wheat and barley land races are tall. Dwarf and semi-dwarf varieties which are common in modern agriculture compete poorly with tall varieties when grown in a mixture (Donald and Hamblin, 1983) and obviously could not survive under primitive cultivation. Tallness may be associated with disease resistance as it is with resistance to the septoria leaf disease in wheat.

Uniform maturity has also been suggested to be a product of automatic selection in harvest-planting cycles (Harlan, de Wet and Price, 1973). This is likely to be more important at the early stage of cultivation when the plants have not yet lost their natural mechanism for seed dispersal and uniform ripening could minimize yield lost. In its place of origin the time of crop maturity is usually similar to that of the wild progenitor, unless late and early maturing types have purposely been selected. Introducing the crop to areas of different latitude or to higher altitudes is another aspect of unintentional selection which would favor types with different photoperiodic responses, better cold or heat tolerance and other physiological characteristics related to the prevailing growing conditions and productivity.

If crop plants are introduced to areas where conditions for pollination are inadequate or the pollinator does not exist, selection for better fruit setting might result in change of the pollination system. Grapes are dioecious in the wild but hermaphrodite in cultivation. Figs are monoecious and in some cultivars pollination by the miniscule wasp *Blastophaga psenes* is required for fruit setting. Other varieties are parthenocarpic (seedless) and need no pollination for fruit setting. Since figs are propagated essentially by cuttings, these parthenocarpic clones are easily maintained.

The cultivated strawberry, *Fragaria × ananassa*, evolved from a spontaneous hybrid between the interfertile octaploid species *F. virginiana* and *F. chiloensis*; both are dioecious. Some strawberry lines are also dioecious but modern cultivars have perfect flowers. This characteristic was selected also by the Indians of Chile in *F. chiloense* (Darrow, 1966).

Self-compatibility of peaches, *Prunus persica*, is apparently also associated with cultivation, because all its related species are self-incompatible.

When and how peaches lost their self-incompatibility is not yet clear but some ideas can be obtained from almond. Almond and peach, though assigned to different genera, *Amygdalus communis* and *Prunus persica*, respectively, are fully interfertile, yet the former is self-incompatible and the latter is autofertile. In the last few years self-compatible types have been selected in almond and they differ from the common self-incompatible varieties by a single gene (Socias I Company and Felipe, 1988). It is possible that similar mutation was selected in peach at early stages of domestication.

Selection for one characteristic may lead unintentionally to change in other characteristics as well. The wild progenitors of carrot, radish, beet and cabbage are annual, but many of their domesticated derivatives are biennial. These crops are grown for their vegetative parts which develop in the first year, with flowering taking place in the second year. In cotton, on the other hand, agricultural practice shifted cotton from a perennial to an annual growth habit (Hutchinson, 1976).

#### (b) Intentional selection

This is essentially a directional selection in the crop population grown by man. In characteristics governed by a single gene it may create a new genetic population in a single or a few generations. It may occur following unintentional selection at the stage in which the new mutant is too common to be ignored, usually in field crops, or as keen observation by the cultivator of spontaneous mutation, mainly in horticulture plants. Intentional selection has been applied to any plant part which has economic importance. In seed crops intentional selection removed characteristics which are associated with natural seed dispersal such as seed non-shattering, awnlessness, glabrousness and naked grains. On the other hand, it has intensified the performance of seed and inflorescence characteristics such as size, shape, and color. In so doing, man often created some 'helpful monsters', particularly in sunflower, maize, and pearl millet among seed crops and cabbage, lettuce and beet in horticulture crops.

Removals of toxic and bitter substances are also consequences of intentional selection either among plants of the wild progenitor, or among the cultivated populations which formerly were detoxified by boiling, roasting or leaching.

Another aspect of intentional selection, which requires some unintentional phase as well, is the maintaining of variation within the crop plant population. Unlike modern cultivars which are highly homogeneous, land races which have evolved over many years under certain ecological conditions contain a mixture of morphological and physiological types. Farmers may admit that some of the types are deliberately maintained but not so the others. Wheat and barley in Ethiopia are extremely

variable and it is not uncommon to find several botanical forms in one field, some of which are barely grown outside Ethiopia. In wheat, *T. turgidum*, the free threshing, var. *durum*, var. *polonicum* and the hulled, var. *dicoccum*, may grow in the same field, though the proportions between them may vary from one field to another. In barley, two, four and six rowed types may be found in the same field. The *Triticum dicoccum* form of wheat was common in ancient times in the Middle East but it has not been a crop there for the last 2000 years or more. The main shortcoming of this wheat is the need for double threshing, firstly breaking the spike to individual spikelets, usually at the threshing ground, and later separating the seeds from the husks by pounding the spikelets in a mortar. When Ethiopian farmers are asked why they keep growing this wheat which requires much more labor than other wheat types, they often say that it is more nutritious and has a good effect on sick old men and children. If asked further why they do not grow it separately, the answer is that it is better growing it in a mixture with other wheat types. In a country like Ethiopia where drought and famine are common, crop failure is disastrous and to some extent can be curbed by greater variation in the crop populations. Crop stability under this uncertain environment may be achieved by genetic mixtures which in the long run are far more stable than a single genotype that might yield more under specific circumstances. The Ethiopian farmers seem to be so intent upon keeping the variation within their crops that during the socialist regime, the late 1980s, when they were forced to grow wheat and barley cultivars provided to them by the government, they used to add some of their own wheat seeds to the government's barley seeds and their barley seeds to the supplied wheat cultivars. Not only was it the only way they could save their germplasm, it also was an assurance that if the introduced cultivars failed there still would be some harvest.

The deliberate maintenance of variation within each individual crop is apparently common in any subsistence agriculture as can be inferred from an anecdotal account told by E. Hernandez-Xolocotzi (Wilkes, 1989).

In Tlaxcala, Mexico, he encountered an old Indian working in his cornfield and asked him what kind of corn he planted. The old man responded that he grew yellow corn, cream corn and white corn. When asked which was the earliest maturing corn, he said that the yellow took five months, the cream six months, and the white seven months to mature. When asked which yielded the most, he informed Hernandez that the yellow corn gave a little, the cream more and the white corn the most. Hernandez then asked him why he did not plant only the white since that was the most productive. The old man smiled and said, that is the question my

son who works at the factory asks. Tell me Mr Agriculturalist, exactly how much and when will it rain next year? Hernandez-Xolocotzi responded that he could not divine the future. With a knowing look, the old man said, exactly, therefore, I plant all three, so if there is a little rain, I always have some yellow corn to eat. If there is more rain, I'll have enough to eat from the cream corn, and if it's a good year with plenty of rain, I have white corn to sell. He added drolly, usually it isn't a good year.

Maintaining crop diversity in subsistence agriculture requires some kind of human intervention, otherwise it may be reduced due to drift or natural selection. It is common in crops such as maize, sorghum, pearl millet and beans where the performance of a single plant can easily be spotted. In self-fertilized or vegetatively propagated crops it can be accomplished by selecting particular plant types for the next sowing prior to the main harvest. It would be more complicated in cross-breeders crops because out-crossing and recombination are likely to upset desirable character combinations. Racial differences can be maintained if they also manifest variation in flowering time or they are sufficiently distant from each other to avoid cross-pollination. In maize, selection for a morphological characteristic may cause a shift in traits which promote racial stability (Paterniani, 1969). White flint kernel and yellow sweet kernel are contrasting recessive gene markers in maize, yy SuSu and YY susu, respectively. Both characters are easily detectable on the mature cob. In mixed populations of these two types Paterniani selected for next planting cobs showing the smallest degree of intercrossing with the other seed type. In a course of six generations, intercrossing dropped from 35.8% to 4.9% in the white type, and from 46.7% to 3.4% in the yellow type. This change also involved a shift in flowering time. In the beginning the two seed types flowered at the same time, but at the end the flint type flowered five days earlier and the yellow two days later. Controlled pollination with pollen mixture also indicated that the white flint may have a gametophyte gene that favors the fertilization of its own genotype.

Wheat and barley land races raised by individual farmers in Ethiopia occasionally exhibit enormous diversity and in a single field one may find several botanical forms which are sown and consumed with no obvious preference to any of them. Although the farmers are familiar with the different forms, they do not seem to intervene in any way in keeping these mixtures by selecting individual plants as seed stock or preparing deliberate mixtures before sowing. It is difficult to determine if these diversities in wheat and barley fields are maintained by natural selection, drift or a combination of both with some human intervention from time to time in the form of seed exchange between individual farmers.

### 3.1.3 Disruptive selection

Unintentional and intentional selections have been associated with creating new variation under cultivation. Disruptive selection, on one hand, has been a main barrier for gene flow into the cultivated gene pool, and on the other hand created polymorphism (occurrence of several distinct types within one population) within the crop plant by selecting different plant parts as an end product.

Adaptation of a cultivated plant to the ecological conditions of the agricultural system is often another aspect of deviation from its wild progenitor. The two are still interfertile, but ecologically isolated. The crop plant cannot survive in the wild and the wild plant is eliminated by man in the cultivated field as a noxious weed. Hybrids between the two occur from time to time but are usually identified and eliminated either according to seed color as in amaranth, or at seedling and more advanced stages in sorghum (Doggett and Majisu, 1968) and maize (Wilkes, 1977).

Disruptive selection also has been a means of greater diversification within a crop and utilizing different organs for different purposes and end products. Such multipurpose crops are hemp, *Cannabis sativa*, flax, *Linum usitatissimum*, the cole group, *Brassica oleracea*, turnip, *Brassica campestris* and beet, *Beta vulgaris*.

Hemp is an ancient crop believed to originate in temperate Asia. The wild form grows there as an indigenous plant but has diffused to many other parts of the Old and New World following the dissemination of hemp. Wild hemp has been regarded as a 'camp follower' which thrived on manure soil around temporary settlements and campsites and was used primarily as a seed plant. The ancient use of cannabis in China as a textile fiber has been substantiated by archaeological and written records. The oldest are ropes and woven cloth painting on pottery of the Yang-shao culture in Honan Province, dated back to 6200–5200 bp (Li, 1974a, b). As a textile fiber, hemp played the same role in China as flax played in West Asia and cotton in India. In China, hemp cloth was the textile of the masses, and silk of the wealthy. It was used also for fishing nets and played a role in the invention of paper (Li, 1974a). The hallucinogenic property of hemp was probably known to the Chinese and it was used for medicinal and hedonistic purposes, but probably not to the extent that opium has been used (Li, 1974a).

Human selection in hemp has focused on three plant parts, stem fibers, narcotic resin produced by glandular hairs on the leaves and inflorescence stems, and seeds. In selecting any of these types, other traits have been modified as well and eventually three morphologically, physiologically and phenologically distinct types were created. The great morphological and physiological diversity caused great taxonomic confusion but current views regard the narcotic types as ssp. *indica* and

the non-narcotic types ssp. *sativa* (Small, 1995). The different hemp types are distinguished by the following complex of characters:

#### 1. Fiber type

Tall plant, relatively unbranched  
Hollow internodes with limited wood  
Limited level of intoxicating cannabinoides  
Limited seed production  
Growing in wet habitats, mainly in the north temperate zone  
Short-day photoperiodic response

#### 2. Narcotic type

Moderate growth  
High level of intoxicating cannabinoides  
Growing in relatively dry and hot habitats, south of the fiber type zone  
A long-day plant

#### 3. Seed type

Moderate-low growth  
Abundant branching  
A long-day plant  
Early maturing

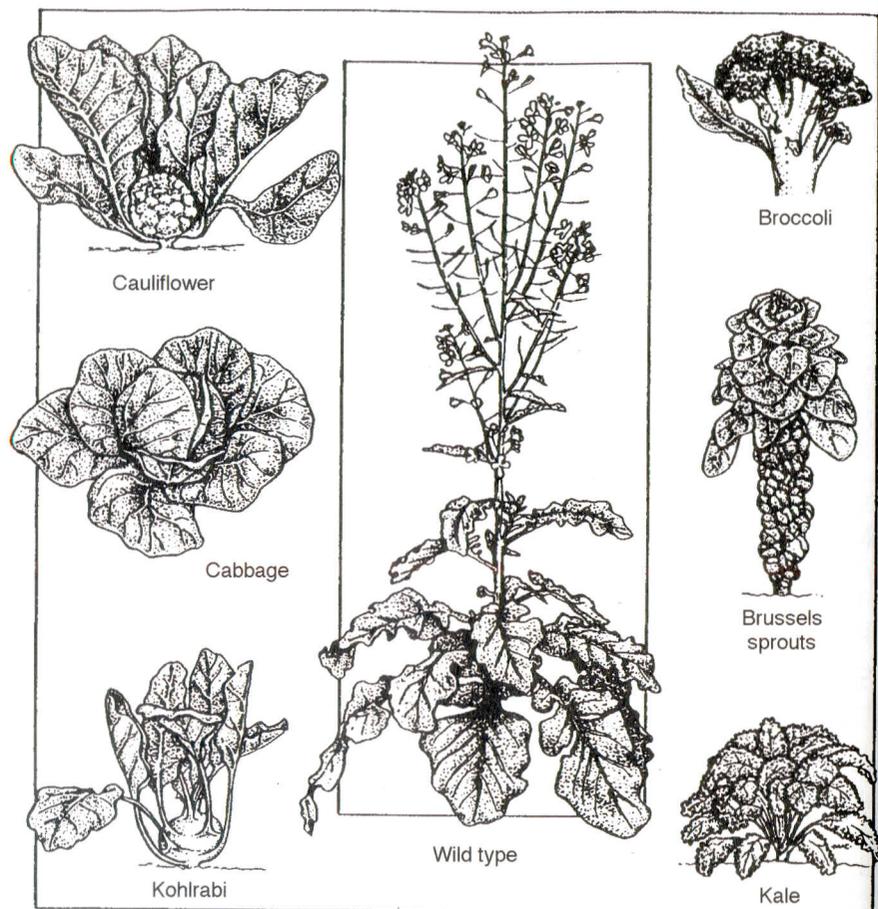
Similarly in flax, disruptive selection resulted in fiber and oil-seed plant types. In West Asia flax was the equivalent of hemp in eastern Asia.

In the cole group of *Brassica oleracea* different plant parts have been modified through disruptive selection to produce an extraordinary diversity: the kale and cabbage with different leaf arrangements, the broccoli and cauliflower with modified inflorescence, the kohlrabi with short thick stem and brussels sprout (Figure 3.1).

In turnip, *B. campestris* and rape, *B. napus*, leafy and bulbous types were selected as vegetables and fodder and seed types as condiments and oil crops. Similarly in beet, *Beta vulgaris*, leafy and hypocotyl-root swollen types have been used as vegetable and the latter also as a fodder and sugar plant.

## 3.2 GENETIC DRIFT

Besides natural and human selection which systematically favor specific genotypes until they reach fixation, diversity of crop plants may also be affected by random events commonly called genetic drift which in extreme cases also may cause genetic fixation. While natural and artificial selection is directional and hence predictable, genetic drift is incidental and its outcome cannot be predicted. Genetic drift may have accounted for several instances of variation in allelic frequency and two of them are the most common:



**Figure 3.1** Crops originated from *Brassica oleracea* subsp. *oleracea*. From Hacock, J. F. 1992. *Evolution and Origin of Crop Plants*. Reprinted with permission of Prentice Hall, Upper Saddle River, New Jersey.

1. Difference of allelic frequency in neighboring populations occupying similar habitats. This variation is believed to be an outcome of sampling error at the time of reproduction which may be more effective in small populations.
2. Variation which is due to the genetic make-up of the founders of the population, known as founder effect (Mayr, 1942). It may occur following migration or a bottleneck situation when the founders of a new population possess only a fraction of the genetic variation of the mother population.

The role of genetic drift in plant and animal evolution has been a subject of considerable controversy because it is almost impossible to

determine if variation of allelic frequency resulted from selection, genetic drift or interaction between them. The debate concerns mainly genetic variation of molecular genes such as allozymes, RFLPs and RAPDs. The 'selectionists' maintain that they are adaptive, though it is still unknown in what way, while the 'neutralists' consider the various alleles as having the same adaptive value, and the different frequency between populations a consequence of random drift.

Founder effect evidently played an important role in crop plant evolution, both at early stages of domestication and later at the phase of diffusion. As indicated in the previous paragraphs many of the major characteristics separating crop plants from their wild progenitors are controlled by a single or small number of genes. When a mutation is occurring in such a gene in a self-pollinated wild plant cultivated by man, the entire domesticated lineage will become not only a faithful copy of the mother plant but will represent a small fraction of the diversity existing in the wild population in regard to all other genes. In a cross-pollinated plant the variation in the basal domesticated population might be a bit larger due to gene flow, but not too extensive because of disruptive selection. Once the domesticated population has been established, the wild progenitor is no longer planted and no additional domesticated mutants would be selected. It is thus reasonable to assume that only a small number of individual plants gave rise to the entire domesticated populations in many crop plants, making plant domestication a clear example of the founder effect (Ladizinsky, 1985b).

### 3.2.1 Evidence of genetic drift

Alleles of different genes which are present in the wild form but absent in the domesticated derivatives strongly indicate genetic drift during the course of domestication. Parallel variation in both populations may be interpreted as multiple domestications, introgression after the initial domestication, mutations or a combination of all three of them. Hidden characteristics which have not been the target of human selection are useful for pursuing genetic drift in crop plants. These are chromosome and molecular markers.

Chromosome variation is relatively rare in diploid crop plants as well as in their wild progenitors. In lentil, *Lens culinaris*, all the tested intervarietal hybrids of the domesticated type had normal meiosis and the chromosomes paired in bivalents indicating no variation in the chromosome structure of the cultigen. The lentil's wild progenitor, ssp. *orientalis*, is variable and several chromosome translocations and paracentric inversions were detected in hybrids involving different populations (Ladizinsky *et al.*, 1984). The common chromosomal arrangement of the wild form is shared by the cultigen, indicating that the other chromosomal stocks have not been involved in domestication. The common

chromosomal arrangement of the wild form is distributed from Turkey to central Asia and therefore chromosomal arrangement by itself could be used for elimination rather than approving populations and geographical areas where lentil was domesticated. Similarly in chili pepper, *Capsicum annuum*, three chromosomal races were identified in the wild form, var. *minimum*, but only one of them has been found in the domesticated *C. annuum* (Pickersgill, 1971; Egawa and Tanaka, 1984).

Evidence of genetic drift during the domestication of bean, *Phaseolus vulgaris* in central America is evident by the electrophoretic pattern of the phaseolin seed protein. While the wild form contains several types only one of them, the S type, has been found in land races of that region (Gepts *et al.*, 1986).

During the last two decades study of variation in crop plants and their wild progenitors has been accelerated by using allozymes and DNA markers. These are also hidden traits which man could not directly select, for or against, unless they were tightly linked to traits of economic value. Results of these studies are meaningful when they are based on several markers and include a sufficient number of accessions. Some of these studies clearly indicate genetic drift during the course of domestication, in others parallel variation has been found in the crop plant and its wild progenitors, and occasionally genetic drift has been suggested by one set of data and parallel variation by other data.

Twenty-three accessions of sunflower, *Helianthus annuus*, and 12 of its wild form were examined for enzyme and cpDNA variation (Riesberg and Sieler, 1990). Extensive polymorphism for both molecular markers was observed among the wild populations, while the cultivated lines were virtually monomorphic and contained a subset of the alleles found in the wild sunflower.

In soybean 423 cultivars and accessions of the cultigen and 139 accessions of its wild progenitor, *G. soja*, were assayed for variation in 23 of enzymic genes. Of the 61 alleles and zymogram types revealed, nine were found only in the wild progenitor populations (Kiang and Marshall, 1983).

Radish, *Raphanus sativus*, is a cross-pollinated species. Examination of the isozyme profile of 16 cultivars representing the main groups of the cultigen, and of four populations of wild radish showed that in each of the loci *Idh*, *est* and *Lap* the wild radish possessed one more allele compared with the cultivated radish. Furthermore, the alleles of the loci *Tap* and *For* of which two and three alleles, respectively, were found in wild radish were absent in all the examined cultivars (Ellstrand and Marshall, 1984).

Variation in the restriction sites of the chloroplast DNA (cpDNA) was found within and among 245 populations of the barley's wild progenitor, *Hordeum vulgare* subsp. *spontaneum*. Three polymorphic restriction

sites defining three distinct lineages were detected. Sixty-two accessions of the cultigen were found, with two exceptions, to belong to just one cpDNA morph of the wild barley (Neale *et al.*, 1988). This clear indication of genetic drift in the early evolution of barley is barely compatible with the isozyme evidence. Kahler and Allard (1981) examined variation in four esterase loci among 1358 accessions of cultivated barley and 148 of wild barley. The cultivated barley accessions were of world wide origin while subsp. *spontaneum* originated from Israel and Turkey. All the 24 active alleles of the cultigen were present also in the wild barley, but two of the wild alleles, Est1 2.3 and Est3 5.8 were missing in the cultigen's germplasm. Another two alleles, Est3 4.1 and Est4 6.8 were missing in the 191 cultivated barley accessions from south west Asia and Afghanistan, which are within the distributional range of subsp. *spontaneum*. The overall immense similarity of the esterase variation observed in wild and cultivated barley seemingly contradicts the results of cpDNA variation.

The restriction pattern of cpDNA in lentil is rather monomorphic. This pattern has been found in 111 lines and cultivars, another three differ by one restriction site. The same general pattern was found in three populations of the wild progenitor, subsp. *orientalis*, from Turkey and Syria and another wild population differed by one restriction site (Mayer and Soltis 1994). Further examination of cpDNA variation in subsp. *orientalis* revealed more variation (van Oss, Aron and Ladizinsky, 1997). Of special interest was the restriction pattern of the central Asiatic populations because, according to their crossability potential with the cultigen, chromosome morphology and isozymes variation, they could be regarded as part of the stock from which lentil evolved. However these populations had a different restriction pattern, indicating that they had no part in the evolution of the domesticated lentil.

### 3.3 CONCLUSIONS

Crop evolution is a process in which human selection favors characters of low selective value in the wild, and acts against others which are indispensable for wild plants. Particularly in the early stages of domestication human selection was largely unconscious and the establishment of domesticated types resulted from the utilization of certain agricultural practices. Although human selection has been a major force in crop evolution, the role of natural selection should not be underestimated. Natural selection affects any character which is not under the immediate interest of the cultivator. Human selection has proceeded in three directions: directional selection has established characters or character combinations never known before; stabilizing selection to maintain variation within the crop; and disruptive selection, selection of cultivars for

different purposes within a single crop, examples being the cabbages and hemp.

Genetic drift has been a major cause of variability reduction in many crop plants. In essence, domestication is a case of genetic drift because the domesticated type contains only a small fraction of the variation existing in the wild progenitor for characters not associated with the domestication syndrome. In more advanced stages, any cases of bottleneck situations following epidemics, devastating climatic conditions or replacement of land races by high yielding cultivars are instances of genetic drift.

## Speciation under domestication

Speciation is a process by which new species are formed. However, before dealing with speciation in general and speciation under domestication in particular, it is important to clarify what a species is.

### 4.1 THE SPECIES CONCEPT

Most laymen believe that a species is something 'real' which scientists only described. The simple truth is that the term species was invented by scientists to cope with the enormous morphological diversity of the animal and plant kingdoms, and to provide a meaningful classification which may promote better communication between scientists. To get a more balanced view on the relations between morphological diversity and what a species is it is useful to examine humans as a natural entity. No one would deny that all human beings, despite differences in shape, size, color and behavior are all members of the same species. However, once it comes to other organisms, similar differences are thought to indicate the existence of several species. Although the term species is a fundamental unit in biology, the subtlety of what is a species and what is not has remained subjective and a topic of long lasting controversy resulting in countless numbers of articles (see Minelli, 1993).

Since the term species was introduced by Linnaeus as a basic unit of classification, it has continued to evolve in an attempt to address the values of different criteria for this term and to what extent they create a natural or artificial classification. A large number of species types have been suggested in the literature, but three seem to be of greatest importance. They are the morphological species, the biological species and the evolutionary species.

#### 4.1.1 The morphological species

This kind of species is known also as a taxonomic or phenetic species. It encompasses individuals sharing the same morphology and

in reference to a type specimen. Usually, a few characteristics (diagnostic characteristics) are employed to separate one species from another. Closely related species are distinguished by discontinuous variation in a single characteristic, or may vary by a combination of characters. The main difficulty with the morphological species concept is that occasionally it seems artificial because discontinuous variation may be due to a single gene while the two types are interfertile and grow side by side in the same habitat. The mode of spikelet disarticulation at maturity has been utilized as a major diagnostic character in *Avena*. Two types occur, one in which individual florets shed separately and each of them forms a dispersal unit, and the second type in which all the florets of the same spikelet shed as one unit. Among the diploid species the mode of spikelet disarticulation has been used to distinguish between *A. clauda* in which individual florets disperse, and *A. eriantha* with the entire spikelet as a dispersal unit. These two species are interfertile and grow side by side throughout most of their distributional range. Despite this, some taxonomists insist on keeping them as two separate species (Baum, 1977).

Another problem of the morphological species is that similar morphology does not necessarily indicate a coherent group as it may with many sibling species. These are species which morphologically are almost identical but which are reproductively isolated. An example of sibling species in *Avena* are *A. prostrata* and *A. strigosa*. When the former was first collected in southern Spain it was treated as another ecotype of wild *A. strigosa*. Subsequent hybridization between the two revealed that they differ from each other by five chromosomal rearrangements and their hybrids are sterile.

While most contemporary biologists recognize the weakness of the morphological concept, it is worth noting that most known plant and animal species are in essence morphological species. In many instances they have remained valid after re-evaluation by more rigorous criteria.

#### 4.1.2 The biological species

To reach a better definition of the species entity, geneticists proposed the biological species concept (Mayr, 1942). According to this concept a species is a breeding community in which the individuals are capable of interbreeding, form one gene pool, and are reproductively isolated from other species. Over the years this concept has expanded to include other elements such as morphology and ecological attributes as elements of the biological species (Grant, 1985; Mayr, 1987). In the sense that it reflects evolutionary dynamics and offers a simple testing procedure, the biological species seems more natural than the morphological species. It is, however, not free of drawbacks. By definition, the biological species is applicable to sexually reproducing organisms and cannot be used for uniparental organisms. Secondly, while breeding potential is a simple

distinctive measure between distantly related groups, there are many instances in which divergent species are still capable of producing partially fertile hybrids. Furthermore, certain intraspecific barriers such as occasional chromosome rearrangements may cause partial sterility within population, or between populations of the same species. So, with the biological concept, circumscribing a species is still liable to subjective judgements.

#### 4.1.3 The evolutionary species

To curb some of the difficulties of the biological species concept, and particularly its inapplicability to uniparental organisms, the evolutionary species was proposed (Simpson, 1961). According to Simpson the evolutionary species is 'a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies'. Roles are definable by their equivalence to ecological niches and morphological peculiarities of adaptive nature. While the evolutionary species concept can be applied to uniparental and biparental species, unlike the former two species concepts it lacks operational measures regarding species delimitation. Furthermore, the 'unitary evolutionary role' is also ambiguous. How should morphological variants and ecotypes be treated? Are they different species?

In addition to these three species concepts a few others have been proposed by several authors which emphasize different aspects of the former species. Others have taken a much broader view of the species concept trying to link elements from both the taxonomic and biological species concepts (Wagner, 1984). According to Wagner, a species is 'a convenient taxonomic category that defines a unit of organismic diversity in a given time frame and composed of individual organisms that resemble one another in all or most their structural and functional characters, that reproduce true by any means, sexual or asexual, and constitute a distinct phylogenetic line that differs consistently and persistently from populations of other species in gaps in character state combinations including geographical, ecological, physiological, morphological, anatomical, cytological, chemical, and genetic, the character states of number and kind usually used for species discrimination in the same and related genera, and if partially or wholly sympatric and coexistent with related species in the same habitats, unable to cross or, if able to cross, able to maintain the special distinction'. While many would agree that this is what a species is, the problem remains how to circumscribe a group of individuals as a species and whether all the characteristics mentioned are of equal weight in so doing. It seems that circumscribing a species remains a subjective matter and some characteristics will be seen as of greater importance by different authors.

## 4.1.4 Species concepts in crop plants

The issue of species concept is even more difficult in crop plants because of their immense morphological variability. Traditionally, and along with the morphological species concept, several species have been described in many individual crops. The number is even larger if one considers also the synonyms of these species. As an example, for the common oat, *Avena sativa*, 36 synonyms have been listed (Baum, 1977), all with specific morphological or geographical peculiarities. Progress toward more natural classification and utilizing genetic criteria has been more common in crop plants than in general plant taxonomy. The reason is that this kind of genetic information became available as a result of hybridization experiments between different taxa within the crop and with wild relatives, conducted by plant breeders and plant geneticists. The trend toward reducing the number of species within a given crop is well illustrated in wheat (Table 4.1). On morphological grounds Jakubziner (1958) recognized 10 cultivated tetraploid and seven hexaploid species. These numbers were reduced to only one tetraploid and a single hexaploid species by Bowden (1959), and to two tetraploids and a single hexaploid species by Morris and Sears (1967).

In some other crops the morphological species concept is still being used. The three pepper species *Capsicum annum*, *C. chinense* and *C. frutescens* grow in different geographical regions, though they occasionally overlap. They share the same white flower, are interfertile and can be regarded as conspecific. Species concept in the genus *Citrus* is also in flux. Tanaka (1977) proposed 162 species, while Swingle and Reece (1967) recognized only 16, and Scora (1988) only three biological species: *C. medica* L. (citron), *C. reticulata* Blanco (mandarin) and *C. maxima* (Brum.) Merrill (pomelo). All the potatoes have been considered by Dodds (1962) as members of *Solanum tuberosum* which have been divided into cultivar groups, while Hawkes (1990) regards each of these groups as separate species.

Not only have different morphological types within a crop been regarded as distinct species, but so have their wild progenitors. In traditional taxonomic literature they are often considered as independent species and occasionally a wild progenitor has been divided further into several species. In oats, where the cultivated form is treated as a single polymorphic species, the wild progenitor had been fragmented into five species (Baum, 1977). It is, however, more and more common that the crop and its wild progenitor are assigned to the same species in ranks of subspecies or varieties (Table 4.2). Similarly, wild diploid potatoes have been divided into approximately 20 species by Hawkes (1990), but considered as one polymorphic species by Grun (1990). On the other hand, sometimes, for practical reasons, different wild ecotypes may be retained at species rank because they possess unique diversity as in the grape vine.

Table 4.1 Taxonomic treatment of polyploid wheats by different authors

	Jakubziner (1958)	Bowden (1959)	Morris & Sears (1967)
(4x)			
Wild		<i>T. turgidum</i>	<i>T. turgidum</i> var. <i>dicoccoides</i>
	<i>T. araraticum</i> , <i>T. dicoccoides</i>		
Cultivated		Groups of cultivars	Group of varieties:
Hulled:	<i>T. timopheevi</i> , <i>T. paleocolchicum</i>	<i>turgidum</i> , <i>polonicum</i> , <i>durum</i> <i>carthilicum</i> , <i>turanicum</i> , <i>paleocolchicum</i> , <i>aethiopicum</i>	<i>dicoccon</i> , <i>durum</i> , <i>turgidum</i> <i>polonicum</i> , <i>carthilicum</i> <i>T. timopheevi</i>
<i>T. dicoccum</i>		var. <i>dicoccoides</i>	<i>T. timopheevi</i>
Naked:	<i>T. durum</i> , <i>T. turgidum</i> , <i>T. turanicum</i>	var. <i>timopheevi</i>	var. <i>timophaevi</i>
<i>T. polonicum</i> , <i>T. carthilicum</i> , <i>T. aethiopicum</i>		var. <i>tumaniani</i>	var. <i>zhukovskiy</i> (6x)
			<i>T. aestivum</i>
6x		<i>T. x aestivum</i>	
Hulled:	<i>T. zhukovsky</i> , <i>T. macha</i> , <i>T. spelta</i>		Groups of varieties:
Naked:	<i>T. aestivum</i> , <i>T. compactum</i> , <i>T. varilovi</i>	Groups of cultivars:	<i>spelta</i> , <i>varilovi</i> , <i>aestivum</i> <i>compactum</i> , <i>sphaerococcum</i>
<i>T. sphaerococcum</i>		<i>aestivum</i> , <i>spelta</i> , <i>compactum</i> <i>sphaerococcum</i> , <i>macha</i> , <i>varilovi</i>	

**Table 4.2** Taxa of the primary and secondary gene pools of different crops

Crop	Ploidy	Primary gene pool		Secondary gene pool
		Cultivated	Wild	
<b>Cereals</b>				
Einkorn	2x	<i>Triticum monococcum</i>	<i>T. boeoticum</i>	<i>Triticum</i> , <i>Secale</i> , <i>Aegilops</i>
Barley	2x	<i>Hordeum vulgare</i>	<i>H. spontaneum</i>	none
Rye	2x	<i>Secale cereale</i>	<i>S. cereale</i>	<i>Secale</i> , <i>Aegilops</i> , <i>Triticum</i>
Rice	2x	<i>Oryza sativa</i>	<i>O. rufipogon</i>	<i>Oryza</i> spp.
Sorghum	2x	<i>Sorghum bicolor</i>	<i>S. bicolor</i>	<i>S. halepense</i>
Pearl millet	2x	<i>Pennisetum americanum</i>	<i>P. violaceum</i>	<i>P. purpureum</i>
Maize	2x	<i>Zea mays</i>	<i>Z. mexicana</i>	<i>Z. perennis</i> , <i>Tripsacum</i> sp.
Emmer	4x	<i>Triticum turgidum</i>	<i>T. dicocoides</i>	<i>Triticum</i> , <i>Aegilops</i> , <i>Secale</i>
Bread wheat	6x	<i>Triticum aestivum</i>	none	<i>Triticum</i> , <i>Aegilops</i> , <i>Secale</i>
Common oat	6x	<i>Avena sativa</i>	<i>A. sterilis</i> , <i>A. fatua</i>	<i>Avena</i> spp.
<b>Pulses</b>				
Pea	2x	<i>Pisum sativum</i>	<i>P. elatius</i> , <i>P. humile</i>	<i>P. fulvum</i>
Lentil	2x	<i>Lens culinaris</i>	subsp. <i>orientalis</i>	<i>L. odemensis</i> , <i>L. ervoides</i>
Chickpea	2x	<i>Cicer arietinum</i>	<i>C. reticulatum</i>	<i>C. echinospermum</i>
Broad bean	2x	<i>Vicia faba</i>	none	none
Groundnut	4x	<i>Arachis hypogea</i>	<i>A. monticola</i>	<i>Arachis</i> spp.
Soybean	4x	<i>Glycine max</i>	<i>G. soja</i>	none
Common bean	2x	<i>Phaseolus vulgaris</i>	<i>Ph. vulgaris</i>	<i>Phaseolus</i> spp.
Lima bean	2x	<i>Phaseolus lunatus</i>	<i>Ph. lunatus</i>	none
Runner bean	2x	<i>Phaseolus coccineus</i>	<i>Ph. coccineus</i>	<i>Phaseolus</i> spp.
Cowpea	2x	<i>Vigna unguiculata</i>	<i>V. unguiculata</i>	none

**Table 4.2** Continued

Crop	Ploidy	Primary gene pool		Secondary gene pool
		Cultivated	Wild	
<b>Vegetable</b>				
Carrot	2x	<i>Daucus carota</i>	<i>D. carota</i>	<i>Daucus</i> spp.
Onion	2x	<i>Allium cepa</i>	none	none
Lettuce	2x	<i>Lactuca sativa</i>	<i>L. serriola</i>	<i>Lactuca</i> spp.
Cabbage	2x	<i>Brassica oleracea</i>	<i>B. oleracea</i>	none
Cucumber	2x	<i>Cucumis sativus</i>	<i>C. sativus</i>	none
Watermelon	2x	<i>Citrullus lanatus</i>	<i>C. lanatus</i>	<i>C. colocynthis</i>
Pepper	2x	<i>Capsicum annum</i> , <i>C. frutescens</i> , <i>C. chinense</i>	<i>C. annum</i> , <i>C. frutescens</i> , <i>C. chinense</i>	<i>Capsicum</i> spp.
Tomato	2x	<i>Lycopersicon esculentum</i>	<i>L. esculentum</i> , <i>L. pimpinelifolium</i>	<i>Lycopersicon</i> spp.
Potato	4x	<i>Solanum tuberosum</i>	<i>S. andigena</i>	<i>Solanum</i> spp.
Eggplant	2x	<i>Solanum melongea</i>	<i>S. incanum</i>	<i>Solanum</i> spp.
Squash	2x	<i>Cucurbita pepo</i>	<i>C. fraterna</i> , <i>C. texana</i>	
<b>Fruit trees</b>				
Apple	4x	<i>Malus domestica</i>	<i>Malus</i> sp.	<i>Malus</i> spp. <i>Cydonia</i>
Peach	2x	<i>Prunus persica</i> , <i>Amygdalus communis</i>	<i>P. davidiana</i> , <i>P. mira</i> , <i>Amygdalus</i> sp.	<i>Prunus</i> spp.
European plum	6x	<i>Prunus domestica</i> , <i>P. insititia</i>	<i>P. spinosa</i>	<i>Prunus</i> spp.
Grapes	6x	<i>Vitis vinifera</i>	<i>V. vinifera</i>	<i>Muscadinia</i> spp.
<b>Nut trees</b>				
Walnut	2x	<i>Juglans regia</i>	<i>J. regia</i>	<i>Juglans</i> spp.
Pistachio	2x	<i>Pistacia vera</i>	<i>P. vera</i>	none

(a) *The gene pool system*

To avoid an excessive number of taxonomic species and to enable better reflection of genetic affinities, Harlan and de Wet (1971) proposed, along with the biological species concept, a system of grouping crop plants and their relatives, wild and cultivated, in the form of gene pools (GP) and the potential of gene flow between them. They proposed three possible gene pools for each crop plant.

1. The primary gene pool, GP I, includes all the taxa of a crop plant and its wild progenitor. Members of the GP I are interfertile, form one gene pool and are regarded as one polymorphic species despite their previous taxonomic ranking. The message for the breeder is that no restriction of gene exchange exists between members of this group.
2. The secondary gene pool, GP II, includes more distantly related species which still can be hybridized with the crop and their hybrids and hybrid derivatives are sufficiently fertile to enable gene flow.
3. The third gene pool, GP III, includes all other botanically related species of the cultigen from which gene flow is naturally not possible because of crossability barriers, hybrid lethality and sterility and breakdown of hybrid derivatives. Some of these barriers may be overcome by experimental techniques such as chromosome doubling and embryo culture, which then may enable assigning a particular species of the GP III to GP II. The GP I of lentil, *L. culinaris*, includes all the cultivars and land races of the cultivated forms which are regarded as ssp. *culinaris*, and its wild progenitor, ssp. *orientalis*. Only a single species, *L. odemensis*, could be assigned to GP II. It is cross-compatible with members of the GP I; the hybrids are normal but only partially fertile because of meiotic irregularities. The GP III contains two species, *L. nigricans* and *L. ervoides*. Both are cross-incompatible with members of the GP I because of early hybrid embryo abortion. However, using embryo culture techniques, it became possible to rescue the *L. culinaris* × *L. ervoides* hybrid embryos and to rear them to maturity. These hybrids are partially fertile and fully fertile derivatives can be selected in the segregating generations. Thus, *L. ervoides* which formerly had been a member of the 3rd gene pool of lentil and of no use for the breeder, has been elevated to the GP II by introducing the embryo culture technique. Taxa of the primary and secondary gene pools of several crop plants are listed in Table 4.2.

All crop plants have a primary gene pool which encompasses the various cultivated forms. Occasionally, as in peach and plum, the GPI contains taxa of other crops. The almond is a member of the peach's primary gene pool and the damson plum, *P. insititia*, is a member of the European, *P. domestica*. Not all crops have wild forms in their GP I. This is the case with the broad bean, sesame, cassava and onion whose wild

progenitors have not been identified yet. Another group of crop plants which have no wild forms in their primary gene pool are all those which have evolved through hybridization and polyploidization under domestication. Among others are the bread wheat *Triticum aestivum*, potato *Solanum tuberosum* and tobacco *Nicotiana tabacum*. Most crop plants have a secondary gene pool which mostly includes species of the same genus. Exceptional are wheats with GP II having other genera such as *Aegilops* and *Secale*. Some crops such as barley, soybean, broad bean and onion do not have a secondary gene pool. The tertiary gene pool has no defined borders and is of no interest to the breeder because no genetic diversity can be obtained from it by classical methods. However, members of this GP are the target of genetic research in an attempt to devise methods which would enable gene transfer from them to the cultigen.

## 4.2 THE PROCESS OF SPECIATION

The ways in which new species are formed depend upon how the species is defined. With the morphological species concept speciation is achieved by accumulation of sufficient morphological variation to differentiate the emerging species from its mother species. These morphological and even ecological differences may or may not be associated with the establishment of reproductive isolating barriers (RIB). With the biological species concept establishment of RIBs is essential for the formation of new species. How then are such RIBs formed, and particularly under what conditions? There is some confusion in the literature regarding the actual formation of RIBs and the circumstances under which they can be achieved. In fact, most of the speciation models indicate the circumstances and physical pre-conditions for species formation but to a much lesser extent how RIBs are formed and established. Thus, the commonly used terms 'allopatric speciation' and 'sympatric speciation', for example, depict whether or not geographical isolation has been required for the evolution of new species, but not to what extent they are necessary for the development of RIBs.

Reproduction barriers may be by-products of genetic changes associated with morphology, adaptation to new environment, or reproduction time. Occasionally, as in the case of chromosomal rearrangement, the change itself creates a RIB. RIBs can be acquired in two ways, gradually or instantly, and so the speciation process may be gradual or abrupt.

## 4.2.1 Gradual evolving of RIBs

The basic requirement for gradual accumulation of RIBs, and hence gradual speciation, is some sort of primary isolation between the mother and the evolving populations. This initial separation is essential for the

differentiation of the evolving population by accumulation of unique variation without the risk of being diluted or even totally swept out by massive gene flow from the mother population. This primary isolation can be provided by:

1. Geographical barriers, or otherwise, in the same geographical area, under the shield of self-pollination
2. Ecological barriers
3. Through modification of reproduction time or behavior.

#### (a) Geographical isolation

This mode of speciation is known also as allopatric or geographic speciation (Mayr, 1942). It is of prime importance in animal speciation but may be applied also to cross-pollinating plants. Following the emergence of a geographic barrier such as a mountain range, desert or sea, a part of a large population is separated to a degree that gene exchange with the mother population is no longer possible. As a result of environmental changes and directional selection, new variation is acquired until the point where sufficient RIBs have accumulated. The geographic isolation by itself, no matter how long it lasted, would not guarantee the development of RIBs. The Old World *Platanus orientalis* and *P. occidentalis*, a New World species, were separated from one another about 300 million years ago, have acquired adaptation to different habitats and morphological differences, but are still interfertile (Stebbins, 1950). Similarly, Old and New World wild grapes were isolated at about the same time but remained interfertile.

Sympatric distribution of closely related species, even growing side by side, seems to weaken the requirement of geographic separation for speciation. A common explanation for such overlapping is post-speciation redistribution of the new species, or of its mother species. In any case, geographic separation is not the only way by which primary separation could be provided.

#### (b) Isolation between sympatric populations

Here the primary isolation occurs in the same geographical area, and is vaguely comparable to sympatric speciation. This is a rather confused expression because it may include a situation where the evolution of the new species has taken place in a separate habitat within the same geographical area or actually in the same habitat of the mother species. Primary isolation for sympatric speciation in plants can be provided by any of the three mechanisms or combination between them:

1. Self-fertilization, which is an effective shield against gene flow.
2. Variation in flowering time which provides a seasonal barrier.

3. Ecological variation, or niche differentiation, which is an important element of disruptive selection.

#### Self-fertilization

Establishment of RIBs as a result of genetic differentiation can be accelerated in self-pollinated plants, for two main reasons: new genetic variation is rapidly fixed in a homozygous condition in specific linkage groups; and it is protected from being diluted by alleles of the mother population, and linkage groups are protected from being disintegrated by recombination.

The effectiveness of self-pollination in promoting accumulation of RIBs within the same habitat has recently been demonstrated in natural populations of the lentil's wild progenitor, *Lens culinaris* subsp. *orientalis*. Cultivated and wild lentils are selfers with outcrossing rates below 1%. Most of the subsp. *orientalis* populations are interfertile when subjected to artificial hand pollination. A few other populations, which under the same circumstances are also cross-compatible with one another, are cross-incompatible with the rest because of hybrid embryo abortion. At least three genes control hybrid embryo abortion in this case, indicating their gradual accumulation. The populations with the unique crossability behavior still share the same morphology and ecological requirements with populations of the main crossability group and occasionally grow in the same site side by side (Ladizinsky and Abbo, 1993).

#### Seasonal barriers

Variation in flowering time can be a major cause of differentiation in sympatric populations. In cross-pollinating plants it may become a RIB by itself and may promote development of additional RIBs.

The wild lettuce species *Lactuca graminifolia* and *L. canadensis* are largely allopatric but interfertile when subjected to hand pollination. Where they grow sympatrically they remain distinct because the former flowers in early spring, the latter in the summer (Whitaker, 1944).

The species *Aegilops longissima* and *Ae. sharonensis* grow sympatrically and in the same habitat. They are cross-fertile and their hybrids are partially fertile, but such interspecific hybrids are totally absent or extremely rare in natural populations. The reason is that *Ae. sharonensis* flowers during March and early April, and *Ae. longissima* during May.

A combination of shifting toward self-pollination and flowering time was documented in *Clarkia xantina* (Moore and Lewis, 1965). In this cross-pollinating species two populations at the edges of the distribution range contained individuals which essentially became selfers due to changes in the position of the anthers toward the stigma. About 30% of the selfers also flowered 1–2 weeks earlier compared with the usual flowering time. Two flower color types were found among the selfers, red, as in the outcross type, and white. The red-flowered selfer was interfertile with

the outcross type, but the white type differed by a chromosomal rearrangement and their hybrids were only partially fertile. To what extent the white-flowered type is bound to the chromosomal rearrangement is not clear, but it illustrates how additional variation and initiation of RIB development may be promoted by self-pollination.

### Ecological barriers

Perhaps the most detailed examples of ecological barriers to gene flow between adjacent populations have been documented in the pasture plant *Agrostis tenuis* and to some extent also in *Anthoxanthum odoratum*. Both are perennial grasses, outcrossing self-incompatible species. Populations of *A. tenuis* were found in unused lead and zinc mines in Wales which are about 1000 years old. The soil there has been contaminated with these two heavy metals, approximately 1% lead and 0.03% zinc (Bradshaw 1952) and except for *A. tenuis* no plant life occurred. In the mine's soil the *A. tenuis* plants grew in small patches about 1 m apart. When pasture plants were transplanted into mine soil about 50% of the tillers died within three months, and the rest produced small roots, not longer than 2 mm. Mine plants transplanted into pasture soil grew slowly and were distinctively smaller than the pasture plants. The border between the heavy metal resistant and susceptible was clear and abrupt, according to the level of contamination. Naturally, under these circumstances massive gene flow must occur across the contamination line, nevertheless, these two populations maintained their identity due to disruptive selection favoring the heavy metal resistant type in the mine soil and the sensitive type in the pasture soil. The heavy burden of genetic load imposed on the mine population by gene flow from the pasture population had encouraged self-fertilization to a degree which was up to four times higher than in the pasture population (Antonovics, 1968). Similar copper tolerance was detected in *A. tenuis* (McNeilly and Bradshaw, 1968).

The above examples indicate that disruptive selection can be an important and effective isolation even across distances of a few meters. The side by side alignment of different habitats may provide the necessary arena and the appropriate shelter for the emergence of new variation which later may also produce the necessary RIBs for the completion of the speciation process.

## 4.3 INSTANTANEOUS FORMATION OF RIBS

Instantaneous speciation was viewed by Mayr (1963) as 'genetic revolution' and as 'speciation by saltation' by Lewis (1966). While in gradual speciation RIBs are usually by-products of genetic variation, spontaneous formation of RIBs, regardless of accumulation of genetic changes in other

traits, marks the instantaneous establishment of a new species. This kind of speciation is often associated with chromosomal irregularity, either structural or numerical. Instantaneous speciation may not require temporal primary isolation, and if does, it is usually for a much shorter time than in gradual speciation.

### 4.3.1 Chromosomal rearrangements

Reciprocal translocation, paracentric and pericentric differences are not uncommon between populations and may even occur within populations. They may affect the wealth of the population and its total selective value, usually when they are in a heterozygous state. Heterozygous individuals are likely to be only semi-fertile because considerable parts of their gametes are likely to be aborted or non-functional (Figures 2.2–2.4). Hence, chromosomal rearrangements have always been regarded as an important step in speciation, and among the few RIBs whose formation and effect have been studied in much detail. However, a single chromosomal rearrangement can barely be regarded as sufficient RIB for the establishment of a new species. In cases where several such rearrangements differentiate related species, their evolution is thought to be gradual, but can be spontaneous as well.

A chromosomal rearrangement requires two simultaneous breakages, either in two different chromosomes, or in a single one, and reunion in a new fashion – change of chromosomal segments between two non-homologous chromosomes in the case of reciprocal translocation, and reunion of the same broken segment but in reverse orientation in the case of inversion. Such chromosome breakages are as rare as gene mutation. Statistically, therefore, it is unlikely that several such chromosomal mutations would occur simultaneously, hence the common concept of gradual accumulation of chromosomal rearrangements in speciation. This is definitely a possibility, and occasionally can even be documented by the type and number of chromosomal rearrangements among closely related species. There are, however, too many cases in which closely related species are separated by several chromosomal rearrangements, but the intermediate links between them are missing. Such a loss of all the intermediate phases seems odd because in gradual accumulation, each of the intermediate forms has to be sufficiently established to produce the next rearrangement of the series.

An inevitable conclusion is that two types of chromosomal rearrangements must occur during speciation, a moderate one, in which a single rearrangement occurs at a time, and a more radical one which revolutionizes the chromosomal arrangement.

Spontaneous chromosomal breakage may be triggered by natural ultra violet irradiation or by certain metabolites of mutagenic effect, and perhaps more so by internal mechanisms such as transposable elements

moving from one chromosome site to another affecting gene action and causing chromosomal breakage (Nevers and Sedler, 1977). These elements, which usually rest unnoticed in certain locations in the chromosome, under specific genetic, and probably environmental conditions, may be provoked to move in and out, causing chromosome breakage. While not every chromosome breakage can be attributed to transposable elements, spontaneous mass chromosomal breakage and rearrangement are probably mediated by such elements. There are a few reported cases in which certain individuals in wild populations exhibit extraordinary chromosome breakage as in *Elymus fractus* (Heneen, 1963) and *Aegilops longissima* (Feldman and Strauss, 1983). In a few individuals of the *Ae. longissima* population in the southern Judean hills, Israel, an extraordinary breakage occurred in mitotic and meiotic chromosomes. All the chromosomes were affected and in a non-random fashion. The frequency and number of the observed aberrations were increased by elevating the temperature from 25°C to 30–32°C. Spontaneous chromosomal breakage seemed heritable and was observed in the few progeny of that plant. Furthermore, in crosses with normal plants, chromosome breakage appeared to be governed by a single recessive gene, and the proportion of the chromosome breaking homozygous gene was affected by the cross direction, indicating cytoplasmic involvement. Another important aspect of the massive chromosomal rearrangements in both *Elymus* and *Aegilops* is that they have not entailed any obvious morphological changes.

Spontaneous chromosomal breakage of that magnitude which may be triggered by environmental or genetic stress offers a rather simple mechanism for instantaneous speciation by genome reconstruction. Massive and abrupt chromosomal rearrangements apparently were involved in formation of *Clarkia franciscana* from *C. rubicunda*. The two differ by three chromosomal interchanges and four inversions (Lewis 1966). Among genera of economic importance such massive chromosomal rearrangements have been recorded in oat and lentil.

The diploid oat species *A. strigosa* and *A. prostrata* are morphologically very similar but differ from one another by five chromosomal rearrangements. Since no intermediate cytogenetic forms between the two were known at the time, radical chromosomal rearrangement by one step was the most plausible explanation. Only later, another diploid species was discovered, *A. damascena* which cytogenetically appeared to be an intermediate form between the former two. Since this species is so rare, and another four intermediate links are still missing, it could be assumed that *A. damascena* represents an independent case of radical chromosomal rearrangement.

An even greater chromosomal rearrangement occurs between *A. strigosa* and *A. longiglumis*. Here the two are morphologically distinct, but grow side by side wherever *A. longiglumis* occurs.

Similar massive chromosomal rearrangements were recorded in two different species groups of the genus *Lens*. *L. tomentosus* differs from *L. culinaris*, by its unique karyotype. One pair of chromosomes appeared much larger than in the *L. culinaris* karyotype, and became the largest in the complement, while the satellite which normally constitutes almost the entire arm became extremely small. Chromosome pairing in their hybrid revealed that the two differ from one another by five rearrangements. Since plants of the two species grow side by side where no intermediate chromosomal forms have been identified, it is tempting to assume that this massive rearrangement arose in one step.

A similar situation also occurs between *L. nigricans* and *L. lamottei*. The common chromosomal type of *L. nigricans* prevails throughout its distribution range from Turkey to Spain and Morocco. An isolated population in the Canary Island, La Palma, differs by a single reciprocal translocation. The distribution of *L. lamottei* is much more restricted and a few populations are known in France, Spain and Morocco, and all share the same chromosomal arrangement. Karyotypically *L. nigricans* and *L. lamottei* are indistinguishable from each other, but appear to differ by five rearrangements and consequently their hybrids are completely sterile. In this case similar chromosome segments were involved in the rearrangement leaving no karyotypic testimony to the immense reshuffling which had occurred. Since these two sibling species are effectively isolated from one another and cytogenetic intermediate forms between them have not been found it is reasonable to assume that this massive chromosome reshuffling occurred instantaneously.

The origin of rye, *Secale cereale*, probably also involved two instantaneous chromosomal rearrangements. The number of species in the genus *Secale* differs according to various authors. Sencer and Hawkes (1980) have recognized five main species, two perennial and three annuals, all diploid with the same chromosome number ( $2n=14$ ), and present the following character combinations:

- S. montanum*, perennial, self-incompatible, montanum chromosome type.
- S. africanum*, perennial, self-fertile, montanum chromosome type.
- S. sylvestre*, annual, self-fertile, montanum chromosome type.
- S. vavilovii*, annual, self-fertile, cereale chromosome type.
- S. cereale*, annual, self-incompatible, cereale chromosome type.

Montanum and cereale chromosome types differ by two chromosomal rearrangements involving three of the seven basic chromosome sets (Riley, 1955; Kush and Stebbins, 1961; Stutz, 1972). The distribution of the above three characters among the *Secale* species suggests that annual growth habit and self-fertility are not associated with the chromosomal rearrangement. A similar conclusion has been drawn from genetic analysis of  $F_2$  *S. montanum* × *S. cereale* (Stutz, 1957). By its morphology and breeding system *S. cereale* is closer to *S. montanum* than to any of

the other two annual species. The question is whether *S. cereale* evolved directly from *S. montanum* or from one of the two self-compatible annual forms. Stutz (1972) is in favor of the idea that *S. sylvestre* was an intermediate form between *S. montanum* and *S. cereale*. Such an evolutionary pathway must be based on the rather unlikely assumption of regaining self-incompatibility after it has been lost in *S. sylvestre*. For the same reason *S. vavilovii* is more likely to be a derivative form of *S. cereale* and not the other way around. The major difficulty of direct emergence of *S. cereale* from *S. montanum* is the chromosomal difference between them, and particularly, how such a homozygous type could emerge in a population of a self-incompatible plant such as *S. montanum*. Kush and Stebbins (1961) were in favor of gradual accumulation of the chromosomal difference between the two, but such intermediate chromosome types have not been found. In addition, establishment of a homozygous to a single chromosomal rearrangement is not much less problematic than establishment of two in the same chromosome. The main obstacle is not so much the 30% fertility of the spontaneous heterozygote for two rearrangements, but the constant pollination of the new cereale-chromosomal type by *S. montanum*. On one hand such continuous pollination seems necessary for the accumulation of sufficient number of alleles in the self-incompatible gene in the cereale-chromosome type, but on the other hand it would delay, if not prevent, the establishment of the cereale-chromosome type. A faster establishment could be achieved if the heterozygous genotypes and the homozygous cereale-type had some adaptive advantage over the montanum-type, and further deviation by acquiring an annual growth habit.

While it seems more likely that *S. cereale* evolved directly from *S. montanum*, the actual course of events is still obscure. However, the absence of an intermediate chromosomal type between them may suggest that the two translocations occurred simultaneously.

Besides massive chromosomal rearrangements in which the segments involved were sufficiently large to be detected at meiosis of the interspecific hybrid, there are apparently many more cryptical changes. In the intergeneric *Lolium perenne* × *Festuca pratensis* hybrid, chromosome pairing was perfect and even the number of chiasmata per cell was in the range of the parental parents. Despite this, the hybrid was completely self-sterile with only 13% pollen fertility (Peto, 1933). Similar normal pairing and complete sterility was reported in the diploid wheat hybrid *Triticum boeoticum* × *T. urartu* (Johnson and Dahaliwal, 1976) and in the interspecific diploid oat hybrid *Avena canariensis* × *A. damascena*. The sterility in such hybrids is supposed to result from cryptic intercalary chromosomal changes which are too small to be detected cytologically. However, any recombination between the two genomes is liable to be lethal because of deficiency or duplication of chromosomal segments.

#### 4.3.2 Change of chromosome numbers

Change of chromosome numbers among closely related species provides an instant barrier to gene flow because hybrids having an uneven chromosome number are likely to be sterile. Change in chromosome numbers can be achieved by aneuploidy, addition or deletion of one or more chromosomes of the basic number, or polyploidy, by doubling of the chromosome number.

##### (a) Aneuploidy

The kind of aneuploidy which seems to play a role in evolution and speciation is that which involves the reduction of chromosome number, creating descending aneuploid series among closely related species. It can be achieved by chromosome fusion known also as Robertsonian translocation, or non-reciprocal translocation (Figure 2.4). Such a fusion usually takes place between two telocentric chromosomes following loss of one centromere. As a result of the fusion, the number of chromosome arms remains the same but the  $2n$  chromosome number is reduced by two. Ascending aneuploidy is more difficult to explain because it requires not merely redistribution of existing chromatin material, but also creation of a new stable centromere.

Robertsonian translocations are relatively common in the animal kingdom, but occur in plants as well. It was reported in *Crepis* (Tobgy, 1943), *Haplopappus gracilis* (Jackson, 1965) and in *Chaenactis* (Kyhos, 1965). Aneuploidy in *Chaenactis* is interesting because it occurred twice. *C. glabriuscula* is an annual Compositae, ( $n=6$ ), which gave rise to the  $n=5$  *C. fremonti* and  $n=5$  *C. stevoides*. Each of the resulting species was derived from loss of a different chromosome of *C. glabriusculata*. The reduction of chromosome number was associated also with shift in adaptation. While the  $n=6$  species grows in mesic habitats, the two derived  $n=5$  species are desert plants.

Among crops' wild relatives descending aneuploidy apparently occurred in the formation of  $n=10$  species from  $n=11$  species in *Carthamus* (Esilai and Knowles, 1976), and in *Allium* (Kollman, 1969).

Difference by a small number of chromosomes between closely related species may be the first indication of an aneuploid series. This, however, is not necessarily the case, as in *Brassica*. Chromosome number in the diploids *B. campestris*, *B. oleracea* and *B. nigra* are  $n=10$ ,  $n=9$  and  $n=8$ , respectively, but in no way do they represent a simple aneuploid series. It is indicated both by their chromosome morphology (Röbbelen, 1960) and the pattern of chromosome pairing in the *B. campestris* × *B. oleracea* diploid hybrid, and in the spontaneous triploid hybrid developed as a shoot mutation in one plant of this hybrid combination.

Another example of a seemingly aneuploid series was found in vetch, *V. sativa* (*sensu lato*). Three chromosome numbers have been recorded in

this vetch:  $2n=14$ ,  $2n=12$  and  $2n=10$ . In this case simple aneuploidy evolution has been dismissed on grounds of chromosome morphology and chromosome pairing in hybrids involving types with different chromosome numbers (Ladizinsky and Temkin, 1978).

The reproductive barrier imposed by aneuploid reduction involves irregular chromosome pairing in hybrids between the diploid parent and the aneuploid derivative. The chromosomes involved in the translocation pair as trivalents in many cells and occasionally their segregation at anaphase is irregular, resulting in unbalanced gametes (Figure 2.4). Sterility resulting from Robertsonian translocation is similar to that of reciprocal translocation.

#### (b) Doubling of chromosome numbers

Chromosome doubling may produce two different types of polyploidy: autopolyploidy, following chromosome doubling of a diploid plant, or of an intra-specific hybrid, and allopolyploidy, following chromosome doubling of an interspecific hybrid. Polyploidy constitutes an effective RIB causing instantaneous speciation.

#### Autopolyploidy

Spontaneous autotetraploid individuals are reproductively isolated from their neighboring diploid individuals because their hybrids are triploids and highly, if not totally sterile, because of irregular chromosome behavior at meiosis. Genetically, these autotetraploids can store much greater variation in each locus compared with their diploid progenitors (section 2.1.3). Following hybridization between  $2\times$  and  $4\times$  individuals a few genes may introgress across the ploidy barrier, but this introgression may be much more to the advantage of the  $4\times$  cytotype than the  $2\times$ .

Among crop plants, speciation via autopolyploidy took place in potato, strawberry, banana, and in the forages alfalfa and perhaps also white clover. Some of the pasture grasses such as *Dactylis glomerata*, *Chloris gayana* and *Cynodon dactylon* also contain diploid and autotetraploid derivatives. In some crop plants spontaneous autopolyploidy may occur and polyploid cultivars are in use such as in grapes, apples, pears, cherry, pineapple and tea. Induced autopolyploidy has been attempted in several crops, but generally they are of limited use.

#### Allopolyploidy

This kind of polyploidy emerges from chromosome doubling of sterile interspecific diploid hybrids, and may be the most common type of instantaneous speciation. The allopolyploid combines the genetic properties of its diploid progenitor, but reproductively is isolated from them.

For an allopolyploid to be formed several conditions must be met:

1. The two progenitor species are capable of crossing with each other, uni- or bilaterally.
2. The interspecific hybrid is vegetatively normal.
3. The chromosomes of the parental species are sufficiently divergent and barely pair in the interspecific diploid hybrid.
4. Chromosome doubling of the zygote or in an apical shoot cell or cells.
5. Occurrence of genetic mechanism which would prevent homologous pairing in the raw polyploid.

Chromosome doubling of an interspecific hybrid provides to the chromosomes of each parental species a homologue with which it can normally pair at meiosis. In that sense an allotetraploid behaves like a diploid and only bivalents are formed at meiosis. Since chromosomes of different species, even if they possess similar genetic information, do not intermix, allopolyploids are characterized by disomic inheritance (Figure 2.6). Only rarely, however, are diploid species which are capable of hybridizing with each other cytogenetically divergent to the degree that their chromosomes are so different that they cannot pair even partially. In most hybrids between related diploid species some pairing does occur as a result of residual homology. This may be a source of irregular bivalent pairing between homologous chromosomes in the resulting allotetraploid. It is well established now that bivalent pairing in allopolyploids is under genetic control as in the case of wheat in which a specific segment on the long arm of chromosome 5B carries major genetic factor(s) governing bivalent pairing in the tetraploid and hexaploid wheat species. Some of these genetic factors could have evolved after the formation of the allopolyploid through directional selection, but others most probably originated in the diploid parents prior to their inclusion in the polyploid formation. Such genetic factors may exhibit themselves under experimental conditions where chromosomes of a certain genome have the choice to pair with their homologue or with partially homologous chromosomes of an alien genome. Given this choice, different degrees of affinity for homologous pairing were found among the three diploid oat species *A. strigosa*, *A. prostrata* and *A. longiglumis* (Ladizinsky, 1974). Pairing patterns were compared in diploid, triploid and tetraploid levels in which a tested genome and an alien one were presented in 1:1, 2:1, and 2:2 ratios. It appeared that *A. strigosa* has the greatest potential for preferential pairing and *A. longiglumis* the poorest. Although multivalents were common in the diploid hybrids involving *A. strigosa*, mostly bivalents were observed in allotriploids and allotetraploids having two *A. strigosa* genomes. The bivalent pairing was even more pronounced in combinations involving *A. strigosa* and *A. prostrata*, but in all combinations when *A. longiglumis* genome was combined with *A. prostrata*, in similar or greater proportions, mainly multivalents were formed.

Another circumstantial indication for the existence of genetic factors in diploid species which can affect regular chromosome pairing is in *Aegilops*. Of the seven diploids two have been involved in the formation of polyploid species. *Ae. umbellulata* (Cu genome) participate in the formation of six allotetraploids and one allohexaploid, and *Ae. squarrosa* (D genome) in three allotetraploids and two allohexaploids. Other diploid species were involved in these polyploids, but none of them has been a major partner (Zohary and Feldman, 1962). The homologous pairing suppressor elements on the 3D chromosome of the hexaploid wheats originating from *Ae. squarrosa* genome have the same potential as genotypes of the diploid *Ae. squarrosa* (Attia, Ekingen and Robben, 1977). It is tempting to speculate that specific genotypes of these two diploids possessing genes for preferential chromosome pairing at meiosis at the polyploid level were involved in the origin of allopolyploids.

Only a few crops are of certain natural allopolyploid origin with a known wild progenitor. Among them are the tetraploid wheat, *Triticum turgidum*, the hexaploid oat, *Avena sativa*, and perhaps also the European plum *Prunus domestica*. On the other hand, allopolyploidy has been a major avenue of speciation under domestication and some of the most important crop plants originated this way.

#### 4.4 SPECIATION UNDER DOMESTICATION

Theoretically, plant domestication and agriculture practices contain the necessary components for speciation. Selection under domestication has resulted in enormous morphological and physiological diversity, crop diffusion to areas away from the nuclear center of origin has provided geographical isolation, and bottleneck situations following severe weather conditions and epidemics could entail 'genetic revolution' and formation of new species. In some crop plants such as *Capsicum* and *Gossypium* several species are recognized within the cultigen. Each is characterized by a complex of morphological and physiological characters and has its own wild form. Nevertheless, the various species are interfertile. In others, such as in *Hordeum*, *Avena* and *Triticum*, the enormous morphological diversity which in the past was used to circumscribe a number of species, is being regarded now as intraspecific variation and each cultigen is defined as a single polymorphic biological species. Similarly, in most crops, the cultigen and its wild progenitor are considered conspecific. This is not to suggest that under domestication no reproductive barriers have begun to emerge. Reduced intervarietal crossability and moderate chromosomal rearrangements are not uncommon in many crops, but they are still regarded as intraspecific variation. Various degrees of sterility have been observed in many

intervarietal hybrids between and within rice races (Sampath, 1964), and were attributed to chromosomal rearrangements and genetic factors. Differential sterility in reciprocal crosses also indicated cytoplasmic differentiation. In African rice evidence has been presented to show the initiation of reproductive barriers between the crop *O. glaberrima* and its wild form (Chu and Okay, 1972). Some  $F_1$  *O. glaberrima*  $\times$  *O. barthii* are fertile but weak due to two complementary dominant gene systems. Most wild lines contain the  $W_1$  and most cultivated types the  $W_2$  gene. Weakness in the  $W_1$   $W_2$  genotype results from disturbed tissue differentiation in adventitious roots. The weakness expression is affected also by modifiers.

Indication of evolution of an isolation mechanism has also been reported in common bean. Abnormal seedlings with stunted growth and chlorosis were observed in hybrids between lines originating from Guatemala and Venezuela. These abnormalities appeared to be controlled by two independent dominant genes D11 and D12. The degree of the abnormalities depends upon allelic dosage.  $F_2$  plants homozygous in both loci were lethal, and those homozygous at one locus and heterozygous at the other locus perished but at a lower rate (Shi *et al.*, 1980). So, gradual build up of morphological, physiological and chromosomal diversity under domestication has progressed to various extents in different crop plants, but it is common to regard them all as tolerable disturbances which have not reached the threshold of complete speciation.

Yet, new species have emerged under domestication, following instantaneous speciation derived from allopolyploidy. The indication that a certain allopolyploid crop plant originated under cultivation and not by domesticating a wild form stems from the absence of genuine wild forms. This is the case with bread wheat, *Triticum aestivum*, and probably also with the tetraploid *Brassica* species, *B. carinata* and *B. napus*, tobacco, *Nicotiana tabacum*, and cotton, *Gossypium* spp.

##### 4.4.1 The hexaploid wheat

Morphologically the hexaploid bread wheat is extremely variable, and in the past it was divided into several species (Table 1.3), but current views regard them all as members of a single species, *Triticum aestivum*. Unlike other diploid and tetraploid domesticated wheat species which have wild counterparts, no wild hexaploid wheats is known to exist. Studies on the origin and phylogeny of the hexaploid indicated that it stemmed from an interspecific cross between tetraploid ( $2n=28$ , AABB) wheat and the diploid ( $2n=14$ , DD) *Aegilops squarrosa* = *T. tauschii*, followed by chromosome doubling of the sterile triploid hybrid (McFadden and Sears, 1946). A synthetic hexaploid of this cross combination was similar to a primitive hexaploid subsp. *spelta*.

It seems likely that the tetraploid parent of the hexaploid wheats was a domesticated form, for the following reasons. Firstly, the distribution ranges of the wild tetraploid wheat, *T. turgidum* var. *dicoccoides* and *Ae. squarrosa* do not overlap; the wild tetraploid is confined to the western portion of the 'fertile crescent' in the Middle East, while *Ae. squarrosa* occurs in central Asia and its western flank at the Caspian sea area. Secondly, a cross involving two wild species is likely to produce a wild hexaploid which disperses its seeds at maturity; this kind of hexaploid does not occur. The common view is that the hexaploid wheats emerged in tetraploid wheat fields in the eastern Caspian area of Iran where *Ae. squarrosa* is a common weed in cultivation. This hypothesis has been confirmed by the esterase and alpha-amylase zymogram of certain biotypes of subsp. *strangulata* from that region. *Ae. squarrosa* is adapted to cold weather and the raw hexaploid wheat apparently had similar cold tolerance which enabled it to expand beyond the limits of the domesticated tetraploid wheat.

#### 4.4.2 The tetraploid *Brassica* species

The tetraploid *Brassica* species are all amphidiploids derived from three diploid species. The diploids differ in their chromosome number, and each contains wild and cultivated forms with overlapping ranges of distribution. Their main characteristics are:

- B. campestris*, 2n=20 (AA genome). A common weed in Europe with the domesticate derivative, turnip, used as an oilseed and fodder crop, and also as a vegetable with swollen hypocotyl and root.
- B. oleracea*, 2n=18 (CC genome). It contains various wild ecogeographical forms which some regard as independent species, but collectively can better be referred to as var. *sylvestris*, occurring on sea-facing cliffs in England and southern Europe. The domesticate derivatives are all vegetables, but come in various forms, cabbage, kale, cauliflower, broccoli, kohlrabi and brussels sprout (Figure 3.1).
- B. nigra*, 2n=16 (BB genome). Wild forms of this diploid species are common in south west Asia where the cultivated form, black mustard, is grown. Another group of cultivated forms are in Europe, Africa and China. Occasionally, *B. nigra* is confused with another mustard crop, *Sinapis alba*, and to a great extent has been replaced by *B. juncea*.

Of the three tetraploid *Brassica* species no truly wild populations of *B. carinata* and *B. napus* occur (Parkash and Hinte, 1980). The few so-called wild forms are likely to be escaped.

- B. napus*, 2n=38 (AACC), the oilseed rape, of Mediterranean origin but currently of much wider distribution.

- B. juncea*, 2n=36 (AABB), brown, or leaf mustard, an ancient oil crop in India, China and recently in other parts of the world. Weed forms of *B. juncea* are quite common and therefore it is difficult to establish whether the leaf mustard emerged under cultivation or in the wild.
- B. carinata* (BBCC), Ethiopian mustard, is of limited use and value.

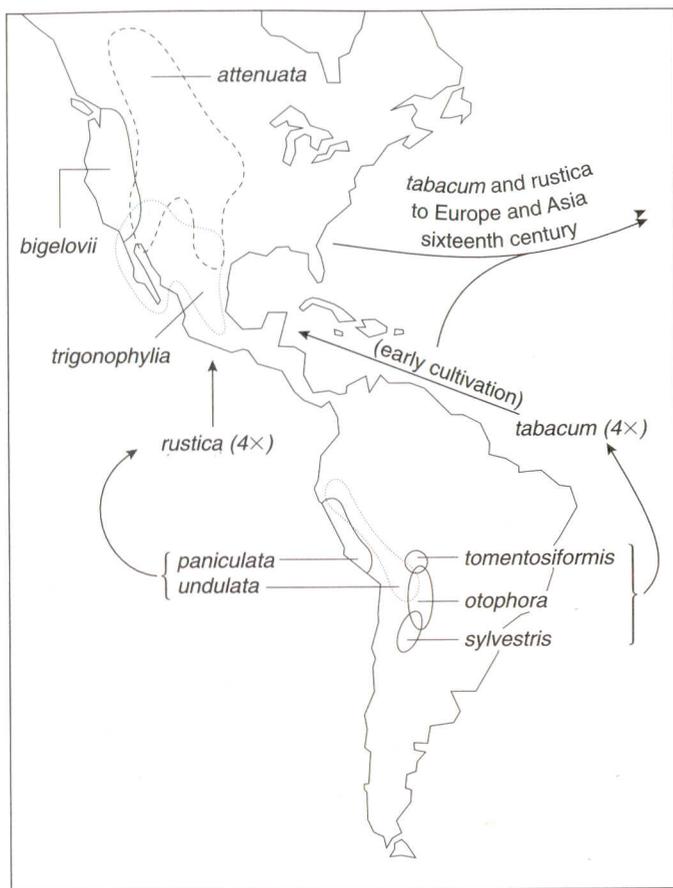
The cytogenetic relationships between the three diploid and three tetraploid *Brassica* species were established by U (1935) (Figure 1.1) to show the diploid progenitors of each of the tetraploid *Brassicacae*. These relationships have been corroborated by resynthesizing *B. juncea* and *B. napus* from their alleged diploid progenitors (Olsson, 1960a, b).

#### 4.4.3 Tobacco, *Nicotiana tabacum*

Among the 66 recognized *Nicotiana* species (Reed, 1991) a number of indigenous species in western North America contain nicotine in their leaves and have been used by the Indians for ritualistic, medicinal and hedonistic purposes. Of such species *N. bigelovii* (n=24) of southern California seems the most used and occasionally even cultivated. Others, less frequently used, are wild *N. trigonophylla* and *N. attenuata*, both n=12 (Goodspeed, 1954).

The two major nicotine containing species, *N. tabacum* and *N. rustica*, are cultivated and their chromosome numbers, n=24, indicate their polyploid origin. They are extensively used not only in the West, but worldwide. *N. tabacum* is the cornerstone of the tobacco industry and is grown wherever the climatic and soil conditions are suitable. Currently, *N. rustica* is grown on a much smaller scale, particularly for its nicotine to be used as insecticide. Unlike the former three *Nicotiana* species, *N. tabacum* and *N. rustica* are known only in cultivation, though occasional escapes near cultivation and road sides may be regarded as wild forms (Gerstel and Sisson, 1995).

The ancestral diploid species of *N. tabacum* have been determined by cytogenetic analyses. They are *N. sylvestris* (n=12) of the *Alatae* Section, and either *N. otophora* or *N. tomentosiformis*, both with n=12, of Section *Tomentosae*. Accordingly, the tobacco genomes are designated SSTT. These three diploid species grow on the eastern slopes of the Andes, *N. otophora* and *N. sylvestris* overlap on part of their range of distribution, while *N. tomentosiformis* grows further north where *N. sylvestris* does not occur (Figure 4.1). This, and the general morphology of synthetic *N. sylvestris* × *N. otophora* amphidiploid which was similar to *N. tabacum*, and the fertility of the synthetic amphidiploid were the reasons for preferring *N. otophora* as the donor of the TT genome (Goodspeed, 1954). On the other hand, cytogenetically, *N. tomentosiformis* seems the preferred one. Chromosome pairing is more regular in the triploid hybrid *N. tabacum* × *N. tomentosiformis*, than in *N. tabacum* ×



**Figure 4.1** The distribution of the tobacco wild diploid progenitors and other nicotine-containing species. Reproduced with permission from Gerstel, D.U. and Sisson, V.A. 1995. Tobacco, in *Evolution of Crop Plants* (eds J. Smartt and N.W. Simmonds), p. 549, Blackwell Science, Oxford.

*N. otophora* (Goodspeed, 1954), and genetic segregation in synthetic hexaploids between *N. tabacum* and either *Tomentosae* species is more regular in the hybrid involving *N. tomentosiformis*, suggesting its greater affinity to the TT chromosomes of *N. tabacum* (Gerstel, 1960).

More certain is the cytoplasm donor of *N. tabacum*. Study of the chloroplast coded large Fraction I Protein subunit indicated similarity between *N. sylvestris* and *N. tabacum* (Gray, Kung and Wildman, 1974).

Even with this knowledge of the tobacco phylogeny, the mystery of tobacco's origin has not been fully unveiled. Both ancestral species of tobacco have no nicotine in their leaves due to a dominant gene which by demethylation converts the nicotine into undesirable nor nicotine, and

it is unlikely that they had been used by the Indians for the purposes the tobacco plant offers. This gene is weaker in *N. sylvestris* and some believe that this wild species was used to some extent, but the dominant nature of the nicotine converting genes indicate that leaves of the raw amphidiploid also were nicotine-less.

#### 4.4.4 The New World tetraploid cottons

The tetraploid cultivated cottons have been thought to be a result of speciation under domestication (Hutchinson, Silo and Stephanes, 1947). The additional information about these tetraploid cottons indicates a much more complicated story.

The New World cultivated cottons *Gossypium hirsutum* and *G. barbadense* differ from each other mainly by leaf shape, position of the anthers, capsule surface and lint length. Both are allotetraploids ( $2n=4x=52$ ) with AADD genomic designation. Each of them has non-cultivated forms; those of *G. hirsutum* are found in the Caribbean Islands and in some Pacific islands, while non-cultivated *G. barbadense* are confined to coastal Ecuador and the Galapagos Islands, occasionally referred to as *G. darwinii*. Other non-cultivated tetraploid taxa are *G. mustelianum* = *G. caicoense* in NE Brazil, and *G. tomentosum* = *G. sandvices* in Hawaii. All the cultivated and non-cultivated taxa are interfertile (Stephens, 1971; Hasenkampf and Menzel, 1980); however, some deformations may be seen among the  $F_2$  progeny.

The donor of the 13 larger pairs of chromosomes, the AA genome, of the tetraploid taxa is an Old World species. They are either the Indian cultivated diploid *G. arboreum* or *G. herbaceum*, of which cultivated forms are known in Africa and Asia and wild forms particularly in South Africa. The two differ by a single reciprocal translocation (Gerstel, 1953). The chromosomes of *G. herbaceum* differ from the AA chromosomes of the tetraploid cottons by two translocations while those of *G. arboreum* differ by three, indicating that the former was more likely to be involved in the origin of the New World tetraploid cottons.

The other progenitor is the New World diploid *G. raimondi* occurring in Peru (Phillips, 1963). Chromosome doubling of *G. herbaceum* × *G. raimondi* sterile hybrid produced a plant similar to the natural tetraploids and was interfertile with the natural tetraploid cotton (Beasley, 1940; Harland, 1940). The monophyletic origin of all the tetraploid cottons is indicated by their interfertility and their common cytoplasm which is similar to that of the A genome species (Wendel, 1989). The small number of mutations in the chloroplast DNA of tetraploids has been taken as evidence of their relatively recent origin.

The above information has been employed in the various attempts to reconstruct the evolution of the New World tetraploid cottons. Three main questions had to be addressed:

How could the Old and the New World diploids have engaged in an interspecific cross?

When did it happen?

Did it occur in the wild or in cultivation?

For the first question, three explanations have been offered. The first is that the tetraploids evolved before Africa and South America drifted apart. This theory is incompatible with the recent origin as indicated by the cpDNA evidence. The second is that seeds of the A genome species were carried by sea currents from southern Africa, where *G. herbaceum* is a native plant, to the shores of South America. There are two difficulties with this theory: (1) seeds of *G. herbaceum* var. *africanum* cannot tolerate such a long journey in sea water (Stephens, 1966), and (2) landing on a South American shore is still too far away from the *G. raimondii* range of distribution in Peru. This latter problem may be allayed by assuming arrival at the western coast of America via Asia and Polynesia, but here the sea barrier is even more formidable, and floating against the sea currents is unlikely. The final explanation put forward is that seeds of the A genome species were brought to the West by man. This is also an argument which is difficult to substantiate. It implies early pre-Columbian contacts between the Old and the New Worlds, for which evidence is faint and circumstantial.

The time when the tetraploid cotton was formed must be earlier than the earliest archaeological cotton remains in America. The oldest *G. peruvianum* remains are from Ocampo Cave in the state of Tamaulipas, Mexico, dated to about 5800 BC (Smith and MacNeish, 1964), and from Huaca Prieta, north Peru at about 3000 BC. In both places cotton was one of several plants which had been used. Interestingly, the earliest cotton remains in the Old World are from the Harappan culture of India, about 3000 BC.

Naturally, any of the above evidence must be considered in an attempt to reconstruct the origin of the New World tetraploid cottons. Arrival of the A genome species in the West by natural means implies that the non-cultivated forms were the predecessor of the cultivated cotton, while introduction by man suggests their origin in cultivation, and accordingly, the non-cultivated forms should be regarded as escapes. None of the present theories on the origin of the New World tetraploid cottons is satisfactory, but if one has to choose, introduction by man seems to be supported by arguments not previously emphasized. Besides lack of solid evidence to support pre-Columbian contacts between the Old and the New Worlds, some of the objection to this theory is that no other major Old World crop plants were used in the Americas at the time of the first European landing there. This is not altogether accurate because the bottle gourd, *Lagenaria siceraria* has been there for 10 000 years. Its dry fruit has been used as cups, bowls, ladles and bottles, as it is used in

the Old World. Besides bottle gourd another plant, *Crescentia cujete* L. is also used for similar purposes in tropical America, but on a much smaller scale. It has been argued that the dry bottle-like fruit of *L. sericaria* floated across the Atlantic ocean to reach the Americas. If so, the bottle gourd had to naturalize in tropical America to an extent that man could appreciate its usefulness. The fact is that the bottle gourd in America is confined only to cultivation. Introduction by man is presently rejected because there is no evidence of such early contacts. Ignoring for a moment this disturbing fact, one may query whether there is any meaning to the endurance of these two crop plants, and if so, whether they have anything in common. Most West Asiatic traditional Old World crop plants such as wheat, barley, pea and lentil that one might consider favorable introductions by Old World migrating people, are ill-adapted to the ecological conditions of lowland Meso-America. Barley was introduced by Columbus in his second voyage but it did not succeed in Hispaniola (Harlan, 1995). The bottle gourd and cotton, however, are of African origin and potentially better adapted to the ecological conditions of Meso-America. Perhaps even more important, both offer products of better quality than any of the native Central American traditional crop plants. Several plants are used there as sources of fiber, i.e. several *Agave* species and *Apocynum cannabinum*, but they are not used for textiles.

#### 4.4.5 Triticale

Triticale is a purposely man-made crop plant species which has gained economic importance. It derives from chromosome doubling of hybrids between either 4x or 6x wheats and the diploid rye. Accordingly, there are hexaploid AABBRR ( $2n=6x=42$ ) and octaploid AABBDDRR ( $2n=8x=56$ ) triticale types.

Spontaneous wheat × rye hybrids have been observed occasionally, but they are completely sterile. Rimpau, in 1891, was the first to detect fertile wheat × rye hybrid, which later was named triticale. Artificial production of triticale began after colchicine treatment became the main method of chromosome doubling (Blackslee and Avery, 1937). Starting as a botanical cytogenetic curiosity this intergeneric hybrid has developed into another cereal crop plant, though not nearly as important as wheat. Triticale, and particularly the hexaploid types, show varying degrees of seed shrivelling. It appears to be associated with late DNA replication and mitotic irregularities in the endosperm nuclei (Bennett, 1977). Additional lines of hexaploid wheat possessing individual rye chromosomes revealed that the genetic factors governing seed shrivelling are located on the rye chromosomes 4R/7R, 5R and 6R. Also, 3R monosomic triticale shows less seed shrivelling (Darvey, 1974). Despite intensive international breeding programs triticale has not been found superior to wheat in terms of total yield and quality. Worldwide it is

currently grown on about 500 000 ha, and it is used mainly as forage and animal feed.

To some extent, the 6× triticale and 6× wheat are similar. Both contain the tetraploid wheat genome but diverge in their third genome, of *Secale cereale* RR in the former and *Aegilops squarrosa* DD in the latter. These two diploids spontaneously hybridize with the 4× wheats and occasionally spontaneous amphipolyploids may emerge. So, why did 6× wheats become a major cereal thousands of years ago, and 6× triticale only recently and by active human intervention? Perhaps one of the main reasons is that spontaneous 6× triticale produced high proportions of shrivelled seeds which were rejected for further sowing.

Taxonomically, triticale is an interesting case because it is perhaps the first economic plant to have been developed from intergeneric hybridization. Furthermore, 6× and 8× triticale have different genomic constitutions and obviously are two different biological entities. The varying numbers of rye chromosomes in some triticale lines, as a result of cytogenetic manipulation, have made the taxonomic problem even more confusing. The inconsistent taxonomic ranking is well reflected by the different botanical names attached to the wheat × rye amphiploids such as (*Triticum* × *Secale*), *Triticosecale*, *Triticale*, × *Triticale*, × *Triticosecale* (Baum, 1971).

Another purposely produced stable intergeneric crop is the lolium × fescue pasture plant. It was developed by chromosome doubling of the sterile intergeneric hybrids between diploid *Lolium* and tetraploid *Festuca* species (Smith, 1995).

#### 4.5 CONCLUSIONS

The term species is widely used by laymen and scientists, but there is no generally agreed definition of this term, and criteria for placing the boundaries between species. Each of the various definitions emphasizes different aspects of the species and have their merits and disadvantages. Many plant geneticists and breeders favor the biological species concept, which essentially regards a species as a reproductive community which forms one gene pool and is isolated from other gene pools. Other attributes are unique morphology and adaptation to specific habitat or habitats. By definition, the biological concept can be applied only to sexually reproducing organisms, but for these it is more convenient than other definitions.

Speciation is the process by which new species are formed. For biological species, speciation is the acquisition of reproductive barriers which prevent gene exchange between the new and the mother species. The acquisition of reproductive barriers can be gradual or abrupt. A gradual build-up of reproductive barriers requires temporary means of isolation,

such as geographical, ecological or pollination behavior, between the mother and the emerging species. Abrupt speciation is usually associated with change of chromosome number and chromosome architecture. Crop evolution contains many elements required for speciation, but partial reproductive isolation between cultivars of a given crop or between them and their wild progenitor are not regarded as sufficient for creation of new species. Speciation under domestication involved interspecific hybridization followed by chromosome doubling of the sterile interspecific hybrid. In this way, the bread wheat, *Triticum aestivum* was formed and probably several *Braasica* species, tobacco and the tetraploid cotton.

# Weeds and their evolution

That weeds are as old as agriculture is indicated by the finding of some obligatory weeds such as *Lolium temulentum* among cereal seeds from 3200 BC (McCreery, 1979). Weeds are undesirable companions of crop plants, reducing their yield and quality, and man's attitude toward them has always been negative and considerable efforts have been made to eradicate them, evidently with only relative success. The continuous engagement with weed control and shifts in agricultural practices have been powerful enough to create in weeds changes of evolutionary significance. Before elaborating more on these changes, let us look at some of the biological and ecological properties of weeds.

## 5.1 DEFINITIONS OF WEEDS

For a layman, weed and wild plants are the same, but any farmer or gardener knows the difference between them very well. They know the weeds on their land and the harm they cause. However, a general unequivocal definition of a weed is by no means simple. Various definitions have been proposed (for review see Harlan and de Wet, 1965), which can be arranged in two groups.

The first group consists of definitions emphasizing human attitudes to weeds, such as useless, obnoxious, a nuisance or undesirable. Because such definitions are subjective it is not uncommon to find that the same plant species may be regarded as a weed in some circumstances and desired one on others. The African kikuyu grass, *Pennisetum clandestinum*, grows in primary and disturbed habitats through many parts of tropical Africa. It was introduced to other parts of the world as lawn grass. Occasionally it proliferates to other cultivated lands where it is an obnoxious weed.

The second group is of definitions indicating weeds' biological attributes such as pioneers and successful competitors in disturbed habitats and in agricultural and urban ecosystems. In this sense they may include also ruderal plants thriving on waste land and dump heaps.

Harlan and de Wet (1965) combined these two types of definitions to propose that weeds are 'generally unwanted organisms that thrive in

habitats disturbed by man'. They suggested that some animals such as the house mouse, starling and the fruit fly, may also be regarded as weeds. Along the same line of thinking one could suggest the inclusion of pests and pathogens infecting crop plants as 'weeds' as well.

## 5.2 ORIGIN OF WEEDS

On geological and evolutionary scales, agriculture is recent and so are the habitats created by cultivation. What is then the origin of the flora associated with these new habitats? The origin of some weed species can be traced with no difficulty; with others such as *Lolium temulentum*, *Phalaris tuberosum* and *Convolvulus arvensis*, it is more problematic because they seem to grow only in cultivated fields. Weeds may be derived from three main sources: local flora; introduction from other areas; direct derivatives of crop plants, or the product of hybridization between crop plants and their wild progenitor.

### 5.2.1 Local flora

Weed species of many areas are members of the local flora. Some are restricted to disturbed habitats but others may grow in primary habitats, as with the tetraploid and hexaploid wild oats, *Avena barbata* and *A. sterilis* respectively. Both are members of the annual plant communities of the Mediterranean region and their populations vary from a few individual plants to more dense clumps, but they never form pure large stands. These two wild oats are also common weeds of the region and may form large, nearly pure, populations in cultivation, roadsides and edges of fields. It is not known whether their wide ecological amplitude is due to phenotypic plasticity, genetic differentiation or both.

### 5.2.2 Introduction by man

Many weed species are alien to the native floras and have been introduced by man. Weed migration can coincide with crop migration and the weeds arrive as undesired companions. A major part of the crop assemblage in the Ethiopian plateau is of Mediterranean origin and so are the weeds. Introduction of the Old World weeds into the Americas only began in post-Columbian times; some of them are ubiquitous and have even replaced some local species. The exact introduction time of some weeds may be traced accurately, as with the annual weed *Parthenium hysterophorus*. It arrived in India in the early 1960s as a contaminant in grain shipments donated by the USAID program, and rapidly spread over large areas in southern India. It is a particularly

problematic weed because it contains a toxin which irritates human skin. Its common name 'Aid' identifies it with the AID program.

Weed movement is greatly facilitated by introductions of new cultivars and crop plants, by trading and tourists. For many areas the current weed flora is composed of many introduced species either because they are cosmopolitan, pre-adapted to local conditions, or genetically flexible.

### 5.2.3 Derivatives and hybrids

Weeds may originate from crop plants in two ways: directly from the crop by back mutation and re-acquiring characteristics of the wild progenitor, and indirectly, through hybridization between the crop and its wild ancestor.

#### (a) Derivatives of crop plants

Certain crop plants may go wild in the form of a weed. Some wild hems in the Mediterranean region and elsewhere are most probably derived from cultivated forms. They grow exclusively in man-made habitats such as roadsides and edges of cultivation long after the hemp is no longer a crop. Morphologically, they can be distinguished from cultivated types by their small, easily disarticulating achenes. Some species presently regarded as weeds in Great Britain, such as chess, *Bromus secalinus* and fat hen, *Chenopodium album* formerly were cultivated there (Salisbury, 1961). Other weeds were used as medicinal plants or garden herbs.

Fatuoids in oats are weed forms believed to originate spontaneously from the cultigen (O'Mara, 1961). They are distinguished by spontaneous seed disarticulation, and geniculate, twisting awns. Cultivated oats have straight, non-twisting awns, or they lack them altogether, and they retain their seeds. Evidently, fatuoids can emerge from natural crosses between oat and the weed form *A. fatua*, but then they segregate for lemma color and germination behavior, some may stay dormant as seeds of *A. fatua* do, others germinate readily as cultivated oat. Some fatuoids, however, may emerge from selfed oat plants which have been homozygous for a few generations. They all have the lemma color of the cultivars in which they occur, germinate instantly when the appropriate conditions are provided, and segregation for these traits do not occur. The idea that fatuoids have emerged by mutation is dismissed on the grounds that seed disarticulation and awn formation are governed by two separate genes and simultaneous mutations in both loci are unlikely to occur. A more probable explanation is that fatuoids result from a small deletion on the chromosome bearing epistatic genes of the fatuoid gene. While cytologically it is difficult to detect such small deletions, some monosomic oat plants ( $2n=41$ ) are fatuoids.

Another weed-derived crop was indicated in sorghum in the USA (Harlan, 1976b). Wild and weed sorghum disperse their seeds by abscission, but in the USA another weed type appeared which disperses seeds in a different way. The inflorescence branches become thin and fragile a short distance below the basal spikelet of the raceme. Several spikelets may fall together or the rachis may fragment between them, but no abscission layer is formed. Genetically this mode of seed shattering is controlled by a single recessive gene.

Wild barley, *H. spontaneum* occurs as weed in regions bordering its natural distributional zone in the 'fertile crescent'. They are believed to be either relicts of much older distribution of *H. spontaneum*, or products of hybridization between the cultivated and wild barley. A few *H. spontaneum* populations have been observed south east of Marrakech, Morocco, on the hillsides of Djebel Siroua. They grow as weeds in barley fields in non-irrigated lands, but never in the surrounding natural habitat dominated by *Artemisia herba-alba*. A few more populations were observed near Azrou, about 400 km northeast of Djebel Siroua (Molina-Cano, Gomez-Campo and Conde, 1982). It is unlikely that the occurrence of these restricted few populations of *H. spontaneum* so far away from the main distributional range of wild barley have originated from hybridization with wild barley. The two possible explanations are that they have been introduced with seeds from areas where *H. spontaneum* grows naturally, but more likely that they are a result of back mutation in the tough rachis gene. Such mutants are likely to be as adapted to the cultivated field as the barley crop is, and maintain themselves by spontaneous reseeding before harvest. A similar situation probably occurs in pearl millet where the shibras, subsp. *seiberanum* occurs as an obligate weed in pearl millet fields. It differs from the crop only by having deciduous involucre (de Wet, 1995). These weed forms do not persist for more than one year after a cultivated field has been abandoned.

#### (b) Hybrids

Some weed forms of crops' wild progenitors are likely to be products of gene flow from the crop plant. The consequences of such gene flow, discussed in Chapter 4, are that the main effect of gene flow in such situations is on the wild plant population. Wider adaptation is perhaps the most readily introgressed character from the crop to its wild relative, enabling rapid expansion of the weed population and better adaptation to changing crop technology.

Introduction of cytoplasmic male sterility (CMS) in sugar beet seed production has increased the number of hybrid seeds between sugar beet and wild beet. Replacement of hand weeding by chemical weed control and diminution of hand roguing enabled these hybrid plants to bolt and distribute their seeds. The hybrid origin of wild beet in sugar

beet in western Europe has been proven by genetic studies (Hornsey and Arnold, 1979) and analyses of cpDNA and mtDNA (Boudry *et al.*, 1993).

The occurrence of brittle six-rowed barley in several locations in Israel, along roadsides and edges of cultivation where cultivated six-rowed barley was grown in the past (Chapter 2), is another indication of a crop-derived weedy form.

### 5.3 BIOLOGICAL CHARACTERISTICS OF WEEDS

What makes a plant a successful weed, when other plant species are not? There is no single trait which confers weediness, but a combination of several traits, some of which may be more important in one species than others. The following biological attributes seem to be common to most weeds:

1. Adaptation to a wide range of disturbed habitats
2. Germination pattern adapted to the prevailing agricultural practice
3. Rapid growth and phenotypic plasticity
4. High seed production, or other means of efficient reproduction
5. Effective dispersal
6. Resistance to weeding.

#### 5.3.1 Wide adaptation

Weeds are adapted to disturbed habitats. They grow successfully in cultivated land where other members of the local flora cannot survive. Weed species normally growing also in habitats free of man's interference are either restricted to niches disturbed by animals, or more temporarily, by fire, landslide or inundation which disturbed the native vegetation. Weeds are colonizing species, adapted to unstable habitats and can establish extensive populations in a relatively short time. Some species apparently have the potential of thriving in native as well as in disturbed niches. It is not known if this is due to ecological plasticity or if it is genetically determined; the latter is more probable.

#### 5.3.2 Germination peculiarities

Seeds of most crop plants have been selected to germinate instantly when the appropriate conditions are available. This capacity is usually limited to a number of years, after which the seeds lose their ability to germinate. Seeds of some weed species also share these attributes. Quick germination and rapid seedling establishment are crucial elements in later stages when fierce competition for light, minerals and water may occur.

Another germination strategy of weeds, as of wild plants growing in primary habitats, is distribution of germination in time. Seeds of various weed species may stay dormant for many years before germinating. In wild oat *Avena sterilis* the germination pattern enables both rapid expansion into open habitat by germination of about 50% of the seeds, and safeguard of the other half for future germination. The dispersal unit of this wild oat contains two seeds, sometimes more, the lower one germinates in the first year and the upper a year or two later. In some weed populations the two seeds germinate in the same year, a possible adaptation to disturbed habitats and a means for rapid establishment of massive stands in a short time.

#### 5.3.3 Rapid growth

The adverse effect of weeds is their competition for the same needs of the crop at the same place and the same time. The competition is for light, nutrients and water, and usually they are more successful in obtaining them. In the competition for light broad-leaf weeds have the advantage over narrow-leaf crop plants, many of these weeds are also taller than the crop plants and at maturity outstrip them.

Weeds usually have more extensive root systems compared with crop plants enabling them better access to nutrients and water. Per unit of dry matter the N P K content of weeds is usually greater than that of crop plants. Water use efficiency, as measured by dry matter produced by a unit of water, is similar in weeds and crop plants but the former have wider and deeper root systems to obtain it.

The intensive growth rate of weeds and competition with the crop plants for the same needs at the same time results in yield loss, reduction in quality and extra cost on weed control. The economic damage is proportionate to weed density and may be total in extreme cases. On a national and international scale losses due to weeds reach staggering

**Table 5.1** Total crop loss by crop groups for the United States

Group	BMP (\$ × 1,000)	No Herb (\$ × 1,000)
Field crops	3359671.39	16239790.84
Non-citrus fruits	201181.48	752446.10
Citrus fruits	118943.22	628186.98
Tree nuts	46541.75	106021.04
Vegetables	386418.19	1845905.85
U.S. total	\$4112756.03	\$19572350.81

BMP=Estimated loss with current practices;

No Herb=Best management practices, less herbicides

Source: Bridges, D.C. and Anderson, R.L. 1992. Crop loss due to weeds in the United States. Weed Sci. Soc. Amer. (Page 8) with permission

figures (Table 5.1). Reduced quality makes the crop less valuable and in some cases even renders it useless. Annual ryegrass, darnel, *Lolium temulentum* is a common weed in wheat fields in the Mediterranean region and western Europe where wheat is sown by broadcasting. It is harvested with the crop but cannot be separated by winnowing from wheat because the seeds have the same shape, color and density as wheat. When ground with wheat the flour becomes darker and eating the bread may be harmful. With the advent of drill sowing the darnel problem has diminished because the weed plants outside the wheat rows can be weeded out.

### 5.3.4 Propagation and dispersal

Characteristically, most weeds are extremely productive and a single plant may produce over a million seeds (Table 5.2). Some perennial weeds are propagated by seeds and also vegetatively by stolons as Bermuda grass, *Cynodon dactylon*; rhizomes, Johnson grass *Sorghum halepensis*; bulbs, wild garlic *Allium* subsp.; and tubers, nutsedge *Cyperus rotundus*. Dispersal by vegetative means is rather limited compared to seeds and is largely dependent upon man. *Cyperus rotundus* reproduces vegetatively and has worldwide distribution, probably with the aid of man. As with other non-cultivated plants, weeds are equipped with diverse means of natural seed dispersal. Mature seeds may be ejected from pods and capsules; other dispersal mechanisms are associated with the external morphology of the dispersal unit, enabling them to move by themselves with the aid of twisting awns, on animals due to bristles, prickles and thorns attaching to their hide and fur, or by wind with the aid of the parachute-like structure (pappus) attached to the seed.

**Table 5.2** Number of seeds produced per plant for several common weeds

Common name	Number of seeds per plant
Buckwheat, wild	11 900
Charlock	2700
Dock, curly	29 500
Kochia	14 600
Lambsquarters	72 450
Medic, black	2350
Mullein	223 200
Mustard, black	13 400
Plantain, broadleaf	36 150
Primrose, evening	118 500
Purslane	52 300
Stinkgrass	82 500
Wormwood	1 075 000

Adapted from: Stevens, O.A. 1932. Amer. J.Bot. 19:784-794.

Some weed species have developed dual seed dispersal strategies, such as wild rye, *Secale cereale* and *Phalaris paradoxa*, which are weeds in wheat fields. At maturity seeds of the upper part of the spike shed to the ground while those at the lower part persist, are threshed with the crop and disseminated in the next year with the wheat seeds.

## 5.4 WEED EVOLUTION

As a category weeds do not exist in nature. They are a by-product in agricultural and urban ecosystems, and their evolution has much in common with that of crop plants. The role of humans is central in weed evolution, though indirectly through agricultural practices.

Changes in the weed flora and the spectrum of weed species are associated with the introduction of new techniques and plant material. Mechanical deep tillage automatically eliminates weeds which cannot germinate from such depth. Similarly, improved seed cleaning drastically reduces the distribution of a number of weeds into new fields. Salisbury (1961) has listed a number of formerly serious weeds in Great Britain which presently are quite rare because of improved seed cleaning. Among others are corn cockle, *Agrostema githao*, blue cornflower, *Centaurea cyanus* and flixweed, *Descurania sophia*. Yet the main change of weed species spectrum is by introduction. Weed diffusion is parallel to crop diffusion and in a new territory some may become major pests. Elimination of major weeds by herbicides may encourage the expansion of others, previously considered of minor importance. It therefore seems that the history of the weed flora is a reflection of changes in agricultural practices and husbandry.

Weed evolution is not considered here as a history of the weed flora, but the genetic shift in existing weeds enabling better adaptation to their habitat and moderating the selection pressures of agricultural practices. Such evolution is evident in crop mimicry and lately in herbicide resistance.

### 5.4.1 Mimicry

Mimicry is presenting with a similar appearance and behavior, enabling the mimic to exploit the selective advantage of the model organism. Barrett (1983) distinguished two types of mimicry in crop-weed complexes: vegetative mimicry, in which similarity occurs during seedling and vegetative growth periods, presumably having evolved in response to weed control by hand weeding, or other implements directly operated by man; and seed mimicry, i.e. resemblance of the weed and crop seeds or fruits in appearance, weight and density.

## (a) Vegetative mimicry

Vegetative mimicry should not be confused with natural similarity between closely related species or between crop plants and their wild progenitors resulting from gene flow. Real mimicry is seen when a crop plant and its mimic are members of different genera or are congeneric but reproductively isolated. This is the case with *Camelina sativa*, a common weed in flax (Stebbins, 1950). *C. sativa* subsp. *linicola* grows exclusively in flax fields in Russia. By its leaf shape, the little branched, slender, long internodes stems, and fewer flowers on spreading branches, it comes closer to flax than any other *C. sativa* subspecies. Other flax weeds such as *Spergula maxima* and *Silena linicola* and some other flax weeds also have vegetative characteristics of flax, but whether these similarities are the product of mimetic processes is unclear. Vegetative mimicry of the flax weeds renders hand weeding almost impossible at the vegetative stage. Roguing at flowering time is usually impractical because it may cause the crop more harm than good.

The rice weed *Echinochloa crus-galli* is another example of vegetative mimicry. Two weed forms are recognized, var. *crus-galli* a weed within and outside rice fields, and var. *oryzicola* found almost exclusively in rice fields. The latter exhibit much greater morphological similarity with the crop. Fifteen quantitative morphological and growth characters of the crop and the two *E. crus-galli* forms were analysed by multivariate methods; the crop and var. *oryzicola* occupied similar overall positions while var. *crus-galli* was separated by a considerable distance (Barrett, 1983). Furthermore, innate seed dormancy is rather weak in var. *oryzicola* but usually much stronger in var. *crus-galli*. Because of vegetative mimicry, seedlings of var. *oryzicola* can not be identified during the transplanting operation or later during the growing period.

## (b) Seed mimicry

Seed mimicry involves characters associated with harvest, threshing and winnowing. Successful seed mimicry includes seed retention until harvest, seed release during threshing and seed shape and density similar to the crop plant. All these may pertain to fruits as well. Besides vegetative mimicry false flax, *C. sativa*, also displays seed mimicry. Its pods are indehiscent, the plants are harvested and threshed with the flax plants and because of similar seed size and density they cannot be separated from flax seeds. Mimicry in *C. sativa* was so successful that it became a minor oil crop in some parts of Europe and west Asia.

Weedy rye, *Secale cereale*, also presents seed mimicry. It contains several interfertile races occurring in west Asia, differing from one another mainly by the pattern of their seed dispersal: a brittle spike type, botanically known as *S. ancestrale*, a semi-brittle spike, *S. afghanicum* and

a tough spike type, *S. segetale*. The latter two are common weeds in wheat fields and cannot be separated from wheat by winnowing. As with *Camelina sativa*, the successful mimic rye became a crop in its own right, particularly on sandy and marginal soils.

Mimicry of barley by *Avena abyssinica* in Ethiopia is similar to wheat mimicry by rye in west Asia. *A. abyssinica* also has all the necessary attributes of a successful mimic: it does not disperse its seeds naturally but by threshing, the kernels are covered with husks as barley seeds are, and the seed size, shape and density are the same as barley and they can be used for the same purposes as barley. But unlike *Camelina sativa* and *Secale cereale*, *A. abyssinica* has not become an independent crop and it is still in a state of tolerated weed.

Seed mimicry was recorded in weedy *Vicia sativa* in lentil fields in Nepal, Russia and recently in the USA and Canada. *V. sativa* seeds are usually spherical, but in lentil fields a flattened-seed type has emerged. The resemblance is not only in shape, but in size as well and is comparable to that of the local lentil type: they are small in Nepal where small seeded lentil is grown, and larger in the USA and Canada where large seeded cultivars are predominant (Erskine, Smartt and Muehlbauer, 1993). Seed mimicry of lentil by *V. sativa* causes a serious weed problem because *V. sativa* seeds are bitter and cannot be used as human food. The contamination may reach such a degree that it reduces the value of the crop.

## 5.4.2 Genetics and evolution of mimicry

The key characters of mimetic species may be controlled by a single or multiple genes. The latter is more likely to occur in vegetative mimicry (Barrett, 1983), but in seed mimicry as well, particularly in traits of a quantitative nature. There are only a few reports on the genetics of seed mimicry, but they are nevertheless instructive. The lens shape of the mimetic *V. sativa* in lentil is controlled by a single recessive gene (Rowlands, 1959). Seed retention of *Avena abyssinica* is under the control of four (Jones, 1940) or two (Ladizinsky, 1975c) recessive genes.

The involvement of a few genes in the evolution of seed mimicry is therefore not much different from what is known on the genetic shift occurring during the emergence of domesticated crop plants. The evolution of mimetic genotypes in weed species is also a direct response to pressures of agriculture practices without any intentional encouragement by man. Evolution of mimicry in weedy species can be regarded as an undesirable parallel of plant domestication which evidently started after the crop was established enough to become a model. The evolution of domesticated-like characters in weed species reflects back on the role of unconscious selection in crop plants. They provide evidence that crop plants could emerge solely by unconscious selection.

## 5.4.3 Herbicide resistance in weeds

Introduction of chemical weed control is one of the most significant developments in agriculture during the last few decades. When properly applied, herbicides are the most effective means of weed control and have been accepted worldwide. However, the belief that with the advent of herbicides the weed problem would be solved, was soon proved wrong. Continuous application of the same herbicide, or herbicides with similar mode of action, on the same land, was followed by the emergence of biotypes resistant to these herbicides. Radosevich and Holt (1984) listed intraspecific differences in tolerance and resistance to herbicides in 136 crop plants and weed/herbicide combinations. LeBaron (1991) enumerated 107 herbicide-resistant weed biotypes that have evolved in various locations around the world including 40 broad-leaved and 17 grass weed species with biotypes resistant to atrazine herbicides, and 33 broad-leaved and 17 grass species with biotypes resistant to 14 other classes of herbicides. The list of herbicide resistance in weed species probably has grown since then but the general situation and trend are clear.

Another potential source of herbicide resistance in weeds is via gene flow from herbicide-resistant cultivars. Growing such cultivars is being proposed as a more elaborate strategy of weed control, allowing the use of herbicide to which the crop has been generally susceptible. The risk here is that the herbicide-resistant gene would be introgressed into a weedy form of the crop's wild progenitor, or other closely related wild species. The immediate risk is in areas where these wild species are native. Even if these herbicide resistant cultivars were not grown deliberately in sensitive areas, it would not be possible to eliminate the possibility that they would arrive as a commodity and would spread along road sides and around locations where they are being processed. For a more comprehensive discussion of this problem see Keeler, Turner and Bolick (1996).

Genetic studies of some of the herbicide-resistant biotypes, both in crop plants and weeds, have revealed that in most cases the resistance is governed by a single gene (Tables 5.3 and 5.4). While the dramatic increase and the rapid expansion of herbicide-resistant biotypes may come as a surprise and disappointment to many agriculturalists, they should have been expected by those who are familiar with the response of biological material to strong selection against such forces as chemical weed control. If there is any surprise in the establishment of herbicide-resistant biotypes it is that they have appeared relatively late after chemical weed control has been widely adopted.

Natural populations usually possess a great deal of diversity, partially of an adaptive nature and partially neutral. Mutations occurring in different genes at low frequency may immediately be wiped out by

Table 5.3 Mendelian inheritance of herbicide resistance in weed biotypes

Herbicide	Species	Plant material	Resistance test	Scoring	Number of genes	Ref.
Atrazine	<i>Abutilon theophrasti</i>	F <sub>1</sub> F <sub>2</sub> F <sub>3</sub>	1 ppm in hydroponics	Dead/alive + intermediate	1 semidominant	74
Chlortoluron	<i>Alopecurus myosuroides</i>	Bulk F <sub>1</sub>	Leaf fluorescence	Inhibition recovery	2 additive	77
Diclofop	<i>Lilium multiflorum</i>	F <sub>1</sub> F <sub>2</sub>	7.5 kg ha <sup>-1</sup> <i>in vitro</i> test	Dry weight and visual injury rating	1 semidominant	92
Fenaxoprop	<i>Avena sterilis</i>	F <sub>1</sub> F <sub>2</sub>	0.6 kg ha <sup>-1</sup> at 2-leaf stage	Visual injury rating	1 semidominant	94
Fluazifop	<i>Avena sterilis</i>	F <sub>2</sub>	0.55 kg ha <sup>-1</sup>	Visual injury rating	1 semidominant	94
Haloxifop	<i>Lolium rigidum</i>	F <sub>1</sub> F <sub>2</sub>	Up to 0.2 kg ha <sup>-1</sup>	Dead/alive	1 semidominant	93
Metsulfuron	<i>Lactuca serriola</i>	F <sub>1</sub> F <sub>2</sub> F <sub>3</sub>	0.5 ppm	Dead/alive + intermediate	1 semidominant	86
Paraquat	<i>Arctotheca calendula</i>	F <sub>1</sub> F <sub>2</sub> BC	0.8 kg ha <sup>-1</sup> at 5- to 6-leaf stage	Visual injury rating	1 semidominant	84
Paraquat	<i>Conyza philadelphicus</i>	F <sub>1</sub> F <sub>2</sub> BC	0.5 kg ha <sup>-1</sup> on seedlings	Dead/alive	1 dominant	79
Paraquat	<i>Conyza bonariensis</i>	F <sub>1</sub> F <sub>2</sub>	10 <sup>-5</sup> M at rosette stage or <i>in vitro</i> test	Dead/alive	1 dominant	80
Paraquat	<i>Erigeron canadensis</i>	F <sub>1</sub> F <sub>2</sub>	10 <sup>-5</sup> M at germination and at cotyledon stages	Dead/alive	1 dominant	81
Paraquat	<i>Hordeum glaucum</i>	F <sub>2</sub> F <sub>3</sub>	0.1 kg ha <sup>-1</sup> at tillering	Dead/alive - intermediate	1 semidominant	83
Paraquat	<i>Hordeum leporinum</i>	F <sub>1</sub> F <sub>2</sub>	0.2 kg ha <sup>-1</sup>	Visual injury rating	1 semidominant	84
Siduron	<i>Hozdeum jabatum</i>	F <sub>2</sub>	2.2 kg ha <sup>-1</sup> at germination	Radicle length	3 complimentary	75
Trifluralin	<i>Setaria viridis</i>	F <sub>2</sub>	0.6 ppm at germination	Radicle length	1 recessive	100

Source: Darmency, H. Genetics of herbicide resistance in weeds and crops, 276-277, in, *Herbicide Resistance in Plants*, Powles, S.B., Holtum, J.A.M., eds, Lewis Publishers, an imprint of CRC Press, Boca Raton, Florida, ©1994. With permission

Table 5.4 Mendelian inheritance of herbicide resistance in crops

Herbicide	Species	Plant	Resistance material	Scoring test	Number of genes	Ref.
Atrazine	<i>Zea mays</i>	F <sub>1</sub> F <sub>2</sub> BC	Recommended rate	Dead/alive	1 dominant	8
Barban	<i>Hordeum vulgare</i>	F <sub>2</sub> F <sub>3</sub>	0.8 kg ha <sup>-1</sup>	Leaf chlorosis or apical inhibition	1 recessive	101
Bensulfuron	<i>Oryza sativa</i>	F <sub>1</sub> F <sub>2</sub>	Germination on 10 <sup>-5</sup> M agar	Visual rating	1 or 2 recessive	103
Bentazon	<i>Capsicum annuum</i>	F <sub>1</sub> F <sub>2</sub> BC	4.5 kg ha <sup>-1</sup> on 25-day-old seedling	Visual rating	1 dominant	104
Butachlor	<i>Oryza sativa</i>	F <sub>1</sub> F <sub>2</sub>	30 kg ha <sup>-1</sup> 3- to 4-leaf seedling	Visual rating	1 recessive	105
Chlortoluron	<i>Triticum aestivum</i>	Substitution lines F <sub>1</sub> F <sub>2</sub>	4.8 kg ha <sup>-1</sup>	Visual rating	1 dominant	55
2,4-D	<i>Triticum aestivum</i>	F <sub>1</sub> F <sub>2</sub>	0.6 kg ha <sup>-1</sup> on 45-day-old plant	Dead/alive	1 dominant	106
Diclotop	<i>Avena sativa</i>	F <sub>2</sub> BC	0.7 kg ha <sup>-1</sup> at 3-leaf stage	Visual rating	2 semidominant	107
Difenzoquat	<i>Triticum aestivum</i>	F <sub>2</sub> monosomic lines, F <sub>4</sub>	1.7 kg ha <sup>-1</sup> 3- to 4-leaf stage	Visual rating	1 dominant	56, 108
Metoxuron	<i>Triticum aestivum</i>	F <sub>3</sub> F <sub>4</sub> F <sub>5</sub>	13.5 kg ha <sup>-1</sup> at 2-leaf stage	Visual rating	1 recessive	109
Metribuzin	<i>Glycine max</i>	F <sub>1</sub> F <sub>2</sub> BC	0.12 ppm in hydroponics	Dead/alive	1 dominant	110
Metribuzin	<i>Lycopersicon esculentum</i>	Diallel (F <sub>1</sub> ) F <sub>2</sub> BC	0.25 ppm in hydroponics	Dead/alive height and weight	1 recessive	102
Metribuzin	<i>Solanum tuberosum</i>	F <sub>1</sub> F <sub>2</sub> BC	0.12 ppm in hydroponics	Visual rating	1 dominant	111
Oxyfluorfen	<i>Oryza sativa</i>	F <sub>1</sub> F <sub>2</sub>	2 kg ha <sup>-1</sup> on 10-day-old seedling	Visual rating	1 recessive	103
Trifluralin	<i>Cucurbita moschata</i>	F <sub>1</sub> F <sub>2</sub> BC	1.1 kg ha <sup>-1</sup> soil incorporated	Visual rating	1 dominant and 1 epistatic	112

Source: Darmency, H. Genetics of herbicide resistance in weeds and crops, 276-277, in: *Herbicide Resistance in Plants*, Powles, S.B., Holtum, J.A.M., eds. Lewis Publishers, an imprint of CRC Press, Boca Raton, Florida, ©1994. With permission.

natural selection or survive a few generations. An ill-adapted mutant under a certain selection regime may become highly adaptive when circumstances are changed and a new selection pressure is applied. Usually, the stronger the selection, the faster the new mutant becomes established. The evolution of herbicide resistance in weed and crop plants is therefore not an exception to this general scenario. Introducing chemical weed control would expose resistant or tolerant genotypes if they exist. A few survivors of the herbicide treatment may be regarded as escapes, but equally are likely to be resistant genotypes. When herbicide-resistant genotypes are adaptively inferior and are lacking in the weed population prior to the herbicide treatment, they may emerge by mutation following continuous use of the same herbicide for a sufficient period of time.

The dramatic evolution of herbicide resistance in weed populations during the last few decades is, however, not different from other incidences of response to effective human selection. The uniqueness, perhaps, is the scope of the selection and the rapid response by the different weed species, which is parallel to insecticide resistance of various pests. Recognizing the origin and evolution of herbicide resistance is not only of theoretical importance but it is also instrumental in formulating steps to curb and impede the distribution of herbicide-resistant genotypes and the evolution of new ones. A reasonable approach is the utilization of herbicides with different modes of action and target in a rotation which would considerably slow down, if not preclude, the establishment of herbicide-resistant genotypes. Where monoculture has been established following the use of herbicides, seed rotation may be another way in which build-up of herbicide resistance may be controlled. As in natural selection, where dominance of a single genotype is avoided by the existence of diverse selection pressures, diversifying the means of weed control is the only appropriate and effective measure against the establishment of herbicide resistance. Unfortunately, the rapid development of herbicide-tolerant cultivars by transgenesis makes the situation even worse. A number of crops now contain ROUND UP tolerant cultivars; for these, treatment with this herbicide is a simple and cheap means of weed control with no residual effect on soil. Growing the herbicide-tolerant cultivars as monoculture or in rotation with similar cultivars of other crops, creates strong selection pressures for ROUND UP resistant weeds, which sooner or later will appear. The trend of growing herbicide-resistant cultivars may be even more hazardous as time passes.

## 5.5 CONCLUSIONS

Weeds are as old as agriculture and are undesirable companions of crop plants. They are adapted to disturbed habitats in agricultural and urban

ecosystems. Weed species have in common a number of biological characteristics which make them so successful in these habitats. The history of the weed flora reflects the changes of agriculture practice and management. Many weed species which were a major problem in traditional farming have vanished in modern agriculture, but have been replaced by others which can cope with the new agricultural practices.

Evolution of weeds is expressed by genetic changes making them more successful weeds. Crop mimicry has been employed successfully by a number of weeds. Vegetative mimicry protected them from hand weeding, and seed mimicry from their separation from the crop in threshing. Some of these weeds have been so successful that man adopted them as secondary crops. Herbicide resistance is a recent development in weed evolution and is becoming an acute problem of modern agriculture. The growing number of weed biotypes tolerant to herbicides with different modes of action is directly related to the universal chemical weed control and utilization of the same herbicide for too long a time in the same field. With the growing demand for food, chemical weed control will continue and so will the evolution of more herbicide-resistant biotypes in weed populations.

## Evolution of selected crop plants

In the previous chapters elements operating in the evolution of various crop plants have been examined. This chapter deals with the evolution of 12 crops. The various crops have not been selected according to their economic importance, nor do they represent systematically crop types as attempted by Smartt and Simmonds (1995). The main reason for choosing them is that they exemplify different aspects of crop domestication and evolution. Among the selected crops are seed crops, vegetables, fruit and nut trees, and forages, and they represent annuals and perennials, selfers and outcrossers, diploids and polyploids, those having wild progenitors and others whose progenitors have not yet been identified, crops with and without a secondary gene pool, and crops having and lacking weedy forms. The evolution of other crop plants may bear some similarity to those discussed in this chapter, but it is not the intention to offer them as models of crop domestication and evolution as attempted by Raamsdonk (1995), because the author is in favor of Harlan's (1976b) idea that each crop has its own peculiarities and evolved under unique circumstances. The 12 crops are broad bean, chickpea, barley, maize, oat, lettuce, carrot, potatoes, grapes, banana, almond and vetch.

### 6.1 FABIA BEAN, *VICIA FABIA* (LEGUMINOSAE-PAPILIONIDEAE)

The faba bean, also known as broad bean or horse bean, is an important legume in the Mediterranean regions, the north temperate zone and in high elevations of the sub-tropical region. It is also extensively grown in China. The faba bean is grown mainly for its protein-rich seeds but also as a fodder plant.

Intraspecific classification of the faba bean is based primarily on seed characteristics such as size and shape. Moratova (1931) recognized two subspecies in *V. faba*: subsp. *faba* with three varieties (*faba*, *equina* and *minor*) and subsp. *paucijuga*. Hanelt (1972) also recognized two