

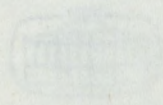
A. BELEA
**INTERSPECIFIC
AND
INTERGENERIC
CROSSES IN
CULTIVATED
PLANTS**

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BUDAPEST

**Interspecific and Intergeneric Crosses
in Cultivated Plants**

A. Belea

Associate Professor
of the Department of Botany
University of Debrecen
Hungary
and
Researcher
Hungary



Akademi Kiadó, Budapest 19

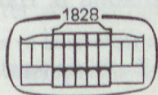
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Interspecific and Intergeneric Crosses in Cultivated Plants

A. Belea

Agricultural Research Institute
of the Hungarian Academy of Sciences,
Martonvásár, Hungary
and
Agricultural University,
Gödöllő, Hungary



Akadémiai Kiadó, Budapest 1992

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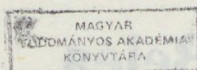


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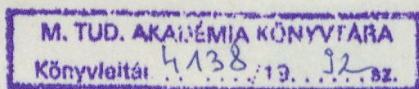
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Preface

No independent work on interspecific and intergeneric crosses in plants has previously appeared on the Hungarian book market. In other countries, too, the subject has only generally been dealt with in certain chapters of books on genetics or practical plant breeding, and even these chapters only touch on generalities, or are restricted to interspecific crosses in certain genera or in the plants of a single geographical region. Much more has been written on the subject in papers published in scientific journals.

The possibility of crossing plant species which are only distantly related to each other, the genetic, biochemical, etc. obstacles which hinder or prevent the production of plant hybrids, and the methods which hold out the promise of success, have always had a fascination for the public, and this is truer than ever today.

It is thus worth providing the reader with a brief summary of the major theoretical and practical results so far achieved in plant hybridisation. Due to the enormous amount of material available, it would be quite impossible to include everything in a book of this size. The aim is rather to illustrate the major aspects of the subject, so only the most characteristic problems arising in cultivated plants belonging to the group of sexually propagating plants (cereals, industrial crops, vegetables, berries and flowers) will be discussed.

The book is in the nature of a manual, so basic terms are only explained in exceptional cases. It is assumed that the reader is already acquainted with the subject at the university level. The main aim of the book is to assist the work of researchers, but it is hoped that specialists working in this field will find that the survey presented here will not only satisfy their interest in the subject, but also broaden their range of vision and perhaps provide them with information which will be of practical use to them.

A detailed discussion of a single topic (interspecific and intergeneric hybridisation) is presented on examples taken from a number of plants. The vast amount of information accumulated and the limited space have forced the author to be selective. The choice of examples is necessarily arbitrary, but the author has endeavoured to give equal weight to all aspects of the problem. The fact that certain sections are discussed in more detail, while others are dealt with more superficially can be attributed partly to the importance of the information in question for plant breeders and producers, and partly to the level of knowledge currently achieved: very little is still known on a number of extremely

important questions. If there is deemed to be a lack of proportion over and beyond this, it must be put down to the partiality of the author, who is himself a researcher. It is thus hardly surprising if the discussion of aspects connected with his own research field (primarily wheat genetics) is in some cases more exhaustive and complex than that of other plants.

Any suggestions or observations which might contribute to improvements in later editions of the book will be received by the author with grateful thanks.

1. Introduction

Exactly where or when man first began to cultivate and domesticate plants is not known. It is certain, however, that one of the earliest homes of civilised man was in the lower basin of the Rivers Tigris and Euphrates in South Western Asia, the site of the traditional Garden of Eden.

The fact that dates were cultivated in Mesopotamia in ancient times is demonstrated by Babylonian and Assyrian monuments and was also recorded by several early Greek historians; the monuments not only show that dates were cultivated, but also give a clear illustration of the process of hand pollination.

It was thus recognised, from very early times, that date trees were of two kinds, sterile and fruit-bearing, in other words, "male" and "female", and that a substance produced by a sterile "male" tree was needed in order to ensure that a fertile "female" tree would bear fruit.

In fact, seedlings originating from any given variety of any plant show a very wide range of variation, and it is said that the original parent type seldom re-appears among the progeny. This diversity of type among seedling plants has led to the establishment of a great number of varieties in the course of cultivation.

ROBERTS (1965) mentions that CAMERARIUS (1665–1721) appears to have been the first botanist to discover, by actual experimentation, that pollen is indispensable to fertilisation, and that the pollen-producing flowers or plants are therefore male and the seed-bearing plants female. The experiments were conducted on spinach and hemp, both of which are dioecious, and on Indian corn or maize. Camerarius was likewise the first investigator to discover, two hundred years after the introduction of maize into Europe, the fact that on removing the staminate inflorescence of an isolated plant the seeds remained unfertilised.

Nevertheless, more than fifty years passed before Camerarius' investigations on sex in plants received substantial recognition, and before the first recorded instance of an actual experiment in hybridisation.

It is a well-known fact that in the plant kingdom intervarietal crosses within the species are one of the most widespread and successful methods by which breeders produce new varieties.

The efficiency of plant breeding depends to a great extent on the choice of method and on the precision with which the method is applied. Even more important is the correct choice of initial breeding stock. Breeding may be based

on a local variety, i.e. a natural population which owes its development to the work of breeders. In this case the breeder first selects suitable basic stock for his purpose from the natural population. If the natural population (the local variety) is characterised by the desired economic, ecological, biological, etc. traits, it is unnecessary to carry out crossing or any other technique designed to increase the variability of the plant properties. If, on the other hand, traits required due to economic or other considerations are absent, variability must be artificially increased. In this case the breeder will analyse various varieties and weigh up the advantages of other possibilities before deciding whether to employ crossing or some other method (mutation, polyploidy, other genetic techniques) to produce a new population from which selection can be made. The greater the variability and heterogeneity of the initial stock, the more successful breeding is likely to be. Before making combinations the plant breeder should take great care to select individual plants which seem best adapted to his purpose, as in this way many years of experiment and much needless expense will be avoided. The differences in the individuals which the plant breeder has to work on are sometimes very slight indeed.

If, for any plant species, no varieties are known to contain the desired properties, intervarietal crosses are unlikely to lead to any resounding success. In such cases other species belonging to the same genus or even species belonging to other genera are used as crossing partners. Using this method it is possible, for example, to transfer the sand tolerance of rye (*Secale*), the disease resistance and high protein content of *Aegilops* and wheat-grass (*Agropyron*) and their ability to grow in any type of soil, the non-race-specific disease resistance of certain wheat species (*Triticum timopheevii*, *T. zhukovskyi*, *T. monococcum*, ssp. *dicoccoides*), the high protein and lysine content of ssp. *dicoccoides*, conv. *durum*, ssp. *carthlicum* and *T. zhukovskyi*, the good milling percentage of *T. aestivum* ssp. *sphaerococcum* and the large number of grains per ear of *T. turgidum* into cultivated wheat. In a similar manner, *Brassica* species resistant to various diseases (e.g. *Plasmodiophora brassicae*), potato (*Solanum*) varieties resistant to the Y virus and leaf-roll, cotton (*Gossypium*) varieties resistant to *Verticillium* wilt and tomato varieties tolerant of salt, an extremely important property under desert conditions, and resistant to various diseases (tomato leaf curl virus = TLCV, *Phytophthora infestans*, *Verticillium dahliae*, *Fusarium oxysporum*, etc.) can best be produced by means of interspecific, or in some cases intergeneric crossing. In this way the variability of the basic breeding stock can be broadened enormously.

In addition to its practical importance, work on interspecific and intergeneric crosses in plants also bears extremely great theoretical significance. Among other things it greatly helps in clarifying the hybridisability of various plant species and genera, the extent to which they are mutually fertile, etc. It also advances knowledge on the origin, evolution, development and degree of relationship of the species.

Hybridisation does not usually play a role in evolution alone, but in combination with selection, polyploidy, micromutation or apomixis. A stable population

of the fertile progeny of a hybrid may turn into a new species under conditions of reproductive isolation (GRANT, 1971). A substantial bulk of information is available on the natural and artificial hybridisation of numerous plants (particularly the *Gramineae*) and detailed studies have been made on their cytology.

The possibility that hybridisation might play an important role in evolution was first expounded by LORSY (1916), whose principal contribution was the demonstration of complex, rich segregation in advanced generation hybrids. Although other botanists of the early twentieth century (e.g. JEFFREY, 1915) also assigned a dominant role to hybridisation, most were reluctant to acknowledge more than the occasional occurrence of hybrids. The minor role accorded to hybrids was even more vividly expressed by zoologists, especially since animal hybrids were recorded much less frequently than plant hybrids.

Hybridisation may be an important evolutionary phenomenon if accompanied by the selective incorporation of genes from the non-recurrent population system (introgression) or by the stabilisation of hybrid derivatives with or without polyploidy, or if population systems diverge in areas of contact to avoid hybridisation and the attendant loss of gametes. A prerequisite for gene exchange or stabilisation is the production of vigorous, partially fertile F_1 and advanced generation hybrids. To the best of our current knowledge, the only way to produce new synthetic species is to employ interspecific crossing.

The work of interspecific and intergeneric crossing has its roots in the methods and results of a number of sciences. These connections and interactions with various branches of science are depicted in Fig. 1. In this field, as is so often the

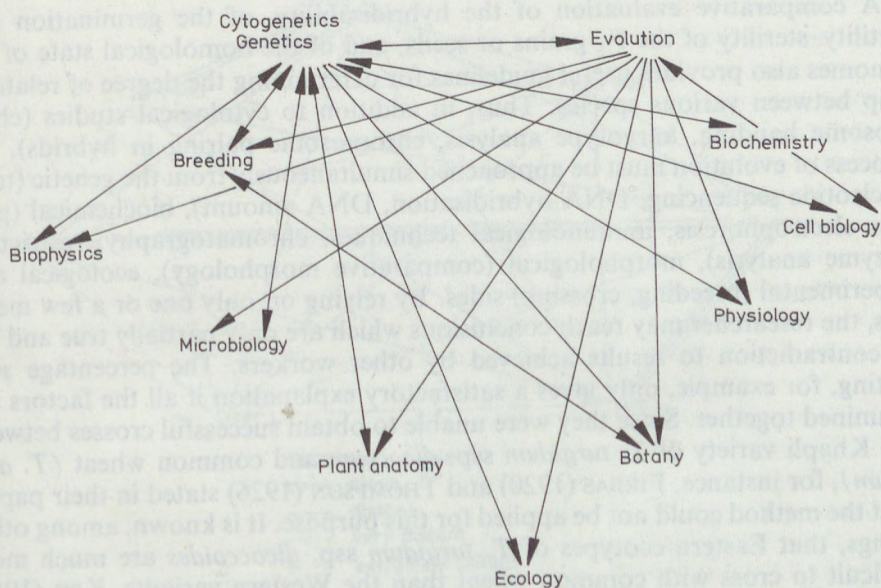


Fig. 1. Mutual relations between the major branches of science used in interspecific and intergeneric crosses in plants

case, it is only possible to achieve outstanding results and solve the practical and theoretical problems arising in the course of the work by jointly applying the results achieved and the methods elaborated in many different branches of science.

* * *

McCLUNG-NAVASHIN (1938) were the first to appreciate the significance of cytological results in evolution and plant classification. At their suggestion, work began on the comparison of the genomes of related species using cytological techniques. The karyotypic analysis of the chromosomes of various plant species offers an enormous amount of valuable data for the pinpointing of relationships. In recent years the heterochromatic staining technique (Giemsa C-band technique) elaborated for the identification of plant chromosomes has made it possible to draw even more reliable conclusions on the evolution of species (HADLACZKY-BELEA, 1975; BELEA, 1975). It has also been demonstrated that the individuals in wild populations are generally cytologically and genetically heterogeneous. The genes can often be put into various orders on the basis of changes in the chromosome segments. The chromosomes may alter spontaneously after chromosome fractures due to changes occurring in the gene order. This contributes to the operation of the isolation mechanism, which would appear to be associated with the evolution of plant species. The examination of chromosomal organisation and karyotypes in individuals, species and genera thus provides confirmation of the role of the chromosomal mechanism in evolution.

A comparative evaluation of the hybridisability, of the germination and fertility—sterility of the F_1 grains or seeds, and of the homological state of the genomes also provides useful guidelines for determining the degree of relationship between various species. Thus, in addition to cytological studies (chromosome banding, karyotype analysis, chromosome pairing in hybrids), the process of evolution must be approached simultaneously from the genetic (total nucleotide sequencing, DNA hybridisation, DNA amount), biochemical (protein electrophoresis, immunological techniques, chromatography, restriction enzyme analysis), morphological (comparative morphology), ecological and experimental (breeding, crossing) sides. By relying on only one or a few methods, the researcher may reach conclusions which are only partially true and are in contradiction to results achieved by other workers. The percentage seed setting, for example, only gives a satisfactory explanation if all the factors are examined together. Since they were unable to obtain successful crosses between the Khapli variety of *T. turgidum* ssp. *dicoccum* and common wheat (*T. aestivum*), for instance, FIRBAS (1920) and THOMPSON (1926) stated in their papers that the method could not be applied for this purpose. It is known, among other things, that Eastern ecotypes of *T. turgidum* ssp. *dicoccoides* are much more difficult to cross with common wheat than the Western variants. KISS (1955) reported that the *T. aestivum* wheat varieties which gave the best seed setting with rye were impossible to cross with other wheat species. FALK-KASHA (1981),

on the other hand, found that the wheat varieties which could be most easily crossed with *Hordeum bulbosum* were those which gave a relatively good seed setting with rye (see below).

The question of how reliable the seed setting percentage is as an indication of the degree of relationship also arises in connection with the use of biotypes with good combining ability selected from individual varieties (to the best of our knowledge FIRBAS was the first to draw the attention of researchers to this problem in 1920).

In the 90s of the last century, MACFARLANE (1890) published a number of papers based on a histological study of the characters of hybrids and their parents, which did much to throw light on the ultimate character of the hybrid condition in the F_1 generation. As the result of these histological investigations, MacFarlane was able to state a much more exact point of view regarding the structural characters of hybrids than most of his contemporaries, a view for which few data then existed, and in which investigations do not seem to have been continued until the post-Mendelian work of DARBISHIRE (1908) on the structure of the starch grains in pea crosses.

Biosynthetic processes in the development of plant hybrids are poorly understood. Genetic tumours are produced in hybrids belonging to several genera. In *Nicotiana*, tumour formation is associated with the presence of excessive amounts of auxins. The biosynthesis of secondary products may be disrupted, leading to the accumulation of precursors or the production of novel com-

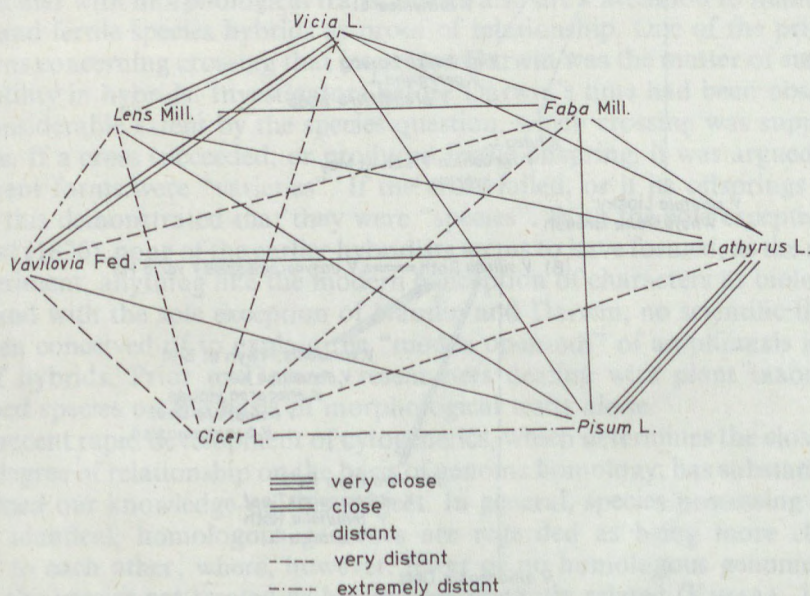


Fig. 2. Relationships between genera belonging to the *Viciae* tribe as demonstrated by the immunochemical analysis of the seed proteins of various species (KONAREV et al., 1983)

pounds (WILLIAMS-YOUNG, 1974). The molecular approach to the study of hybrids extends to chromosomes, where studies on pairing relationships are now concentrated on the level of unique DNA divergence and the amount and divergence of redundant DNA (NARAYAN-REES, 1977), and on ribosomal-DNA constancy and nuclear organiser expression (BICUDO-RICHARDSON, 1977). If the genomes of F_1 hybrids have antagonistic or incompatible regulatory systems, evidence of this should be forthcoming from physiological as well as biochemical studies. Unfortunately, little attention has been given to the tissue, organ or whole-organism physiology of hybrids.

The ever wider use of polyacrylamide gel electrophoresis (PAGE) and isoelectric focussing (IEFPG) is also of great assistance in research on evolution, providing confirmation of results achieved with other (e.g. cytogenetic) methods (FEJÉR-BELEA, 1978a).

When studying the seed proteins of genera belonging to the *Vicieae* tribe using immunochemical methods, KONAREV and co-workers (1983) found that the

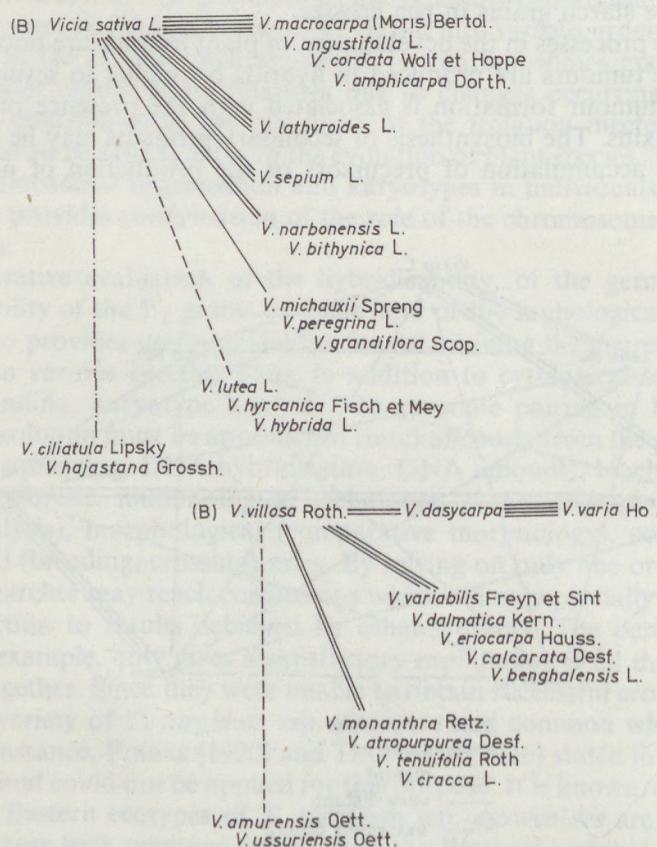


Fig. 3. Relationships between *Vicia sativa* and *V. villosa* and other *Vicia* species as demonstrated by the immunochemical analysis of seed proteins (KONAREV et al., 1983)

differences in the globulin component enabled extremely reliable conclusions to be drawn on the origin of plant species. Similarly, a comparative analysis of the albumin antigens in the protein also gave an indication of degrees of relationship. It was discovered, for example, that the degree of relationship between the genera *Lens* and *Vicia*, *Vavilovia* and *Vicia* and *Vavilovia* and *Lathyrus*, and especially between *Pisum* and *Lathyrus*, was substantially closer than that between *Vicia* and *Faba*, *Faba* and *Lathyrus*, *Vavilovia* and *Lens*, *Cicer* and *Vicia*, *Faba* and *Vavilovia*, and *Cicer* and *Faba* (Fig. 2).

Considerable differences in this respect are also found between the various species of *Vicia*. *V. sativa*, for instance, is in extremely close relationship with *V. macrocarpa*, *V. angustifolia*, *V. cordata* and *V. amphicarpa*. The relationship between *V. sativa* (vetch), *V. lathyroides* and *V. sepium* is somewhat more distant, while that between *V. lutea* and *V. ciliatula* is even more distant (Fig. 3).

1.1 The concepts: species, genus and hybrid

Before turning to a detailed discussion of interspecific and intergeneric crossing, a slight digression is perhaps necessary to clarify what is meant by the terms species, genus and hybrid.

The concepts of species and genus are outlined by descriptive taxonomy. DARWIN (1859), too, dealt with the distinguishing traits of certain plant species, in particular with morphological traits, but he also drew attention to numerous sterile and fertile species hybrids as proof of relationship. One of the primary questions concerning crossing that interested Darwin was the matter of sterility and fertility in hybrids. Investigators before Darwin's time had been obsessed to a considerable extent by the species question, which crossing was supposed to solve. If a cross succeeded, or produced fertile offspring, it was argued that the parent forms were "varieties". If the cross failed, or if its offsprings were sterile, this demonstrated that they were "species". With the sole exception of SAGERET (1826), none of the earlier hybridists seems to have formed, as the result of experiment, anything like the modern conception of characters as biological units, and with the sole exception of Naudin and Darwin, no scientific theory was even conceived of to explain the "modus operandi" of amphimixis in the case of hybrids. Prior to Darwin, researchers dealing with plant taxonomy described species on the basis of morphological traits alone.

The recent rapid development of cytogenetics, which determines the closeness of the degree of relationship on the basis of genome homology, has substantially broadened our knowledge on this subject. In general, species possessing completely identical, homologous genomes are regarded as being more closely related to each other; where, however, fewer or no homologous genomes are found, the species are treated as being more distantly related (KIHARA, 1924). It has also been proved that species determinations which are still uncertain can be decided more reliably with the aid of interspecific crossing.

Taxonomical and cytogenetic classifications generally coincide. The varieties of a given species usually have identical genomes, though in some cases varieties belonging to the same species may contain different (non-homologous) genomes (e.g. *T. turgidum* ssp. *dicoccoides* var. *nudiforme*). It is even known for the chromosome number to differ within a single species (e.g. *Agropyron intermedium*, *Agr. smithi*, *Agr. repens*, *Elymus condensatus*, etc.).

For the most part, earlier plant hybridisers made a distinction between "hybrids", occurring between "species", and "crosses", occurring between "varieties". Mendel discards this terminology, recognising that the distinction is one of degree, not of kind, a distinction essentially artificial when closely applied.

The fundamental difference between Mendel's hybridisation experiments and all others stands out most clearly in the following statement: "If two plants which differ constantly in one or several characters be crossed, numerous experiments have demonstrated that the common characters are transmitted unchanged to the hybrids and their progeny; but each pair of differentiating characters, on the other hand, unites in the hybrid to form a new character, which in the progeny hybrid is usually variable. The object of the experiment was to observe these variations in the case of each pair of differentiating characters, and to deduce the law according to which they appear in the successive generations. The experiment resolves itself therefore into just as many separate experiments as there are constantly differentiating characters present in the experimental plants." (MENDEL, 1866–1870).

On the basis of a biosystematic classification, OEHLER (1956) distinguishes ecotypes, ecospecies, coenospecies and comparia based on the hybridisability of the species, the sterility–fertility of the species hybrids and an analysis of anomalies arising in reductional cell division.

Nowadays, plant anatomical, genetic, biochemical, cell biological, ecological, etc. analyses are also employed to assist species determinations. In this way the various species can be distinguished from each other with greater accuracy. Nevertheless, it still happens that certain varieties are classified in different species, or completely different types are regarded as the same species because of a failure to carry out examinations on seed setting, germination, the fertility of the first generation, the inheritance of major economic properties and morphological traits, and to make use of methods elaborated in other branches of science. Experience shows that such errors can be eliminated by a thorough and circumspect analysis of the interspecific hybrids and their parent lines.

In 1863, GODRON reported a series of observations on the fecundity of hybrids. He investigated the question of whether this fecundity, in succeeding generations, bore any relation to the ease with which the original hybridisation was effected. From experiments with *Verbascum* hybrids he came to the conclusion that the fertility of hybrids does not always have any relation to the ease with which the cross is effected in the first instance.

Godron concludes, in general, that crosses between two races or varieties of the same species are characterised by absolute fertility, that the sterility of simple hybrids is proof that they come from distinct species, and that crossing between

two species of different "genera" is impossible. At the present time, of course, no special importance is necessarily attached in crossing to the precise systematic position of the organisms it is intended to cross. They may be different "varieties", or different "species", or even belong to different so-called "genera". Attention is necessarily directed primarily to the nature of the characters it is desired to involve in the cross, the behaviour of which it is sought to investigate.

Godron remarks that similar observations have been made by Lecoq in the fertile hybrids of *Mirabilis*, by Naudin in the fertile hybrids of *Nicotiana*, and by several authors in *Primula*, and in *Petunia violacea* $\times$ *P. nyctaginaeflora*.

During the genetic analysis of various species LAMPRECHT (1948) reached the conclusion that, irrespective of the morphological traits, any "varieties" which contained one or more "interspecific genes" should be classified as different species. Without a reduction in the fertility of the hybrid progeny, the characters of these "varieties" cannot be combined in a single progeny by means of crossing. If, on the other hand, the characters of the "varieties" crossed can be combined in a single progeny without any loss of fertility, the varieties in question belong to the same species.

In biochemistry, attempts are now being made to correlate the degree of relationship between various species with the immunological behaviour or amino acid composition of proteins with identical functions.

According to KONAREV (1975), a species is the sum total of generations originating from a common ancestor, which have become segregated from the rest of the living world during the struggle for existence. Among the living organisms there are series of similar forms which are distinct from other series. It was on this fact that Linnaeus based the scientific concept of species, introducing a binominal nomenclature to designate the species and equating the concept of logical species with that of natural species. To Darwin's mind the species was a historical phenomenon, gaining ground after its formation until it reached the full height of its development, later declining as circumstances changed and new, more virile rivals appeared, until it finally became extinct.

It will perhaps be obvious from the above that there is still no generally accepted definition of species. One reason for this is that, despite its constancy, the species nevertheless changes to a certain extent, so the term is somewhat dialectical. The traits which served for the identification of species and were previously considered to be constant, have not only increased in number as biology developed, but have also proved to be variable. Later, emphasis moved to the application of results obtained in reproduction physiology, since in the animal kingdom even related species do not always produce fertile progeny. When defining botanical species, the restriction that fertile hybrid progeny can only be produced by individuals belonging to the same species is not accepted.

Since species are only relatively stable and are in fact continuously changing due to their disintegration into new species or their extinction, they can even be regarded as periods or phases in the process of evolution. It would thus seem that species cannot be defined as a category; at most a specific form of existence can be identified with the help of characteristic traits. The species can be

considered as a biological organism, the essence of which is most clearly visible in its relationship to other, similar types of categories. The *concrete* representative of any species is the population and, vice versa, every population represents a species.

Criteria which would facilitate the selection of the traits providing the best definition of the essence of a species have not yet been elaborated. In practice, however, some form of criteria is needed if living organisms are to be taxonomically classified.

Due to the effect of differing geographical and climatic factors, different gene complexes may accumulate in various populations of the same species. The effect of environmental changes on the origin of species can be best understood if consideration is given to the enormous length of the geohistorical periods and to the climatic and geographical changes.

The role of ecological isolation is of great importance in the origin of species because it is the basis of external isolation mechanisms without which races developing in geographically different situations could not rise to the subspecies or species level. Within the sexually reproducing species, segregation is generally allopatric in nature, i.e. it takes place in different parts of the geographical territory of the species. Due to the isolation factors (e.g. great distances, mountain ranges, waters, etc.) the obscuring effect of crossing cannot be manifested, so the gene systems of segregated populations come to differ from each other. Once this biological isolation has taken place, the separate populations can live side by side on the same area. Various mechanisms promote the occurrence of biological isolation. In the case of plants the difference may be in the structure of the flowers. It frequently happens that certain insect species are incapable of pollinating the flowers while other species are able to do so. In some plant species, for instance, the tubes formed by alien pollen grow too slowly on the stigma or completely cease to develop. Another frequent problem is that after fertilisation has taken place, defence mechanisms come into operation, as a consequence of which the hybrids are sterile, or stop developing at some stage due to some lethal effect. In some species, however, this defence mechanism fails to develop. Basically, there are some differences that prevent the formation of hybrid zygotes, and some that reduce the viability and fertility of the hybrids. Isolating mechanisms per se should not be viewed as adaptations, for they are not properties of single populations or species. In effect, isolating mechanisms reside in the interface between populations and are a function of the interface. They result from incongruities in the adaptive "surfaces" of populations that happen to be paired in nature or by the evolutionist. In the hybrids obtained when crossing these species, there is an enormous range of variability due to the segregation of complicated polygenic systems. Segregation may be so extensive that the introgression of the gene complexes of the species is completely overthrown and the progeny is not able to adjust to the changed conditions. This disharmonious variability explosion either leads to the destruction of the hybrid population or initiates the appearance of new species. It can thus be said that modifications in the internal structure of the genes, changes in the gene com-

position of the chromosomes, new ecological situations, the gradual development of (spatial and biological) isolation and constantly operating selection bring new species into being. Each new species probably develops through the gradual transformation and hybridisation of several populations over a long period of time and on a relatively large area.

The *genus* is a higher taxonomical unit than the *species* and is also perhaps the most important such unit, defined primarily by similarities in the structure of the reproductive organs. Genera which contain a large number of species are divided into *sections*. The largest genera of seed-bearing plants are, for example, *Senecio*, with approx. 2000 species, *Astragalus*, with approx. 1700 species, *Solanum*, with approx. 1400 species, *Carex* with around 1000 species and the tropical *Orchidea*, with several thousand species.

According to STEBBINS (1959) a hybrid is a heterozygotic progeny originating from a cross between two individuals belonging to separate populations with differing characters and different degrees of adaptability. Depending on the number of gene pairs involved, the hybrid is referred to as a mono-, di-, etc. or polyhybrid. If crossing is carried out between different genera, the progeny are referred to as intergeneric hybrids, while the results of crosses between species belonging to the same genus are known as interspecific hybrids. Variety hybrids are produced if varieties belonging to the same species are crossed.

As the number of differing gene pairs rises, the degree of heterozygosis in the hybrids also increases, facilitating the appearance of new traits. Among the progeny generations of the hybrids, only those with adequate adaptability survive the effects of natural selection, while the rest of the hybrid population dies out.

The stabilisation of hybrid derivatives in nature is more likely in plants than in animals owing to their greater penchant for interspecific hybridisation, asexual reproduction and polyploidy. In plants, putative stabilised diploid fertile hybrid entities include *Potentilla glandulosa* ssp. *hansenii* (CLAUSEN et al. 1940), many subspecies of *Gilia capitata* (GRANT, 1950), *Phlox pilosa* ssp. *deamii* and *P. amoena lighthiwei* (LEVIN-SMITH, 1966). GRANT (1979) reports an example of complex reticulate evolution in *Gilia*, in which he distinguishes various types of hybrid complexes. The constituents of the homogamic complex in *Gilia* are a cluster of sympatric annual herbs, which are sexually propagated and predominantly diploid. This complex is noteworthy because of the large number of elements involved. The stabilisation of the *gilia*s was the result of abiotic selective forces. As a point of contrast, Straw (in LEVIN, 1979) describes the stabilisation of hybrid derivatives by pollinators in *Penstemon*. This is one of the best-documented cases of the pre-adaptation of different hybrids to different pollinators not servicing the parental species, and of stabilisation via assortative pollination and selection.

In both plants and animals, the stabilisation of hybrids by asexual mechanisms may be more common than the stabilisation of an intermediate phenotype in a sexual population. In plants, some hybrids can reproduce and spread asexually by agamospermous seed formation as well as by vegetative propaga-

tion. The asexual reproduction of diverse hybrid types from one pair of species may yield what GRANT-GRANT (1971) call a clonal complex.

In nature, hybrids do not usually arise en masse, so their chances of surviving are improved if they back-cross with one of the parental populations. It has been known for the constant pressure of hybridisation to cause genes from one species to be transferred into the genomes of the other species, leading to the appearance of species-level adaptive forms in nature. Since the hybrids are less fertile, there is more likelihood of fertilisation taking place with parental gametes. After suitable selection, progeny produced in this way will continue to multiply, enriched with a number of traits obtained from the "alien species". This process is known as introgression. A fine example of this is the origin of *Iris* species or hybrids, as described by ANDERSON (1949). HEISER (1954) presented evidence of extensive introgression in *Helianthus*, with *H. annuus* as the central figure. This species has given rise to introgressive races varying towards *H. debilis*, *H. petiolaris* and *H. argophyllus*. Other authors have proved the introgressive origin of maize by investigating artificial introgressive *Zea* lines of teosinte (*Euchlaena mexicana*).

The hybrids may also give rise to transgressive segregants in which new quantitative or qualitative characters appear, either eclipsing those of the parents or not resembling those of either parent. This phenomenon can be explained by the fact that the interactions of genes coming together in the hybrids may be additive, in which case these gene combinations may cause new properties to appear in the progeny. Numerous examples of this can be found. If, for example, selection is carried out for large corollas in the hybrid progeny of two tobacco species (*Nicotiana sanderae* and *N. langsdorfii*) with corollas differing in size, shape and colour, by the F₈ generation segregants with large flowers exceeding those of the *N. sanderae* species will be found. A similar observation was made by BELEA (1965), who selected individuals severely infected with powdery mildew from among the hybrid progeny of *Triticum timopheevii* × ssp. *carthlicum* despite the fact that both parental species are well-known for their powdery mildew resistance. Naturally, the opposite of this could also be observed, when extremely resistant individuals arose in the hybrid generations of two parental species susceptible to disease.

Hybrids may also arise through *apomixis*. Apomictic species may have any set of chromosomes. Triploids of apomictic origin are completely fertile, while those which reproduce sexually are generally sterile. Various aneuploid plants of apomictic origin are also fertile. In the case of sexual reproduction, aneuploid plants rarely survive.

Of course, although the apomictic form of reproduction plays an important role in evolution, it also has its disadvantages. Due to the lack of sexual reproduction, the species loses recombination variability, one of the chief sources of evolutionary plasticity in the species. From the point of view of evolution, only genotypes which possess an optimum system of interactions between mutation, recombination and selection can be regarded as progressive. This applies to moderately isolated populations of sexually reproducing plants.

In certain genera, such as *Rubus*, *Poa*, etc., both sexual and apomictic reproduction occur, and this combination leads to great plasticity. In this case, too, apomixis has a decisive influence on the adaptability of the species in question.

One major task now facing geneticists is to clarify the genetic background of apogamy. A combination of heterosis and apogamy could open up enormous horizons for breeders to produce new, unique hybrids.

It is thus obvious that even today it is impossible to give an unequivocal definition of the terms species and genus. The identification of the interspecific and intergeneric hybrids discussed in this book may thus be somewhat inaccurate. The hybrid in question may count as an interspecific hybrid according to one definition and not according to another.

1.2 Historical review

The history of interspecific crossing has been dealt with in most detail by ROBERTS (1965) and ZIRKLE (1935) who present a comprehensive review of work on interspecific crossing prior to Mendel. The first known artificial interspecific hybrid was produced in 1717 by FAIRCHILD, who made a cross between the species *Dianthus caryophyllus* and *D. barbatus*.

A little later, LINNE (1753) reported interspecific crosses between *Mirabilis longiflora* × *M. jalapa*, *Veronica maritima* × *Verbena officinalis*, *Tragopogon pratense* × *Tr. possifolius* and *Verbena hastata* × *V. spuria*. In the same year HAARTMAN (1751) included a number of interspecific crosses in a work entitled *Plantae Hybridae*, which describes a hundred different plants. Mention is made, for instance, of the well-known species *Trifolium hybridum*, which was widespread at one time, and which originated from the *Trifolium pratense* × *T. repens* cross. An alfalfa species hybrid well-known for its intermediate nature (*Medicago falcata* × *M. sativa*) is also included.

The first systematic attempt at interspecific crossing is linked with the name of KOELREUTER (1766). Koelreuter's most important papers; his "Vorläufige Nachricht" and its three "Fortsetzungen", cover the period from 1760 to 1766. In 1760, Koelreuter produced his first hybrid, *Nicotiana paniculata* × *N. rustica*. Experiments carried out over the following six years, 65 of which were described in detail, covered crosses involving 13 genera and 54 species. The first "Fortsetzung" is dated 1762. It is worth mentioning that in connection with his first *Nicotiana* hybrid, Koelreuter records its much more rapid growth, which meant that it could be distinguished from its two parents right from the germinating seed up to complete flowering. Koelreuter's second "Fortsetzung" to the "Vorläufige Nachricht", published in 1764, gives an account of 49 experiments, of which 29 were specifically crossing experiments, the remainder being experiments involving the use of the plant's own pollen simultaneously with that of another species (*Verbascum*, *Nicotiana*, *Dianthus*, *Hibiscus*, *Datisca*, *Mirabilis*, *Leucojum*). Of the 30 *Nicotiana* experiments, eight were species crosses. Of the

eight experiments in crossing species of *Dianthus*, three were species or variety crosses, while three were back-crosses on F_1 hybrids.

Koelreuter's third "Fortsetzung" is dated 1765. In addition to fertile crosses with four species of *Verbascum*, several other fertile combinations were reported in the same genus, involving chiefly the reciprocal crosses of the species native to the locality. All the *Verbascum* crosses proved sterile.

During the period prior to Mendel many other authors, including KNIGHT (1799), HERBERT (1819), WIEGMAN (1828), GAERTNER (1849), NEILREICHT (1852), GODRON (1863), NÄGELI (1865, 1866), etc., also reported a number of interspecific crosses.

HERBERT (1819) noticed the fact that in species crosses (e.g. *Passiflora coerulea* $\times$ *P. onychina*) the ovaries may develop as the result of the fertilisation stimulus, the interior remaining empty, like a bladder, and only the outer coat of the fruit having been fertilised, in consequence of the weakness of the cross-bred pollen. He continued by noting that where adaptation of the two types was perfect, a perfect offspring was produced, but where it was not perfect, inadequate or weak fertilisation occurred, and "it is further to be observed that there is frequently an imperfect hybrid fertilisation which can give life, but not sustain it well". Among such cases he mentions *Hibiscus pabustris* $\times$ *H. speciosus*, of which the seeds always sprouted, but of which only one survived to the three-leaf stage, when it perished. He states that in crosses between *Rhododendron ponticum* and an orange *Azalea* he had never raised seedlings beyond the third or fourth leaf stage.

GAERTNER (1849) worked on prominent genera such as *Antirrhinum*, *Avena*, *Dianthus*, *Nicotiana*, *Digitalis*, *Oenothera*, etc. Later, FOCKE (1881) reported on numerous interspecific and intergeneric crosses in his book "Die Pflanzen-Mischlinge"; the vast majority of his observations are still valid today. He gave the taxonomical classification of species hybrids both in the family (*Ranunculaceae* - *Fucaceae*) and in the genus. After a brief historical review, he deals with the appearance, nature and practical significance of the interspecific hybrids. Focke's own experiments involved the crossing of species of *Raphanus*, *Melandryum*, *Rubus*, *Anagallis*, *Digitalis* and *Nicotiana*. While the actual number of crosses made by Focke was few, and the results, as in the case of most other observers of hybrid phenomena, were not analysed with respect to the generations of the hybrids, yet in the single case of a cross made between *Digitalis purpurea* $\times$ *D. ambigua*, Focke made measurements on certain organs in the parents and in the hybrid, and these, with few exceptions, would appear to constitute the only quantitative measurements made on hybrid cases prior to 1900.

HENSLOW (1891) reported a cross between *Digitalis lutea* $\times$ *D. purpurea*. MACFARLANE (1890) made crosses involving *Rhododendron*, *Hedychium*, *Cytisus*, *Dianthus*, *Drosera*, *Ribes*, etc. MARSCHALL (1892) described species hybrids of *Salix* and *Epilobium*. WILSON (1900) reported on crosses between species of *Passiflora*, *Albica*, *Ribes* and *Begonia*. In a report on an international conference on genetics, CAMUS (1907) listed interspecific hybrids produced between Euro-

pean flowering plants. Similar lists were given by MACDOUGAL (1907) for hybrids produced in the USA and by LEVEILLE (1917) for those found in France. Later, in the first volume of a book entitled *Plantes hybrides de France*, GUETROT (1927) described 69 hybrids, dealing with a further 32 in a volume published in 1929, and finally with *Saxifraga* interspecific hybrids in a 1931 publication. COCKAYNE (1923) lists New Zealand hybrids, and Drice (1928) the 500 or more interspecific hybrids to be found in England. Valuable information on interspecific hybrids within the *Gramineae* family is presented by ULLMANN (1936), MYERS (1947) CARNAHAN-HILL (1961) and KNOBLOCH (1968).

Outstanding work on interspecific crosses was also carried out by BURBANK (1914) in America and by MICHURIN (1925) in the Soviet Union. The success achieved by these authors had a stimulating effect on other researchers in this field. During this period interspecific crosses were carried out in Denmark (ANDERSON, 1931) and France (HANSEN, 1959). GARAY-SWEET (1974) described species hybrids in orchids and YARNELL (1956) in crucifers.

Developments in interspecific and intergeneric crossing can be divided into three phases: the first consisting of Koelreuter's work and his predecessors, a period excellently reviewed by Zirkle, the second being the wide-ranging work on interspecific and intergeneric hybridisation begun in the 1900s and described in a book by Roberts.

Indubitably, these first attempts at interspecific hybridisation were of botanical interest, rather than of practical importance. Nevertheless, great significance is attached to these early endeavours, since they formed the basis for later work which gave rise to numerous theoretical and practical results. Real success was achieved in the third phase, when the investigations were complemented with cytological, genetic, biochemical (electrophoresis, isoenzymes, DNA, histone, etc.) and physiological analyses (ANDERSON, 1949; BELEA, 1976; etc.).

After 1910, mention is made (WINGE, 1917) of fertile interspecific hybrids produced by polyploidisation from sterile hybrids for use in evolution research.

* * *

Details will now be given on the history of interspecific crossing for a number of major plants.

Within the *Gramineae* family the first wheat (*Triticum*) species hybrid was described by HALLET in 1861 (ROSIE, 1955). CIFFERI (1955) mentions even earlier researchers who dealt with interspecific crossing, such as the botanists BELLARDI and BARELLE, who attempted to cross various wheat species in 1807-1809. PERCIVAL (1921) draws attention to the work of Bromsgrove, who reported results achieved in this field at a meeting of the English Agricultural Society in 1846. During the same period RAYNBIRD (1851-1855) produced species hybrids from the *Triticum aestivum* × *T. turgidum* conv. *durum* combination. In the 1860s interspecific hybrids were produced in Scotland by SHIERREFF (1897), as reported by PERCIVAL (1921), in the USA by PRINGLE and BLOUNT and in Germany by RIMPAU (1877-1891). In 1863 the French botanist NAUDIN mentioned interspecific crosses involving tetraploid and hexaploid wheat; this au-

thor also dealt with the segregation of certain outstanding morphological traits of wheat species hybrids and attempted to analyse them. SPILLMAN (1901), too, reported on the genetic analysis of F_1 and F_2 species hybrids of *T. dicoccum* $\times$ *T. aestivum*, etc.

Up to the turn of the century numerous other well-known researchers, such as the German author KÖRNICKE (1885), the Frenchmen GODRON (1873) and VILMORIN (1880, 1889), the Dutchman BEIJERINCK (1884, 1886), the Australian FARRER (1898), etc., dealt with the subject of interspecific crossing in wheat. In a report to the Société Botanique de France on the hybridisation of wheat, Vilmorin stated that the characters of the hybrids in the *sativum* crosses were generally intermediate, sometimes more closely resembling one parent, sometimes the other, and sometimes showing characters found in both. When a pubescent wheat, Blé à duvet, was crossed reciprocally with a reddish, beardless, smooth spelt (*T. spelta*), the products of the cross were intermediate if spelt was the female and Blé à duvet the male parent. The report also mentioned reciprocal crosses made in 1878 between *T. sativum* and *T. turgidum*, *durum*, *polonicum* and *spelta*.

It can thus be said that work on the interspecific crossing of wheat was begun in the middle or second half of the last century and was aimed at the solution of definite theoretical and practical problems. These activities, and especially the work carried out in Sweden in the early 1900s by NILSSON-EHLE (1908–1911) and, as reported by ROBERTS (1965), by BIFFEN (1905) and LOVE-GRAIG (1919), who based their research on modern theories and techniques, attracted many theoretical and practical experts to this untapped area of wheat breeding and research on the origin of wheat.

In Hungary, work on the interspecific crossing of wheat was not commenced until after 1945 (in Magyaróvár, Fertőd and Kompolt) and was aimed chiefly at breeding for disease resistance. Wide-ranging research on interspecific and intergeneric crosses in wheat were begun in 1950 in Martonvásár (LELLEY-RAJHÁTHY, 1955; BELEA, 1964) and later, in 1971, in the Institute of Genetics of the Szeged Biological Centre. In addition to practical aspects, the main aim here was evolution genetics (BELEA, 1971, 1976, 1982, 1984 etc. BELEA-FEJÉR, 1981). In addition to wheat species, these crosses also involved certain species of the *Aegilops*, *Secale*, and later the *Agropyron*, *Hordeum* and *Avena* genera.

After a number of unsuccessful attempts, the first wheat (*Triticum*) $\times$ wheat-grass (*Agropyron*) hybrid was produced by WILSON (1875). This work was continued in the Soviet Union by TSITSIN and co-workers (1957). Tsitsin made his first, unsuccessful, attempts at crossing in 1929, at the instigation of Michurin. Later, his persistence paid off. The wheat $\times$ wheat-grass crosses led to unexpected practical results, which stimulated researchers to carry out further crosses (SZALAY-BELEA, 1962). In addition to various species of *Agropyron* (*A. elongatum*, *A. trichophorum*, *A. glaucum*, *A. junceum*, *A. repens*), hybridisation was extended to include crosses of wheat with *Elymus*, and later *Haynaldia* and *Aegilops* species (WHITE, 1940).

In Hungary, Árpád Kiss carried out the first wheat $\times$ wheat-grass crosses at

the Plant Breeding Institute in Mosonmagyaróvár in 1946. This work was continued in Martonvásár in 1950. The hybrid material produced was later developed by SZALAY (1968), who selected promising lines from combinations of an *Agropyron elongatum* × *Triticum aestivum* hybrid back-crossed several times to *T. aestivum*.

A sterile hybrid of wheat (*Triticum*) × rye (*Secale*) was first described to the Edinburgh Botanical Society by WILSON in 1875. His work was aimed at the unification of the favourable characters of the two crops. Finally, the German breeder Rimpau succeeded in producing the first fertile wheat × rye hybrid in 1890; this became known as *triticale*. After this work was published in 1936, several researchers became interested in the subject (e.g. MÜNTZING, PISSAREV—VINOGRADOVA, 1945; KATTERMAN, WELLENSIEK, 1947) and produced $2n = 56$ -chromosome octoploid wheat × rye amphiploids by means of colchicine treatment. In the 1950s a hexaploid ($2n = 42$) form of triticale was also produced (O'MARA, 1947; NAKAJIMA, 1951 etc.). In Hungary successful wheat × rye crosses aimed at uniting the favourable properties of the two crops were carried out in Magyaróvár by OBERMAYER in 1917 and by GYÖRFFY in 1948, and by FLEISCHMANN in Kompolt in 1943. The first fertile hexaploid and octoploid triticales arose in 1953 as the result of research by KISS-RÉDEI, which later led to the production of the first secondary hexaploid triticales (cultivars No. 57 and No. 64). The triticale breeding now is in progress in Kecskemét under the guidance of Árpád Kiss and his son József has won world-wide recognition. The results obtained in Kecskemét greatly promoted the success of triticale breeding in Mexico (CIMMYT), Europe and India.

Reports on crosses between marrow species (*Cucurbita*) belonging to the *Cucurbitaceae* family were particularly frequent in the 1930s (MACKAY, 1968, 1972; RUTTLE, 1932; WHITAKER, 1954, 1956, 1962 etc.), though similar work was also carried out in previous years. The hybridisation experiments reported by SAGERET (1826) were largely confined to the *Cucurbitaceae*. This French author crossed musk melons with candaloupes, but found that in the two hybrid fruit obtained, the characters were not blended or intermediate at all, but were clearly and distinctly those of one or the other parent. During this same period hybridisation work was also published by KNIGHT (1799) and HERBERT (1819). In 1902 BAILEY was the first to produce a viable F_1 generation from the Japanese 'Crookneck' (*Cucurbita mixta*) × 'Connecticut Field Pumpkin' (*C. pepo*) combination. The 88 F_1 plants were phenotypically more similar to the *C. pepo* species, the only difference being in the state of development of the lower flowers of the plants. In a reciprocal cross ERWIN-HABER (1929) achieved 25% seed setting; this combination also led to the raising of viable plants. CASTELLER (1930) also obtained fertile F_1 plants from a *Cucurbita pepo* × *C. maxima* cross. VAN ESELTINE (1937) successfully carried out interspecific crosses between *C. pepo* and *C. moschata*. Later, WEILING (1955), WHITAKER (1956), BEMIS (1976), etc. made even more extensive crosses between marrow species.

Crosses between *Brassica* species were also initiated at the beginning of the century (MORINAGA, 1928, 1929; OKONAGI, 1934, etc.) and were later continued

by numerous authors (KATO-TOKUMASU, 1976; KISS-BELEA, 1958; KAMALA, 1976; MACKAY-LOW, 1975; MCNAUGHTON, 1973; RÖBBELEN, 1960, etc.).

The first cross between sugar cane (*Saccharum*) species was made in 1914 by BARBER, who crossed *Saccharum officinarum* × *S. spontaneum*. The first intergeneric cross was carried out between *Saccharum officinarum* and *Narenga porphyrocoma* in 1916. Later, VENKATRAMIAN (1931) and JANAKI-AMMAL (1938), BOURNE (1935) and WILLIAMS-CAMERON (1936) reported on crosses between sugar cane and other genera (*Sorgum*, *Panicum*).

The first artificial interspecific cross involving sunflower (*Helianthus*) was described by COCKERELL in 1918 (*H. petiolaris* × *H. annuus*). This work was later continued by HEISER (1954).

1.3 Origin of cultivated plants and interspecific crossing

Before giving details on interspecific and intergeneric crosses, a brief review will first be presented on the current state of knowledge regarding the origin or derivation of cultivated plants.

Many cultivated crops (yellow lupins, castor oil plant, hops, chicory, white mustard, white sweetclover, villous and Hungarian vetch, lettuce, perennial rye-grass, oat-grass, meadow fescue, smooth brome-grass, etc.) have their origin in wild species of the plant; these crops differ from their ancestors only in their cultivated nature. They often lose the traits associated with cultivation and are very similar to their wild forms.

Other cultivated plants (e.g. lentils, forage turnips, carrots, horse beans, flax, hemp, red and purple clover, etc.) developed from a variant of the wild form. As in the previous group of plants, these too differ from the wild species only in their cultivated nature.

Another group of cultivated plants is treated by taxonomists as being completely new species, differing both morphologically and in their cultivated nature from the original wild species. This group includes rice, millet, beans, soybeans, white-flowered lupins, fodder vetch, etc.

Yet another group of plants arose from the wild species through gradual mutations, e.g. barley, bristle-grass.

It has long been known that many cultivated crops are the result of spontaneous interspecific crosses due in large part to repeated mutations and human intervention (selection).

Among the cereals (*Gramineae*) the form of rye now cultivated developed as the result of numerous spontaneous crosses between perennial and annual wild rye species. In the first instance the species *Secale digholicum*, *S. afghanicum* and *S. ancestrale* came into existence through a cross between *S. montanum* (mountain rye) and *S. kuprianovi*, followed by multiple mutation. In the second stage, crosses between these species, together with micromutations, led to the development of *S. segetale*, which subsequently gave rise to the species of rye currently cultivated (Fig. 4).

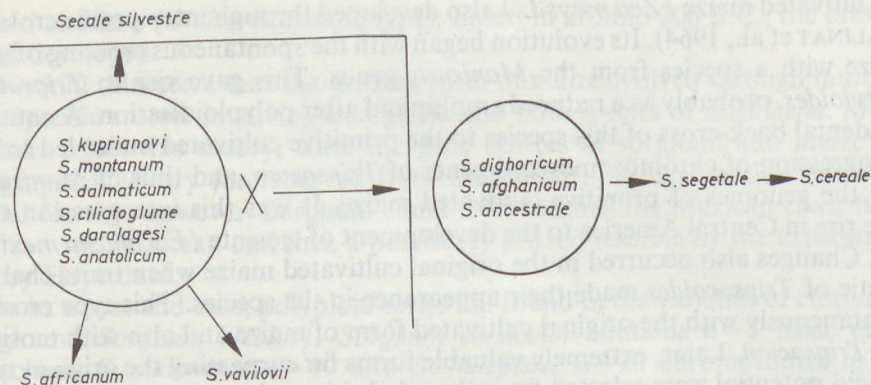


Fig. 4. Hypothetical course of evolution for cultivated rye (MÁNDY, 1972)

Like rye, oats (*Avena sativa*) also developed from a weed plant. Although in Hungary only forage oats (*Avena sativa*) are grown, in various other parts of the world numerous oat species, such as *A. strigosa*, *A. abyssinica* and *A. byzantina* are also in general cultivation. The majority of these species arose from wild-grown related species by means of mutation and interspecific crossing. As in wheat, here too di-, tetra- and hexaploid ($n=7$, genome A; $n=14$, genome AB, AC; and $n=21$, genome ACD) lines can be found. In contrast to wheat, however, in the *Avena* genus original species are known at all polyploid levels (diploid = *A. hirtula*; tetraploid = *A. sterilis*) (Table 1).

Table 1.
Polyploidy series of oat species (after RAJHÁTHY-THOMAS, 1974)

Polyploidy level	Genome	Diaspora		
		floret	spikelet	cultivated
Diploid $2n = 2x = 14$	C_pC_p C_vC_v A_pA_p A_lA_l A_dA_d A_cA_c A_sA_s A_wA_w	<i>clauda</i> Dur. <i>prostrata</i> Lad. <i>longiglumis</i> Dur. <i>damascena</i> Rajh. et Baum <i>wiestii</i> Steud. <i>hirtula</i> Lag.	<i>pilosa</i> M. Bieb. <i>ventricosa</i> Bal. <i>canariensis</i> Baum. et Rajh.	 <i>strigosa</i> Schreb.
Tetraploid $2n = 4x = 28$	AABB	<i>barbata</i> Pott <i>vaviloviana</i> Mordv.	<i>magna</i> Murph. <i>murphyi</i> Lad.	<i>abyssinica</i> Hochst.
Hexaploid $2n = 6x = 42$	AACCDD	<i>fatua</i> L.	<i>sterilis</i> L.	<i>byzantina</i> C. Koch <i>sativa</i> L.

Cultivated maize (*Zea mays* L.) also developed through interspecific crossing (GALINAT et al., 1964). Its evolution began with the spontaneous crossing of wild maize with a species from the *Manisuris* genus. This gave rise to *Tripsacum dactyloides*, probably as a reduced amphiploid after polyploidisation. A natural, accidental back-cross of this species to the primitive cultivated maize led to the introgression of chromosomes and genes of *Tripsacum*, and thus of *Manisuris*, into the genomes of primitive cultivated maize. It was this introgression that gave rise in Central America to the development of teosinte (*Euchlaena mexicana*). Changes also occurred in the original cultivated maize when traits characteristic of *Tripsacoides* made their appearance in the species. This type crossed spontaneously with the original cultivated form of maize and also with teosinte and *Tripsacum*. Later, extremely valuable forms far surpassing the original type in yield potential were selected from these hybrid combinations. The introgression of *Manisuris* chromosomes and genes made it possible for the enormous maize ears to develop. At the same time an intense heterosis effect was manifested, primarily in yield potential. The tripsacoid type is characterised by small maize ears and grains. Mutability also became substantially greater, leading to increases in resistance to drought, heat and diseases.

The other genus which may have played a part in the origin of maize is *Euchlaena*, two species of which are found in Mexico (*E. mexicana*-teosinte and *E. perennis*). The annual teosinte greatly resembles maize in its tillering system and in the fact that the male and female flowers are separately located. *E. perennis*, though slightly resembling teosinte, differs from it considerably in that it is a perennial and has a chromosome number double that of maize ($n=20$). In spite of this, Schiemann (in MÁNDY, 1972) attributes an important role to *E. perennis* in the hypothetic origin of maize through intergeneric hybridisation (Fig. 5).

Archaeological research also provides clear evidence of the appearance of the tripsacoid hybrid *Tripsacum* × *Zea* or *Euchlaena* × *Zea* during the Coxcatlan period. Both early and late types existed, as did crosses between the intergeneric

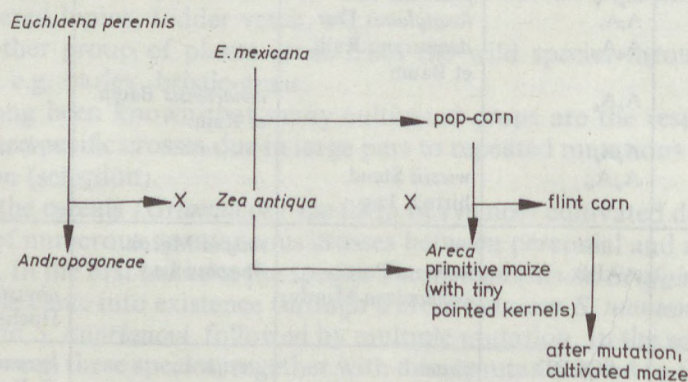


Fig. 5. Outline of the origin of cultivated maize through intergeneric hybridisation (MÁNDY, 1972)

hybrid and *Zea* (*Naltel chapalota* type). Later, in around 200 B.C., the present types developed.

It would thus seem that the modern form of maize evolved through multiple interspecific crosses involving a sorghum and both species of *Euchlaena*. Many authors reject this theory, since the gene centres of sorghum and maize are geographically very far removed from each other. An explanation has been found for this, however. Sorghum could have reached the Mexican coast from Africa with the ocean currents, a possibility proved feasible by the expeditions led by Heyerdahl.

As in wheat and oats, polyploid series are found in the varieties of cultivated sorghum (*Sorghum bicolor*). *Sorghum versicolor* contains $n=5$ basic chromosomes, *S. sudanense* $n=10$ and *S. halepense* $n=20$ chromosomes in the gametes. The two latter species are polyploid. The exceptional richness of forms can be attributed to interspecific crosses between the 23 *Sorghum* species belonging to three major groups (*S. arundinaceum*, *S. verticilliflorum* and *S. aethiopicum*), combined with micromutations.

Italian rye-grass (*Lolium multiflorum*) evolved from an interspecific cross between *L. perenne* and *L. temulentum*, *Trifolium hybridum* from *T. pratense* $\times$ *T. repens*, *Medicago media* from *M. sativa* $\times$ *M. falcata* and *Epilobium roseum* from *E. adunatum* $\times$ *E. montanum*.

Among the root and tuber crops, potato (*Solanum tuberosum*) probably also arose through a spontaneous cross between *S. stenotomum*, indigenous to Peru, and *S. sparsipilum*, followed by genome mutations. Artichoke (*Helianthus tuberosus*), too, may have arisen from a spontaneous hybridisation between an unknown autotetraploid species and sunflower (*Helianthus annuus*). In a similar manner, sunflower (*Helianthus annuus*) itself also derives from an ancient interspecific cross between *H. petiolaris* and the original wild form of *H. annuus*.

The ancestor of beet (*Beta vulgaris*) was *B. vulgaris* ssp. *maritima*, which arose from crosses between other species (*B. macrocarpa*, *B. atriplicifolia*).

Among the horticultural plants, the brassicas owe their richness of form to interspecific crossing, in the opinion of Nagahura. This hypothesis was confirmed by FRANDSEN, who, in 1947, produced the species *B. carinata*, *B. juncea* and *B. napus* from the basic species (Fig. 6). In 1950, RUDORF also successfully produced the amphiploid *B. napus*. It is also known that the subspecies *B. napus* ssp. *oleifera* arose through a cross between *B. oleracea* and *B. campestris*. The brassicas not included in Fig. 6 also originated from natural hybridisation between a number of species (*B. balearica*, *B. montana*, *B. insularis*, *B. rupertis*, *B. cretica*, *B. alboglabra*, etc.) and through a whole series of micromutations. The popular cabbage (*B. oleracea*), however, is not of interspecific hybrid origin. Naturally, in addition to interspecific crossing and multiple micromutations, human intervention in the form of selection also played an essential role in the development of the current forms of brassicas.

The radish (*Raphanus sativus*) probably also arose with human assistance from combinations of the major ancestor of radishes, *R. maritimus*, with wild species (*R. rostratus* and *R. raphanistrum*).

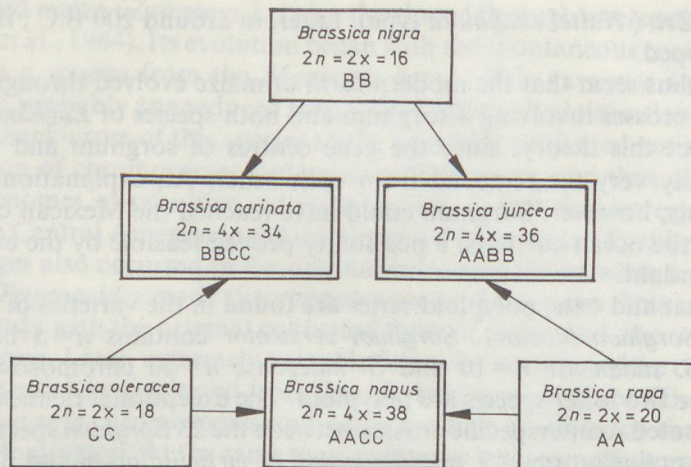


Fig. 6. Allopolyploid species originating from crosses between *Brassica* species (MÁNDY, 1972)

Peas (*Pisum sativum*) are also the result of interspecific crossing. On the Eastern coast of the Mediterranean and in Asia Minor, crosses between the wild species *P. fulvum* and *P. elatium* led to hybrid combinations from which, as the result of recombinations and multiple micromutations, together with various types of selection, two new species, *P. syriacum* (in Asia Minor) and *P. abyssinicum* (in the south-west part of the Arabian peninsula) came into being. Later, in Abessinia, these two species crossed with the *P. elatium* species to give types with extremely favourable economic properties, and these later entered general production as cultivated peas (LEHMANN, 1954).

Many berried plants, such as currants (*Ribes* sp.) arose from crosses between three wild species (*R. rubrum*, *R. spicatum* and *R. sylvestre*). Many authors consider *R. rubrum* to be a hybrid of the two latter species.

Five wild species (*Rubus bolley*, *R. ulmifolius*, *R. tomentosus*, *R. incanescens*, *R. muschus*) played a role in the development of the European relatives of blackberry (*Rubus* sp.). The presently known species of blackberry evolved through crosses between these species, followed by back-crosses, doubling of the chromosome set, the occurrence of diploid gametes and apomixis.

Among the stone-fruits, almond (*Prunus amygdalus*) owes its origin to the species combination *P. bucharica* × *P. fenzliana*, and sour cherry (*Prunus cerasus*) to *P. avium* × *P. fruticosa*. The wide variety of forms existing in the apple and pear subfamilies can also be attributed to crosses with numerous wild species and to polyploidy.

Among the medicinal plants, peppermint (*Mentha piperita*) is probably a derivative of a triple species hybrid (*M. aquatica* × *M. silvestris* × *M. rotundifolia*).

In the same way, numerous ornamentals also arose due to spontaneous

crosses between various wild species. Examples of this are petunia (*Petunia atkinsiana*) from *P. violacea* × *P. nyctaginiflora*, rose (*Rosa* sp.) from *R. gallica* × *R. chinensis*, *Primula elatior* from *P. versis* × *P. vulgaris*, dahlia (*Dahlia pinnata*) and gladiolus (*Gladiolus cultorum*).

Many of the highly valuable crops cultivated today were only able to develop from interspecific and intergeneric crosses because the multiplication of their chromosome sets (auto- and allopolyploidy) meant that the first generation became fertile (see section entitled Polyploidy). Among the cultivated crops, some of the most valuable belong in this group, including wheat, rape, common tobacco, coarse tobacco, white clover, Kentucky bluegrass, cotton, etc.

The strawberry (*Fragaria ananassa*) is also an autotetraploid plant. The different variants can, however, be regarded as vegetatively reproduced hybrid clones originating from crosses between two octoploid species (*F. chiloensis* and *F. virginia*). In later stages a genome from another octoploid species (*F. cuneifolia*) also enriched the genome stocks, thus contributing to the wide variety of forms. Plums (*Prunus domestica*) are an amphiploid of sloes (*P. spinosa*) and myrobalan plums (*P. cerasifera*).

A classic example of the significance of allopolyploidy is the origin of the wheat series (*Triticum*). The basic chromosome number of the *Triticinae* subtribe is $n=7$. As the result of chromosome aberrations, structurally differing genomes arose from the 7-chromosome original genome, and due to the inhibition of gene exchanges, these genomes accumulated differing sets of alleles. This led to the formation of morphologically different species groups, such as *Triticum* (wheat), *Aegilops*, *Agropyron* (wheat-grass), *Secale* (rye) and *Haynaldia*.

It has been known since 1918 that the *Triticum* genus has three polyploid levels ($2n=14$ diploid; $2n=28$ tetraploid and $2n=42$ hexaploid). The pioneering work of KIHARA (1924) and SAX (1922) served to clarify the allopolyploid nature of these polyploid series, indicating that the genome formulae of the *Triticum* genus are AA, AABB or AAGG, and AABBDD or AAAAGG.

There are various theories as to the origin of the individual wheat species. The taxonomists are unanimous in tracing the A genome to diploid wheat ($n=7$). Opinions differ, however, as to which diploid what was the original parent. Right up until 1937, when TUMANYAN discovered *T. urartu*, the most primitive form of the diploid series yet known, *T. monococcum* ssp. *boeoticum*, discovered by Balansa in 1854, was regarded as the most ancient species of wheat (LELLEY-MÁNDY, 1963).

The diploid wild species widespread in the hills of Western Asia and in the Balkan peninsula are endemic under fairly isolated ecological conditions. This situation has led to ecogeographical types developing within the same polyploid level. One strange type, var. *aegilopoides*, has a single grain per spikelet and a single floral glume awn, and has adapted itself to a very limited, extremely arid climate. The greatest grain yield is given by this type between different diploid wheat species *T. monococcum* (eincorn), which is still cultivated in some regions, probably originated from this form. In Central Anatolia the var. *thaoudar* appeared, which has two awns and often two grains per spikelet. The third type,

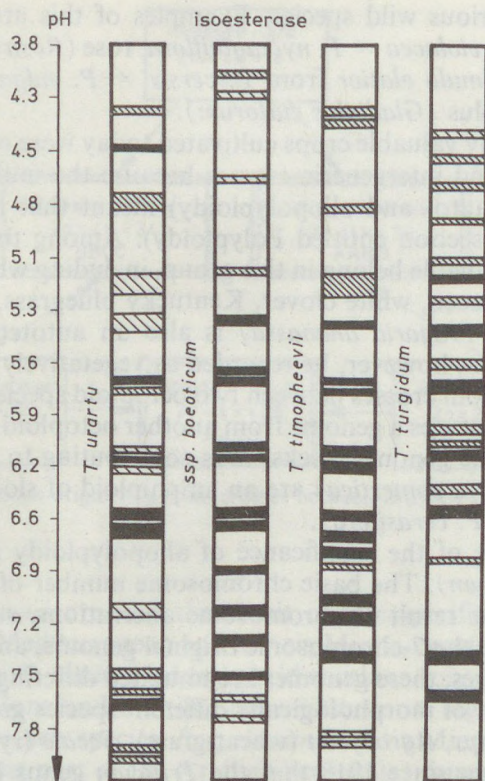


Fig. 7. Isoesterases of various *Aegilops* and *Triticum* species (BELEA, 1976)

T. urartu, where the awns are again two in number, but are shorter and diverging, is indigenous in the eastern part of the area mentioned (Lebanon, Taurus mountain range) (JOHNSON, 1975). Spontaneous crosses can take place between these types with no difficulty whatsoever.

Karyologically (as regards the ratio of the long and short arms of the chromosomes), *T. urartu* does not differ substantially from the other diploid species. Immunochemical methods showed quite different protein patterns, however (JOHNSON, 1975; KONAREV, 1975). Slight differences were found in the spectra of focussed isoesterases (Fig. 7) (JAASKA, 1974; BELEA, 1976) and in the course of chromosome identification by means of the heterochromatic staining (C-band) technique. The differences in banding suggest that *T. urartu* did not arise from *ssp. boeoticum*, but evolved parallelly with this subspecies from a common ancestor (BELEA, 1971).

Certain authors claim that there were two paths of evolution. MÁNDY (1971), for instance, states that only species originating from the ancestor (*T. urartu*) of the Western gene centre (*urartu* – *georgicum* – *carthlicum* – *aestivo-compac-*

tum - aestivum) reached the hexaploid level, while the other course of evolution (*boeoticum - monococcum - dicoccoides - durum - turgidum - polonicum*) remained at the tetraploid level. Both diploid wheat species are regarded as separate evolutionary sources by GUBAREVA and co-workers (1975), who consider that the A genome of *T. timopheevii* originates from ssp. *boeoticum*, while the A genomes of the other tetraploid wheats stem from *T. urartu*.

The important role played in evolution by *T. urartu* is confirmed by observations indicating that ssp. *boeoticum* is resistant to stem and leaf rust, while *T. urartu* is susceptible to these diseases. This unfavourable character would appear to be characteristic of wheat species (*georgicum - aestivum*) originating from this species.

For wheat (*Triticum* L.) the first step in polyploidisation is the tetraploid level, the A genome of which, as mentioned above, originated from diploid wheat. The general opinion among early researchers was that these wheat species arose monophyletically. However, the genetically and morphologically very isolated tetraploid *T. timopheevii* (AAGG), discovered in Western Georgia in 1923 by ZHUKOVSKY (1928), suggests biphyletic origin. It is extremely difficult to cross this species with other wheat species, and any hybrid progeny achieved are generally sterile (see section entitled Hybridisability of species and genera).

The genetic isolation of *T. timopheevii*, the second genome of which is designated as G due to desynapsis stemming from genic interaction, is obvious from its karyotype, which differs from that of the other tetraploid wheats (GIORGI-BOZZINI, 1969), its DNA content (REES-WALTERS, 1966), its cytoplasmically male sterile nature (WILSON-RESS, 1962), its immunochemical response (BOZZINI, 1970) and from differences in its esterase and alcohol dehydrogenase zymograms (Fig. 8).

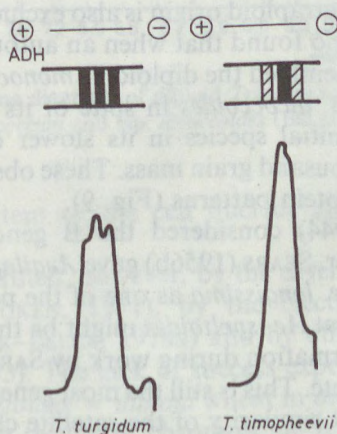


Fig. 8. Alcohol dehydrogenase zymograms of *Triticum turgidum* (AB) and *T. timopheevii* (AG) (BELEA, 1976)

The origin of the G genome of *T. timopheevii* is unknown. On the basis of chromosome pairing analysis (SHANDS-KIMBER, 1973) it has been suggested that *Aegilops speltoides* (S) was the donor of the G genome. This supposition is not confirmed, however, by the results of chromosome identification carried out with Giemsa (C-band) staining. The banding in the heterochromatic material of the two species is not identical, though the similarity between *Ae. speltoides* S and *T. timopheevii* G is greater than that between S and the B genome of the *T. turgidum* group. A similar conclusion can be drawn from a comparison of the isoesterases obtained by isoelectric focussing from *T. timopheevii*, ssp. *boeoticum* and *Ae. speltoides* (Fig. 7). KUSHNIR-HALLORAN (1983) suggest that the G genome of *T. timopheevii* (the B genome of the *T. turgidum* group) could have developed through macromutation from the B genome of the *T. turgidum* group. This suggestion was based on the fact that these authors selected *T. timopheevii* types from a ssp. *dicoccoides* population and these gave 55.5% seed setting and fertile F₁ progeny when crossed with natural *T. timopheevii*.

The origin of the B genome of wheat species belonging to the *T. turgidum* group is also unknown. Recently there has been a revival of the theory that tetraploid wheat is simply an autotetraploid of the diploid species (SCHIEMANN, 1932; SCHRIMPF, 1951). On the basis of electrophoresis analyses on grain protein patterns, JOHNSON (1975) considers the species *T. urartu* to be the source of the B genome, mentioning ssp. *boeoticum* (A genome) as the other parent. It was demonstrated using the heterochromatic staining technique that the banding in the A genome of *T. urartu* differed from that of the chromosomes belonging to the B genome, which meant that this species could not be the donor of the B genome. In the course of addition, characters which are missing from *T. urartu* were introduced into emmer wheat from the B genome. There was a distinct improvement in the heat tolerance, adaptability and disease resistance of tetraploid wheats. The more intense vegetative development and the higher chlorophyll content are also characteristic of these wheats alone.

The possibility of autotetraploid origin is also excluded by observations made by BELEA (1965, 1976), who found that when an autotetraploid *T. monococcum* (AA) was produced, it resembled the diploid *T. monococcum* much more closely morphologically than ssp. *dicoccoides* in spite of its $2n=28$ chromosomes. It only differed from the initial species in its slower development, darker leaf colour, larger ears and thousand grain mass. These observations were confirmed by the electrophoretic protein patterns (Fig. 9).

McFADDEN-SEARS (1944) considered the B genome to be derived from *Agropyron triticeum*. Later, SEARS (1956b) gave *Aegilops bicornis* and GUBAREVA and co-workers (1975) *Ae. longissima* as one of the parents. An earlier suggestion by PATHAK (1940) that *Ae. speltoides* might be the source of the B genome received cytological confirmation during work by SARKAR-STEBBINS (1956) and RILEY-CHAPMAN (1958), etc. This is still the most generally accepted hypothesis, based as it is on the great similarity of the satellite chromosomes (1B and 6B) belonging to the B genomes of *Ae. speltoides* and tetraploid wheat and on the fact that *Ae. speltoides* and diploid wheat are found on the same geographical

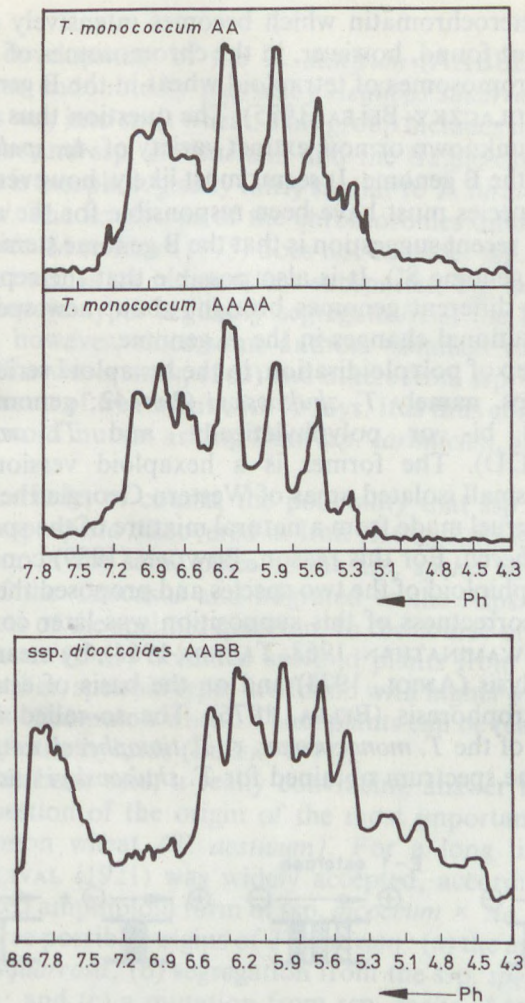


Fig. 9. Protein focusing diagrams of diploid *Triticum monococcum*, autotetraploid *T. monococcum* and *ssp. dicoccoides* (BELEA-FEJÉR, 1980)

areas. The DNA content of the cell nucleus also appears to back up this assumption.

The hypothesis is refuted, however, by the diverse cytoplasmic nature of *Ae. speltoides* (MAAN-LUCKEN, 1971), by the electrophoretic protein patterns (JOHNSON, 1972; FEJÉR-BELEA, 1978a) and by differences in immunochemical responses (ANIOL, 1973). The lack of success experienced so far in attempts to amphiploidise *Ae. speltoides* × *diploid* wheat in order to synthesise a tetraploid wheat species, and the results of chromosome identification by staining with Giemsa (C-band) also exclude this possibility. All the chromosomes of *Ae.*

speltoidea have heterochromatin which becomes intensively stained. Such intense banding is not found, however, in the chromosomes of *T. turgidum*. Nor can the marker chromosomes of tetraploid wheat in the B genome be found in *Ae. speltoidea* (HADLACZKY-BELEA, 1975). The question thus arises of whether perhaps an as yet unknown or now extinct variety of *Ae. speltoidea* could have been the donor of the B genome. It seems most likely, however, that some other diploid *Aegilops* species must have been responsible for the addition of the B genome. The most recent suggestion is that the B genome stems from the species *Ae. searsii* ($n=7$; genome S^e). It is also possible that the repeated crossing of species containing different genomes brought about new species without any substantial constitutional changes in the A genome.

In the second step of polyploidisation, in the hexaploid series, there are again two natural groups, namely *T. zhukovskyi* ($2n=42$; genomes=AAAAGG), which originated bi- or polyphyletically, and *T. aestivum* ($2n=42$; genomes=AABBDD). The former is a hexaploid version of the species *T. timopheevii*. In small isolated areas of Western Georgia the local inhabitants still eat a form of gruel made from a natural mixture of the species *T. monococcum* and *T. timopheevii*. For this reason, BOWDEN (1959) considered this to be a spontaneous amphiploid of the two species and proposed the genome formula AAAAGG. The correctness of this supposition was later confirmed cytologically (UPADHYA-SWAMINATHAN, 1963; TAVRIN, 1964), by means of comparative grain protein analysis (ANIOL, 1973) and on the basis of esterase zymograms obtained by electrophoresis (BELEA, 1976). The so-called fast moving (EI) esterase spectrum of the *T. monococcum* $\times$ *T. timopheevii* amphiploid coincides completely with the spectrum obtained for *T. zhukovskyi* under the same conditions (Fig. 10).

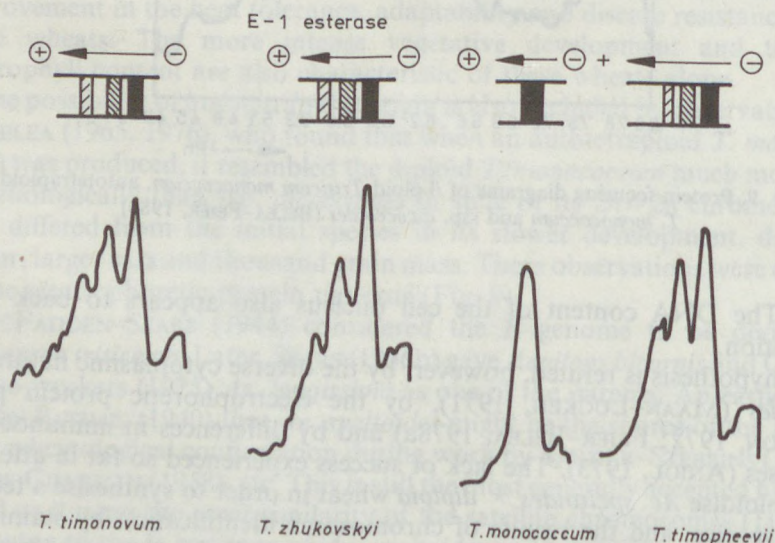


Fig. 10. Esterase zymograms of wheat species belonging to the AG genome group and their parental species (BELEA-FEJÉR, 1981)

A role in the development of the *T. aestivum* (AABBDD) group of the hexaploid level was undoubtedly played by *Aegilops squarrosa*, the D genome of which found its way into spelt wheat. This group includes the smooth-grained ssp. *sphaerococcum* and ssp. *compactum*, and the fragile-eared, closed awned ssp. *macha*, which is morphologically fairly similar to *T. turgidum* ssp. *dicoccum* and *T. zhukovskyi*. The karyotype of the chromosomes differs, however, from that of these species. MAC KEY (1975) does not consider ssp. *vavilovii*, another member of this group, as an independent subspecies, but as a variety of ssp. *spelta*, since vavilovoid types regularly segregate from the latter. This is not decisive evidence, however, since some authors obtained vavilovoid mutants from *T. aestivum* (SWAMINATHAN, 1963) and others from ssp. *carthlicum* (BARABÁS, 1959) as the result of treatment with X-rays. It is thus conceivable that ssp. *vavilovii* is a vavilovoid mutant arising from ssp. *carthlicum*, and an amphiploid of *Ae. squarrosa*.

This does not exclude, of course, the possibility that ssp. *spelta* had some other origin. The ssp. *spelta* discovered in Iran (KUCKUCK, 1959) did not arise in the same way or in the same place as the ssp. *spelta* which arose on the northern slopes of the Caucasus and migrated to the Alps. This then raises phylogenetic aspects of the speltoid question. In the course of mutation experiments, SWAMINATHAN (1963) obtained speltoid plants from *T. aestivum*. Depending on the weather, speltoid types are found with higher or lower frequency in field populations of common wheat. These plants can be readily crossed with ssp. *spelta*, giving fertile hybrids (BELEA, 1971).

Despite what has been said, a really convincing answer has not yet been received to the question of the origin of the most important species for the human race, common wheat (*T. aestivum*). For a long time the *Aegilops hypothesis* of PERCIVAL (1921) was widely accepted, according to which the species was a reduced amphiploid form of ssp. *dicoccum* $\times$ *Ae. cylindrica*. SEARS (1959) mentions three possible origins of *T. aestivum*: (a) the amphiploid of ssp. *carthlicum* $\times$ *Ae. squarrosa*; (b) segregation from the ssp. *spelta* $\times$ ssp. *carthlicum* combination; and (c) a mutation from ssp. *spelta*. According to BELEA (1976), all three routes are conceivable, as are other paths of evolution. This opinion is based on the fact that constant aestivoid types were found among sterile individuals with squarehead and compactoid ears segregating from the F_2 generation of a ssp. *spelta* $\times$ ssp. *carthlicum* cross. These plants resembled cultivated wheat in every respect and when crossed with common wheat gave completely fertile progeny and a seed setting equivalent to that obtained in variety crosses. In a paper published in 1980, ZHIROV submits a new theory on the origin of *T. aestivum*. He suggests that the species *T. militinae* (A^bA^bGG+q), a smooth-grained variant of *T. timopheevii* possessing the q factor, may have crossed spontaneously with *Ae. squarrosa* ($A^bA^bGGDD+q$), followed by amphiploidisation. The new species produced in this way was named *T. miguschovae* Zhir. and is virtually identical to *T. aestivum*, being smooth-grained and easily threshed. The disease resistance found in certain varieties of *T. aestivum* may have been borrowed from this source (Fig. 11). The

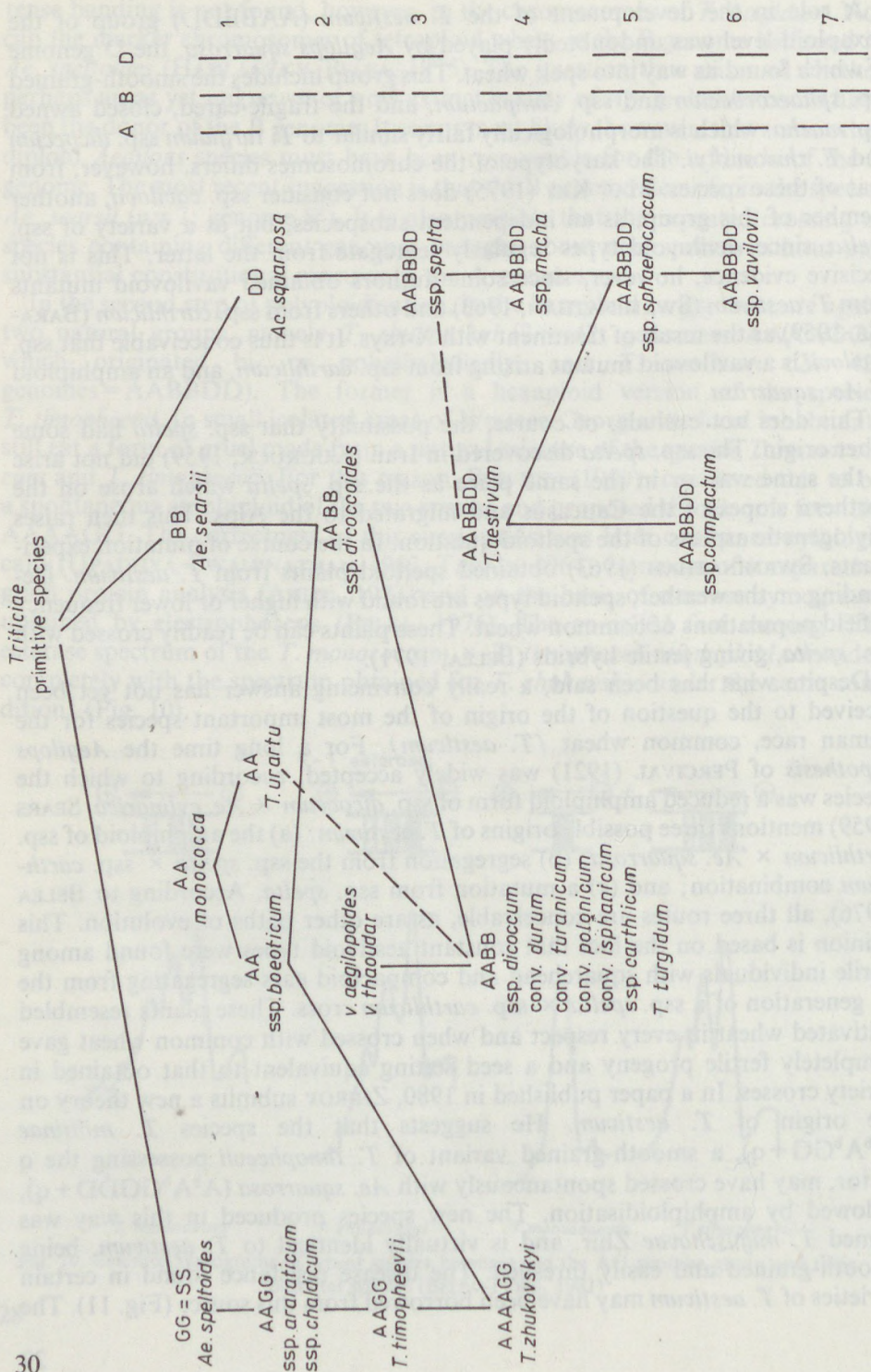


Fig. 11. Origin and relationships of wheat (MAC KEY, 1975)

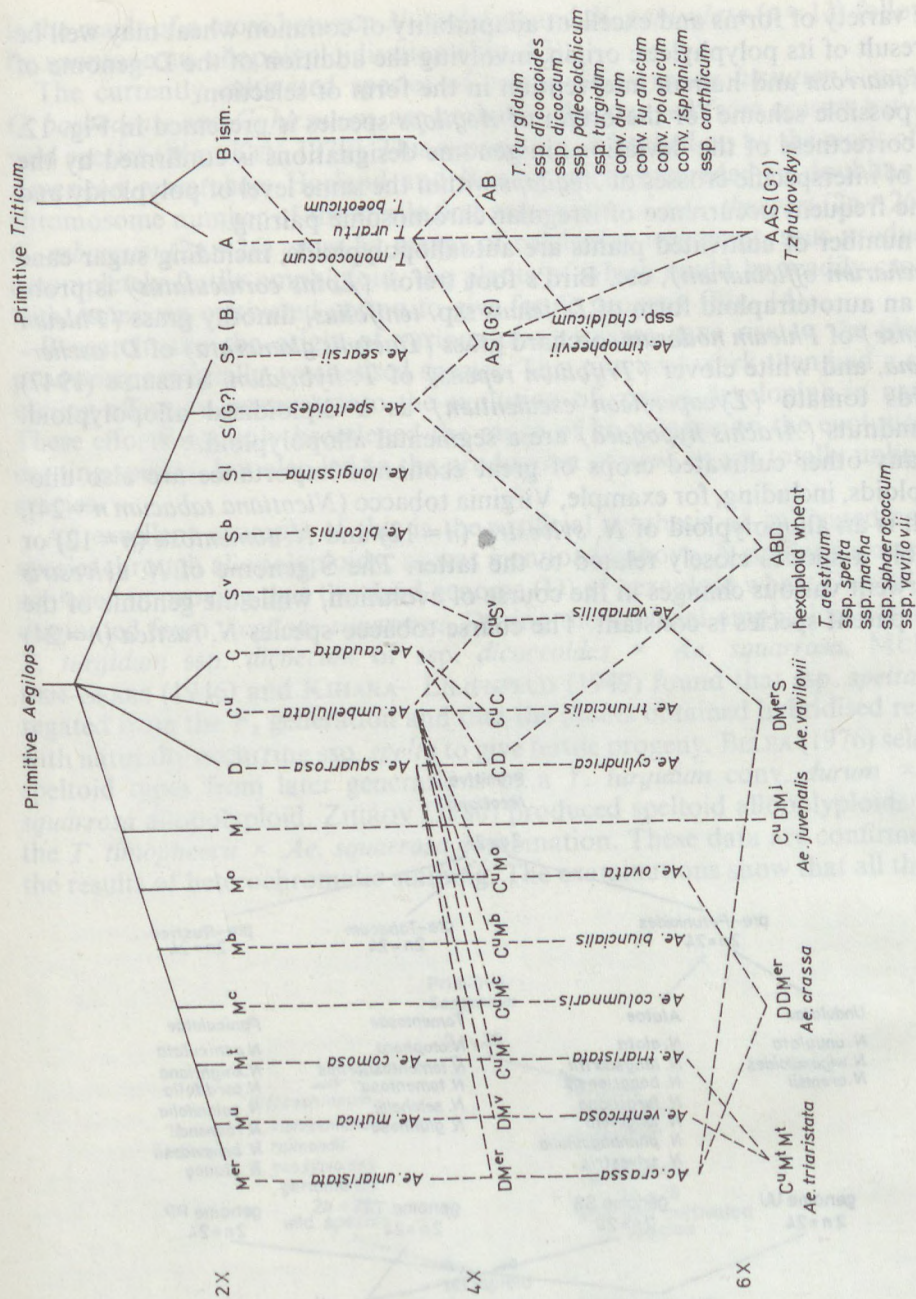


Fig. 12. Hypothetical origin of *Aegilops* species (BELEA, 1976)

wide variety of forms and excellent adaptability of common wheat may well be the result of its polyphyletic origin, involving the addition of the D genome of *Ae. squarrosa* and human intervention in the form of selection.

A possible scheme for the origin of *Aegilops* species is presented in Fig. 12. The correctness of the deviations in genome designations is confirmed by the data of interspecific crosses of *Aegilops* within the same level of polyploidy and by the frequent occurrence of irregular chromosome pairing.

A number of cultivated plants are autoallopolyploids, including sugar cane (*Saccharum officinarum*), etc. Bird's foot trefoil (*Lotus corniculatus*) is probably an autotetraploid form of *L. tenuis* ssp. *tenifolius*, timothy grass (*Phleum pratense*) of *Phleum nodosum*, orchard grass (*Dactylis glomerata*) of *D. ascher-soniana*, and white clover (*Trifolium repens*) of *T. hybridum*. STEBBINS (1947) regards tomato (*Lycopersicon esculentum*) as a diploidised allopolyploid. Groundnuts (*Arachis hypogaea*) are a segmental allopolyploid.

Many other cultivated crops of great economic importance are also allopolyploids, including, for example, Virginia tobacco (*Nicotiana tabacum* $n=24$), which is an allopolyploid of *N. sylvestris* ($n=12$) and *N. tomentosa* ($n=12$) or possibly a species closely related to the latter. The S genome of *N. sylvestris* underwent various changes in the course of evolution, while the genome of the other parent species is constant. The coarse tobacco species *N. rustica* ($n=24$)

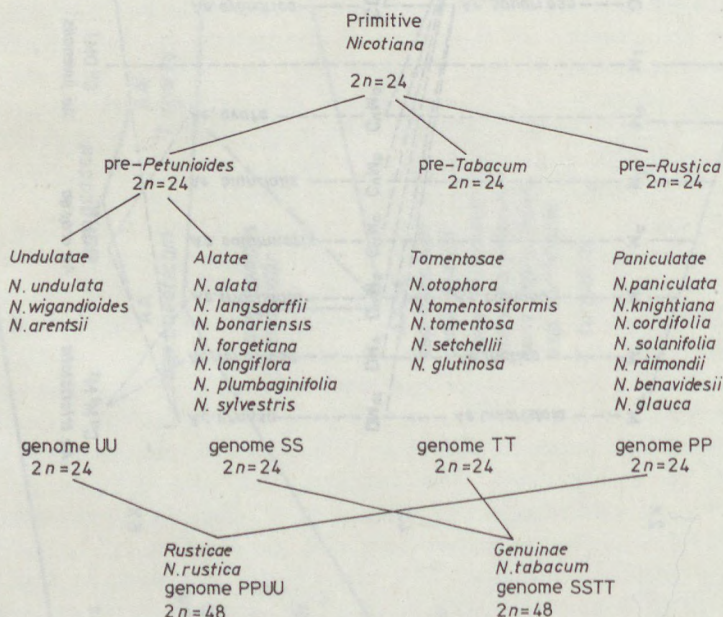


Fig. 13. Outline of the origin of tobacco (MAC KEY, 1970)

is the result of a cross between *N. undulata* and *N. paniculata* ($n=12$) followed by spontaneous allopolyploidisation (Fig. 13).

The currently cultivated species of cotton (*Gossypium hirsutum*), namely *G. barbadense* and *G. hirsutum*, are probably also derived from crosses between wild species (MAC KEY, 1970). This supposition is backed up by the work of the American researchers Harland and Beasley, who succeeded in doubling the chromosome number of the sterile first generation of a *G. thurberi* ($2n=26$) $\times$ *G. arboreum* ($2n=26$) cross by means of colchicine treatment, thus producing a completely fertile amphiploid, the plants of which could be readily crossed with American cultivated cotton to give fertile progeny (Fig. 14).

Research into the origin of various plant species gave rise to the idea of producing artificially synthesised species. This practical work then had a stimulating effect on research into the evolution of species developing in nature. These efforts not only broadened the range of knowledge on the evolution of existing species, but also led to the production of new, as yet totally unknown species.

An excellent example of this is the artificial synthesis of cultivated cotton species through allopolyploidy, as was mentioned above. A similar success was achieved in proving that the third genome (D) of hexaploid wheat (AABBDD) originated from *Aegilops squarrosa*. During the artificial amphiploidisation of *T. turgidum* ssp. *dicoccum* or ssp. *dicoccoides* $\times$ *Ae. squarrosa*, MCFADDEN-SEARS (1946) and KIHARA-LILIENFELD (1949) found that ssp. *spelta* segregated from the F_2 generation and that the plants obtained hybridised readily with naturally occurring ssp. *spelta* to give fertile progeny. BELEA (1976) selected speltoid types from later generations of a *T. turgidum* conv. *durum* $\times$ *Ae. squarrosa* allopolyploid. ZHIROV (1980) produced speltoid allopolyploids from the *T. timopheevii* $\times$ *Ae. squarrosa* combination. These data are confirmed by the results of heterochromatic staining. The examinations show that all the *Ae.*

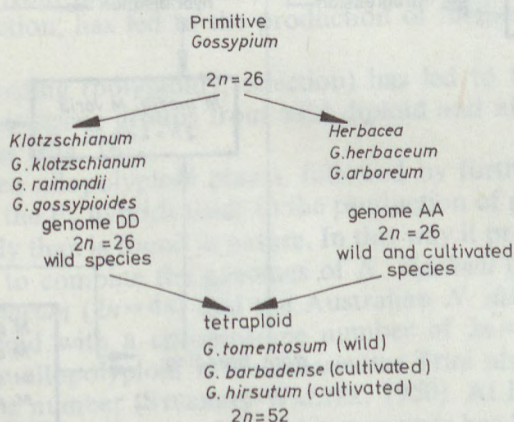


Fig. 14. Outline of the origin of cotton (MAC KEY, 1970)

squarrosa chromosomes have a characteristic staining pattern coinciding with the banding found for the chromosomes belonging to the D genome of hexaploid wheat.

The characteristic staining of the most distinctive marker chromosomes is as follows: on the shorter arm of the 7D chromosome there is a distinctive terminal band, below which a tiny heterochromatic dot can be observed. Below the centromere, which is poor in heterochromatic regions, two dots can be found on the longer arm (7D^L). The heterochromatic region of two-thirds of the arm is intensively stained. At the terminal end of the satellite of the 2D chromosome and its shorter arm (2D^S) there is a double band of intense staining, with a characteristic dot above the centromere. There is a double terminal band on the 2D^L arm. An intense interstitial band of staining can also be observed on the 5D^L chromosome. The centromere is not stained. Chromosome 6D contains the largest quantity of chromatin. Due to the very intense staining of the terminal heterochromatin, this chromosome is always easily recognised (BELEA, 1976). This is confirmed by chromosome pairing and traditional karyotypic analysis carried out by RILEY-CHAPMAN (1960).

A considerable amount of karyotypic similarity can be observed between *Gossypium* and the *Triticum-Aegilops* complex. In the *Triticum* genus, the gene regulating chromosome pairing is located on the 5B^L chromosome. Among the *Gossypium* species the A genomes of *G. barbadense* and *G. hirsutum* are constant, while the D genomes are modified. The A genome is homologous with that of an Asian diploid species which bears domesticated, self-fertile perennial traits. The D genome may have arisen from the wild American species *G. klatschianum*

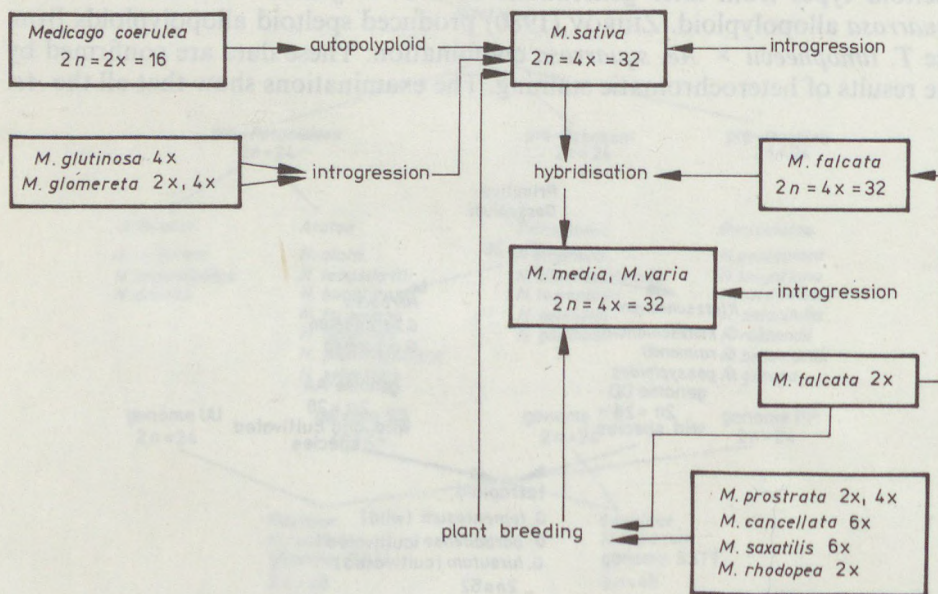


Fig. 15. Outline of the origin of cultivated alfalfa (SIMMONDS, 1976)

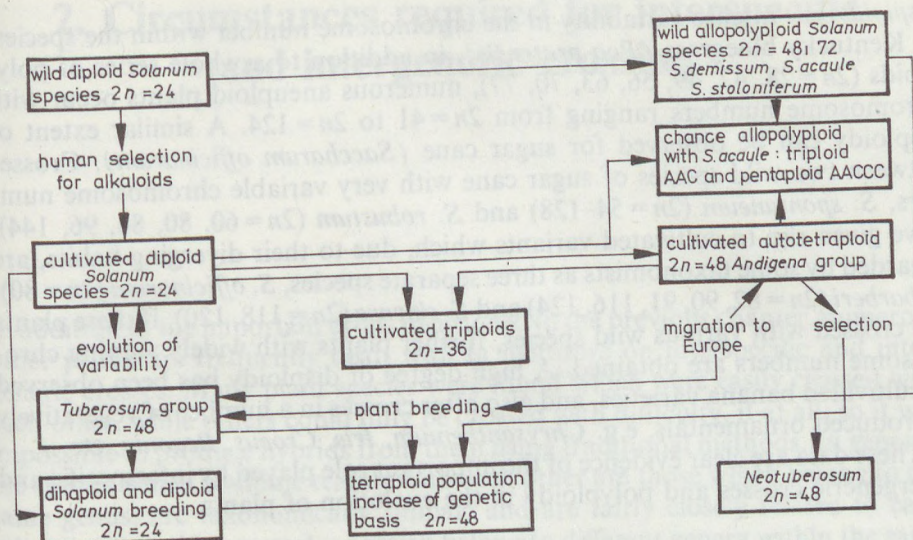


Fig. 16. Outline of the origin of cultivated potatoes (SIMMONDS, 1976)

or *G. raimondii*. Both diploid species are perennials, suitable for pollination by insects, and allogamous. The flowers of the former are large and deep red, while the flowers and stigmata of the latter are smaller. These structural differences are also very reminiscent of what has been said on the allopolyploid origin of *Nicotiana* and *Triticum-Aegilops*.

The *Aegilops cylindrica* (CD) species has also been artificially synthesised by the allopolyploidisation of the *Ae. caudata* (C) and *Ae. squarrosa* (D) species.

Crosses between the autotetraploid species *Medicago sativa*, *M. media*, etc. arising naturally from the diploid alfalfa species *Medicago coerulea*, followed by adequate selection, has led to the production of further *Medicago* species (Fig. 15).

Purposeful breeding (polyploidy, selection) has led to the creation of the *Tuberosum* and *Andigena* groups from wild diploid and allopolyploid potato (*Solanum*) species (Fig. 16).

Crosses between allopolyploid plants, followed by further doubling of the chromosomes of the F_1 hybrids leads to the production of plants with a higher level of polyploidy than is found in nature. In this way it proved possible in the *Nicotiana* genus to combine the genomes of *N. bigelovii* ($2n=48$), the South American *N. tabacum* ($2n=48$) and the Australian *N. debnigi* ($2n=48$) in a fertile allopolyploid with a chromosome number of $2n=144$ (KEHR-SMITH, 1952). The fertile allopolyploid *Bromus carinatus* Trini also has an extremely high chromosome number (STEBBINS-WALTER, 1950). At higher ploidy levels, the loss or introduction of one or more chromosomes has less influence on the equilibrium of the genome as a whole. This gives rise to the phenomenon of

disploidy, i.e. intense variability in the chromosome number within the species. In Kentucky bluegrass (*Poa pratensis*), in addition to a whole series of polyploids ($2n=28, 42, 49, 56, 63, 70, 77$), numerous aneuploid plants occur with chromosome numbers ranging from $2n=41$ to $2n=124$. A similar extent of dispoloidy can be observed for sugar cane (*Saccharum officinarum*). Crosses between two wild species of sugar cane with very variable chromosome numbers, *S. spontaneum* ($2n=54-128$) and *S. robustum* ($2n=60, 80, 84, 96, 144$), have given rise to cultivated variants which, due to their diverging habits, are regarded by some taxonomists as three separate species, *S. officinarum* ($2n=80$), *S. barberi* ($2n=82, 90, 91, 116, 124$) and *S. sinense* ($2n=118, 120$). If these plants are crossed with various wild species, further plants with widely varying chromosome numbers are obtained. A high degree of dispoloidy has been observed in cultivated banana varieties, and also after crosses in a number of vegetatively reproduced ornamentals, e.g. *Chrysanthemum*, *Iris*, *Crocus*, *Begonia*, etc.

These data are clear evidence of the important role played by interspecific and intergeneric crosses and polyploidy in the evolution of plants.

2. Circumstances required for interspecific and intergeneric crossing

In addition to the important crops mentioned in the previous chapter, numerous other plants are frequently dealt with in literature on interspecific and intergeneric crosses. Many plant species were found which were easily crossed with each other, while others could only be crossed with difficulty, if at all, so it was impossible to produce hybrids from them using traditional methods. In general, the species which combine readily with each other are those which belong to the same genus, are taxonomically similar, and are fairly closely related to each other (interspecific crosses), or which belong to different genera within the same family, where the species themselves are not too distantly related (intergeneric crosses). The majority of hybridisable genera belong to the same tribe of the given family (Fig. 17). Hybrids between genera belonging to different tribes are

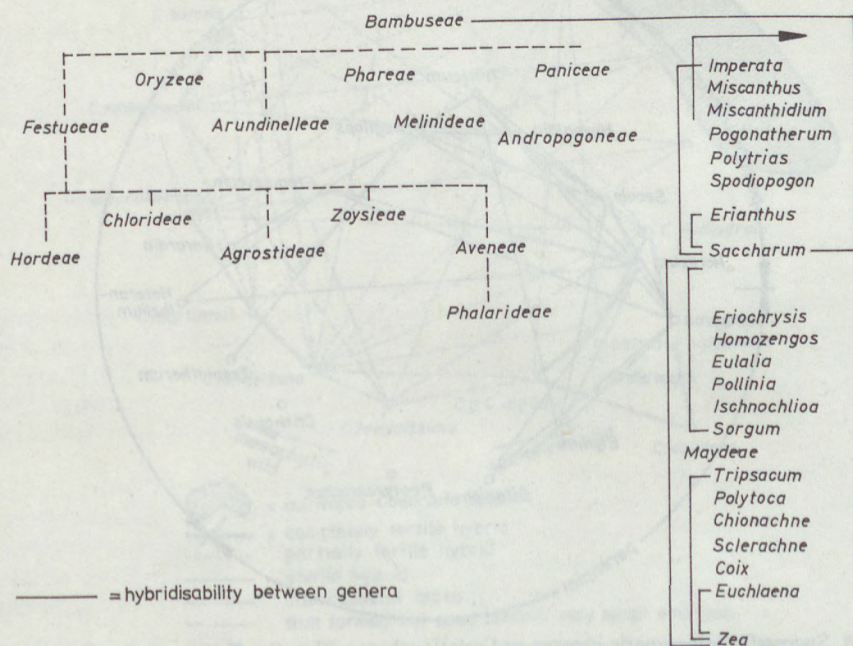


Fig. 17. Intergeneric hybrids (KRISHNAWAMY-CHANDRASEKHARAN, 1960)

extremely rare. According to the modern idea of biosystematics, the species of hybridisable genera should be considered rather as members of a comparium. Crosses between species belonging to different families are unknown to date in the case of higher plants, though research in this field (DNA hybridisation, protoplast fusion, gene manipulation) is extremely promising. Throughout the world, interest is centred on the possibility of crossing distant forms using experimental techniques.

A relatively large number of interspecific and intergeneric hybrids are known within the *Triticeae* tribe of the *Gramineae* family between genera belonging to the *Triticinae* subtribe (*Triticum*, *Secale*, *Agropyron*, *Avena*, *Aegilops*) (AHOKAS, 1973.; DEWEY, 1971) and the *Hordeae* subtribe (*Hordeum*, *Elymus*, *Sitanion*) (Fig. 18), and particularly between species within the various genera (BRINK et al., 1944; QUINCKE, 1940; RAJ-HÁTHY-SYMKO, 1963). Hybrids can be produced with similar ease in the *Andropogoneae* between *Sorghum*, *Iperata*, *Miscanthus* and *Saccharum* (LOH-WU, 1950; JANAKI AMMAL, 1938; RAGHAWAN, 1952; PRITCHARD, 1965), between various species (*Zea* – *Euchlaena*) of the *Maydeae* genus and within these genera (EMERSON-BEADLE, 1930; MANGELSDORF, 1947; FARQUHARSON, 1957), between various species of *Festuca* and *Lolium* (HESZKY, 1972a, b) and within the genera *Agrostis*, *Bromus*, *Poa*, *Phleum*, and *Stipa* (MYERS, 1947; ULLMANN, 1936; etc.).

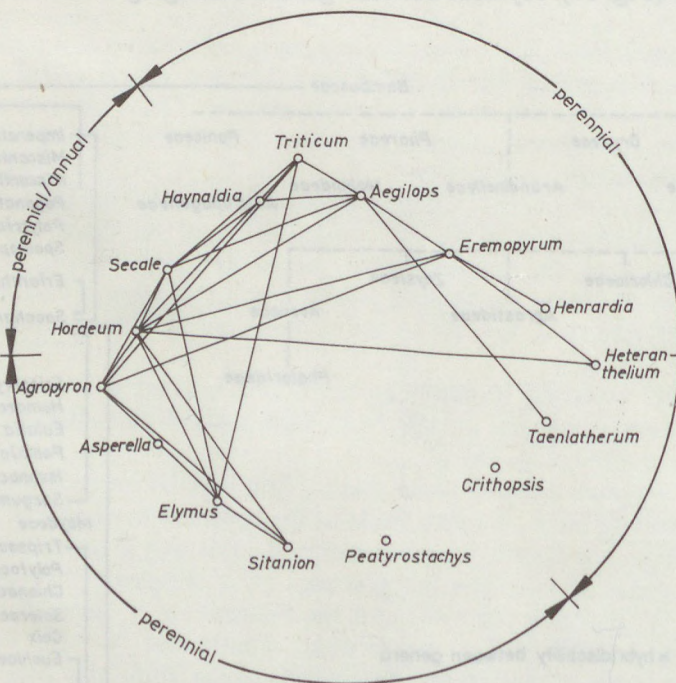


Fig. 18. Successful intergeneric crosses and relationships within the *Triticeae* tribe (SAKAMOTO, 1973)

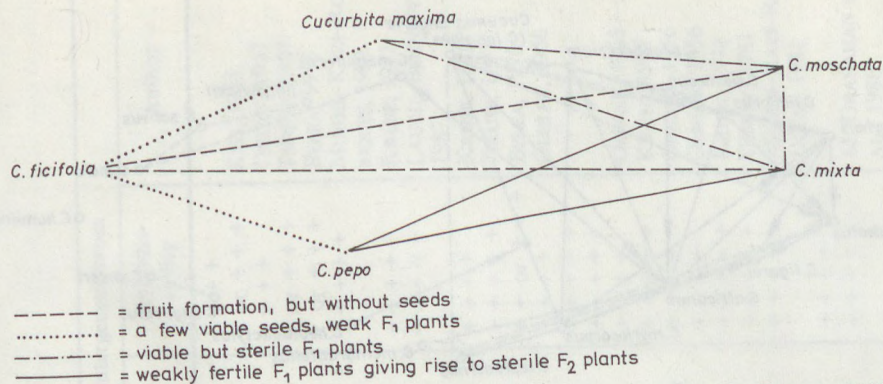


Fig. 19. Hybridizability of cultivated marrow species (ESQUINAS-ALCAZAR-GULIEK, 1983)

A large number of interspecific hybrids have also been described within the *Solanaceae* between various species of *Solanum* (PROPACH, 1938; HAWKES, 1958; SWAMINATHAN-HOWARD, 1953; HOUGAS-PELOGUNS, 1959), *Nicotiana* (BRIEGER, 1928, 1929; SUBHASHINI, 1973; EAST, 1928; GUPTA, 1969; GOODSPEED, 1945; KOSTOFF, 1930; TAKENAKA,

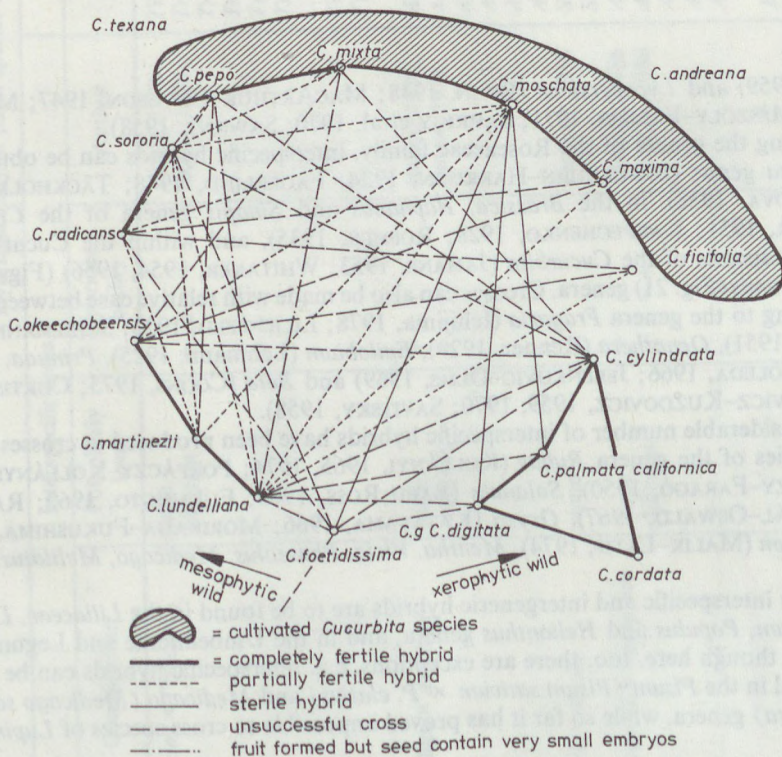


Fig. 20. Hybridizability of marrow species within the *Cucurbita* genus (ESQUINAS-ALCAZAR-GULIEK, 1983)

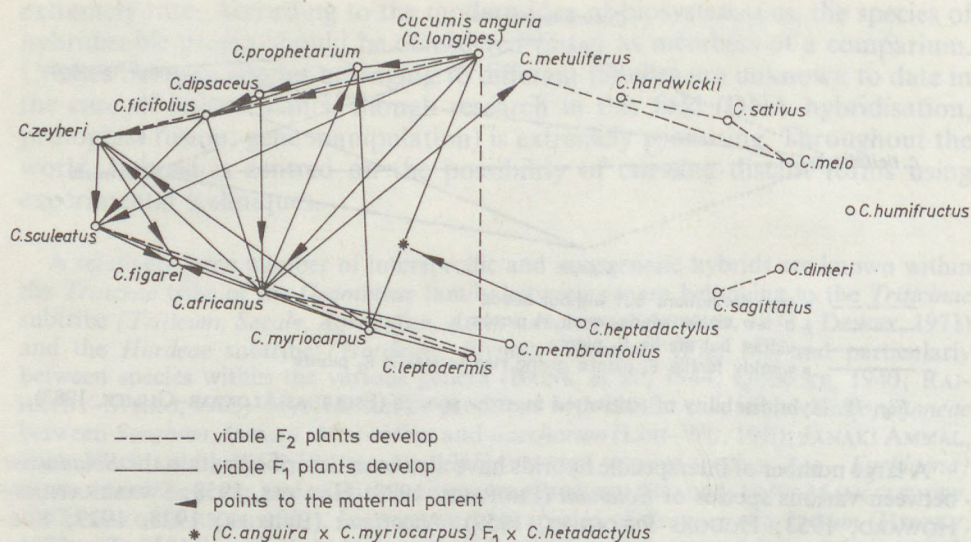


Fig. 21. Hybridisability of cucumber species (ESQUINAS-ALCAZAR-GULIEK, 1983)

1958, 1959) and *Lycopersicon* (BOHN, 1948; MACARTHUR-CHIASSON, 1947; MÉSZÖLY, 1968; MÉSZÖLY-FARKAS, 1971; SAHRIGY et al, 1970; SAWANT, 1958).

Among the genera of the *Roseaceae* family, interspecific hybrids can be obtained in the *Rosa* genus (BLACKBURN-HARRISON, 1924; FAGERLIND, 1948; TÄCKHOLM, 1922; ROZANOVA, 1938), in the *Brassica*, *Raphanus* and *Sinapis* genera of the *Cruciferae* (BECKER, 1951; KARPECHENKO, 1928; ROEMER, 1935), and within the *Cucurbitaceae* between species of the *Cucurbita* (JAMANE, 1953; WHITAKER, 1954, 1956) (Figs 19, 20) and *Cucumis* (Fig. 21) genera. Crosses can also be made with relative ease between species belonging to the genera *Fragaria* (Ichijima, 1978; LILIENFELD, 1933; SCHIEMANN, 1951; Staudt, 1951), *Oenothera* (Renner, 1929), *Epilobium* (Lehmann, 1925), *Primula*, *Prunus*, *Vitis* (KOLEDA, 1966; JELENKOVIC-OLMS, 1969) and *Beta* (COONS, 1975; CURTIS, 1967; FILUTOWICZ-KUZDOVICZ, 1959, 1970; SAVITSKY, 1958).

A considerable number of interspecific hybrids have been produced in crosses involving species of the genera *Rubus* (KOLLÁNYI, 1965, 1974; PORPÁČZY-KOLLÁNYI, 1963; PORPÁČZY-FARAGÓ, 1950), *Solanum* (BABU ROSS, 1965; FUKUMOTO, 1962; RAJKI E., 1966; PÁL-OSWALD, 1967), *Oryza* (KATAYAMA, 1966; MORINAGA-FUKUSHIMA, 1946), *Gossypium* (MALIK-LATIF, 1974), *Mentha*, *Vicia*, *Phaseolus*, *Medicago*, *Melilotus*, *Lotus*, etc.

Fewer interspecific and intergeneric hybrids are to be found in the *Liliaceae*, *Lactuca*, *Verbascum*, *Populus* and *Helianthus* genera, and in the *Umbelliferae* and *Leguminosae* families, though here, too, there are exceptions, e.g. interspecific hybrids can be readily produced in the *Pisum* (*Pisum sativum* × *P. elatius*) and *Medicago* (*Medicago sativa* × *M. falcata*) genera, while so far it has proved impossible to cross species of *Lupinus* and *Vicia*.

A similar lack of success in interspecific hybridisation can be observed in the genera *Papaver*, *Digitalis*, *Salvia*, *Lavandula* (WETTSTEIN, 1933), *Salix* (HÄKANSSON, 1929), etc.

Table 2.
Hybridisability of plant species and genera

Interspecific cross				Intergeneric cross		
Combination	Polyploidy level	Hybridisability	Author	Combination	Hybridisability	Author
<i>Triticum</i> × <i>Triticum</i>	same	+	BELEA, 1976	<i>Triticum</i> × <i>Elytrigia</i>	+	KISS, 1955
	different	+	BELEA, 1976	<i>Triticum</i> × <i>Secale</i>	+	TSITSIN, 1957
<i>Aegilops</i> × <i>Aegilops</i>		+		<i>Triticum</i> × <i>Haynaldia</i>	+	TSITSIN, 1957
		+		<i>Triticum</i> × <i>Agropyron</i>	+	BELEA, 1976
		+		<i>Triticum</i> × <i>Aegilops</i>	+	MUJEEB-KAZI-RODRIQUES, 1980
		+		<i>Triticum</i> × <i>Elymus</i>	+	KRUSE, 1973
		+		<i>Triticum</i> × <i>Hordeum</i>	+	LAURIE-BENNETT, 1987
		+		<i>Triticum</i> × <i>Zea</i>	+	KRUSE, 1973
<i>Aegilops</i> × <i>Aegilops</i>	same	+	BELEA, 1976	<i>Aegilops</i> × <i>Hordeum</i>	+	KRUSE, 1973
	different	+	BELEA, 1976	<i>Aegilops</i> × <i>Agropyron</i>	+	BELEA, 1976
		+		<i>Aegilops</i> × <i>Secale</i>	+	OEHLE, 1956
		+		<i>Aegilops</i> × <i>Haynaldia</i>	+	
<i>Secale</i> × <i>Secale</i>	same	+	OEHLE, 1956	<i>Aegilops</i> × <i>Elymus</i>	+	
		+		<i>Aegilops</i> × <i>Elytrigia</i>	+	
		+		<i>Secale</i> × <i>Agropyron</i>	+	
<i>Agropyron</i> × <i>Agropyron</i>	same	+	OEHLE, 1956	<i>Secale</i> × <i>Hordeum</i>	+	OEHLE, 1965
	different	+	OEHLE, 1956	<i>Agropyron</i> × <i>Haynaldia</i>	+	KRUSE, 1967
		+		<i>Agropyron</i> × <i>Sitanion</i>	+	OEHLE, 1956
		+		<i>Agropyron</i> × <i>Hordeum</i>	+	OEHLE, 1956
<i>Hordeum</i> × <i>Hordeum</i>	same	+	OEHLE, 1956	<i>Agropyron</i> × <i>Elymus</i>	+	KRUSE, 1974
	different	+		<i>Agropyron</i> × <i>Secale</i>	+	DEWEY, 1981
		+		<i>Elymus</i> × <i>Secale</i>	+	MUJEEB-KAZI-RODRIQUES, 1981
		+		<i>Hordeum</i> × <i>Agropyron</i>	+	McGRANAHAN ET AL., 1986
		+		<i>Hordeum</i> × <i>Aegilops</i>	+	FEDAK, 1980

Table 2. (continued)

Interspecific cross				Intragenic cross		
Combination	Ployploidy level	Hybridisability	Author	Combination	Hybridisability	Author
<i>Avena</i> × <i>Avena</i>	same	+	BROWN, 1964	<i>Hordeum</i> × <i>Elymus</i>	++	DEWEY, 1971
	different	++	BROWN, 1964	<i>Hordeum</i> × <i>Sitanion</i>	++	OEHLER, 1956
		++	BOHN ET AL., 1988	<i>Hordeum</i> × <i>Haynaldia</i>	++	OEHLER, 1956
<i>Panicum</i> × <i>Panicum</i>			MANGELSDORF-REEVES, 1931	<i>Avena</i> × <i>Triticum</i>	++	KRUSE, 1973
<i>Zea</i> × <i>Zea</i>	same	++		<i>Tripsacum</i> × <i>Panicum</i>	++	WILLIAMS-CAMERON 1936
<i>Oryza</i> × <i>Oryza</i>	same	++	OEHLER, 1956	<i>Zea</i> × <i>Euchlaena</i>	++	OEHLER, 1956
	same	+	BORGAONKAR, 1962	<i>Zea</i> × <i>Tripsacum</i>	++	MANGELSDORF-REEVES, 1931
<i>Pisum</i> × <i>Pisum</i>	same	++	OEHLER, 1956	<i>Oryza</i> × <i>Panicetum</i>	++	OEHLER, 1956
<i>Vicia</i> × <i>Vicia</i>	same	++	OEHLER, 1956	<i>Pisum</i> × <i>Vicia faba</i>	++	OEHLER, 1956
<i>Glycine</i> × <i>Glycine</i>	same	++	OEHLER, 1956	<i>Vicia</i> × <i>Vavilovia</i>	++	KONAREV ET AL., 1983
<i>Phaseolus</i> × <i>Phaseolus</i>	same	++	OEHLER, 1956	<i>Phaseolus</i> × <i>Vigna</i>	++	BALLON-YORK, 1959
<i>Cicer</i> × <i>Cicer</i>	same	++	JAISWAL, 1986			
<i>Lupinus</i> × <i>Lupinus</i>	same	++	OEHLER, 1956	<i>Medicago</i> × <i>Melilotus</i>	++	OEHLER, 1956
<i>Medicago</i> × <i>Medicago</i>	same	+	OEHLER, 1956	<i>Melilotus</i> × <i>Trigonella</i>	++	OEHLER, 1956
<i>Melilotus</i> × <i>Melilotus</i>	same	+	OEHLER, 1956	<i>Alyoria</i> × <i>Cajanus</i>	++	PUNDIR-SINGH, 1986
<i>Onobrychis</i> × <i>Onobrychis</i>	same	++	NASKIDASH-VILI-LOMSADZE, 1986			
<i>Lens</i> × <i>Lens</i>	same	+	OEHLER, 1956			

Table 2. (continued)

Interspecific cross				Intergeneric cross		
Combination	Ployploidy level	Hybridis-ability	Author	Combination	Hybridis-ability	Author
<i>Solanum</i> × <i>Solanum</i>	same	+	OEHLER, 1956	<i>Cassava</i> × <i>Manihot</i>	++	NASSAR-SILVA, 1986
<i>Manihot</i> × <i>Manihot</i>	different	++	OEHLER, 1956		++	SCREENIVASAN ET AL., 1984
<i>Beta</i> × <i>Beta</i>	same	++	NASSAR-SILVA, 1986		++	OEHLER, 1956
			OEHLER, 1956		++	SCREENIVASAN ET AL., 1984
<i>Saccharum</i> × <i>Saccharum</i>	same	+	OEHLER, 1956	<i>Saccharum</i> × <i>Euchlaena</i>	++	SCREENIVASAN ET AL., 1984
	different	++	OEHLER, 1956	<i>Saccharum</i> × <i>Sorghum</i>	++	OEHLER, 1956
				<i>Saccharum</i> × <i>Erlanthis</i>	++	SCREENIVASAN ET AL., 1984
				<i>Saccharum</i> × <i>Imperata</i>	++	SCREENIVASAN ET AL., 1984
				<i>Saccharum</i> × <i>Bambusa</i>	++	SCREENIVASAN ET AL., 1984
				<i>Saccharum</i> × <i>Zea</i>	++	SCREENIVASAN ET AL., 1984
<i>Arachis</i> × <i>Arachis</i>	same	++	MURTY-JAH-NAVI, 1986	<i>Saccharum</i> × <i>Miscanthus</i>	++	JELENKOVIC-OLMS, 1968
<i>Helianthus</i> × <i>Helianthus</i>	same	++	OEHLER, 1956	<i>Vitis</i> × <i>Vitis</i>	++	
	different	++	NORDENSKIÖLD, 1937			
<i>Gossypium</i> × <i>Gossypium</i>	same	+	OEHLER, 1956	<i>Jatropha</i> × <i>Ricinus</i>	++	
	different	++	OEHLER, 1956			
<i>Linum</i> × <i>Linum</i>	same	+	OEHLER, 1956	<i>Brassica</i> × <i>Sinapis</i>	++	OEHLER, 1956
	different	++	OEHLER, 1956	<i>Brassica</i> × <i>Diplotaxis</i>	++	RINGDAHL ET AL., 1987
	same	+	OEHLER, 1956	<i>Brassica</i> × <i>Eruca</i>	++	OEHLER, 1956
	different	++	OEHLER, 1956	<i>Eruca</i> × <i>Raphanus</i>	++	MATUZAWA-SARASHIMA, 1986
<i>Brassica</i> × <i>Brassica</i>		+		<i>Raphanus</i> × <i>Brassica</i>	+	OEHLER, 1956

Table 2. (continued)

Interspecific cross				Intergeneric cross		
Combination	Polyploidy level	Hybridisability	Author	Combination	Hybridisability	Author
<i>Lycopersicon</i> × <i>Lycopersicon</i> <i>Cucumis</i> × <i>Cucumis</i>	same different same different	+ ++ ++ ++ ++ ++	OEHLER, 1956 OEHLER, 1956 OEHLER, 1956 ESQUINAS-AL-CAZAR-GUILER, 1983 OEHLER, 1956 ESQUINAS-AL-CAZAR-GUILER, 1983	<i>Lycopersicon</i> × <i>Solanum</i>	++	O'CONNELL ET AL., 1986
<i>Cucurbita</i> × <i>Cucurbita</i>	same different	++ ++ ++ ++ ++ ++	OEHLER, 1956 ESQUINAS-AL-CAZAR-GUILER, 1983			
<i>Lactuca</i> × <i>Lactuca</i>	same different	+	OEHLER, 1956			
<i>Allium</i> × <i>Allium</i>	same	++	OEHLER, 1956			
<i>Papaver</i> × <i>Papaver</i>	same	+	OEHLER, 1956			
<i>Daucus</i> × <i>Daucus</i>	same	+	SALAMON, 1919			
<i>Capsicum</i> × <i>Capsicum</i>	same different	++ ++ ++ ++ ++ ++	STACE, 1975 CSILLÉRY, 1983 CSILLÉRY, 1983	<i>Capsicum</i> × <i>Lycopersicum</i>	++	WOJCIECHOWSKI-ANDRZEJEWSKI, 1986
<i>Rumex</i> × <i>Rumex</i>	same	++	STACE, 1975			
<i>Argemone</i> × <i>Argemone</i>	different	++	SHARMA, 1986			
<i>Setaria</i> × <i>Setaria</i>	same	+	OEHLER, 1956			
<i>Agrostis</i> × <i>Agrostis</i>	same	+	OEHLER, 1956	<i>Agrostis</i> × <i>Calamagrostis</i> <i>Agrostis</i> × <i>Polypogon</i>	++ ++	OEHLER, 1956 STACE, 1975
<i>Alopecurus</i> × <i>Alopecurus</i>	same	++	OEHLER, 1956			
<i>Bromus</i> × <i>Bromus</i>	same	++	OEHLER, 1956	<i>Bromus</i> × <i>Festuca</i>	++	STACE, 1975
<i>Festuca</i> × <i>Festuca</i>	same	++	OEHLER, 1956	<i>Festuca</i> × <i>Lolium</i> <i>Festuca</i> × <i>Glyceria</i>	++ ++	OEHLER, 1956 OEHLER, 1956

Table 2. (continued)

Interspecific cross				Intergeneric cross		
Combination	Polyploidy level	Hybridisability	Author	Combination	Hybridisability	Author
<i>Glyceria</i> × <i>Glyceria</i> <i>Dactylis</i> × <i>Dactylis</i> <i>Lolium</i> × <i>Lolium</i>	same	+	OEHLER, 1956	<i>Glyceria</i> × <i>Lolium</i>	+	OEHLER, 1956
	same	+	OEHLER, 1956	<i>Cynosurus</i> × <i>Dactylis</i>	++	OEHLER, 1956
	same	+	OEHLER, 1956	<i>Lolium</i> × <i>Dactylis</i>	+++	OEHLER, 1956
<i>Phleum</i> × <i>Phleum</i> <i>Poa</i> × <i>Poa</i>	same	++	OEHLER, 1956	<i>Lolium</i> × <i>Festuca</i>	+++	OEHLER, 1956
	same	+	OEHLER, 1956	<i>Lolium</i> × <i>Avena</i>	+++	OEHLER, 1956
<i>Nicotiana</i> × <i>Nicotiana</i>	same	++	OEHLER, 1956	<i>Phleum</i> × <i>Festuca</i>	+++	PRENDERGAST ET AL., 1988
	different	++	OEHLER, 1956	<i>Chloris</i> × <i>Cynodon</i>	+	FOJTIK ET AL., 1987
		++	OEHLER, 1956	<i>Arrhenatherum</i> × <i>Festuca</i>	++	
<i>Crocus</i> × <i>Crocus</i>	same	++	OEHLER, 1956	<i>Nicotiana</i> × <i>Lycopersicum</i>	++	OEHLER, 1956
		++	OEHLER, 1956	<i>Nicotiana</i> × <i>Petunia</i>	+++	OEHLER, 1956
<i>Lotus</i> × <i>Lotus</i>	same	+	CAIOLA-CHIRICCO, 1986	<i>Hyoscyamus</i> × <i>Nicotiana</i>	++	ZENKTELER-SLUSARKIEWICZ, 1985
<i>Lathyrus</i> × <i>Lathyrus</i>	same	++	O'DONOUGHNE, 1988			
<i>Viola</i> × <i>Viola</i>	same	++	OEHLER, 1956			
<i>Amaranthus</i> × <i>Amaranthus</i>	same	++	STACE, 1975			
<i>Malva</i> × <i>Malva</i>	same	++	STACE, 1975	<i>Hibiscus</i> × <i>Abelmoschus</i>	++	HAMON-YAPO, 1986
		++	KRISTOFFERSON, 1926			
<i>Spiraea</i> × <i>Spiraea</i>	same	++	STACE, 1975			
<i>Rosa</i> × <i>Rosa</i>	same	++	BLACKBURN-HARRISON, 1924			
<i>Ocimum</i> × <i>Ocimum</i>	different	++	KHOSLA, 1988	<i>Achillea</i> × <i>Chrysanthemum</i>	++	STACE, 1975
<i>Chrysanthemum</i> × <i>Chrysanthemum</i>	same	++	CONTANT, 1963			
<i>Delphinium</i> × <i>Delphinium</i>	same	+	BORGAONKAR, 1962			

Table 2. (continued)

Interspecific cross			Intergeneric cross		
Combination	Polyploidy level	Hybridis-ability	Author	Combination	Hybridis-ability
<i>Digitalis</i> × <i>Digitalis</i>	same	++	STACE, 1975		
<i>Saxifraga</i> × <i>Saxifraga</i>	same	++	STACE, 1975		
<i>Oenothera</i> × <i>Oenothera</i>	same	++	STACE, 1975		
<i>Pimpinella</i> × <i>Pimpinella</i>	same	++	STACE, 1975		
<i>Primula</i> × <i>Primula</i>	same	++	STACE, 1975		
<i>Veronica</i> × <i>Veronica</i>	same	++	STACE, 1975		
<i>Mentha</i> × <i>Mentha</i>	same	++	STACE, 1975		
<i>Salvia</i> × <i>Salvia</i>	same	++	STACE, 1975		
<i>Narcissus</i> × <i>Narcissus</i>	same	++	MASHANOV— LODYINENKO, 1986		
<i>Lavandula</i> × <i>Lavandula</i>	same	++	SAPRE—DESH— PANDE, 1987		
<i>Coix</i> × <i>Coix</i>	same	++	SHIONTANI— KAWASE, 1987		
<i>Ipomoea</i> × <i>Ipomoea</i>	same	++	DWVAL—BIES— BOER, 1988		
<i>Zizania</i> × <i>Zizania</i>	same	++	OEHLER, 1956		
<i>Ribes</i> × <i>Ribes</i>	same	++	BALLINGTON ET AL., 1986		
<i>Vaccinium</i> × <i>Vaccinium</i>	same	++	OEHLER, 1956		
<i>Rubus</i> × <i>Rubus</i>	different	++	OEHLER, 1956		
<i>Rubus</i> × <i>Rubus</i>	same	+	FADDEVA, 1966	<i>Fragaria</i> × <i>Potentilla</i>	+++
<i>Fragaria</i> × <i>Fragaria</i>	same	++	JANKUN— KOVANDA, 1988	<i>Fragaria</i> × <i>Rubus</i>	+
<i>Sorbus</i> × <i>Sorbus</i>	same	++			
					OEHLER, 1956
					OEHLER, 1956

Table 2. (continued)

Interspecific cross				Intergeneric cross		
Combination	Polyploidy level	Hybridis-ability	Author	Combination	Hybridis-ability	Author
<i>Laurus</i> × <i>Laurus</i>	same	++	TODUA, 1986			
<i>Cinnamomum</i> × <i>Cinnamomum</i>	same	+++	TODUA, 1986			
<i>Citrus</i> × <i>Citrus</i>	same	+	KAHN-DE-MASON, 1986	<i>Citrus</i> × <i>Poncirus</i>	+++	TUTBERIDZE, 1986
<i>Coffea</i> × <i>Coffea</i>	same	+	ZAPATA-RUIZ, 1985	<i>Fortunella</i> × <i>Citrus</i>	+++	KOKAYA, 1987
<i>Salix</i> × <i>Salix</i>	same	+	OEHLER, 1956			
<i>Populus</i> × <i>Populus</i>	same	++	OEHLER, 1956			
<i>Ficus</i> × <i>Ficus</i>	same	++	RAMIREZ, 1986			
<i>Malus</i> × <i>Malus</i>	same	+	OEHLER, 1956	<i>Cydonia</i> × <i>Malus</i>	++	SMYKOV ET AL., 1985
<i>Pyrus</i> × <i>Pyrus</i>	same	+	OEHLER, 1956	<i>Cydonia</i> × <i>Pyrus</i>	++	OEHLER, 1956
<i>Pyrus</i> × <i>Pyrus</i>	different	++	OEHLER, 1956	<i>Pyrus</i> × <i>Malus</i>	++	OEHLER, 1956
		++		<i>Pyrus</i> × <i>Cydonia</i>	++	OEHLER, 1956
		++		<i>Pyrus</i> × <i>Sorbus</i>	++	AHMAD KUSHAIRI, 1985
<i>Prunus</i> × <i>Prunus</i>	different	++	OEHLER, 1956	<i>Corozo</i> × <i>Elaeis</i>	++	
<i>Morus</i> × <i>Morus</i>	same	++		<i>Pterocarya</i> × <i>Juglans</i>	++	MCGRANAHAN, 1986
<i>Juglans</i> × <i>Juglans</i>	same	++			++	

+ = very easy; ++ = easy; +++ = fairly difficult; ++++ = difficult; +++++ = very difficult

It is very difficult to achieve hybridisation between *Zea* and *Coix lacryma-jobi*, and between species of *Scleranchne* (which is related to *Coix*, but has $2n = 20$ chromosomes) and the *Polytoca* genus with *Zea*.

Though it is impossible to give a complete list, a wide range of interspecific and intergeneric hybrids are summarised in Table 2.

The success or lack of success of this work is influenced by numerous factors, the most important of which are the crossing technique, the climatic conditions, the flowering time, the hybridisability of the species – varieties – cultivars – biotypes, the direction of crossing, the polyploid level, genome differences, etc. A number of these factors act constantly, so it is very difficult to decide which of the factors inhibiting success play the most important roles, and which reduce or increase the effects of other factors in the course of hybridisation. If breeding is to be successful, a knowledge of the flower structures and flowering biology of the various plants, which will be dealt with below, is essential.

In the flowers of 70% of flowering plants both stamens and pistils develop. Such flowers are known as hermaphroditic (or androgynous) and are found in wheat, barley, oats, flax, rape, potatoes, etc. If only stamens or only pistils mature in the flowers, they are referred to as diclinous male or female flowers. Plants which have separate staminate and pistillate flowers on the same individuals are referred to as monoecious (e.g. maize, marrow, cucumber, walnut, oak, etc.), while those where the staminate and pistillate flowers develop on separate individuals are known as dioecious (e.g. hemp).

During pollination, the pollen is deposited straight onto the ovule in gymnosperms and onto the stigma in angiosperms. Both self-pollinating plants (wheat, barley, peas, flax, etc.) and cross-pollinating plants are known, the latter being considerably more frequent. In cross-pollinated hermaphrodites, self-pollination is prevented by various mechanisms. Most frequently, the anthers and the stigma mature at different times. If the stigma has not matured when the anthers ripen, the flowers are proterandrous, whereas if the stigmata ripen before the dehiscence of the anthers, the flowers are proterogynous.

If pollination takes place without outside interference, we speak of direct pollination. This is facilitated by the location of the anthers and the stigma. More frequently, however, even in the case of self-pollination, external forces (water, wind, insects) assist the transfer of the pollen to the stigma.

2.1 Flower opening

Before crossing can be carried out, it is important to know the flowering time of the plants. There are considerable differences between plants in this respect. Depending on the variety and the temperature, various plants flower at different times and for longer or shorter periods. The flowering of flax, maize, aubergine, etc. lasts for some two weeks. Depending on the variety and the production environment, cotton bushes may flower for several weeks. The flowering of

green peppers may also extend for a considerable period. The flowering of many plants lasts for only 2–3 or at most 12 days (barley, sorghum, millet, potatoes, etc.). Wheat flowers a few days after heading. First the ears of the main shoot and then those of the side-shoots flower. The flowers open first in the middle of the ear, followed by the upper and finally the lower third.

The opening of the flowers also depends on the time of day. The flowers of some plants open in the morning (sorghum, maize, aubergine, etc.), others at mid-day (e.g. millet), and some during two periods (from 6–8 a.m. and from 3–5 p.m.), such as barley and rice. The flowers of convolvulus, morning glory, chicory, dandelion, etc. open at dawn, while those of hesperis, evening primrose, etc. open at dusk.

2.2 Flowering time

One of the major difficulties encountered in interspecific and intergeneric crossing is the lack of synchronisation in the flowering of the parent species, though this difficulty is fairly easy to overcome. It is now possible, using suitable storage conditions, to prolong the germination ability of the pollen, and the stigma can also be made fit for fertilisation. Nevertheless, crosses are not always successful. There may be numerous reasons for this, one of which is differences in flowering time.

The success of many interspecific and intergeneric crosses depends largely on the adequate synchronisation of the flowering times of the parent species. If crosses are to be made, the single or composite flowers of the two parents must open at the same time. The closer the flowering times of the two parent species, the more likely the cross is to be successful; and the greater the difference in flowering times, the less chance there is of achieving satisfactory results. It is particularly important for the flowering times to coincide for plant species which produce few flowers or which only flower for a short period. There is more likelihood of the flowering times coinciding if each flower remains open for a longer period. In the *Triticinae* subtribe, for instance, the synchronisation of flowering times is a more important factor in interspecific and intergeneric crossing than the closeness of the relationship between the species, or differences in chromosome number and genome quality. Early ripening wheat varieties give 20–50% seed setting with rye, while wheat varieties flowering 2–3 weeks later give a seed setting of only 0–7%. In the crosses *Aegilops* × *Triticum* and *Aegilops* × *Secale*, seed setting is again substantially better if the parent species flower at the same time than when the flowering times are very diverse.

Several methods are available for the elimination or reduction of the flowering time differences which hinder interspecific and intergeneric crosses. It is often possible to synchronise the flowering of the parent species by preliminary raising in the greenhouse, by cutting back the first shoots of one of the parents or keeping them refrigerated to delay the flowering time. In the case of grasses, for example, it may be sufficient to cut the ears and keep them in water in a warm, sunny room. If the difference between the flowering times of the parents

is too great, periodic sowing or photoperiodic treatment may lead to success. The spring sowing of vernalised winter parental species may also be successful, depending on whether the flowering time needs to be lengthened or shortened. Repeated cloning may also be a suitable method in the case of certain flowers, or for wild species of *Agropyron*, *Hordeum*, etc.

2.3 Climatic conditions

The flowering time is greatly influenced by the temperature, the air humidity, the sunlight duration, the wind, etc. On sunny, warm days, flowering begins earlier and lasts for a shorter time. In moist, rainy weather, on the other hand, the plants flower later, but for a longer period. Aubergines, for example, begin flowering in the morning hours at high temperature and humidity, while low temperature and humidity delay the opening of the flowers.

Crosses are more successful if the optimum flowering time of the plants is also taken into consideration. Crosses between species belonging to various genera (*Triticum*, *Aegilops*, *Hordeum*, *Secale*, *Agropyron*) of the *Triticinae* subtribe are much more likely to succeed if carried out under warm dry conditions, while the species of other genera (*Avena*, *Brassica*, etc.) can be better crossed in cool, humid weather. The most satisfactory conditions for fertilisation in the *Gramineae* are a temperature of 20–25° C and a relative humidity of 60–70%. CARTER-McNEILLY (1973, 1975, 1976) found great differences when they examined the effect of humidity on pollination, the germination of the pollen tube, and seed setting. As the humidity rose and the temperature dropped, crosses became more successful, particularly if species-alien pollen was used to stimulate fertilisation.

Certain interspecific crosses in potato (*Solanum*), such as *S. polyadenium* × *S. jamesii*, are only successful in autumn, when the weather has turned cooler. In potatoes, temperatures higher than 20° C cause a serious reduction in the seed setting percentage, especially if the plant is exposed to high temperature 48 hours prior to flower opening or for the next 72 hours. In a similar manner, crosses between tobacco (*Nicotiana*) and tomato (*Lycopersicon*) species also give different results in autumn and spring. This is why quite different results may be achieved in many cases for the same interspecific and intergeneric crosses, depending on where they were carried out and under what climatic conditions. If the flowering of the parent species is extended over a longer period, the success of the cross is determined by the climatic conditions observed during various periods. The heat effect is more closely correlated with the maturity of the flowers than with the date of pollination.

There are also considerable differences between the plants as regards the ability of the stigma to become fertilised. The stigma of the sunflower can be fertilised for a period of 23–25 days. ROSS-WEBSTER (1959) found that the stigma of male sterile sorghum could only be fertilised with difficulty after the 5th day from full flowering, and not at all by the 6–7th day. The stigmata of

Table 3:
Effect of the state of development of the wheat stigma on seed setting, expressed as a percentage

Effect of the state of development of the wheat stigma on seed yield															
No. of days after castration	<i>T. timopheevii</i> × ssp. <i>carthlicum</i>					<i>T. timopheevii</i> × ssp. <i>dicoccum</i>					<i>T. timopheevii</i> × <i>T. aestivum</i>				
	I.	II.	III.	IV.	V.	I.	II.	III.	IV.	V.	I.	II.	III.	IV.	V.
	state of development of the stigma														
	No. of seeds, % *														
1						1.3									
2						0.8						14.1			
3							0.3					7.5			
4							15.5						2.5		
5		0.8	13.3				26.9						4.2		
6			8.3					19.7						2.5	
7				30.8				25.8						2.5	
8				34.1					17.2					4.2	
9					15.8				9.4						
10										8.6					
										0.5					0.8

* where the number of fertilised stigmata = 100%

cereals can be fertilised for 2–3 days, or possibly for as long as 12 days, depending on the weather.

For the pollination of wheat, too, sufficiently mature stigmata and pollen are required. BELEA (1964) examined wheat stigmata at various phases of development in order to determine the optimum time for crossing. If the lobes of the stigma are still completely undeveloped and the pappus is still missing, the stigma is in development phase I. In the following phase (II), the pappus appears and the lobes become more distinct. Development phase III is characterised by the development of the stigma lobes. In development phase IV the stigma lobes are completely developed, while in the last phase of development (V) the lobes can be seen emerging from among the glumes, and the ovaries, too, are well developed. Depending on the plant species, the stigma is most suitable for pollination when it is still young and not completely developed, or (in the case of wheat) in development phase IV (Table 3). When crossing barley species, however, very undeveloped (phases II–III) stigmata, still in “boot”, give the best results, due to the strictly self-fertilising (flowering “in boot”) nature of barley.

In wheat, anthers which are yellowy green and have not yet opened are most suitable for pollination. When placed on the stigma, particularly in warm, sunny weather, they will split open within a short time and be capable of pollination. If possible, the flowers of the main ear should be fertilised, as the flowers in the side-ears produce less viable stigmata. Pollen should best be collected in the early morning. Pollination carried out in bright sunshine at mid-day is usually unsuccessful. If, for any unforeseen reason, the pollen cannot be used on the day it is collected, it can be kept in a refrigerator at 0° C until the next morning without suffering any damage. The best temperature for long-term storage is –90° C, for instance in the case of maize. Pollen frozen in this way can be stored for an unlimited period.

The best time for pollinating potatoes is from two days before flower opening to three days after opening. Within this period, the best results are obtained by pollinating on the day of flowering or the next day. For maize, too, it has been observed that if the stigma becomes too long, i.e. if pollination is delayed, there is a reduction in seed setting.

2.4 Crossing techniques

Depending on the plant species, countless crossing methods are known, of which only a few of the most important will be outlined here. In principle, the technique of interspecific and intergeneric crossing within the same tribe is basically the same as that for variety crossing.

In practice, various crossing methods are employed, depending on the crossing partners and the aim of the cross. Within the *Triticinae* subtribe, for example, the anthers are removed from the ears of the female parent using tweezers and the ear is then isolated with a cellophane bag. Following this, pollen from the chosen male parent is placed on the stigma using tweezers or

a brush. The Lukyanenko method of group pollination can also be applied, in which case several pollinator ears are cut and tied beside the castrated female ear. They are then stood in a phial of water and covered with a parchment bag. This method can only be employed if a sufficient quantity of well flowering pollinator plants are available. A slightly modified version of Borlaug's pollination method can also be successfully applied, particularly for the crosses *Triticum* $\times$ *Secale* and *Aegilops* $\times$ *Secale*. In this case, a quarter or a third of the rye glume is cut back with scissors, after which the three immature (green) anthers extending above the stigma are removed in a single action, taking care not to damage any of them. Finally, after isolation under cellophane for 1–2 days, the pollinator and the castrated female ear are placed under a common parchment isolator.

The anthers of the hermaphroditic brassicas must also be removed in the yellow bud stage before they reach maturity, after which the flower is isolated using a cellophane bag. In the same way, flowers with which the female plant is to be pollinated must also be isolated in the bud.

If the flowers are monoecious it is sufficient to isolate the female flowers (using cellophane or parchment bags) in order to avoid cross-pollination. The pollen of the chosen male species is introduced onto the stigma in various ways. In maize, sorghum, millet, etc. the pollen collected is simply sprinkled onto the flower, while in sunflower the pollen is brushed onto the stigma using a cloth. After pollination the female flower must again be isolated until the grain, seed or pods are formed. It is important to label these plants or shoots.

One way of castrating en masse, in the case of sorghum for instance, is to place the panicle in water at 50° C for 10 minutes, thus destroying the pollen. There are various other methods of mass castration, though these are not used in interspecific and intergeneric crosses. These include the production of cytoplasmically or genically male sterile female plants, a method widely used for maize and sorghum, and which is still being elaborated for wheat and other plants (e.g. tobacco). More recently the pollen of the female plants is made male sterile using chemicals (2,4-dichlorophenoxyacetic acid 50 mg/kg; naphthylacetic acid 50 mg/kg; maleic acid hydrazide, triiodobenzoic acid, or unknown compounds produced by various chemical works), making castration unnecessary. This method is gaining ground for wheat in particular.

Although in many cases it is still not clear why difficulties are encountered in crossing certain plant species, numerous methods have been elaborated to overcome the factors inhibiting the success of crossing. It is the general experience that sometimes one method will lead to success and sometimes another, depending on the local conditions, on the species or biotypes employed, and on many other factors.

Frequently there are differences in the flower structures of the parental species, as in the case of *Nicotiana*, where one parental species has an extremely long style and pappus, while those of the other species are short. The pollen tubes of the short-styled parent are incapable of reaching the ovaries of the other parent due to the length of the style. This problem can be overcome by cutting

back the style and pollinating the cut surface (*Zea* × *Tripsacum*) or by using a section of style from the pollinator. Successful crosses made in this way are reported in *Datura* (GARDELLA, 1950) and *Linum* (SIZOVA, 1958).

In the Soviet Union good results were achieved by mixing a little pollen from the female with that of the male parent, e.g. in the case of the *Agropyron* × *Triticum* cross (MICHURIN, 1925). Successful crosses were also made using this method in *Brassica* species combinations (OCKENDON, 1977), where observations showed that a seed setting of 12–14% could be achieved with mixed pollen, as opposed to only 2–4% when the pollen of the alien parent was applied alone. There were also differences in the degree of seed setting depending on the period that elapsed between the application of the plant's own pollen and that of the alien pollen. Both ROGGEN (1975) and MÉSZÖLY (1968) successfully crossed *Lycopersicon esculentum* with *L. peruvianum*. The stigma of the female species was first lightly pollinated with its own pollen, after which the pollen of *L. peruvianum* was placed on the *L. esculentum* stigma on five occasions on five consecutive days.

Another method which can be successfully employed in interspecific and intergeneric crosses is the vegetative approximation, whereby the young embryos of the female parent are placed in the endosperm of the male species (MICHURIN, 1925; PISSAREV-VINOGRADOVA, 1945). When transplanting wheat embryos into rye endosperms, HALL (1954) obtained and raised considerably more F_1 plants than by simple crossing. Various other approaches are reported by PETROV (1955); these methods can be usefully employed in practice.

The use of an intermediate species is also a well-known practice in crosses between cultivated plant species. This has been a generally applied method of overcoming hybridisation problems especially since the work of MICHURIN (1925). SEARS (1955) transferred the disease resistance of *Aegilops umbellulata* into common wheat (*Triticum aestivum*) through the intermediary of conv. *durum*, since this species can be more readily crossed with *Ae. umbellulata*. In the cross *Ae. comosa* × *T. aestivum* RILEY (1966) used ssp. *dicoccum* as the intermediate, while KISS (1956) employed conv. *durum* as the intermediate when crossing *T. aestivum* with *T. timopheevii*. BELEA (1960, 1961, 1976) found ssp. *carthlicum* and ssp. *dicoccum* suitable for this purpose in the combination *T. aestivum* × *T. timopheevii*.

The use of larger numbers of anthers (1, 2, 3), i.e. varying quantities of pollen, may be successful, depending on the amount of pollen contained by the anthers. In the cross *T. timopheevii* × *T. aestivum* an increase in the number of anthers significantly increased the seed setting, since the anthers of common wheat contain relatively little pollen. In the reciprocal cross an increase in the number of anthers did not affect the percentage seed setting. In the combination *T. timopheevii* × ssp. *dicoccum* it proved sufficient to use two anthers (Table 4). This is probably due to the fact that ssp. *dicoccum* has large anthers, more than two of which can only be placed on the stigma of the female plant with difficulty.

Table 4.

Success of crossing as a function of the number of anthers utilised

Combination	1 anther			2 anthers			3 anthers		
	No. of flowers crossed	No. of seed obtained	% Seed setting	No. of flowers crossed	No. of seed obtained	% Seed setting	No. of flowers crossed	No. of seed obtained	% Seed setting
<i>T. timopheevii</i> × <i>T. aestivum</i>	456	7	1.5	456	26	5.7	432	33	7.6
<i>T. aestivum</i> × <i>T. timopheevii</i>	120	2	1.6	120	1	0.8	120	2	1.6
<i>T. timopheevii</i> × <i>ssp. dicoccum</i>	936	147	14.7	936	164	17.5	936	163	17.4

Repeated pollination may also be successful in crosses between numerous plant species or genera (MICHURIN, 1925). In the combinations *T. aestivum* × *T. timopheevii* and *ssp. dicoccum* × *T. aestivum*, for example, better results are obtained by pollinating twice or three times, rather than just once (Table 5). Improved seed setting was also achieved by repeated pollination for tomatoes, cotton and cabbages.

Hormones and other stimulants are also used to overcome difficulties in crossing. In various interspecific crosses of marrow, for instance, where the growth rate of the pollen tube is extremely slow (e.g. in the combinations *C. dipsaceus* × *C. figarei* and *C. dipsaceus* × *C. pepo*) and thus rarely reaches the ovary, and when crossing certain species of *Solanum*, where the pollen of *S. verrucosum*, for example, is incapable of penetrating the stigmata of certain self-sterile biotypes of diploid potatoes, hormones are used to stimulate the growth of the pollen tubes (DUNWELL-SUNDERLAND, 1973). On the stigma of *Brassica napus* conv. *oleifera* the pollen does not produce tubes until after a period of 45 minutes and the process of fertilisation takes 18–24 hours if stimulants are not applied (KAVECKA, 1958). Certain researchers used microelements (e.g. boron) to stimulate pollen germination (TUKEY, 1954; SMITH, 1957).

Table 5.

Effect of repeated pollination on seed setting

Combination	No. of flowers crossed	1 pollination		2 pollinations		3 pollinations	
		No. of seed obtained	% Seed setting	No. of seed obtained	% Seed setting	No. of seed obtained	% Seed setting
<i>T. timopheevii</i> × <i>T. aestivum</i>	543	23	4.2	26	4.8	33	6.1
<i>T. aestivum</i> × <i>T. timopheevii</i>	480	7	1.5	23	4.8	29	6.0
<i>ssp. dicoccum</i> × <i>T. aestivum</i>	120	15	12.5	19	15.8	34	28.3
<i>T. aestivum</i> × <i>ssp. dicoccum</i>	160	17	10.6	19	11.9	20	12.5

BATES and co-workers (1975) experimented with various animal immune suppressors (E-amino caproic acid = EACA; acriflavine, chloramphenicol, salicylic acid, etc.), the most efficient of which proved to be the lysine analogue E-amino caproic acid (EACA). Using this compound a 10% rate of hybrid embryos was obtained (and successfully raised) in the combinations *Triticum* × *Hordeum*, *Zea* × *Sorghum*, *Hordeum* × *Avena* and *Hordeum* × *Secale*. In intraspecific crosses (*Zea* × *Tripsacum*, *Zea* × *Euchlaena*) gibberellic acid (GA_3) was also used with success.

ROGGEN-VAN DIJK (1972) promoted seed setting with the aid of electric currents, thus achieving success in the raising of viable hybrid plants in inter-specific *Brassica* crosses.

2.5 Hybridisability of species

The extremely extensive literature on interspecific and intergeneric crosses provides a summary of the major theoretical findings and practical results achieved by researchers. Numerous data are available to show that, irrespective of the chromosome number, the genome quality (both of which will be discussed later) and the reasons mentioned above (e.g. differences in flower structure), different species can be crossed with each other to various extents.

Several authors have dealt with the phenomenon and causes of compatibility-incompatibility and with ways of overcoming it. As we know, the majority of flowers are androgynous. In many species self-fertilisation is a regular occurrence. There are many other species, however, such as cabbage (*Brassica*), where a special genetic mechanism prevents self-fertilisation. In cabbages, this character depends on the fact that the S genes have a whole series of alleles, designated by the symbols S^1 , S^2 , S^3 . Some plants only contain the allele pairs S^1S^2 or S^1S^3 . If the same allele is found in the pollen as in the stigma, the pollen will fail to germinate, or will only germinate extremely slowly. It is obvious that in such cases self-fertilisation becomes impossible, since the stigma and the pollen are found in the flowers of the same plant and contain the same alleles. The homologous nature of the alleles in the pollen and the stigma results in genetic incompatibility in the plants to be crossed.

Thus, any two plants containing the same S^n allele cannot be crossed with each other. If, however, the plants to be crossed do not contain homologous alleles (e.g. S^1S^2 × S^3S^4), the pollen germinates well and develops a normal pollen tube (OLSSON, 1960). It is clear that, in the case of natural crosses, the larger the number of S alleles present in the population, the lower the incidence of incompatibility. The evolutionary system of incompatibility excludes the possibility of self-fertilisation in androgynous plants, but promotes the cross-pollination of many plants.

Crosses were carried out by BELEA (1976) on numerous *Triticum*, *Aegilops* and *Secale* species belonging to the same subtribe, *Triticinae*, for various theoretical

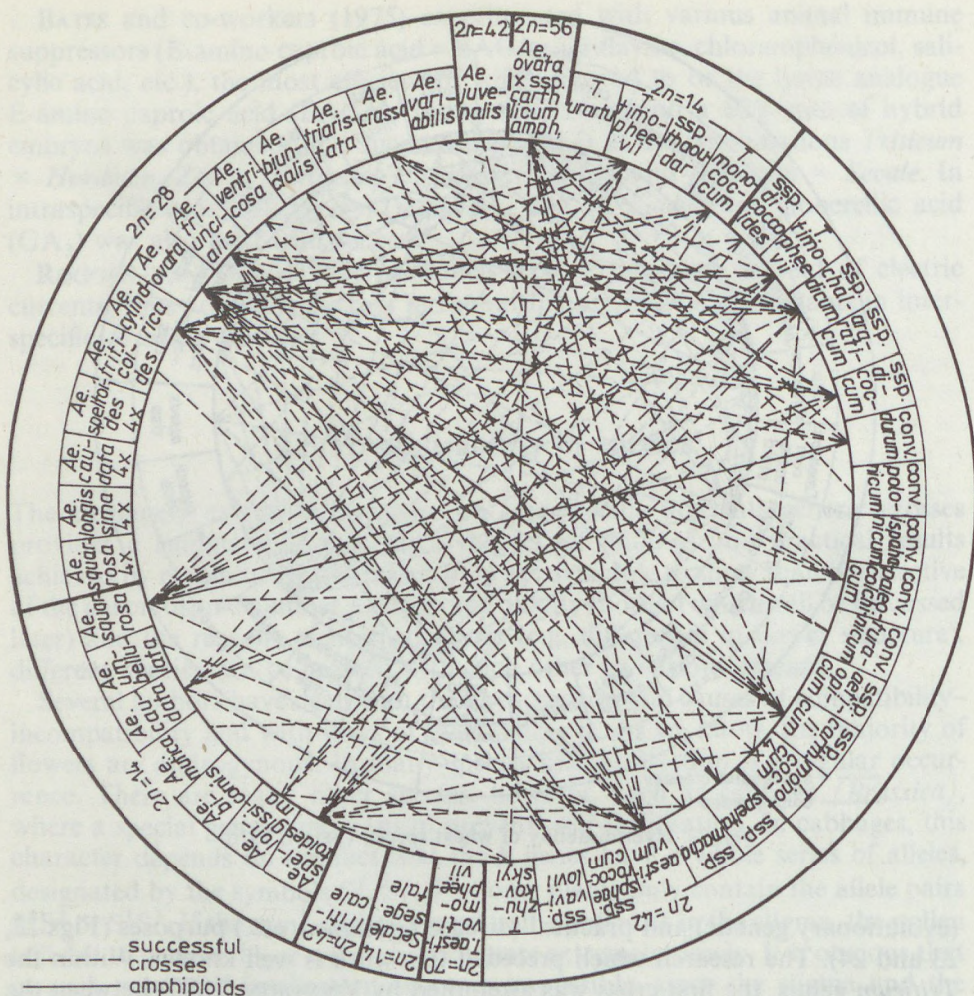


Fig. 23. Hybridisability between *Aegilops* and *Triticum* species (BELEA, 1976)

skyi ($2n=42$) arose from a spontaneous cross between the primitive Georgian local *T. monococcum* species Zanduri and *T. timopheevii*. It is to this origin that the species can thank its excellent disease resistance. BELEA (1976) also experienced difficulty in crossing *T. monococcum* with tetra- and hexaploid wheat species. Relatively good seed setting (11.9%) was only achieved with ssp. *cartholicum*. A cross between autotetraploid *T. monococcum* ($2n=28$), produced by treatment with colchicine, and *T. aestivum* was fairly successful (Table 6).

The species *T. timopheevii* and ssp. *chaldicum*, which are also difficult to cross, are used as one possible way of producing disease-resistant varieties. It is only recently, after long years of experiments, that in crosses with *T. monococcum*,

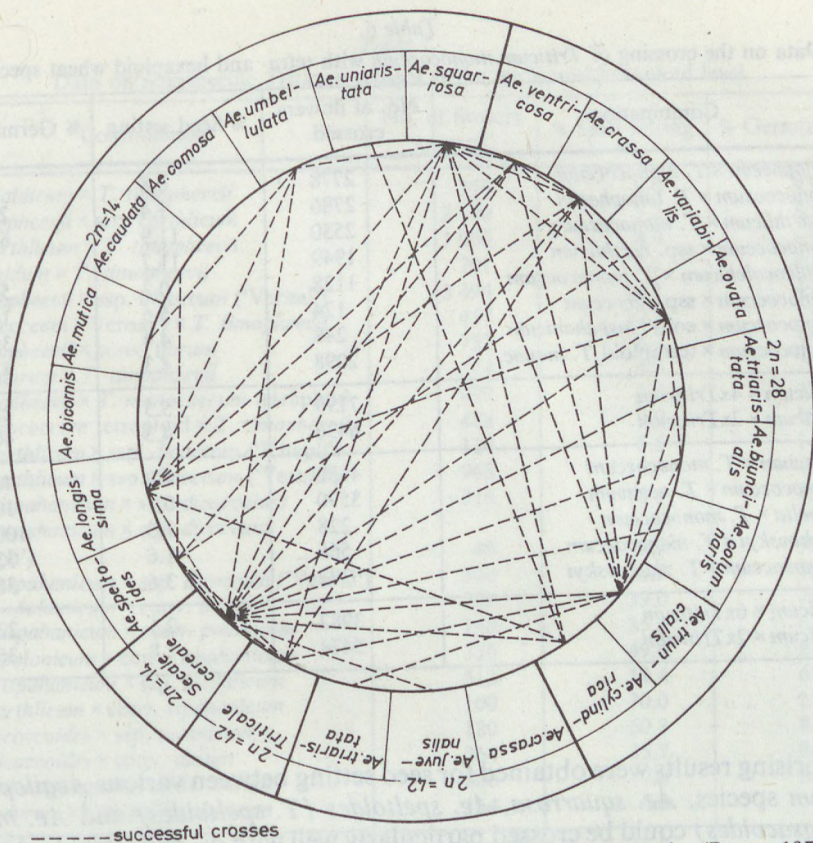


Fig. 24. Hybridisability between *Aegilops*, *Secale* and *Triticale* species (BELEA, 1976)

these two species have finally given a few hybrid grains, from which fertile progeny have been raised. Poor seed setting was also obtained by BELEA when using *T. timopheevii* in other combinations (Table 7). Relatively good seed setting was only found in crosses with ssp. *carthlicum* and ssp. *dicoccum* cv. Vernal (14.1%).

T. zhukovskyi, currently used as a source of disease resistance, is difficult to cross even with its assumed parental lines (*T. monococcum* and *T. timopheevii*). By contrast, ssp. *carthlicum*, which is known for its resistance to leaf rust and powdery mildew, can be easily crossed not only at the same level of polyploidy, but also with di- and hexaploid species. The recently discovered conv. *ispahanicum* can also be successfully combined with various wheat species (Table 7).

The *Aegilops* species are generally difficult to cross with each other. The most successful are various combinations of *Ae. squarrosa* (*T. tauschii*), *Ae. longissima* (*T. longissimum*), *Ae. triuncialis* (*T. triunciale*) and *Ae. biuncialis* (*T. macrochaetum*), which belong to the di- and hexaploid series (Table 8).

Table 6.

Data on the crossing of *Triticum monococcum* with tetra- and hexaploid wheat species

Combination	No. of flowers crossed	% Seed setting	% Germination
<i>T. timopheevii</i> × <i>T. monococcum</i>	2778	0.8	0.4
<i>T. monococcum</i> × <i>T. timopheevii</i>	2780	1.4	20.8
ssp. <i>carthlicum</i> × <i>T. monococcum</i>	2530	11.9	63.1
<i>T. monococcum</i> × ssp. <i>carthlicum</i>	1949	11.7	5.6
ssp. <i>paleocolchicum</i> × <i>T. monococcum</i>	1128	0.2	50.0
<i>T. monococcum</i> × ssp. <i>dicoccum</i>	124	5.6	14.3
<i>T. monococcum</i> × conv. <i>inspahanicum</i>	248	4.4	36.3
<i>T. monococcum</i> × tetraploid <i>T. monoc.</i>	2098	4.3	42.8
2x <i>Triticum</i> × 4x <i>Triticum</i>	7199	5.5	23.9
4x <i>Triticum</i> × 2x <i>Triticum</i>	6436	4.3	40.8
<i>T. aestivum</i> × <i>T. monococcum</i>	4680	1.9	48.2
<i>T. monococcum</i> × <i>T. aestivum</i>	3590	0.7	10.0
ssp. <i>spelta</i> × <i>T. monococcum</i>	228	1.8	100.0
<i>T. zhukovskyi</i> × <i>T. monococcum</i>	566	1.6	33.3
<i>T. monococcum</i> × <i>T. zhukovskyi</i>	392	3.6	35.7
2x <i>Triticum</i> × 6x <i>Triticum</i>	3982	2.1	22.8
6x <i>Triticum</i> × 2x <i>Triticum</i>	5474	1.8	36.2

Surprising results were obtained for seed setting between various *Aegilops* and *Triticum* species. *Ae. squarrosa*, *Ae. speltoides* (*T. speltoides*) and *Ae. mutica* (*T. tripsacoides*) could be crossed particularly well with di- and tetraploid wheat species. Even greater success was achieved when crossing certain *Aegilops* species with hexaploid wheat species (Table 9). *Aegilops* species with various levels of polyploidy also combine fairly well with *Secale cereale* (Table 10). The best species for crossing with rye are *Ae. crassa* (*T. crassum*), *Ae. squarrosa* and *Ae. triuncialis*, especially when the *Aegilops* species is used as the female parent.

Among the *Avena* species, the wild species (*A. hirtula*, *A. vaviloviana* and *A. sterilis*) can be readily crossed with each other, and it is from these combinations, together with micromutations, that the fodder oats, Byzantine and Abyssinian oats now generally cultivated have developed (Fig. 25).

Successful crosses were carried out by FRANDSEN (1947), JOARDER-EUNUS (1970), KAMALA (1976) and MACKAY (1972) between *Brassica campestris* and other cabbage species, and by TOKUMASU (1970) between *B. japonica* and other species. Observations recorded by these authors indicate that *B. napus* × *B. rapa* and *Raphanus sativus* × *B. oleracea* can be crossed with ease, while *B. oleracea* × *B. rapa* is a difficult cross. THOMPSON (1964) produced triple hybrids using the species *B. chinensis*, *B. pekinensis*, *B. carinata*, *B. juncea* and *B. napus*.

A review of the hybridisability of green pepper species (*Capsicum* L.) is presented in Table 11 as compiled by CSILLÉRY (1983). Experience shows that

Table 7.

Data on interspecific *Triticum* crosses at the tetra- and hexaploid level

Combination	No. of flowers crossed	% Seed setting	% Germination
<i>ssp. chaldicum</i> × <i>T. timopheevii</i>	256	9.0	43.4
<i>T. timopheevii</i> × <i>ssp. carthlicum</i>	2 870	7.2	80.2
<i>ssp. carthlicum</i> × <i>T. timopheevii</i>	1 900	4.4	63.8
<i>T. turgidum</i> × <i>T. timopheevii</i>	701	2.1	40.0
<i>T. timopheevii</i> × <i>ssp. dicoccum</i> ('Vernal')	3 494	14.1	49.2
<i>ssp. dicoccum</i> ('Vernal') × <i>T. timopheevii</i>	457	10.7	53.3
<i>T. timopheevii</i> × <i>conv. durum</i>	722	4.7	55.8
<i>conv. durum</i> × <i>T. timopheevii</i>	594	4.8	70.7
<i>T. timopheevii</i> × <i>T. monococcum</i> tetraploid	472	1.3	83.3
<i>T. monococcum</i> tetraploid × <i>T. timopheevii</i>	488	2.0	10.0
<i>ssp. carthlicum</i> × <i>ssp. dicoccum</i> ('Khapli')	124	5.6	14.3
<i>ssp. carthlicum</i> × <i>ssp. dicoccum</i> ('Vernal')	968	15.3	41.7
<i>conv. ispahanicum</i> × <i>ssp. dicoccoides</i>	316	16.5	42.3
<i>conv. ispahanicum</i> × <i>ssp. dicoccum</i> ('Khapli')	48	8.3	50.0
<i>conv. ispahanicum</i> × <i>ssp. dicoccum</i> ('Vernal')	540	28.9	70.5
<i>conv. ispahanicum</i> × <i>conv. durum</i>	268	39.0	70.3
<i>conv. ispahanicum</i> × <i>conv. polonicum</i>	140	35.6	63.5
<i>conv. polonicum</i> × <i>conv. ispahanicum</i>	356	49.6	87.0
<i>conv. ispahanicum</i> × <i>ssp. carthlicum</i>	512	19.4	63.5
<i>ssp. carthlicum</i> × <i>conv. ispahanicum</i>	100	30.0	83.3
<i>ssp. dicoccoides</i> × <i>ssp. turanicum</i>	120	50.8	81.9
<i>ssp. dicoccoides</i> × <i>conv. durum</i>	264	35.7	85.7
<i>ssp. paleocolchicum</i> × <i>conv. durum</i>	606	7.8	85.1
<i>conv. durum</i> × <i>ssp. paleocolchicum</i>	164	0.0	0.0
4 × <i>Triticum</i> × 4 × <i>Triticum</i>	16 480	16.8	57.87
<i>T. monococcum</i> tetraploid × <i>T. aestivum</i>	1 831	7.2	29.8
<i>T. aestivum</i> × <i>T. monococcum</i> tetraploid	3 956	3.7	26.1
<i>ssp. carthlicum</i> × <i>ssp. spelta</i>	482	41.2	69.2
<i>conv. ispahanicum</i> × <i>ssp. spelta</i>	144	27.1	75.0
<i>T. aestivum</i> × <i>ssp. carthlicum</i>	1 594	21.5	62.6
<i>ssp. carthlicum</i> × <i>T. aestivum</i>	4 349	30.2	57.9
<i>T. aestivum</i> × <i>ssp. dicoccum</i>	860	21.6	70.0
<i>ssp. dicoccum</i> × <i>T. aestivum</i>	2 220	36.2	27.6
<i>T. aestivum</i> × <i>conv. durum</i>	974	10.2	70.8
<i>conv. durum</i> × <i>T. aestivum</i>	532	26.1	52.9
<i>T. aestivum</i> × <i>T. turgidum</i>	279	1.1	66.7
<i>T. turgidum</i> × <i>T. aestivum</i>	4 207	14.2	22.2
<i>T. zhukovskyi</i> × <i>ssp. dicoccoides</i>	511	8.2	71.0
6x <i>Triticum</i> × 4x <i>Triticum</i>	8 183	11.1	61.2
4x <i>Triticum</i> × 6x <i>Triticum</i>	13 765	26.3	47.8
<i>T. aestivum</i> × <i>T. timopheevii</i>	5 367	2.1	43.7
<i>T. timopheevii</i> × <i>T. aestivum</i>	6 479	4.1	27.1
<i>ssp. spelta</i> × <i>T. timopheevii</i>	744	4.0	51.7
<i>T. timopheevii</i> × <i>ssp. spelta</i>	394	11.7	21.7
<i>ssp. chaldicum</i> × <i>T. aestivum</i>	84	11.7	71.0
<i>T. timopheevii</i> × <i>T. zhukovskyi</i>	2 436	2.7	30.2
6x <i>Triticum</i> × <i>T. timopheevii</i>	6 111	3.1	47.1
<i>T. timopheevii</i> × 6x <i>Triticum</i>	9 393	7.5	37.5

Table 8.
Data on crosses between *Aegilops* species

Combination	No. of flowers crossed	% Seed setting	% Germination
<i>Ae. speltoides</i> × <i>Ae. caudata</i>	455	0.2	0.0
<i>Ae. caudata</i> × <i>Ae. speltoides</i>	394	0.0	0.0
<i>Ae. mutica</i> × <i>Ae. speltoides</i>	162	0.0	0.0
<i>Ae. speltoides</i> × <i>Ae. comosa</i>	58	6.9	50.0
<i>Ae. squarrosa</i> × <i>Ae. longissima</i>	80	16.2	61.0
<i>Ae. squarrosa</i> × <i>Ae. mutica</i>	106	0.0	0.0
<i>Ae. squarrosa</i> × <i>Ae. caudata</i>	222	0.0	0.0
<i>Ae. caudata</i> × <i>Ae. squarrosa</i>	120	0.0	0.0
<i>Ae. squarrosa</i> × <i>Ae. umbellulata</i>	54	3.7	50.0
<i>Ae. umbellulata</i> × <i>Ae. squarrosa</i>	230	0.0	0.0
<i>Ae. squarrosa</i> × <i>Ae. sharonensis</i>	258	16.0	33.3
<i>Ae. umbellulata</i> × <i>Ae. mutica</i>	48	6.2	66.6
2x <i>Aegilops</i> × 2x <i>Aegilops</i>	2187	4.4	21.2
<i>Ae. squarrosa</i> × <i>Ae. triuncialis</i>	40	0.0	0.0
<i>Ae. squarrosa</i> × <i>Ae. crassa</i>	100	0.0	0.0
<i>Ae. crassa</i> × <i>Ae. squarrosa</i>	114	3.5	50.0
<i>Ae. squarrosa</i> × <i>Ae. ovata</i>	210	0.0	0.0
<i>Ae. squarrosa</i> × <i>Ae. ventricosa</i>	44	4.5	50.0
<i>Ae. ventricosa</i> × <i>Ae. squarrosa</i>	166	0.6	100.0
<i>Ae. longissima</i> × <i>Ae. ovata</i>	94	0.0	0.0
<i>Ae. ovata</i> × <i>Ae. longissima</i>	24	16.6	66.6
<i>Ae. longissima</i> × <i>Ae. cylindrica</i>	86	0.0	0.0
<i>Ae. longissima</i> × <i>Ae. crassa</i>	60	0.0	0.0
<i>Ae. ventricosa</i> × <i>Ae. longissima</i>	68	6.8	66.6
<i>Ae. speltoides</i> × <i>Ae. triuncialis</i>	272	0.0	0.0
<i>Ae. variabilis</i> × <i>Ae. speltoides</i>	72	0.0	0.0
<i>Ae. triuncialis</i> × <i>Ae. caudata</i>	68	0.0	0.0
2x <i>Aegilops</i> × 4x <i>Aegilops</i>	906	0.6	6.2
4x <i>Aegilops</i> × 2x <i>Aegilops</i>	512	4.6	47.0
<i>Ae. triuncialis</i> × <i>Ae. crassa</i>	124	4.1	100.0
<i>Ae. crassa</i> × <i>Ae. triuncialis</i>	74	0.0	0.0
<i>Ae. crassa</i> × <i>Ae. ovata</i>	116	0.0	0.0
<i>Ae. triuncialis</i> × <i>Ae. ventricosa</i>	218	16.6	33.3
<i>Ae. triuncialis</i> × <i>Ae. biuncialis</i>	132	8.9	66.9
<i>Ae. biuncialis</i> × <i>Ae. triuncialis</i>	84	8.3	66.9
<i>Ae. triuncialis</i> × <i>Ae. ovata</i>	56	0.0	0.0
<i>Ae. cylindrica</i> × <i>Ae. triuncialis</i>	90	2.2	50.0
<i>Ae. ovata</i> × <i>Ae. ventricosa</i>	128	0.0	0.0
<i>Ae. ovata</i> × <i>Ae. biuncialis</i>	48	4.1	50.0
<i>Ae. biuncialis</i> × <i>Ae. ovata</i>	70	7.1	66.9

Table 9.
Data on crosses involving *Aegilops* × *Triticum* species

Combination	No. of flowers crossed	% Seed setting	% Germination
4x <i>Aegilops</i> × 4x <i>Aegilops</i>	1140	4.7	39.5
<i>Ae. speltoides</i> × <i>T. monococcum</i>	596	0.0	0.0
<i>T. monococcum</i> × <i>Ae. speltoides</i>	2252	0.8	66.6
<i>Ae. speltoides</i> × ssp. <i>boeoticum</i>	1120	0.0	0.0
ssp. <i>boeoticum</i> × <i>Ae. speltoides</i>	456	4.2	100.0
<i>Ae. squarrosa</i> × <i>T. urartu</i>	108	38.9	50.0
<i>Ae. squarrosa</i> × ssp. <i>boeoticum</i>	112	24.1	74.0
<i>Ae. squarrosa</i> × <i>T. monococcum</i>	1022	4.5	64.0
ssp. <i>boeoticum</i> × <i>Ae. longissima</i>	176	2.7	100.0
ssp. <i>boeoticum</i> × <i>Ae. caudata</i>	696	4.7	60.6
<i>Ae. caudata</i> × ssp. <i>boeoticum</i>	50	4.0	100.0
<i>Ae. caudata</i> × <i>T. monococcum</i>	72	0.0	0.0
<i>T. monococcum</i> × <i>Ae. caudata</i>	710	1.5	33.3
2x <i>Aegilops</i> × 2x <i>Triticum</i>	3074	10.2	41.1
2x <i>Triticum</i> × 2x <i>Aegilops</i>	4390	2.7	72.1
ssp. <i>chaldicum</i> × <i>Ae. longissima</i>	146	0.0	0.0
ssp. <i>chaldicum</i> × <i>Ae. umbellulata</i>	142	0.0	0.0
ssp. <i>chaldicum</i> × <i>Ae. speltoides</i>	144	1.3	50.0
<i>T. timopheevii</i> × <i>Ae. speltoides</i>	374	0.8	33.3
<i>Ae. speltoides</i> × <i>T. timopheevii</i>	384	0.0	0.0
<i>Ae. speltoides</i> × ssp. <i>carthlicum</i>	234	10.2	75.0
<i>Ae. speltoides</i> × ssp. <i>dicoccoides</i>	500	0.0	0.0
<i>Ae. speltoides</i> × <i>T. monococcum</i> tetrapl.	374	1.6	66.6
conv. <i>aethiopicum</i> × <i>Ae. speltoides</i>	96	0.0	0.0
ssp. <i>paleocolchicum</i> × <i>Ae. speltoides</i>	211	0.0	0.0
ssp. <i>paleocolchicum</i> × <i>Ae. caudata</i>	244	0.0	0.0
ssp. <i>carthlicum</i> × <i>Ae. mutica</i>	72	5.5	100.0
<i>Ae. caudata</i> × ssp. <i>chaldicum</i>	64	1.5	0.0
<i>Ae. caudata</i> × conv. <i>durum</i>	874	0.4	50.0
<i>Ae. caudata</i> × <i>T. timopheevii</i>	204	0.8	50.0
<i>T. timopheevii</i> × <i>Ae. caudata</i>	224	0.0	0.0
<i>Ae. squarrosa</i> × ssp. <i>dicoccoides</i>	180	5.5	100.0
<i>Ae. squarrosa</i> × ssp. <i>dicoccum</i>	306	7.5	86.9
ssp. <i>dicoccum</i> × <i>Ae. squarrosa</i>	144	7.6	81.6
<i>Ae. squarrosa</i> × ssp. <i>chaldicum</i>	162	24.1	66.6
<i>Ae. squarrosa</i> × ssp. <i>paleocolchicum</i>	106	17.9	52.6
<i>Ae. squarrosa</i> × ssp. <i>carthlicum</i>	114	0.0	0.0
<i>Ae. squarrosa</i> × conv. <i>durum</i>	197	8.0	62.5
<i>Ae. longissima</i> × <i>T. turgidum</i>	148	0.0	0.0
<i>Ae. longissima</i> × ssp. <i>dicoccoides</i>	98	1.0	0.0
2x <i>Aegilops</i> × 4x <i>Triticum</i>	3179	4.9	38.1
4x <i>Triticum</i> × 2x <i>Aegilops</i>	1953	1.5	30.4

Table 9.
(continued)

Combination	No. of flowers crossed	% Seed setting	% Germination
<i>Ae. squarrosa</i> × <i>T. aestivum</i>	1062	2.3	78.0
<i>T. aestivum</i> × <i>Ae. squarrosa</i>	212	0.0	0.0
<i>Ae. squarrosa</i> × ssp. <i>spelta</i>	94	0.0	0.0
<i>Ae. speltoides</i> × <i>T. aestivum</i>	336	0.0	0.0
<i>Ae. speltoides</i> × ssp. <i>macha</i>	90	2.2	50.0
<i>T. zhukovskyi</i> × <i>Ae. speltoides</i>	345	1.4	60.0
<i>Ae. caudata</i> × <i>T. zhukovskyi</i>	188	0.5	0.0
<i>T. zhukovskyi</i> × <i>Ae. caudata</i>	336	1.1	50.0
<i>Ae. caudata</i> × <i>T. aestivum</i>	126	0.0	0.0
ssp. <i>spelta</i> × <i>Ae. caudata</i>	160	0.0	0.0
<i>Ae. longissima</i> × <i>T. aestivum</i>	297	1.3	75.0
<i>Ae. longissima</i> × ssp. <i>spelta</i>	150	0.0	0.0
2x <i>Aegilops</i> × 6x <i>Triticum</i>	2293	0.7	25.4
6x <i>Triticum</i> × 2x <i>Aegilops</i>	1053	0.6	27.5
ssp. <i>boeoticum</i> × <i>Ae. crassa</i>	261	5.6	83.3
ssp. <i>boeoticum</i> × <i>Ae. variabilis</i>	231	3.4	75.0
<i>Ae. triuncialis</i> × ssp. <i>boeoticum</i>	130	0.7	100.0
<i>Ae. triuncialis</i> × <i>T. monococcum</i>	136	0.0	0.0
ssp. <i>boeoticum</i> × <i>Ae. triuncialis</i>	112	0.0	0.0
ssp. <i>boeoticum</i> × <i>Ae. ovata</i>	389	0.7	0.0
<i>Ae. ovata</i> × ssp. <i>boeoticum</i>	324	33.3	75.0
ssp. <i>boeoticum</i> × <i>Ae. cylindrica</i>	94	1.0	0.0
<i>Ae. ovata</i> × <i>T. monococcum</i>	144	6.8	33.3
<i>Ae. variabilis</i> × <i>T. monococcum</i>	54	0.0	0.0
4x <i>Aegilops</i> × 2x <i>Triticum</i>	788	8.1	41.6
2x <i>Triticum</i> × 4x <i>Aegilops</i>	1087	1.9	31.6
<i>Ae. triuncialis</i> × ssp. <i>dicoccoides</i>	70	2.8	50.0
<i>Ae. triuncialis</i> × ssp. <i>chaldicum</i>	114	7.9	44.4
<i>Ae. triuncialis</i> × <i>T. timopheevii</i>	50	10.0	60.0
<i>Ae. triuncialis</i> × ssp. <i>dicoccum</i>	182	1.0	0.0
<i>Ae. triuncialis</i> × conv. <i>durum</i>	288	2.4	42.8
<i>Ae. triuncialis</i> × <i>T. turgidum</i>	112	5.3	50.0
<i>Ae. triuncialis</i> × ssp. <i>carthlicum</i>	128	1.5	50.0
<i>Ae. ovata</i> × ssp. <i>dicoccoides</i>	158	6.3	80.0
<i>Ae. ovata</i> × ssp. <i>chaldicum</i>	116	2.5	33.3
ssp. <i>chaldicum</i> × <i>Ae. ovata</i>	256	0.0	0.0
<i>Ae. ovata</i> × <i>T. timopheevii</i>	312	2.5	25.0
<i>Ae. ovata</i> × ssp. <i>dicoccum</i>	114	5.2	50.0
<i>Ae. ovata</i> × ssp. <i>paleocolchicum</i>	118	13.5	62.5
ssp. <i>paleocolchicum</i> × <i>Ae. ovata</i>	194	0.0	0.0
<i>Ae. ovata</i> × conv. <i>durum</i>	153	8.4	76.9
conv. <i>durum</i> × <i>Ae. ovata</i>	262	0.0	0.0
<i>Ae. ovata</i> × ssp. <i>carthlicum</i>	88	27.2	83.3

Table 9.
(continued)

Combination	No. of flowers crossed	% Seed setting	% Germination
<i>Ae. ovata</i> × <i>T. turgidum</i>	55	14.5	37.5
<i>Ae. ovata</i> × <i>T. monococcum</i> tetraploid	168	6.5	45.2
<i>Ae. cylindrica</i> × ssp. <i>dicoccum</i>	680	6.1	85.7
<i>Ae. cylindrica</i> × ssp. <i>chaldicum</i>	172	0.0	0.0
ssp. <i>chaldicum</i> × <i>Ae. cylindrica</i>	378	2.9	36.4
<i>Ae. cylindrica</i> × ssp. <i>paleocolchicum</i>	166	1.8	33.3
<i>Ae. cylindrica</i> × conv. <i>durum</i>	225	12.4	57.1
<i>Ae. cylindrica</i> × ssp. <i>carthlicum</i>	60	8.3	80.0
<i>Ae. triaristata</i> × conv. <i>durum</i>	168	1.7	0.0
<i>Ae. variabilis</i> × ssp. <i>dicoccum</i>	60	0.0	0.0
<i>Ae. crassa</i> × ssp. <i>dicoccum</i>	238	4.2	80.0
<i>Ae. crassa</i> × ssp. <i>paleocolchicum</i>	42	2.3	0.0
<i>Ae. crassa</i> × conv. <i>durum</i>	72	12.5	66.6
<i>Ae. crassa</i> × ssp. <i>chaldicum</i>	112	3.6	25.0
ssp. <i>chaldicum</i> × <i>Ae. crassa</i>	40	0.0	0.0
<i>Ae. biuncialis</i> × ssp. <i>paleocolchicum</i>	40	7.5	33.3
4x <i>Aegilops</i> × 4x <i>Triticum</i>	4279	5.5	45.2
4x <i>Triticum</i> × 4x <i>Aegilops</i>	1090	1.0	7.3
<i>Ae. triuncialis</i> × <i>T. aestivum</i>	1487	11.8	55.4
<i>T. aestivum</i> × <i>Ae. triuncialis</i>	790	3.2	18.5
<i>Ae. triuncialis</i> × ssp. <i>macha</i>	140	0.7	0.0
<i>Ae. ovata</i> × <i>T. aestivum</i>	1847	9.4	36.2
<i>T. aestivum</i> × <i>Ae. ovata</i>	540	2.1	14.3
<i>Ae. ovata</i> × ssp. <i>vavilovii</i>	132	3.2	0.0
<i>Ae. ovata</i> × ssp. <i>sphaerococcum</i>	216	18.7	33.3
<i>Ae. ovata</i> × ssp. <i>macha</i>	80	21.2	29.9
<i>Ae. ovata</i> × ssp. <i>spelta</i>	154	7.4	50.0
<i>Ae. cylindrica</i> × <i>T. aestivum</i>	2346	14.9	48.3
<i>T. aestivum</i> × <i>Ae. cylindrica</i>	760	4.1	33.3
<i>Ae. cylindrica</i> × ssp. <i>sphaerococcum</i>	130	26.6	50.0
<i>Ae. cylindrica</i> × ssp. <i>vavilovii</i>	312	28.5	79.4
<i>Ae. biuncialis</i> × <i>T. aestivum</i>	340	9.2	36.8
<i>Ae. crassa</i> × <i>T. aestivum</i>	128	25.7	66.6
<i>T. aestivum</i> × <i>Ae. crassa</i>	110	7.8	36.2
<i>Ae. ventricosa</i> × <i>T. aestivum</i>	48	14.5	71.4
<i>Ae. variabilis</i> × <i>T. aestivum</i>	156	0.0	0.0
<i>Ae. variabilis</i> × ssp. <i>spelta</i>	36	0.0	0.0
<i>Ae. variabilis</i> × ssp. <i>macha</i>	140	0.8	0.0
4x <i>Aegilops</i> × 6x <i>Triticum</i>	7692	13.8	37.1
6x <i>Triticum</i> × 4x <i>Aegilops</i>	2200	4.3	25.6
<i>Ae. juvenalis</i> × <i>T. aestivum</i>	774	3.4	55.5
<i>Ae. juvenalis</i> × ssp. <i>spelta</i>	120	10.8	76.9
6x <i>Aegilops</i> × 6x <i>Triticum</i>	894	47.1	66.2

Table 10.
Data on *Aegilops* × *Secale* intergeneric crosses

Combination	No. of flowers crossed	% Seed setting	% Germination
<i>Secale cereale</i> × <i>Ae. squarrosa</i>	433	11.1	62.5
<i>Secale cereale</i> × <i>Ae. longissima</i>	64	6.2	50.0
<i>Secale cereale</i> × <i>Ae. umbellulata</i>	142	0.7	0.0
<i>Secale cereale</i> × <i>Ae. speltoides</i>	244	0.8	0.0
<i>Ae. speltoides</i> × <i>Secale cereale</i>	182	11.5	33.3
<i>Secale segetale</i> × <i>Ae. speltoides</i>	144	5.5	37.5
2x <i>Aegilops</i> × 2x <i>Secale</i>	182	11.5	33.3
2x <i>Secale</i> × 2x <i>Aegilops</i>	1027	4.8	30.0
<i>Secale cereale</i> × <i>Ae. cylindrica</i>	736	0.5	50.0
<i>Ae. cylindrica</i> × <i>Secale cereale</i>	609	5.0	80.7
<i>Secale cereale</i> × <i>Ae. biuncialis</i>	340	2.2	37.5
<i>Ae. biuncialis</i> × <i>Secale cereale</i>	501	8.5	34.9
<i>Secale cereale</i> × <i>Ae. ventricosa</i>	679	1.2	50.0
<i>Secale cereale</i> × <i>Ae. triaristata</i>	314	0.9	0.0
<i>Ae. triaristata</i> × <i>Secale cereale</i>	56	0.8	25.0
<i>Secale cereale</i> × <i>Ae. crassa</i>	128	8.5	45.4
<i>Ae. crassa</i> × <i>Secale cereale</i>	562	28.1	82.8
<i>Secale cereale</i> × <i>Ae. triuncialis</i>	1458	6.8	57.5
<i>Ae. triuncialis</i> × <i>Secale cereale</i>	1299	3.0	37.0
4x <i>Aegilops</i> × 2x <i>Secale</i>	3027	7.5	50.7
2x <i>Secale</i> × 4x <i>Aegilops</i>	3655	3.3	40.6
<i>Triticale</i> × <i>Ae. crassa</i>	730	1.8	35.7
<i>Ae. speltoides</i> × <i>Triticale</i>	140	10.0	25.0
<i>Ae. squarrosa</i> × <i>Triticale</i>	96	16.6	62.5
<i>Ae. triuncialis</i> × <i>Triticale</i>	66	6.6	50.0
<i>Aegilops</i> × <i>Triticale</i>	302	11.1	45.8
<i>Triticale</i> × <i>Aegilops</i>	730	1.8	35.7

the vast majority of pepper species can generally be crossed with ease. When crossing species which are more distantly related to each other the hybrids can be raised by means of embryo cultures, or success can be achieved by using a multi-stage hybridisation programme (e.g. *C. pubescens* × *C. eximium* F₁₋₃ × *C. praetermissum* – F₁₋₃ × *C. baccatum* – F₁₋₃ × *C. annuum*) or an intermediate species. Raising hybrid plants in embryo cultures (in vitro) is substantially faster than producing hybrids in a multi-stage hybridisation programme. It is clearly visible from the table that *C. chinense* and *C. frutescens* can be crossed fairly readily and that the fertility of their hybrids is generally satisfactory. For this reason, certain authors (TERPÓ, 1966) classify both species as a single species, *C. conicum*.

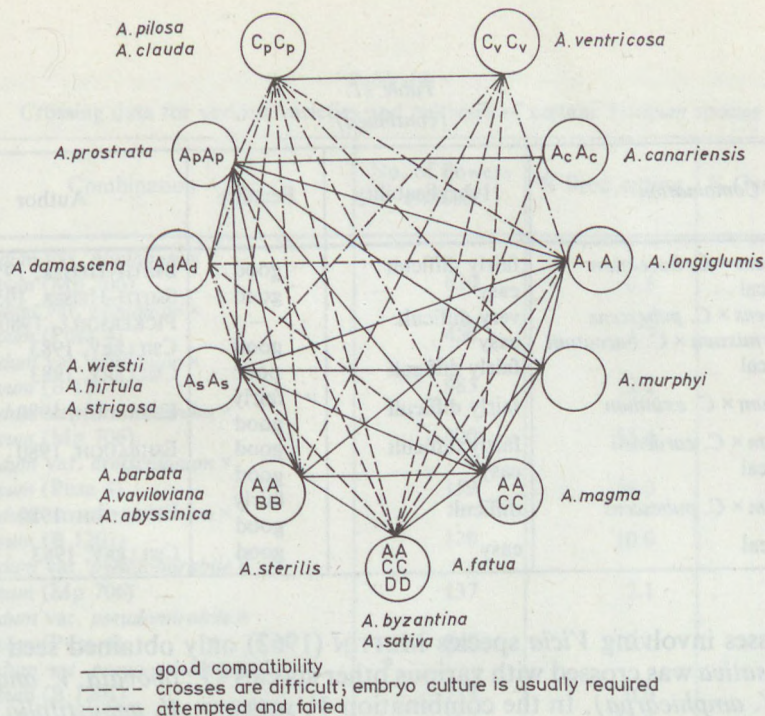


Fig. 25. Hybridizability of oat species (RAJHÁTHY-THOMAS, 1974)

Table 11.
Hybridizability of *Capsicum* species

Combination	Hybridizability	Fertility	Author
<i>C. annuum</i> × <i>C. chinense</i> reciprocal	easy	good	CSILLÉRY, 1983
<i>C. annuum</i> × <i>C. frutescens</i> reciprocal	fairly difficult	poor	CSILLÉRY, 1976
<i>C. annuum</i> × <i>C. chacoense</i> reciprocal	difficult	poor	CSILLÉRY, 1983
<i>C. annuum</i> × <i>C. chacoense</i> reciprocal	very difficult	poor	PICKERSGILL, 1980
<i>C. annuum</i> × <i>C. galapagoense</i>	easy	poor	PICKERSGILL, 1980
<i>C. annuum</i> × <i>C. baccatum</i> reciprocal	fairly difficult	—	CSILLÉRY, 1983
<i>C. annuum</i> × <i>C. pubescens</i>	very difficult	—	
<i>C. annuum</i> × <i>C. pubescens</i>	fairly easy	good	
<i>C. annuum</i> × <i>C. pubescens</i>	difficult	poor	MOLHOVA-MICHAILOVA, 1982
<i>C. chinense</i> × <i>C. frutescens</i> reciprocal	very difficult	poor	HEISER, 1957
<i>C. chinense</i> × <i>C. chacoense</i> reciprocal	easy	good	CSILLÉRY, 1976
<i>C. chinense</i> × <i>C. chacoense</i> reciprocal	difficult	good	PICKERSGILL, 1980
<i>C. chinense</i> × <i>C. baccatum</i> reciprocal	difficult	poor	PICKERSGILL, 1980
<i>C. chinense</i> × <i>C. baccatum</i> reciprocal	difficult	poor	
<i>C. praetermissum</i> × <i>C. chinense</i>	difficult	fairly good	
<i>C. praetermissum</i> × <i>C. chinense</i>	difficult	good	
<i>C. praetermissum</i> × <i>C. chinense</i>	difficult	—	PICKERSGILL, 1980
<i>C. chinense</i> × <i>C. pubescens</i>	very difficult	poor	SMITH-HEISER, 1957

Table 11.
(continued)

Combination	Hybridisability	Fertility	Author
<i>C. frutescens</i> × <i>C. baccatum</i> reciprocal	fairly difficult easy	good good	SMITH-HEISER, 1957 SMITH-HEISER, 1957
<i>C. frutescens</i> × <i>C. pubescens</i>	very difficult	—	PICKERSGILL, 1980
<i>C. praetermissum</i> × <i>C. baccatum</i> reciprocal	easy fairly difficult	good poor	CSILLÉRY, 1983 CSILLÉRY, 1983
<i>C. baccatum</i> × <i>C. eximium</i>	fairly difficult	fairly good	ESHBAUGH, 1980
<i>C. eximium</i> × <i>C. cardensii</i> reciprocal	fairly difficult easy	good good	ESHBAUGH, 1980
<i>C. eximium</i> × <i>C. pubescens</i> reciprocal	difficult easy	fairly good good	ESHBAUGH, 1980 CSILLÉRY, 1983

In crosses involving *Vicia* species METTIN (1962) only obtained seed setting when *V. sativa* was crossed with various other species (*V. obovata*, *V. angustifolia* and *V. amphicarpa*). In the combination *V. sativa* × *V. angustifolia* YAKAMOTO (1959) achieved 14% seed setting.

2.6 Hybridisability of varieties, cultivars and biotypes

Differences can also be observed within the various plant species in the hybridisability of varieties, cultivars and even of biotypes selected from cultivars. As can be seen from Table 12, a number of varieties of *T. turgidum*, for example, act quite differently in crosses with different cultivars of common wheat. The best seed setting was obtained when the stigmata of var. *dreischianum* were pollinated with pollen from the cultivars Mp. 706 and Pusa 4. Less success was achieved when these cultivars were crossed with the *plinianum* and *pseudomirabile* varieties of the species *T. turgidum*.

Considerable differences in seed setting were also found when crossing *T. turgidum* ssp. *dicoccum* with various cultivars of common wheat (B 1201, F 481, Produttore, Fortunato, Lee, etc.). The cultivars Aniversario and Newthatch could best be crossed with *T. monococcum*, and the cultivars Ardito, Norin 10 and Thatcher with rye (KISS, verbal communication).

When examining the combining ability of 56 wheat varieties, FALK-KASHA (1981) found that cultivars which gave 0.0–95.0% seed setting with rye also crossed relatively well with *Hordeum bulbosum* (wild barley) (0.0–32.2%). The cultivars which gave especially good seed setting with *Hordeum bulbosum* were those which also gave above-average results with rye (Table 13). In crosses between the two plant species the correlation coefficient was $r=0.75$. Cultivars

Table 12.

Crossing data for various varieties and cultivars of certain *Triticum* species

Combination	No. of flowers crossed	% Seed setting	% Germination
<i>T. turgidum</i> var. <i>plinianum</i> × <i>T. aestivum</i> (Mp 706)	620	0.5	0.0
<i>T. turgidum</i> var. <i>plinianum</i> × <i>T. aestivum</i> (Pusa 4)	450	1.7	12.5
<i>T. turgidum</i> var. <i>plinianum</i> × <i>T. aestivum</i> (B 1201)	985	2.1	23.8
<i>T. turgidum</i> var. <i>dreischianum</i> × <i>T. aestivum</i> (Mp 706)	220	55.4	12.2
<i>T. turgidum</i> var. <i>dreischianum</i> × <i>T. aestivum</i> (Pusa 4)	159	54.0	13.9
<i>T. turgidum</i> var. <i>dreischianum</i> × <i>T. aestivum</i> (B 1201)	120	10.0	33.3
<i>T. turgidum</i> var. <i>pseudomirabile</i> × <i>T. aestivum</i> (Mp 706)	137	2.1	33.3
<i>T. turgidum</i> var. <i>pseudomirabile</i> × <i>T. aestivum</i> (Pusa 4)	247	12.1	0.0
<i>T. turgidum</i> var. <i>pseudomirabile</i> × <i>T. aestivum</i> (B 1201)	133	0.0	0.0
ssp. <i>carthlicum</i> × <i>T. aestivum</i> ('F 481')	562	44.8	9.1
ssp. <i>carthlicum</i> × <i>T. aestivum</i> ('B 1201')	671	31.2	5.2
ssp. <i>dicoccum</i> (Vernal) × <i>T. aestivum</i> (B 1201)	1020	25.0	15.3
ssp. <i>dicoccum</i> (Vernal) × <i>T. aestivum</i> (Produktore)	360	5.5	0.0
ssp. <i>dicoccum</i> (Vernal) × <i>T. aestivum</i> (Lee)	320	24.1	6.5
ssp. <i>dicoccum</i> (Vernal) × <i>T. aestivum</i> (Fortunato)	180	3.3	50.0
<i>T. aestivum</i> (F 481) × ssp. <i>dicoccum</i> (Vernal)	560	26.6	75.2
<i>T. aestivum</i> (Aniversario) × ssp. <i>dicoccum</i> (Vernal)	300	12.3	48.6

originating directly or indirectly from the cultivar Chinese Spring, such as the 5A substitution line of Chinese Spring/Hope and the cultivars Songlen, Mendos (Australian), Salmon, 79-275 (American) and Norin 29 (Japanese) showed outstandingly good combining ability, as did the cultivars CI 12632 and CI 52633, derived from *T. timopheevii*. Similarly good seed setting values were reported by SNAPE and co-workers (1979) in crosses of the cultivars Songlen, Wren, Gamut, Mendos (Australian) and TH 3929 (Chinese) with rye or *Hordeum bulbosum*. According to FALK-KASHA (1983) suppressor genes located on chromosomes 5A and 5B influence hybridisability. The Kr_1 gene, found on chromosome 5B, has the greatest effect on hybridisability. The Kr_2 gene located on chromosome 5A has less influence on combining ability.

Table 13.

Hybridisability of wheat cultivars with rye and *Hordeum bulbosum* (after FALK-KASHA, 1981)

Wheat cultivar ♀	Origin	♂ Secale cereale		♂ Hordeum bulbosum	
		No. of flower crossed	% Seed setting	No. of flowers crossed	% Seed setting
Big Club	USA	72	0.0	—	—
Centurk (CMS)	USA	218	0.0	174	0.0
China 3	China	60	0.0	—	—
G4-1	USA	40	0.0	92	0.0
Gabo	Australia	62	0.0	—	—
Holdfast	UK	52	3.8	126	0.0
Marquis	Canada	110	0.0	—	—
Penjamo 62	Mexico	58	0.0	—	—
Red Bobs	Canada	56	0.0	—	—
S615	Portugal	56	0.0	—	—
Timstein	Australia	48	0.0	—	—
Tordo	Mexico	68	0.0	126	0.0
DFT 7-11	USA	124	0.8	278	0.0
G4-8	USA	94	1.1	86	0.0
CI 6223	China	84	1.2	—	—
Purple Straw	USA	254	1.2	—	—
Rescue	Canada	68	1.5	—	—
DFT 16-27	USA	64	1.6	70	0.0
Cadet	Canada	58	1.7	—	—
Lerma Rojo 64	Mexico	58	1.7	—	—
Timvera	Australia	108	1.8	—	—
Olesen's dwarf	Rhodesia	52	1.9	84	0.0
Dong Fang Hong	China	36	2.8	208	0.0
FS6/3 Bo69	USA	140	2.9	140	0.0
Nong Da 139	China	32	3.1	172	0.0
Pitic 62	Mexico	64	3.1	—	—
Gala	Australia	60	3.3	—	—
Gamut	Australia	62	58.0	90	10.1
TH 3929	China	85	88.2	138	35.5
Timgalen	Australia	176	23.0	484	6.0
Wren	Australia	172	66.0	434	1.6
15-6-14	USA	60	3.3	134	0.0
Red Egyptian	Ethiopia	58	3.5	—	—
Froid	USA	166	3.6	134	0.0
Timson	Australia	156	3.8	—	—
Lancota	USA	31	6.5	119	0.0
Pau 45	China	108	6.5	58	0.0
CI 13005	USA	54	7.4	—	—
Frederick	Canada	159	9.4	484	0.2
Yorkstar	USA	176	10.2	—	—
Chinese Sp./Hope 5B	USA	90	13.3	144	0.0
15-5-6	USA	108	16.7	—	—
Winalta	Canada	61	19.7	352	0.3
Chinese Sp./Hope 5A	USA	84	23.0	148	14.9
CI 13113	USA	97	28.9	—	—

Table 13. (continued)

Wheat cultivar ♀	Origin	♂ <i>Secale cereale</i>		♂ <i>Hordeum bulbosum</i>	
		No. of flower crossed	% Seed setting	No. of flowers crossed	% Seed setting
Chancellor	USA	94	40.4	102	0.0
Songlen	Australia	162	43.8	654	11.8
Peking 10	China	39	46.2	—	—
SW 41	USA	547	48.1	—	—
Mendos	Australia	48	54.2	110	23.6
SW 42	USA	538	55.8	—	—
Salmon	USA	112	56.2	158	20.9
CTW 3	Mexico	79	63.3	—	—
Zaragosa 75	Mexico	187	69.5	351	18.2
SW 47	USA	86	69.8	—	—
Norin 29	Japan	62	74.2	418	18.2
CI 12633	USA	60	83.3	178	7.3
Chinese Spring	China	210	86.7	870	32.2
CI 12632	USA	90	90.0	224	3.6
79-72S	USA	88	95.4	142	30.3
Chinese		112	82.1	501	7.4
Sp./Songlen		168	30.9	68	0.0
Chinese Sp./G4-1		110	30.0	174	0.6
Sp./Zaragosa 75		362	27.9	164	1.2
Chinese Sp./DFT 7-11		48	18.7	186	0.0
Chinese		169	12.5	240	0.0
Sp./Holdfast		88	9.1	82	6.1
Chinese		78	7.7	220	0.9
Sp./Fredrick		318	6.2	218	0.0
Songlen/Zaragosa 75					
Chinese Sp./G4-8					
Centurk/Chinese Spring					

It was observed by THOMAS and co-workers (1980) that wheat cultivars which hybridised well with rye had good combining ability not only with *Hordeum bulbosum*, but also with species belonging to other genera (Table 14).

FIRBAS (1920) found that the Polish wheat cultivar Bochara combined well with rye. Other authors obtained a seed setting of 60% in crosses between the wheat cultivar Chinese 466 and rye, while the cultivars Marquis and Peragis only gave 1.9% seed setting when the flowers were fertilised with rye pollen.

DUBROVAET and co-workers (1959) obtained only 7.8% seed setting in the cross *Lutescens* 62 (*T. aestivum*) × *Melanopus* 69 (conv. *durum*), but 47% in the combination Durable (conv. *durum*) × *Lutescens* 62 (*T. aestivum*). The cultivar Khapli (*T. turgidum* ssp. *dicoccum*) combines very poorly with any

Table 14.

Data on crosses carried out on wheat cultivars hybridisable with rye and on species from other genera (after THOMAS et al., 1980)

Wheat-rye hybridisa- bility group, female parent	Male parents							
	<i>Secale montanum</i>	<i>Aegilops variabilis</i>	<i>Triticum timopheevii</i>	<i>Triticum monococcum</i>	<i>Agropyron junceum</i>	<i>Agropyron elongatum</i>	<i>Elymus arenarius</i> ⁺	
							+ GA ³	- GA ³
	* * *	* * *	* * *	* * *	* * *	* * *	* * *	* * *
50-100%	83 : 265	35 : 17	103 : 86	49 : 13	13 : 49	28 : 86	15 : 285	2 : 193
10-50%	13 : 253	—	54 : 95	—	2 : 22	8 : 72	0 : 30	0 : 126
0-10%	4 : 214	17 : 25	1 : 194	2 : 44	1 : 59	2 : 33	0 : 142	0 : 102

* Grains

** No grains

+ Flowers treated with 75 mg/kg gibberellic acid (GA₃) 24 hours after fertilisation

wheat species or cultivar, by contrast to the Indian cultivar Vernal, which also belongs to ssp. *dicoccum* and which can be successfully used in the production of species hybrids. For this reason, several authors classify the cultivar Khapli in a genetically isolated variety (var. *nudiglumis*), often considered to belong to the species *T. timopheevii*.

In crosses between *Cucurbita pepo* and *C. moschata*, JAMANE (1953) used numerous Japanese cultivars, some of which gave seed settings of 20%. Nine F₁ generations were raised in embryo cultures and the plants exhibited a considerable heterosis effect with respect to quantitative traits. A seed setting of 52% was reported by HAYASE (1950) in the interspecific cross *C. moschata* × *C. maxima* (Delicious). In a later publication TAKASHIMA (1953) claimed a 78% result for this same combination.

It was FIRBAS (1920) who first drew the attention of researchers to the fact that differences in hybridisability existed not only between species, varieties and cultivars, but even between different biotypes of the same cultivar population. Certain biotypes (B 1201-4) of the wheat cultivar B 1201 (*T. aestivum*), for

Table 15.

Crossing data for biotypes selected from the *T. aestivum* cultivar Bánkúti 1201

Combination	No. of flowers crossed	No. of seed obtained	% Seed setting	% Germination
B 1201-6 × <i>T. monococcum</i>	575	24	4.2	69.5
B 1201-10 × <i>T. monococcum</i>	231	12	5.2	29.6
B 1201-33 × <i>T. monococcum</i>	199	8	4.0	37.5
B 1201-66 × <i>T. monococcum</i>	150	7	4.7	42.8
average of cultivars				
<i>T. aestivum</i> × <i>T. monococcum</i>	2790	4	0.2	50.0

example, and various biotypes of the cultivars F 481 and Thatcher hybridise with rye much more easily than the cultivar average. In the same way, a number of biotypes selected from B 1201 (B 1201-6 and B 1201-10) gave higher seed setting (5.2%) than the cultivar average (0.2%) with *T. monococcum* (Table 15). This character is generally inherited, though not in all cases. These biotypes do not give satisfactory seed setting with rye, for instance. By using biotypes with good combining ability, it is possible to reduce the number of crosses. Naturally, in this case, too, economic or theoretical value must be given prime consideration when choosing the crossing partners.

2.7 Crossing direction

References in the literature indicate that the direction of crossing has a very great effect on the extent of seed setting and on the germination vigour. Whether the parent species are used as the male or female parent is not a matter of indifference. In many cases, crosses are only successful in one direction and not in the other. There may be numerous reasons for this phenomenon, including the morphological differences mentioned above. If the flowers of one parent have very long styles, while those of the other parent are short, the pollen tubes of the long-styled species have no difficulty in reaching the ovary of the other species. In the opposite case, fertilisation takes place with difficulty, if at all, since the growth rate of the pollen tubes is generally proportionate to the length of the style in the species from which the pollen originates.

DARWIN frequently comments, in the "Origin of Species" (1859), on the fact that the hybrids produced from reciprocal crosses often differ in fertility and that, while two species may be difficult to cross, there is no strict parallelism between the difficulty of effecting the cross and the degree of sterility of the hybrids resulting therefrom.

As DARWIN (1859) observes, differences in the results, in respect to the relative ease of making reciprocal crosses, had been previously noted by Koelreuter, who conducted some two hundred trials over a period of eight years and found that, while *Mirabilis jalapa* could easily be fertilised by *M. longiflora*, the reverse cross could not be effected. There may be some fundamental resemblance between the facility with which reciprocal crosses can be made and the ease with which reciprocal grafts can be achieved: Darwin mentions the fact that the currant can, with some difficulty, be grafted on the gooseberry, while the reciprocal graft is quite impossible.

One of the earliest successful experiments of this nature was that of LAIBACH (1925) involving the cross *Linum perenne* $\times$ *L. austriacum* and its reciprocal. When *L. perenne* is the female parent the embryo reaches maturity, but cannot sprout from the seed. In the reciprocal cross, hybrids can be obtained by dissecting the very young embryos out of the developing seed and growing them in a nutrient solution. Similar success was obtained using this method in crosses between *Secale cereale* $\times$ *Hordeum jubatum* by BRINK et al. (1944).

During research on the origin of wheat, much thought was given to the direction in which wheat may have crossed with various species of *Aegilops* in nature. It seems likely that *Aegilops* was the female parent. BELEA (1976), for instance, obtained better seed setting if the *Aegilops* species were used as female parents in the *Aegilops* × *Triticum* and *Aegilops* × *Secale* crosses (Tables 9 and 10). THOMAS and co-workers (1980) also achieved better seed setting if the wheat species acted as pollinators in crosses with *Aegilops* and *Elymus*. This assumption is also confirmed by observations made by SUEMOTO (1969) and others, who found that individuals in which the cytoplasm originated from *Aegilops speltoides* and the cell nucleus from tetraploid wheat were generally fertile, while in the reciprocal crosses the progeny were sterile. Observations made by KISS (1955) however, indicate that in *Triticum* × *Secale* crosses, the best seed setting can be achieved in every case when wheat is the female parent. The reciprocal cross is rarely successful.

In other plants, too, great differences can often be experienced in the seed setting and even more so in the fertility as a function of the crossing direction. The genetic, physiological and plasmatic reasons for this phenomenon will be discussed later. In the cross *Phaseolus vulgaris* × *Ph. multiflorus*, LAMPRECHT (1948) obtained a seed setting of 42.3%, whereas this value was only 0.5% in the

Table 16.
Effect of back-crossing on seed setting in interspecific *Triticum* hybrids

Combination	No. of flowers crossed	No. of seed obtained	% Seed setting
<i>T. aestivum</i> × ssp. <i>carthlicum</i>	247	86	34.8
(<i>T. aestivum</i> × ssp. <i>carthlicum</i>) × <i>T. aestivum</i>	656	29	4.4
(<i>T. aestivum</i> × ssp. <i>carthlicum</i>) × <i>T. aestivum</i> BC ²	504	27	5.3
(<i>T. aestivum</i> × ssp. <i>carthlicum</i>) × <i>T. aestivum</i> BC ³	2574	561	21.8
ssp. <i>carthlicum</i> × <i>T. aestivum</i>	1233	462	37.5
(ssp. <i>carthlicum</i> × <i>T. aestivum</i>) × <i>T. aestivum</i>	352	118	33.5
(ssp. <i>carthlicum</i> × <i>T. aestivum</i>) × <i>T. aestivum</i> BC ²	280	152	54.3
<i>T. aestivum</i> × <i>T. turgidum</i>	279	3	1.1
(<i>T. aestivum</i> × <i>T. turgidum</i>) × <i>T. aestivum</i>	3352	528	15.8
(<i>T. aestivum</i> × <i>T. turgidum</i>) × <i>T. aestivum</i> BC ²	1400	237	16.9
(<i>T. aestivum</i> × <i>T. turgidum</i>) × <i>T. aestivum</i> BC ³	416	85	20.4
<i>T. turgidum</i> × <i>T. aestivum</i>	750	70	9.3
(<i>T. turgidum</i> × <i>T. aestivum</i>) × <i>T. aestivum</i>	423	18	4.3
(<i>T. turgidum</i> × <i>T. aestivum</i>) × <i>T. aestivum</i> BC ²	1240	86	6.9
(<i>T. turgidum</i> × <i>T. aestivum</i>) × <i>T. aestivum</i> BC ³	1632	280	17.1
<i>T. aestivum</i> × ssp. <i>dicoccum</i>	560	149	26.5
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × <i>T. aestivum</i>	336	70	20.8
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × <i>T. aestivum</i> BC ²	3216	1062	33.0
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × <i>T. aestivum</i> BC ³	360	159	44.0
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × ssp. <i>dicoccum</i>	720	72	10.0
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × ssp. <i>dicoccum</i> BC ²	192	31	16.2
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × ssp. <i>dicoccum</i> BC ³	280	97	34.6

reciprocal cross. SWAMINATHAN-RADHAKRISHNA (1957) reported on successful crosses between *Nicotiana rustica* × *N. tabacum* and *N. debneyi* × *N. tabacum*. In the reciprocal crosses, no seed setting was obtained. In a cross between *Epilobium luteum* and *E. hirsutum*, the F_1 was fertile if *E. luteum* was the female parent and sterile if the reciprocal cross was made.

2.8 Effect of back- and top-crossing on seed setting

Back- and top-crossing also have an effect on seed setting, and this is of particular significance in making pollen-sterile interspecific hybrids fertile. Observations made by BELEA indicate that the first back-cross (BC^1) in interspecific crosses of wheat causes a temporary reduction in the seed setting percentage compared to the original interspecific cross. This was especially evident in the

Table 17.
Effect on seed setting of back-crossing with various *Triticum aestivum* cultivars

Combination	No. of flowers crossed	% Seed setting	% Germination
[<i>T. aestivum</i> (Fortunato) × ssp. <i>dicoccum</i>] × <i>T. aestivum</i> (Fortunato) BC^2	192	23.9	74.4
[<i>T. aestivum</i> (Glutinoso) × ssp. <i>dicoccum</i>] × <i>T. aestivum</i> (Glutinoso) BC^2	576	23.6	69.1
[<i>T. aestivum</i> (Mara) × ssp. <i>dicoccum</i>] × <i>T. aestivum</i> (Mara) BC^2	432	25.4	41.8
[<i>T. aestivum</i> (Produttore) × ssp. <i>dicoccum</i>] × <i>T. aestivum</i> (Produttore) BC^2	216	21.8	80.8
[<i>T. aestivum</i> (San Pastore) × ssp. <i>dicoccum</i>] × <i>T. aestivum</i> (San Pastore) BC^2	138	4.3	83.3
	1556	22.2	63.8
<i>T. aestivum</i> (Mara) × ssp. <i>dicoccum</i> × <i>T. aestivum</i> (Mara × San Pastore)	196	25.5	76.0
[<i>T. aestivum</i> (Mara) × ssp. <i>dicoccum</i>] × <i>T. aestivum</i> (Mara × Etoile de Choisy)	192	23.9	54.3
<i>T. aestivum</i> (Mara) × ssp. <i>dicoccum</i> × <i>T. aestivum</i> (Mara × Bezostaya 1)	248	9.7	72.5
[<i>T. aestivum</i> (Glutinoso) × ssp. <i>dicoccum</i>] × <i>T. aestivum</i> (Glutinoso × Bezostaya 1)	360	50.8	60.1
[<i>T. aestivum</i> (Glutinoso) × ssp. <i>dicoccum</i>] × <i>T. aestivum</i> (Glutinoso × San Pastore)	336	60.1	29.7
[<i>T. aestivum</i> (San Pastore) × ssp. <i>dicoccum</i>] × <i>T. aestivum</i> (San Pastore × Produttore)	120	64.1	69.6
[<i>T. aestivum</i> (San Pastore) × ssp. <i>dicoccum</i>] × <i>T. aestivum</i> (San Pastore × Bezostaya 1)	208	64.4	70.8
	1660	43.1	54.6

Table 18.
Effect of top-crossing on seed setting in interspecific Triticum crosses

Combination	No. of flowers crossed	No. of seed obtained	% Seed setting
<i>T. turgidum</i> × <i>T. timopheevii</i>	701	15	2.1
(<i>T. turgidum</i> × <i>T. timopheevii</i>) × <i>T. aestivum</i>	146	9	6.2
(<i>T. turgidum</i> × <i>T. timopheevii</i>) × <i>T. aestivum</i> BC ²	687	154	22.4
<i>T. timopheevii</i> × ssp. <i>carthlicum</i>	1760	193	11.0
(<i>T. turgidum</i> × <i>T.</i> × ssp. <i>carthlicum</i>) × <i>T. aestivum</i>	3516	94	2.7
(<i>T. timopheevii</i> × ssp. <i>carthlicum</i>) × <i>T. aest.</i> BC ²	2448	230	9.4
ssp. <i>carthlicum</i> × <i>T. timopheevii</i>	1900	81	4.3
(ssp. <i>carthlicum</i> × <i>T. timopheevii</i>) × <i>T. aestivum</i>	443	17	3.8
(ssp. <i>carthlicum</i> × <i>T. timopheevii</i>) × <i>T. aest.</i> BC ²	520	42	8.1
<i>T. turgidum</i> × conv. <i>durum</i>	147	42	28.5
(<i>T. turgidum</i> × conv. <i>durum</i>) × <i>T. aestivum</i>	133	8	6.0
(<i>T. turgidum</i> × conv. <i>durum</i>) × <i>T. aestivum</i> BC ²	872	94	10.8
(<i>T. turgidum</i> × conv. <i>durum</i>) × <i>T. aestivum</i> BC ³	1534	267	17.4
(<i>T. turgidum</i> × conv. <i>durum</i>) × <i>T. aestivum</i> BC ⁴	1344	196	14.6
<i>T. aestivum</i> × ssp. <i>dicoccum</i>	560	149	26.6
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × conv. <i>durum</i>	408	51	12.5
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × conv. <i>durum</i> BC ²	480	76	15.8
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × conv. <i>durum</i> BC ³	240	102	42.5
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × <i>carthlicum</i>	96	8	8.3
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × ssp. <i>carthlicum</i> BC ²	210	24	11.4
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × conv. <i>dur.</i> × <i>T. aest.</i>	240	61	25.4
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × conv. <i>dur.</i> × ssp. <i>dic.</i>	312	50	16.0

combinations *T. aestivum* × ssp. *carthlicum* and *T. aestivum* × ssp. *dicoccum* (Table 16). In the second (BC²), and particularly in the third (BC³) back-cross there was a substantial rise in seed-setting percentage. In some cases better seed setting was obtained even in the first back-cross, e.g. in the combination *T. aestivum* × *T. turgidum*. Differences in seed setting were also found when the back-cross was carried out using different cultivars. Better seed setting but somewhat poorer germination of the hybrid grains were obtained when different wheat cultivars were used for the second back-cross (Table 17).

Pollen-sterile F₁ hybrid plants can be successfully crossed with a third species, in which case we speak of top-crossing. As can be seen in Table 18, when the *T. turgidum* × conv. *durum* combination was top-crossed with *T. aestivum*, or the *T. aestivum* × ssp. *dicoccum* combination with ssp. *carthlicum*, there was again a temporary reduction in the extent of seed setting, but in the BC², and particularly in the BC³, there was a perceptible rise in the percentage seed setting.

Numerous trigeneric hybrids have been reported in the literature, and these can be used to increase the degree of seed setting. Examples of this are *Hordeum vulgare* × *Triticum aestivum* × *Secale cereale* or *Gossypium hirsutum* × *G. herbaceum* × *G. harknessii* (BROWN-MENZEL, 1950).

2.9 Influence of chromosome number on the success of crossing

Substantial differences in the seed, grain or pod yield in reciprocal crosses are also found if the parents have different chromosome numbers or if the genomes are not homologous. Deviations in the chromosome number are an extremely important factor in certain plant species, even though they cannot be regarded as the sole reason for the differences experienced in reciprocal crosses.

2.10 Pollen tube growth in style tissues

A number of authors have studied the germination of the pollen and the growth of the tube in the tissues of the style. The somatic chromosome number of the latter is diploid: $2n$, while the pollen grain and the pollen tube are haploid (n). This suggests that the chromosome number of the pollen and the style tissue may have a role in pollen grain germination and pollen tube growth. When two species with the same chromosome number are crossed, or in the case of self-fertilisation, the chromosome ratio is 1:2. When crossing parental species with different chromosome numbers this ratio changes and will differ depending on whether the parent with the larger or smaller chromosome number is used as the female parent. This causes disturbances in the normal physiological relationship between the pollen tube and the style.

In numerous interspecific crosses, especially in the case of autotetraploid plants, the pollen tube growth will be better if the parent with the higher chromosome number is used as the female (KATAYAMA, 1933; WATKINS, 1932). In this case the ratio of the chromosome number of the pollen tube to that of the style tissue is greater than 1. When crossing $2n = 48 \times 24$ chromosome *Datura* species, for example, the pollen tube growth rate is 67.4%, whereas in the reciprocal cross it is only 13.7%. In this latter case the pollen tube rarely reaches the ovary. The chromosome number ratio of the pollen tube to the style tissue is 1:4 in the first case and 1:1 for the reciprocal cross. The ratios are similar in interspecific crosses of *Nicotiana* (EAST, 1935), *Solanum* (JÖRGENSEN, 1928), *Galeopsis* (MÜNTZING, 1930) and *Lycopersicon* (COOPER-BRINK, 1945, WOJCIECHOWSKI-ANDRZEJEWSKI, 1986).

The superiority of pollen with a lower chromosome number is clearly illustrated when pollination is carried out with a pollen mixture. In the case of *Secale*, LÖVENSTEIN (1951) placed an $n + 2n$ pollen mixture on the stigma of a tetraploid plant and obtained 26.4% mature ($4n$) grains and 73.6% immature ($3n$) grains. If, however, this same mixture was put onto the stigma of a diploid ($2n$) plant the ratio was 69.7% mature ($2n$) and 30.3% immature ($3n$) grains. If the $4n$ stigma was first pollinated with n pollen, followed half an hour later with $2n$ pollen, 3.2% grains with a chromosome number of $4n$ were obtained, whereas if the stigma of a $2n$ plant was pollinated first with $2n$ pollen and half an hour later with n pollen, 26% $2n$ grains were obtained.

The production of triploid water melon seed is also complicated by the fact that hybridisation is only possible in one direction. Triploid seed is only obtained if the $4n \times 2n$ cross is made. In the reciprocal direction, the thick pollen tube of the tetraploid is unable to penetrate the thin style of diploid water melon, so fertilisation fails to take place. Since $4n$ water melons set only a tenth the number of seeds as $2n$ melons, the production of triploid $3n$ seedless water melons is not economical (KISS-BELEA, 1958).

In other plant species, such as *Triticum* (WAKAKUWA, 1934), *Avena* (KIHARA-NISHIYAMA, 1932), *Helianthus* (WAGNER, 1932), *Rosa* (FAGERLIND, 1948) and numerous grasses, the growth of the pollen tube is better if the parent with the lower chromosome number is the female, when the chromosome number ratio is less than 1:2. In a third group, to which the *Brassica* genus belongs, no differences can be observed in pollen tube growth as a function of crossing direction.

In the cross *Solanum tuberosum* $\times$ *S. acaule*, WAGENHEIM (1954) found that the pollen tube of the male parent stopped growing completely in the style tissue. In the case of the reciprocal cross weak growth was observed. According to BATIKINA and co-workers (1961) the interaction of the female and male gametes depends on the initial development of the pollen tubes. In addition to morphological reasons, other authors, too, put the differences observed in reciprocal crosses down to mainly physiological, genetic or plasmatic causes (FABIG-NOVAK, 1972; NAKANISHI et al., 1969; NAKANISHI-HINATA, 1975; OCKENDON, 1977, etc.). When the stigmata of *T. monococcum* and ssp. *dicoccum* are pollinated with the pollen of hexaploid wheat (*T. aestivum*), abnormal development is often noted after the penetration of the pollen tube. In the case of *Prunus* and *Nicotiana*, a blister forms on the end of the pollen tube, hindering the development of the fruit. In the reciprocal cross, when the species with the greater chromosome number is used as the female parent, this phenomenon rarely occurs.

2.11 Seed or grain formation

The direction of crossing has an effect not only on seed setting, but also on the formation and quality of the hybrid seed or grain, and this also influences the germination of the seed. In addition to morphological reasons, this can be explained chiefly by the differing chromosome numbers in the tissues of the female parent, embryo and endosperm. The abnormal development of the endosperm is a particularly frequent cause of disturbances in hybrid seed formation. In the case of normal fertilisation and seed formation, the ratio of the chromosome numbers of the embryo, the endosperm and the maternal ovary tissue is 2:3:2, since the fertilised endosperm consists of triploid tissue, i.e. two female genomes are combined with one male genome. When crossing parents with different chromosome numbers, this ratio will change, depending on which species is used as the female and which as the male parent (Table 19). If the

Table 19.

Chromosome number of the embryo, the endosperm and the ovary tissue (after OEHLER, 1956)

Chromosome combination	Ratio of chromosome number			Chromosome ratio		
	Embryo	Endosperm	Ovary tissue	between the embryo and the endosperm	between the embryo and the ovary tissue	between the endosperm and the ovary tissue
$2n \times 2n$	2	3	2	0.67	1.0	1.5
$2n \times 4n$	3	4	2	0.75	1.5	2.0
$2n \times 6n$	4	5	2	0.80	2.0	2.5
$4n \times 2n$	3	5	4	0.60	0.75	1.25
$6n \times 2n$	4	7	6	0.57	0.67	1.17

parent with the smaller chromosome number is the female, the embryo has a relatively large chromosome number compared to the endosperm and the female ovary tissue, while in the reciprocal cross its chromosome number will be relatively small. When the chromosome ratio of the embryo: endosperm or endosperm: female ovary is abnormal, as in the case of parent species with different chromosome numbers, this may result in morphological and physiological changes which lead to anomalies in the development of the endosperm. This is much more pronounced if the species with the smaller chromosome number is the female parent. In this case the embryo: endosperm ratio is greater than 2:3 (BOYES-THOMPSON, 1937). In the reciprocal cross the endosperm develops better. In many cases the disturbances are so great that the endosperm completely ceases to develop and the embryo dies.

Anomalous development in the endosperm or embryo can be attributed to genetic or physiological reasons. After analysing the crosses *Solanum acaule* ($8 \times$) $\times$ *S. acaule* ($4 \times$) and *S. stoloniferum* ($4 \times$) $\times$ *S. tuberosum* ($4 \times$), WAGENHEIM (1954) suggested that, in addition to factors inhibiting crossing, which stem from the *S. tuberosum* species, abnormalities in the development of endosperm tissues were responsible in these combinations, too, for the disturbances.

In many interspecific crosses, after successful seed setting, the initial development of the embryo and the endosperm is quite normal. Experiments on *Medicago*, *Nicotiana*, *Lycopersicon*, *Hordeum* and *Zea* species, carried out by COOPER-BRINK (1945), indicate that the development of the endosperm usually only slows down after a number of days. This then leads to obstructions in the transport of nutrients, resulting in abnormal development of the tissues in the nucellus and ovary, which in turn hinders the development of the endosperm.

When crossing *Nicotiana* species, after a few days the wall of the ovary begins to undergo intensive division, which prevents the endosperm from developing. At the same time the differentiation of the transporting tissue between the ovary and the embryo ceases to exist. In the tumours often developing in the ovaries of *Datura* species indolyl acetic acid forms, which could be responsible for the anomalies observed.

In numerous genera (*Zea*, *Secale*, *Hordeum*, etc.) viable triploid hybrids are rarely obtained, because of abnormalities in endosperm development following fertilisation, as the result of which the embryo dies. This is primarily characteristic of plants where the endosperm plays an important role in the nutrition of the embryo. Triploid plants can easily be produced, however, from species where little or no endosperm develops in the seed (*Populus*, *Beta*).

A few days after fertilisation, the endosperm and the embryo died in crosses between artificially produced autotetraploid *Secale* and *Hordeum* species and the original diploid species (HÄKANSSON-ELLERSTRÖM, 1950; HÄKANSSON, 1953). The anomalies are found chiefly in the endosperm development and result in the destruction of embryos which would otherwise develop normally.

The raising of the first generation is often difficult not only when the chromosome number is different ($2x \times 6x$), but also in crosses between species at the same level of polyploidy ($4x \times 4x$ or $6x \times 6x$). It frequently happens that the development of the endosperm ceases 8–10 days after the germination of the pollen and the embryo dies due to lack of nutrients. FORLANI (1950), BRINK-COOPER (1947) and BROWN (1964) refer to this phenomenon as starvation. In other cases, plants developing from shrivelled seeds die off immediately prior to full development due to the effect of late-acting lethality (HERMSEN, 1957; MORRISON, 1953; SACHS, 1953). This difficulty can be overcome by raising the embryo artificially in an embryo culture. If such embryos are dissected out of the young seeds in time (8–12 days after fertilisation) and are fed artificially, they can be raised successfully. In this way viable F_1 plants were raised from interspecific crosses of *Linum* (LAIBACH, 1925), *Lycopersicon* (COOPER-BRINK, 1945), *Datura* (MCLEAN, 1945), *Gossypium* (BEASLEY, 1940), *Cucurbita* (WEILING, 1955), *Hordeum* (BRINK et al., 1944), etc.

Using this method RÉDEI (1954) was able to produce hybrid plants by raising embryos in vitro from the combination *T. turgidum* conv. *durum* $\times$ *Secale cereale*. JAMANE (1953) raised the first generation of the cross *Cucurbita pepo* $\times$ *C. moschata* and its reciprocal. Due to the abnormal development of the endosperm, the hybrid seeds of combinations of the diploid *Iris pallida* ($2n=24$) and the polyploid *I. macrantha*, *I. trajana* and *I. cyprium* ($2n=48$ and $2n=60$) were poorly developed; these, too, could only be raised in embryo cultures. Hybrids of *Gossypium arboreum* $\times$ *G. hirsutum* (GILL-BAJAJ, 1987), *Ornithopus sativus* $\times$ *O. compressus*, etc. could also be raised only in embryo cultures. HESZKY (1972a, b) was only able to raise intergeneric hybrids between *Lolium* (*L. westerwoldicum*, *L. perenne*, *L. multiflorum*, *L. temulenium*) and *Festuca* (*F. arundinacea*, *F. pratensis*) in vitro. The hybrid proembryos were dissected out 7–14 days after fertilisation and raised on Difco Orchid and modified Nitsch nutrient medium. In order to ensure normal development, the hybrid proembryos were kept on a medium supplemented with various osmotic agents, hormones and vitamins. The high osmotic pressure of the endosperm was achieved by increasing the concentrations of saccharose, glucose, casein hydrolysate and KH_2PO_4 . After embryogenesis, the germination of the developed

embryos was induced by transferring them to a nutrient medium with lower osmotic pressure.

Tissue culturing has been successfully employed to raise intergeneric hybrids of *Hordeum* × *Secale*, *Hordeum* × *Triticum*, *Hordeum* × *Agropyron* and *Hordeum* × *Avena* (KRUSE, 1973, 1974, 1967), trigeneric interspecific hybrids between *Hordeum*, *Triticum* and *Secale* (FEDAK-ARMSTRONG, 1980), *Hordeum* × *Triticum* hybrids (MOLNÁR-LÁNG et. al., 1985), interspecific hybrids of *Lycopersicon* (COOPER-BRINK, 1945), etc. If the prepared embryo can be kept completely free of infection, the method is an extremely efficient way of raising hybrid plants from interspecific and intergeneric crosses.

The composition of certain nutrient mediums which have proved useful in embryo cultures is presented in Table 20.

Table 20.
Composition of nutrient mediums used in embryo cultures

After KRUSE (1974)		After TOMASZEWSKI-KUBOK (1968)		After DVORÁK (1981)	
KCl	65 mg/l	Macro:	0.15 g/l	NaH ₂ PO ₄ + H ₂ O	150 mg/l
KNO ₃	100 mg/l	(NH ₄) ₂ SO ₄	(0.25)	KNO ₃	2 500 mg/l
NH ₄ NO ₃	100 mg/l	KNO ₃	0.25 g/l	(NH ₄) ₂ SO ₄	134 mg/l
Ca(NO ₃) ₂	150 mg/l	Ca(H ₂ PO ₄) ₂	0.20 g/l	MgSO ₄ + H ₂ O	250 mg/l
NaH ₂ PO ₄	50 mg/l	Ca(NO ₃) ₂	(0.22)	Fe-EDTA	35 mg/l
KH ₂ PO ₄	50 mg/l	MgSO ₄	0.15 g/l	CaCl ₂ + H ₂ O	150 mg/l
MgSO ₄	70 mg/l	KCl	0.20 g/l	MnSO ₄ + H ₂ O	10 mg/l
adenine	40 mg/l	Micro:	0.15 mg/l	H ₃ BO ₃	3 mg/l
I-inozite	100 mg/l	MnCl ₂	(0.25)	ZnSO ₄ + 7H ₂ O	2 mg/l
kinetin	0.5 mg/l	H ₃ BO ₃	0.15 mg/l	Na ₂ MoO ₄ + 2H ₂ O	0.25 mg/l
IAA	5 mg/l	CuSO ₄	0.05 mg/l	CuSO ₄	0.03 mg/l
(indo- leacetic acid)		ZnSO ₄	0.30 mg/l	CoCl ₂ + 6H ₂ O	0.03 mg/l
		(NH ₄) ₂ MoO ₄	0.15 mg/l	KI	0.75 mg/l
		Vitamins:		nicotinic acid	1.0 mg/l
		B ₁ thiamine	10 mg/l	thiamine	10 mg/l
		B ₂ riboflavin	7 mg/l	inosite	2 000 mg/l
		B ₆ pyridoxine	5 mg/l	glutamine	400 mg/l
		H biotin	5 mg/l	serine	80 mg/l
		PP nicotinic acid	5 mg/l	cysteine	10 mg/l
		C (ascorbic acid)	50 mg/l	sucrose	60 000 mg/l
		(pantothenic acid)	7 mg/l		

2.12 Quality and germination of hybrid seeds

If the hybrid seeds are filled out and develop fairly normally, this means they have a sufficient amount of endosperm. Some seeds, however, will be larger or smaller than the parents and severely shrivelled due to the lack of endosperm. There is no connection between the degree of seed setting and the quality of the hybrid seed, but the quality is correlated with germination. This is particularly obvious in crosses between parents with different chromosome numbers. In interspecific crosses of wheat, for instance, the hybrid seeds are often filled out, but smaller in size if the parent with the larger chromosome number is used as the female, and these seeds have better germination (BELEA, 1964). In the reciprocal cross, although the seeds are larger, they are shrivelled due to lack of sufficient endosperm, so their germination ability is also poorer (Table 21). The direction of crossing also exerts an effect on the mass and length of the seeds. For example, the average mass and length of pentaploid hybrid seeds of wheat are 24.7 mg and 7.9 mm in the tetraploid $\times$ hexaploid direction, while in the reciprocal cross these values are 12.1 mg and 4.4 mm (Table 22). Similar observations were made by KIHARA-NISHIYAMA (1932) when crossing *Avena* species with different chromosome numbers (Table 23). In this case the tissue of the female ovary has a relatively small chromosome number ($2\times$), while those of the embryo ($3\times$) and endosperm ($4\times$) are larger, and this gives rise to larger, but shrivelled hybrid seeds.

WATKINS (1927) was the first to establish the fact that when crossing parents with different chromosome numbers, seed setting was lower, but the hybrid seeds germinated better if the species with the larger chromosome number was used as the female parent. In the reciprocal cross the seed setting was better, but the germination vigour was poorer due to the shrivelled state of the seeds. This conclusion was drawn mainly from crosses between *T. turgidum* and *T. aestivum*.

Table 21.

Seed setting, seed germination and seed formation in direct and reciprocal crosses of *Triticum* species with different chromosome numbers

Chromosome combination	Seed setting		Germination		Seed formation	
	No.	%	No.	%	Size	Quality
$n=7 \times n=14$	211	6.2	16	12.6	large	slightly shrivelled
$n=14 \times n=7$	319	4.4	219	27.3	medium	fairly well filled
$n=7 \times n=21$	18	0.7	2	10.0	large	shrivelled
$n=21 \times n=7$	84	1.9	31	49.6	medium	slightly shrivelled
<i>T. timopheevii</i> $\times$ $n=14$	140	5.0	92	58.9	medium	slightly shrivelled
$n=14 \times T. timopheevii$	846	17.6	592	67.5	large	slightly shrivelled
$n=14 \times n=21$	1851	12.6	857	32.1	large	shrivelled
$n=21 \times n=14$	783	10.7	613	50.8	small	very well filled
<i>T. timopheevii</i> $\times$ $n=21$	335	5.6	84	25.3	large	shrivelled
$n=21 \times T. timopheevii$	156	3.3	93	53.3	small	well filled

Table 22.

Effects of crossing direction on seed mass and length in direct and reciprocal crosses between *Triticum* species with different chromosome numbers

Tetraploid wheat species	Seed mass mg	Seed length mm	numbers						Diploid wheat species	Seed mass mg	Seed length mm
			Crossing direction				4 × <i>T. timopheevii</i>	mm			
			7 × 14		14 × 7						
			mg	mm	mg	mm					
<i>ssp. dicoccum</i> <i>ssp. carthlicum</i> <i>T. timopheevii</i>	28.0	7.8	—	—	16.3	7.2	<i>T. monococcum</i> <i>T. monococcum</i> <i>T. monococcum</i>	35.6	7.8		
	32.1	7.2	20.6	10.1	18.5	9.4		35.6	7.8		
	41.9	8.5	18.2	9.7	15.4	8.1		35.6	7.8		
			19.4	9.9	16.7	8.2					
tetraploid wheat species	Seed mass mg	Seed length mm	Crossing direction						tetraploid wheat species	Seed mass mg	Seed length mm
			<i>T. timopheevii</i> × 4		4 × <i>T. timopheevii</i>	mm					
			mg	mm							
			mg	mm							
<i>T. timopheevii</i> <i>T. timopheevii</i> <i>T. timopheevii</i>	41.9	8.5	35.9	8.3	34.1	7.5	<i>ssp. carthlicum</i> <i>ssp. dicoccum</i> <i>conv. durum</i>	32.1	7.2		
	41.9	8.5	42.4	10.0	36.8	9.6		30.0	7.8		
	41.9	8.5	37.8	8.7	35.4	2.5		20.0	6.1		
			38.7	9.0	35.4	6.5					
tetraploid wheat species	Seed mass mg	Seed length mm	Crossing direction						hexaploid wheat species	Seed mass mg	Seed length mm
			14 × 21		21 × 14		mm				
			mg	mm	mg	mm					
			mg	mm	mg	mm					
<i>ssp. carthlicum</i> <i>ssp. dicoccum</i> <i>T. timopheevii</i>	32.1	7.2	18.1	6.4	7.6	3.9	<i>T. aestivum</i> <i>T. aestivum</i> <i>T. aestivum</i>	40.2	6.5		
	28.0	7.8	30.2	9.0	13.2	4.9		40.2	6.5		
	41.9	8.5	14.5	8.3	11.9	4.3		40.2	6.5		
<i>T. timopheevii</i> <i>T. timopheevii</i> <i>ssp. carthlicum</i>	41.9	8.5	21.9	8.4	11.7	3.6	<i>ssp. spelta</i> <i>ssp. spelta</i> <i>T. aestivum</i>	30.0	8.5		
	32.1	7.2	26.7	8.9	12.1	5.2		30.0	8.5		
	20.0	6.1	35.4	6.2	13.6	4.0		40.2	6.5		
<i>conv. durum</i> <i>T. monococcum</i> 4 ×	20.0	8.6	26.1	7.9	14.5	4.8	<i>T. aestivum</i>	40.2	6.5		
			24.7	7.9	12.1	4.4					

Table 23.

Seed setting, seed germination and seed formation in direct and reciprocal crosses between *Avena* species with the same or different chromosome numbers
(after KIHARA-NISHIYAMA, 1932)

Chromosome combination	Seed setting		Seed germination		Seed	
	No.	%*	No.	%	Size	development
$n=7 \times n=7$	59	85.5	43	87.8	small	well developed
$n=14 \times n=14$	222	96.6	210	97.3	large	well developed
$n=21 \times n=21$	69	86.3	68	98.7	large	well developed
$n=7 \times n=14$	118	81.4	88	74.6	large or small	shrivelled
$n=14 \times n=7$	119	73.5	110	93.2	fairly small	slightly shrivelled
$n=7 \times n=21$	56	71.8	0	—	large	shrivelled
$n=21 \times n=7$	81	62.3	46	56.8	small	somewhat shrivelled
$n=14 \times n=21$	222	95.3	136	61.3	large	very shrivelled
$n=21 \times n=14$	113	71.1	108	98.2	small	well developed

* where 100% is the number No. of fertilised stigmata

tivum. VENEDIKTOV (1958) reached similar conclusions when carrying out crosses between conv. *durum* ssp. *carthlicum* species and hexaploid wheat. GRANHALL (1943), on the other hand, obtained both better seed setting and better germination of the hybrid seeds in the *T. aestivum* $\times$ *T. turgidum* cross if the parent with the larger chromosome number (*T. aestivum*) was used as the female. The probable reasons for this is that the climatic conditions in Sweden do not favour tetraploid wheat species.

Certain authors (THOMPSON-ROBERTSON, 1930) consider this phenomenon to be characteristic only of pentaploid hybrids. BELEA (1976), however, found it to apply not only to pentaploid ($4x \times 6x$) crosses, but also to triploids ($2x \times 4x$) (see Table 18).

KATAYAMA (1933) classifies all plant species characterised by this phenomenon as "*Triticum*" types, the opposite of which is the "*Brassica*" type, where better seed setting and a poorer germination percentage are obtained if the species with the larger chromosome number is the female parent. In yet other species (e.g. *Nicotiana*) no such phenomenon is experienced.

The crossing direction generally has a greater effect on germination than on seed setting. In practice it would thus seem advisable to use the species with the higher chromosome number as the female parent, since this will improve the percentage germination. The associated drop in seed setting can be counter-balanced by using biotypes or cultivars with good combining ability.

As mentioned above, the germination ability of well developed hybrid seeds is usually better. There is no direct correlation between the degree of seed setting and germination. Shrivelled seeds may be obtained even from successful crosses. It may also happen that seed setting is better if the species with the larger chromosome number is used as the female parent. In this case there can be no doubt about which crossing direction is likely to give the best results.

2.13 Effect of genome differences on the success of crossing

As in the case of differences in chromosome number, genome differences, especially in the cereals, also have an effect on the success of crosses between different species. The development of the embryo and the endosperm is influenced not only by quantitative differences in the chromosomes, but also by qualitative (genome) differences. If the genomes of the parents differ in quality, abnormalities will be observed in endosperm development and the embryo may die. If the new genome complexes are homologous with the genomes of the female ovary tissue, the development of the endosperm will be normal, otherwise there will be anomalies.

Table 24.

Genome relations when crossing species having the same or different chromosome numbers with the same or different species (after KATAYAMA, 1933)

Cross	Pollen tube	Style	Embryo	Endosperm	Reciprocal differences
AA × AA	A	AA	AA	AAA	factorial or plasmatic quantitative qualitative qualitative qualitative quantitative and qualitative
AABB × AABB	AB	AABB	AABB	AAABBB	
AAAA × AA	A	AAAA	AAA	AAAAA	
AA × AAAA	AA	AA	AAA	AAAA	
AA × BB	B	AA	AB	AAB	
BB × AA	A	BB	AB	ABB	
AABB × AA	A	AABB	AAB	AAABB	
AA × AABB	AB	AA	AAB	AAAB	

When crossing species with the same chromosome number and homologous genomes ($A \times A$ or $AB \times AB$), differences in seed setting and seed formation depend only on gene activity or the cytoplasm effect, and on interactions between them.

If the species crossed have different chromosome numbers but homologous genomes ($A \times AA$) the success of crossing is influenced only by quantitative factors. When the species have the same chromosome number, but the genomes are not homologous, qualitative differences between the parents are also important. In an $A \times B$ combination the endosperm will have the genome composition AAB, while the style and the ovary tissue are AA. In the reciprocal cross ($B \times A$) the endosperm will be ABB and the style and ovary tissue BB. When crossing species with different chromosome numbers and non-homologous genomes ($A \times AB$), but which belong to the same genus and are not too distantly related to each other, both quantitative and qualitative factors exert an effect. If the species to be crossed belong to different genera and have completely different chromosome numbers and genome quality ($AB \times S$), the success of crossing

depends only on qualitative factors. In an $AB \times A$ cross the endosperm contains 5 genomes (AAABB), while in the reciprocal cross it contains 4 (AAAB) (Table 24). When crossing hexaploid and tetraploid wheat species ($ABD \times AB$) the endosperm develops satisfactorily if the D genome is doubled in the species which has a higher level of polyploidy (AAABBBDD), but will be poor if the D genome is only present once (AAABBBDD).

Cross	Endosperm	Embryo	Endosperm	Embryo	Cross
$AA \times AA$	AA	AA	AA	AA	$AA \times AA$
$AA \times AB$	AA	AB	AA	AB	$AA \times AB$
$AA \times BB$	AA	BB	AA	BB	$AA \times BB$
$AA \times DD$	AA	DD	AA	DD	$AA \times DD$
$AB \times AB$	AAAB	AB	AAAB	AB	$AB \times AB$
$AB \times BB$	AAABB	AB	AAABB	AB	$AB \times BB$
$AB \times DD$	AAABD	AB	AAABD	AB	$AB \times DD$
$BB \times BB$	BB	BB	BB	BB	$BB \times BB$
$BB \times DD$	BB	DD	BB	DD	$BB \times DD$
$DD \times DD$	DD	DD	DD	DD	$DD \times DD$

3. Morphology of interspecific and intergeneric hybrids

Before discussing the morphology of interspecific and intergeneric hybrids, a brief description must be given of the process of fertilisation, the structure of the chromosomes which play a decisive role in heredity, and the rules governing heredity.

3.1 Fertilisation

It has long been known that when the pollen reaches the stigma, it produces a pollen tube which penetrates to the ovule. In 1830 Amici observed that the pollen tube had reached the ovum, but was unable to establish the fact that they had actually united. In his opinion, the pollen tube simply stimulated further development. It only later became known that the pollen fertilised the ovum,

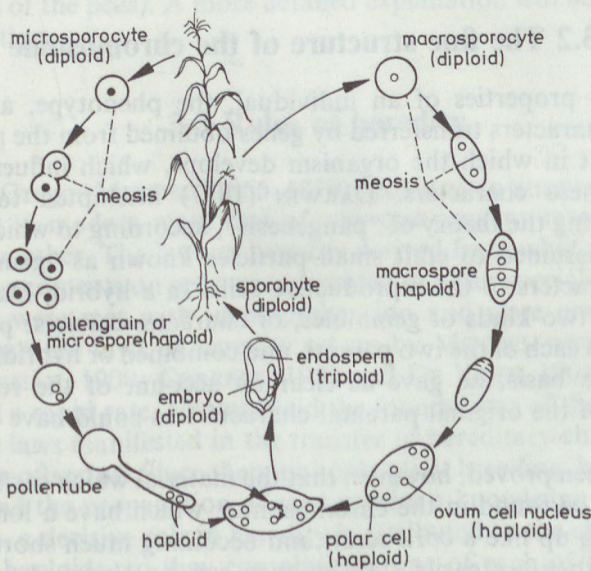


Fig. 26. The life cycle of plants (SINNOTT et al., 1958)

the most important cell in the interior of the ovary. There may be one or more ovules in the ovary. An embryo sac forms in the ovule and, as the result of complicated cell divisions, 8 gametes form in the embryo sac. These are characterised by the fact that they have a chromosome number which is only half that of the somatic cells. Of these 8 cells, 4 are to be found at the lower pole of the embryo sac and 4 at the upper pole. In the following stage, one cell each from the upper and lower groups migrate to the middle and unite, so that the chromosome number of this united cell is the same as that of the somatic cells. This is referred to as the secondary nucleus. Three cell nuclei thus remain at the bottom and three at the top, each surrounded by a separate cell wall. Of the upper 3 nuclei, one forms the ovum and the other two are accessory cells. In general it is the ovum which is fertilised (Fig. 26). After pollination the cell nucleus of the pollen tube divides into two parts in the course of growth, one forming the vegetative cell nucleus and the other the generative cell nucleus. The first develops the pollen tube, the material of which is later absorbed. The generative nucleus divides into two (G_1 and G_2), after which both migrate towards the ovum, with which G_1 unites. This gives rise to the zygote, the first cell of the embryo, which contains a double quantity of chromosomes. After this first fertilisation, G_2 moves on downwards into the embryo sac, where it unites with the secondary nucleus, producing an entity with a triple quantity of chromosomes. This then develops into the endosperm. Since the cell nucleus of the fertilised ovum also contains the cell nucleus of the pollen, and since the chromosomes of the cell nuclei are the carriers of the plant characters, the characters of both parents are to be found in the new embryo.

3.2 The fine structure of the chromosome

The observable properties of an individual, the phenotype, are determined jointly by the characters transferred by genes obtained from the parents and by the environment in which the organism develops, which influences the manifestation of these characters. DARWIN (1877) attempted to explain this phenomenon using the theory of "pangenesis", according to which every cell in the body was assumed to emit small particles known as "gemmules" which carried the characters to the reproductive cells. In a hybrid, Darwin assumed that there were two kinds of gemmules, or character-carriers: pure gemmules originating from each of the two parents, and combined or hybridised gemmules as well. On this basis, he gave as clear an account of the reasons for the re-appearance of the original parental characters as could have been expected at the time.

It has since been proved, however, that the material which carries the various characters is to be found in the chromosomes, which have a long, thread-like structure, coiling up like a cork-screw and becoming much shorter during cell division. Since they are easily stained, they can be observed readily using a microscope. The chromosomes are located in the cell nucleus and the number

of chromosomes is characteristic of the species in question. The basic chromosome number is that of the monoploid and is symbolised by x . The gametes are haploids and have a chromosome number designated by n in diploid species. The somatic cells have a chromosome number of $2n$, since they contain one pair of each type of chromosome.

Each chromosome contains two strands, running parallel to each other and of identical structure. These are known as chromatids. During cell division they become separated and migrate into separate daughter cells, where they duplicate themselves. The old and new chromatids produced in this manner form a new chromosome (in the course of mitosis). When the gametes are formed, in the course of reductional division (meiosis), various homologous chromosomes are located to start with in the equatorial plane of the cell. One member of each pair migrates to one pole of the cell and the other to the opposite pole, where the chromatids separate, as in equational division (mitosis), but instead of two, four new cells are formed, each containing the number of chromosomes characteristic of the somatic cells (e.g. the gametic chromosome number of *Brassica* is $n=9$, that of hexaploid *Triticum* $n=21$, that of *Capsicum* species $n=12$). In the somatic cells $2n=18$, $2n=42$ and $2n=24$ chromosomes are found, respectively. Since the chromosomes of a single cell differ considerably from each other in size, shape, structure and behaviour, they are relatively easy to identify.

The particles which transfer the various characters (the genes) are located at specific sites on the chromosomes, like links in a chain; they are generally designated using the initial letter of the characters they determine. If the inheritance of a particular character is to be traced, there must be at least two distinctive forms of manifestation (e.g. in Mendel's experiment, the yellow and green colours of the peas). A more detailed explanation will be presented in the following section.

3.3 Rules of heredity

The work of Gregor MENDEL (1866–1870) provided an answer to a question of great interest to modern man, that of why one progeny resembles its parents more than the other. The laws of heredity derived from what are now regarded as classical experiments on peas were reported to other specialists on the subject in 1866, but were met with incomprehension and were gradually buried in oblivion. When the laws of heredity set up by MENDEL were rediscovered in 1900 (TSCHERMAK, 1900; CORRENS, 1900 and DE VRIES, 1901), genetics began to develop at a rapid rate. MENDEL laid the foundations of the gene theory and set down the laws manifested in the transfer of hereditary characters from the parents to the offspring. Since then, not only plant breeding, but also the choice of cultivar and the propagation of seed require a knowledge of basic genetics.

Nowadays, a decisive role in heredity is attributed to the chromosomes. The gametes are haploids, so they contain only one of each of the chromosomes characteristic of the somatic cells. In a similar manner, there is only one of each

gene. The zygote arising in the course of sexual reproduction, however, contains a diploid set of chromosomes, so the genes, too, are present in pairs. The gene pairs found at the same loci are referred to as alleles. The allele is thus a morphological term, indicating that the allelic genes are located in the same part of the chromosome, though they may not necessarily contain the same information. If the genes in the gametes are designated as "A" and "a", there are three possible ways in which the genes can pair to form a new genotype, namely: AA, Aa and aa. Each gamete contains one allele, so when two gametes combine, three different genotypes will be produced in the case in question. If both members of the allele pair determine the same characters in the same way (and are thus designated by the same symbols: AA or aa), they form a homozygote. If one member of the allele pair determines the given character differently to the other, the new cell is a heterozygote (Aa or aA).

In the allele pair, "A" determines which character or trait appears in the progeny. In the present case one member of the allele pair, "A", is dominant, while the other, "a", carries a recessive trait. Dominant factors are characterised by the fact that the traits they determine are inherited even if the allele is only present once in the allele pair, while the recessive factor only determines the trait which will be manifested if it is present twice, which means that the allele pair is homozygotic (in the present case the "aa" homozygote is recessive).

If individuals representing the three genotypes mentioned above (AA, Aa and aa) are crossed with each other, the following possibilities will occur:

- | | |
|-------------|-------------|
| 1. AA × AA, | 4. Aa × Aa, |
| 2. AA × Aa, | 5. Aa × aa, |
| 3. AA × aa, | 6. aa × aa. |

It can thus be seen that, in the case of two alleles, there are three possible genotypes, resulting in six crossing types. If these crossing types are examined more closely, it will be seen that in cases 1, 3 and 6 the progeny will form a uniform population, all resembling each other. This means that when crossing homozygotes the first progeny generation is always uniform, though it may contain both homozygotes and heterozygotes. This observation is expressed in Mendel's first law, the principle of uniformity in F_1 .

In cases 2, 4 and 5, heterozygotes are crossed, or at least one of the parents is a heterozygote. In this case the characters are separated in the progeny generation. This is expressed in Mendel's second law, the principle of segregation.

The first two Mendelian laws can only be explained as the behaviour of a pair of alleles, i.e. the factors which determine the character, located on two chromosomes. If, however, the plants crossed have two different pairs of homologous chromosomes, i.e. two pairs of alleles determining different characters, rather than just two homologous chromosomes, the results will be different.

Let us suppose that two alleles, AB (the dominant form) and ab (the recessive form) are present. Four types of gametes are thus possible: AB, Ab, aB and ab. This is well demonstrated by MENDEL's experiment, in which a pea variety

with two dominant characters, round, yellow peas (AABB), was crossed with a variety having two recessive characters, angular, green peas (aabb). All the individuals in the F_1 were round and yellow, their genotype being AaBb (or AABB). In the second generation four types of gametes are produced, in the following numerical ratio:

AB round, yellow	315 plants
Ab round, green	108 plants
aB angular, yellow	101 plants
ab angular, green	32 plants.

The genotypes of progeny arising from these four gametes in all the 16 possible crossing combinations are illustrated in Fig. 27. In nine cases both dominant alleles are found (AB), in three cases one dominant allele is present (Ab), in a further three cases the other dominant allele (aB) and in one case both the recessive alleles (ab). Only one of the sixteen cases produced a homozygotic dominant and one a homozygotic recessive. These observations all go to prove the free combination of the individual factors (alleles). This constitutes Mendel's third law, the principle of independent assortment.

As mentioned above, the genes are located on the chromosomes like links in a chain. During the pachytene phase of meiosis, the formation of synapses between the chromatids allows recombination to take place, i.e. the exchange of various sections of homologous chromatids. In this way maternal genes may be transferred to the paternal chromosome, and paternal genes to the maternal

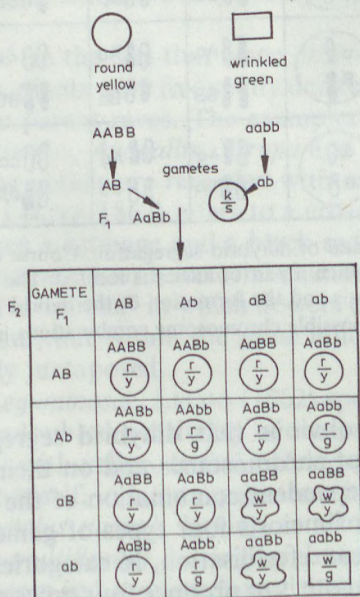


Fig. 27. Independent inheritance of two pairs of characters in a cross between round yellow peas and green wrinkled peas (DUBININ, 1970)

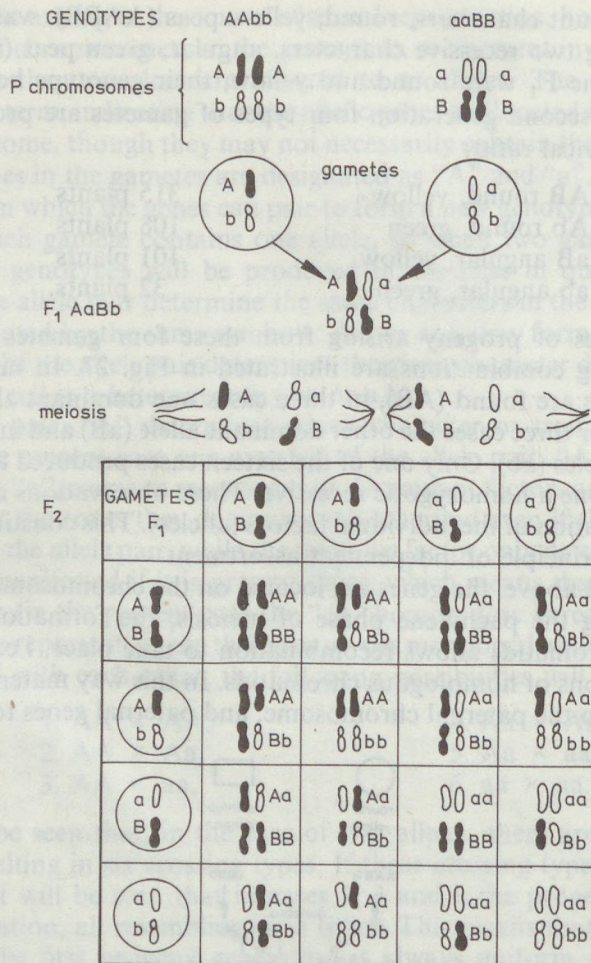


Fig. 28. Cytological background of dihybrid segregation. Course of heredity for two pairs of chromosomes, on each of which a pair of alleles is located. The formation of the parental gametes, the course of meiosis and the formation of the hybrid gametes is illustrated. The diagram also indicates the possible chromosome combinations in the F₂ (DUBININ, 1970)

chromosome. It is thus obvious that dihybrid segregation is based on the inheritance of two pairs of chromosomes and on their independent combination, and also on the independent combination of the alleles within the chromosomes. In the course of meiosis four types of gametes are formed. As the result of free combination and fertilisation, 16 categories of zygotes are possible (Fig. 28). If the diheterozygote is to produce four types of gametes, it is essential for the alleles in question to occupy homologous loci in the homologous chromosome pairs.

A knowledge of dominance relationships is extremely important, as it means that the success or failure of a cross can be judged from the appearance of the F_1 plants, particularly if the plant carrying the dominant traits is used as the male parent. The dominance relationships often determine the conditions under which the hybrids must be raised. The dominance of winter or spring habit and frost resistance or sensitivity, for instance, will determine whether the first generation should be sown in autumn or spring. A knowledge of dominance relationships also facilitates the selection of recessive traits in early generations. In the case of repeated back-crosses, if the desired character of the donor parent is recessive, it is unnecessary to raise an F_3 generation in between back-crosses. This means that selection can be carried out at an earlier stage. Naturally, dominance relationships may differ in different combinations, as will be discussed in more detail below.

3.4 Morphology of the first generation

The more that is known about the genetics of various plant species, the more likelihood there is that the appearance and frequency of new combinations will be reliably predicted, provided the environmental conditions remain unchanged. To this end, genetic analyses must be conducted on the initial stock, studies must be made on inheritance relationships of individual characters, etc., since without this knowledge even simple variety crosses and breeding are unlikely to succeed.

FOCKE (1881) remarked on the fact that when crossing closely related races, especially colour varieties, plants were frequently derived which resembled more or less exactly one of the parent races. The examples cited included *Brassica rapa*, *Linum*, *Pisum*, *Phaseolus*, *Anagallis*, *Atropa* and *Datura*.

A number of interesting details are recorded with respect to crossing plants within different families. LECOQ (1862) refers to a cross in the *Cruciferae* made by SAGERET (1826) between a cabbage and a black radish, the latter serving as the seed parent. Lecoq also mentions a sectorial chimaera in *Dianthus barbatus*, which sometimes shows "variations" in which flowers of different colours occur not only on the same plant, but within the same inflorescence, white and red flowers being immediately juxtaposed.

When discussing the *Leguminosae*, LECOQ (1862) speaks of crosses involving alfalfa, alluding to the undoubted possibility of successfully crossing ordinary alfalfa (*Medicago sativa*) with yellow trefoil (*Medicago lupulina*).

MENDEL (1866–1870) himself, in later experiments involving crosses between dwarf lima beans (*Phaseolus nanus*), having small white seeds, and scarlet runner beans (*Phaseolus multiflorus*), having large seeds with black flecks and splashes on a peach-blossom red ground, found that the colour combinations in the seeds did not appear to follow his laws. Anticipating modern work, which has since confirmed his hypothetical conclusions, he says: "Even these enigmatical results, however, might probably be explained by the law governing *Pisum*,

if we might assume that the colour of the flowers and seeds of *Phaseolus multiflorus* is a combination of two or more entirely independent colours, which individually act like any other constant character in the plant”.

In addition to these authors, an extremely wide-ranging literature has grown up, particularly since the beginning of the 20th century, on the morphology of interspecific and intergeneric hybrids and on the inheritance and segregation of various characters and traits (MUTLY-LAKHAN, 1958; SHARMAN, 1950; SMITH, 1957; KRISTOFFERSON, 1926, etc.).

3.4.1 Uniformity and multiplicity of F_1 hybrids

If the parental species are self-fertilised and are homozygotic with respect to their morphological characters, the plants in the first generation of interspecific and intergeneric hybrids are generally similar to each other in appearance, like hybrids stemming from variety crosses, which obey Mendel's first law, the principle of uniformity. This hybrid form is independent of the crossing direction. If, however, the parents are heterozygotic with respect to their morphological characters, especially if they are also cross-pollinated, it is generally found that the F_1 population consists of individuals with many, extremely varied phenotypes.

As early as 1866, NÄGELI noted that among the species hybrids there were some which showed noticeable variability even in the first generation. This phenomenon was particularly common in crosses between nearly related species, such as the hybrid of *Lychnis diurna* $\times$ *L. vespertina*. The least variability was found as a rule in hybrids where the parent species possessed only a slender mutual relationship.

In the 90s of the last century, MACFARLANE (1890) published considerable work based on a histological study of the characters of hybrids and their parents, which did much to throw light on the ultimate character of the hybrid condition in the F_1 generation. As the result of these investigations, MacFarlane was able to reach a much more exact point of view with regard to the structural characters of hybrids than most of his contemporaries; a view for which few data then existed, and in which investigations do not seem to have been continued until the post-Mendelian work of DARBISHIRE (1908) on the structure of the starch grains in a cross of peas.

MENDEL (1866–1870) himself noted the appearance of several types of F_1 plants in the combination *Hieracium auricula* $\times$ *H. aurantiacum*, the cause of which was the heterozygotic nature of the latter species. In a similar manner, the heterozygotic nature of one or both parents was responsible for the appearance of several types in the F_1 of other hybrids. In certain interspecific crosses in the *Oenothera* genus, for example, 2, 3 or 4 types were found in the F_1 , depending on the combination. DE VRIES (1907) found 4 types in the F_1 of *Oe. nutans* $\times$ *Oe. pycnocarpa* and two in the first generation of *Oe. muricata* $\times$ *Oe.*

lamarckiana. These *Oenothera* species are themselves permanent heterozygotic hybrids, consisting of two components. If the parents are different in all respects, the F_1 will consist of four different types, assuming that the gametes and zygotes are viable. If, on the other hand, one or more gamete or zygote complex is incapable of development, there will be fewer phenotypes in the F_1 .

In the F_1 of the cross *Raphanus sativus* $\times$ *Brassica oleracea*, although the majority of plants were small-flowered and of dwarf habit, enormous individuals of the rosette type with poor flowering and tall, richly flowering plants were also obtained (KARPECHENKO, 1928). In the combination *Helianthus cucumerifolius* $\times$ *H. macrophyllus*, 50% of the first generation was dwarf, while 50% resembled the male parent. In the F_1 of *H. cucumerifolius* $\times$ *H. tuberosus*, every possible transition can be found between the normal growth of the male parent and the weak, unviable dwarf type (WHELAN, 1978). In intergeneric hybrids of *Fragaria* (*F. vesca* $\times$ *F. chilensis*, *F. glauca* $\times$ *F. virginia*) and in the F_1 of *Nicotiana* species (*N. longiflora* $\times$ *N. sanderae*), dwarf, stunted types are frequently found among the normally growing plants. The probable reason for this is the presence of a semi-lethal factor in *N. longiflora* (BRIEGER, 1929). The first generation of *Phaseolus vulgaris* $\times$ *Ph. coccineus* consists of 5 different types: one similar to the male parent, with intense growth, an intermediate type, a sterile dwarf, a sterile semi-dwarf, and a type with early lethality (LAMPRECHT, 1948). A definite ratio, of 3:1 or 1:1, can only be observed between one or two types. The segregation probably depends on a factor found in one of the parents and causing sterility in the heterozygotic state. RUDORF (1953) proved that plants with anomalous development arose irrespective of the direction of crossing. In his opinion, the anomalies were caused by the presence in the parents of alleles inducing different kinds of inheritance. He demonstrated the fact that various inbred lines of the same varieties of *Ph. coccineus* carried different alleles of this species, and these caused the disturbances. In the first generation of *Ph. vulgaris* $\times$ *Ph. multiflorus*, too, types with dwarf habit or exceptionally tall (10 m tall) plants were found among the small number of intermediate plants, depending on the crossing direction. There are also differences in the F_1 interspecific hybrids of the genera *Oenothera*, *Digitalis*, *Epilobium*, *Rubus*, *Medicago*, *Primula* and *Hieracium*, and the appearance of plants of different types depends on which species was used as the female parent. According to MICHAELIS (1937), for example, the cross *Epilobium luteum* $\times$ *E. hirsutum* produces bushy, prostrate, broad-leaved plants bearing fertile androgynous flowers. In the reciprocal cross, however, the plants are all pyramidal and erect, with narrow leaves and exclusively female flowers. The difference is probably caused by deviations in the cytoplasm. In the F_1 populations of crosses between *Helianthus* (sunflower), *Fragaria* (strawberry), *Rubus* (blackberry) and *Nicotiana* (tobacco) species, under-developed short types are to be found among the tall, normally developed plants. The appearance of individuals with different phenotypes can be attributed primarily to the fact that one or both of the parent species is heterozygotic for the majority of the morphological traits, and only homozygotic for one or two characters. In the case of interspecific and inter-

generic crosses, this is the general situation, especially for cross-pollinated species. In the combination *Phaseolus vulgaris* $\times$ *Ph. multiflorus*, for example, the male parent is a cross-pollinator.

Varying types also occur frequently in the F_1 generation of self-fertilising plants. In the F_1 of *Triticum aestivum* $\times$ *T. monococcum*, for instance, individuals in which the glumes are loosely arranged in the lower part of the ear and densely packed in the upper third (squarehead), or having componed ears (vavilovoid), are found amongst the intermediate types (Fig. 29). The plants in the first generation of this combination included some in which 2-3 undeveloped ears covered with a leaf-sheath were formed on the same stalk as the main ear (teratological phenomenon). Deviant types can also be observed among the

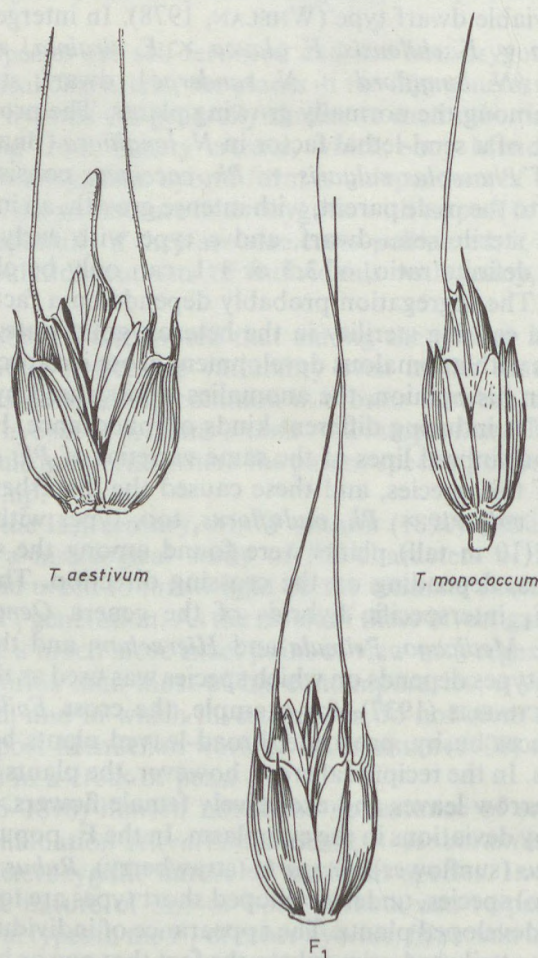


Fig. 29. Spikelet forms of the *Triticum aestivum* $\times$ *T. monococcum* F_1 hybrid and the parental species (BELEA, 1976)

mostly uniform F_1 plants of the combinations *T. timopheevii* $\times$ ssp. *carthlicum* and *T. aestivum* $\times$ *T. timopheevii* as well; these include dwarf compactoid and squarehead individuals. This can again be attributed to the heterozygotic nature of the parent species.

3.4.2 Pseudohybrids resembling the male and female parents

In one group of interspecific hybrids, a substantial proportion of the population resembles the female and male parents, or the offspring resemble only one of the parents. The latter are often referred to as apparent or pseudohybrids. Various *Hieracium* species, for example, develop two kinds of embryo sacs, a normal reduced embryo sac from which a hybrid develops after pollination, and a non-reduced diploid, which develops on its own without fertilisation and produces a plant resembling the female parent. Other *Hieracium* species form exclusively diploid embryo sacs, from which only pseudohybrids develop. In other crosses, for instance in interspecific crosses in the genera *Gramineae* (GAINES-AASE, 1926), *Nicotiana* (KEHR, 1951), *Primula* (ERNST, 1951) and *Brassica* (NISHIYAMA-INAMORI, 1953), plants resembling the female species do not develop alone, but only if species-alien pollen is used in pollination. These pseudohybrids arise due to pseudogamy and develop from non-reduced ovules or from other cells of the gametophytes (*Triticum*, *Nicotiana*, etc.). Diploids may also appear if the chromosomes double at a later stage (*Brassica*, *Primula*, etc.). The haploid plants resemble the female parent as regards their phenotype, but are smaller and less well developed in every respect.

Among the brassicas it is very rare for types resembling the maternal parent to arise in the first generation. Only when pollination is carried out with species-alien pollen do a few individuals correspond to the maternal type. Seed development is induced to a certain extent by pollination (pseudogamy). This phenomenon was investigated by EENINK (1974a, b; 1975a, b), MACKAY (in DIXON, 1968), etc., who gave detailed reports on the inheritance of quantitative characters resembling the female parent, and on the phenomenon of parthenogenesis.

It may also happen that some of the F_1 plants are not uniform, but have differently formed organs (flower colour, flower shape). In the F_1 of *Raphanus raphanistrum* $\times$ *R. sativus*, for example, flowers of both the female and male type (white and yellow) appear and produce two kinds of seeds (RENNER, 1929).

3.4.3 Hybrids of the intermediate type

In general, the F_1 plants of interspecific and intergeneric hybrids give the impression of being intermediate types. In reality, however, this is not so. OEHLER (1956) distinguishes between apparently transitional and real intermediate types. In the first case, due to the countless traits which are inherited

differently in the parents, the hybrids inherit some of the dominant characters from each, so this is really a case of mosaic inheritance. In true intermediates, traits where the dominance of neither parent exerts itself are predominant. This leads to a segregation ratio of 1 : 2 : 1, and the hybrids do not give the impression of being intermediate with respect to certain traits, but as regards the plants as a whole. In reality, as in variety hybrids, they show a colourful mosaic of different morphological characters, and of these traits some have intermediate inheritance, while in others the dominance of male or female parent exerts itself. In addition, there are characters which lead to luxuriance (giant growth) or depression (dwarf growth). This abnormal growth is probably due to the additive or inhibitive effects of growth factors in the progeny.

The majority of F_1 hybrids obtained in the course of interspecific crossing in wheat are also characterised by a mosaic type of inheritance or phenotype. In the case of the *T. timopheevii* $\times$ ssp. *carthlicum* cross, for example, the hairiness of the ear glumes, leaves and auricles in the first generation resembles that of *T. timopheevii*, while the number of awns is reminiscent of the male parent (four-awned ssp. *carthlicum*).

In the case of hexaploid triticale No. 1 (*T. turgidum* var. *buccale* $\times$ *Secale cereale*, stable hybrid), Kiss (1969) examined 28 morphological and 29 quantitative characters. Among the morphological characters the dominance of wheat (*T. turgidum* var. *buccale*) could be observed in 7 cases and the dominance of rye (*S. cereale*) in nine. Eight characters were intermediate in nature, while 4 were completely new (seedling colour, straw colour at maturity, ear colour and number of flowers per ear). Of the quantitative characters, 13 were maternal, 3 paternal, 4 intermediate and 9 completely new (glume length, number of grains per ear, hectolitre mass of the grains, anther size, etc.).

In the F_1 of *Triticum* $\times$ *Secale* crosses, the length and breadth of the rachis, the number of spikelets, the shape of the glume, the pith content of the straw, the duration of flower opening, and the time of flowering and ripening are also inherited in an intermediate manner.

In $2n = 35$ chromosome F_1 plants of the cross *Agropyron tsukushiense* $\times$ *Hordeum bulbosum*, which are sterile but otherwise of intensive development, the plant height and the length of the ears and internodes are transitional between the values found in the two parents; only the flag leaf was longer than that of the parents. With respect to morphological traits, however, the hybrid had a closer resemblance to the male parent.

3.4.4 Maternal or paternal inheritance

In many cases the first generation of interspecific hybrids pronouncedly resembles the phenotype of one of the parents, due to the dominant inheritance of the majority of morphological traits. In this case the inheritance is matroclinal or patroclinal, depending on whether the progeny generation is similar to the

phenotype of the maternal or paternal parent. This phenomenon is observed principally when the species crossed have different chromosome numbers. It is generally the parent with the larger chromosome number which is dominant, since this either contains a larger multiple of the same genomes or has a larger number of different genomes. In this case the presence of more factors, or the fact that different factors act in a similar direction, i.e. the addition of their effects, leads to the dominance of the parent with the greater chromosome number. Thus, in crosses in the genera *Brassica*, *Fragaria* (NISHIYAMA-INAMORI, 1953) *Chrysanthemum*, *Helianthus*, *Gossypium*, *Nicotiana* (KEHR, 1951), *Triticum* $\times$ *Secale* and *Zea* $\times$ *Tripsacum* between parental species with different chromosome numbers, it is nearly always the type of the parent with the higher chromosome number which is manifested. This can also be observed in interspecific crosses of *Triticum*. In the combination hexaploid *T. aestivum* ($2n=42$) $\times$ ssp. *carthlicum* ($2n=28$), for example, the semi-prostrate growth habit of the hexaploid wheat, the stiffer, erect position of the leaves, the shape of the glumes and the absence of awns in the pales are found considerably more frequently than the awned glumes of ssp. *carthlicum*, which are found in very few plants.

The dominance of parents with a higher level of ploidy is particularly apparent in numerous interspecific hybrids if the species with the greater chromosome number is used as the female parent. In this case, not only does inheritance depend on the genotype, but the effect of the maternal cytoplasm is also more pronounced. This also explains instances when the progeny resembles the female parent irrespective of the crossing direction, a phenomenon which is difficult to interpret simply as the gene mechanism of genotypes localised in the chromosomes. The first recorded instance of this was described by WETTSTEIN (1933) in his classic experiment on bryum. Later, similar phenomena were observed in numerous interspecific crosses, e.g. in the genera *Epilobium*, *Aquilegia*, *Saxifraga*, *Antirrhinum*, *Streptocarpus*, *Digitalis*, *Oenothera*, etc.

The hybrids of the crosses *Brassica napus* ($2n=38$) $\times$ *Br. oleracea* ($2n=18$) and *Nicotiana rustica* ($2n=48$) $\times$ *N. paniculata* ($2n=24$) are extremely like the maternal species (ROEMER, 1935; GOODSPEED et al., 1926), while the F_1 hybrids of *Helianthus cucumerifolius* ($2n=34$) $\times$ *H. rigidus* ($2n=102$) and *Fragaria vesca* ($2n=14$) $\times$ *Fr. virginiana* ($2n=56$) resemble the male parent (FADEEVA, 1966).

A fine example of the relationship between gene quality and dominance is also to be found in interspecific hybrids of *Chrysanthemum*, though there are some exceptions. The hybrids of *Ch. makinoi* ($2n=18$) $\times$ *Ch. japonense* ($2n=54$), for example, resemble the female parent, those of *Ch. makinoi* ($2n=18$) $\times$ *Ch. decaisneanum* ($2n=72$) are intermediate and those of *Ch. makinoi* ($2n=18$) $\times$ *Ch. pacificum* ($2n=90$) exhibit the characters of the male parent, despite the fact that, in general, the dominance of the parent with the greater chromosome number is characteristic of *Chrysanthemum* interspecific hybrids.

It frequently happens that the expression of certain morphological traits is much more pronounced if the male parent is the carrier of the dominant traits. In this crossing direction it is easier to recognise the hybrid character. This is experienced in the combination *Triticum aestivum* $\times$ ssp. *carthlicum*, where the

downiness of the stalk and leaves, inherited from the pollinator, is much more intense than in the reciprocal cross. In the same way, the inheritance of hairy leaves, stalk, auricula and ears from *T. timopheevii* is also more pronounced if this species was used as the male parent.

Cases are also known where the characters of the parent with the smaller chromosome number are dominant, for instance in the crosses *Nicotiana longiflora* ($2n=20$) $\times$ *N. sanderae* ($2n=18$) and *Fragaria virginia* ($2n=56$) $\times$ *F. eliator* ($2n=42$), where the plants of both hybrid populations resemble the male parent.

The inheritance of the majority of morphological traits is identical in both crossing directions. Interspecific hybrids in the genera *Digitalis*, *Oenothera* and *Epilobium*, however, differ in the reciprocal crosses. In both crossing directions, the offspring of the *Digitalis purpurea* $\times$ *D. ambigua* combination frequently resemble the female parent, so the inheritance is matroclinal. The F_1 plants of the cross *Epilobium luteum* $\times$ *E. hirsutum* are bushy, prostrate and broad-leaved, with very fertile flowers. In the reciprocal cross, however, the plants are pyramidal, erect and narrow-leaved, with small sterile flowers. It has been suggested that this phenomenon may be due to cytoplasm differences between the parents.

In some interspecific crosses (*Nicotiana*, *Saccharum*, *Solanum*, *Raphanus*, *Brassica*, *Fragaria*, *Zea*) the situation is complicated by the fact that non-reduced gametes are also formed. If, by any chance, these take part in pollination, the F_1 hybrids produced will have a chromosome number which includes an extra haploid set of male chromosomes. These are referred to as sesquidiploids if the original parental species were diploids. In addition to plants with 36 chromosomes, individuals with 48 chromosomes are also found in the progeny of *Solanum tuberosum* ($2n=48$) $\times$ *S. chacoense* ($2n=24$), while all the offsprings from the cross *S. phureja* ($2n=24$) $\times$ *S. tuberosum* ($2n=48$) have 48 chromosomes; these originate from a combination of the non-reduced male or female gametes of diploid parents (PRAKKEN-SWAMINATHAN, 1952). In a similar manner, in the F_1 of *Brassica oleracea* ($2n=18$) $\times$ *Raphanus sativus* ($2n=18$), plants containing 27 chromosomes were obtained as well as those with 18 chromosomes, while in the first generation of the cross *Brassica campestris* ($2n=20$) $\times$ *Raphanus sativus* ($2n=18$), all the plants had 28 chromosomes. Among the 55-chromosome individuals arising from a cross between *Saccharum officinarum* ($2n=80$) and *S. narenga* ($2n=30$), F_1 plants with 95 chromosomes were also observed (RAGHAVAN, 1952). In the interspecific cross *Fragaria vesca* ($2n=14$) $\times$ *F. moschata* ($2n=42$) plants with 28 chromosomes were rarely obtained. The appearance of individuals with 35 chromosomes was more frequent. These arose due to the fertilisation of non-reduced vesca gametes (SCHIEMANN, 1951).

The phenotype of the sesquidiploids often differs from that of the diploids. The hybrid of diploid *Zea mays* ($2n=20$) $\times$ *Euchlaena perennis* ($2n=40$) resembles *Euchlaena*, while those originating from tetraploid *Zea mays* ($2n=40$) $\times$ *Euchlaena* ($2n=40$) are intermediate and resemble the hybrids of diploid *Zea mays* ($2n=20$) and *Euchlaena mexicana* ($2n=20$) (EMERSON-BEADLE, 1930).

Cultivated tuberous begonia hybrids (*Begonia* × *tuberhybrida*) can be divided into various groups depending on their chromosome numbers and morphological characters (Table 25). Varieties belonging to the *Pendula* group are diploids ($2n=28$), while the members of the *Multiflora* group are di-, tri- or tetraploids. *Multiflora maxima*, and in general the large-flowered begonia varieties, are tetraploids. The chromosome number of the diploids fluctuates between 27 and 28, that of the triploids between 41 and 42, and the somatic chromosome number of the tetraploid varieties between 52 and 56.

Table 25.

Connection between morphology and chromosome number as reflected in the chromosome number of begonia cultivars (KUCKUCK, 1979)

Group	No. of cultivars									Total
	diploid		triploid		tetraploid					
	27	28	41	42	52	53	54	55	56	
Pendula type		7								7
Small flowered multiflora	2	7	2	7		1	5	1	1	26
Medium flowered multiflora type					2		2		2	6
Bertinii type				1					1	2
Large flowered single type					2		4		1	7
Double type						1	3	2	13	19
Total	2	14	2	8	4	2	14	3	18	
Grand total		16		10			41			67

When studying the inheritance of certain morphological traits it could be observed that the darker leaf colour of the wheat variety B 1201 (*T. aestivum*), for example, and the purple auricula and ligula coloration of the variety F 481 were dominant in crosses with ssp. *dicoccum* and ssp. *carthlicum*. The awnedness of the ears, on the other hand, proved to be a recessive character, if not to such a pronounced extent, in crosses between awnless varieties of *T. aestivum* (Fortunato and San Pastore) and the awned variety of conv. *durum* Arnaut de Studina. A large proportion of plants in the first generation had a short beak, while only a few plants were awned. In awnless wheats the formation of the awns is depressed by one or more inhibiting factors. *Aegilops* species belonging to the *Pleiothera* section have long awns. If these species are crossed with awnless wheat, there are long awns on the flower glumes of the top spikelets of the hybrids, but not on the cover glumes.

In a similar manner, the dominant traits of the two parents could be observed in the combinations *T. turgidum* conv. *durum* × *T. timopheevii*, *T. timopheevii* × ssp. *dicoccum* and *T. timopheevii* × *T. monococcum* (Fig. 30), when the hairiness of the spikelets inherited from *T. timopheevii* was dominant, as was the darker

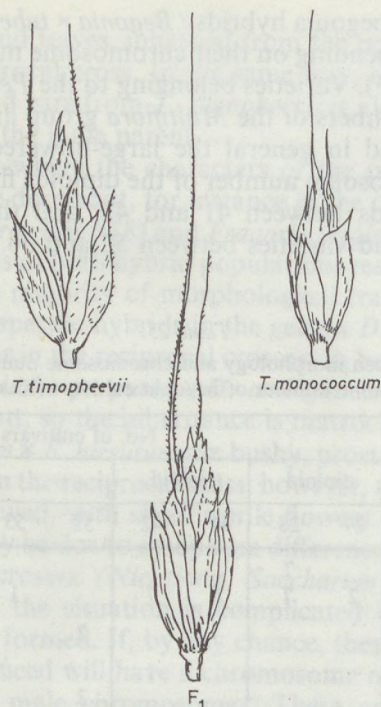


Fig. 30. Spikelet forms of the *Triticum timopheevii* $\times$ *T. monococcum* F_1 hybrid and the parental species (BELEA, 1976)

leaf colour of conv. *durum* in the first cross, the waxiness of stalk and leaves of ssp. *dicoccum* in the second and the ear shape of *T. monococcum* in the third. The dominantly inherited morphological traits of the parents can be observed in the same F_1 plants in the crosses ssp. *dicoccum* $\times$ *T. aestivum*, ssp. *carthlicum* $\times$ *T. monococcum*, etc. In these combinations the waxiness of ssp. *dicoccum*, the leaf downiness and glume awnedness of ssp. *carthlicum*, and the closely knit glumes (ear compactness = D value), rachis fragility and hard-to-thresh ears of *T. monococcum* are all to be found in the plants of the first generation. It can also be observed in these combinations that the outward appearance of the F_1 plants is closer to that of *T. timopheevii* or *T. monococcum* than to that of the other partner (Table 26). Some morphological traits, such as hairiness, are dominantly inherited regardless of the crossing direction.

When crossing cauliflower (*Brassica oleracea* conv. *botrytis*) with other brassicas, WERNER-HONMA (1980) found that the vertical leaf arrangement of cauliflower was inherited dominantly irrespective of the sowing time (summer or winter plants). The additive gene effect was more pronounced in autumn sowings, however.

Other morphological traits, on the other hand, are manifested differently depending on the parental species used. In one cross a certain morphological

Table 26.
Morphological traits of the first generation of certain interspecific Triticum hybrids

Combination	Stem		Leaf			Auricula	
	Hairiness	Wax, downiness	Colour	Hairiness	Hairiness of 3rd leaf	Width	Colour
<i>ssp. carthlicum</i> × <i>T. monococcum</i>	slightly downy	slightly downy	green	slightly downy	rough	narrow	pink
<i>T. aestivum</i> (F 481) × <i>T. monococcum</i>	rough	not waxy	green	rough	rough	medium	purple
<i>T. aestivum</i> (B 1201) × <i>T. monococcum</i>	rough	not waxy	green	rough	rough	medium	white
<i>T. timopheevii</i> × <i>ssp. carthlicum</i>	slightly hairy	not waxy	light green	hairy	hairy	medium	white
<i>T. timopheevii</i> × <i>ssp. dicoccum</i>	slightly hairy	not waxy	light green	hairy	hairy	medium	pink
<i>conv. durum</i> × <i>T. timopheevii</i>	slightly hairy	not waxy	light green	hairy	hairy	medium	white
<i>ssp. carthlicum</i> × <i>ssp. dicoccum</i>	downy	waxy	green	hairy	hairy	medium	white
<i>T. aestivum</i> (B 1201) × <i>ssp. carthlicum</i>	slightly downy	slightly downy	light green	downy	rough	medium	white
<i>T. timopheevii</i> × <i>T. aestivum</i> (F 481)	slightly hairy	not waxy	green	downy	rough	medium	white
<i>ssp. spelta</i> × <i>T. timopheevii</i>	hairy	not waxy	green	hairy	hairy	medium	purple
<i>T. aestivum</i> (F 481) × <i>ssp. dicoccum</i>	rough	not waxy	green	hairy	hairy	broad	white
<i>T. aestivum</i> (B 1201) × <i>conv. durum</i>	rough	waxy	green	slightly downy	rough	medium	purple
	rough	slightly waxy	green	downy	rough	medium	white
<i>T. monococcum</i>	rough	not waxy	green	rough	rough	medium	white
<i>T. timopheevii</i>	hairy	not waxy	light green	rough	rough	narrow	pink
<i>ssp. carthlicum</i>	downy	waxy	light green	hairy	hairy	medium	pink
<i>ssp. dicoccum</i>	downy	waxy	light green	downy	rough	narrow	white
<i>T. aestivum</i> (F 481)	rough	not waxy	green	downy	rough	medium	pale purple
<i>T. aestivum</i> (B 1201)	rough	slightly waxy	green	rough	hairy at base	medium	purple
<i>T. aestivum</i> (B 1201)	rough	waxy	green	rough	hairy at base	medium	white

trait may be dominant, while in another cross the same character may be recessive. In interspecific crosses of wheat, for example, the fragile rachis of ssp. *dicoccum* and ssp. *dicoccoides* is inherited dominantly compared to the steady rachis of conv. *durum* and *T. aestivum*, but is recessive in the cross *Aegilops caudata* × ssp. *dicoccum*.

For certain characters, well defined groups can be set up into which the various individuals can be divided, for instance on the basis of red or white tuber or flower colour. Other characters, such as plant height, tuber size, the pigment content of spice peppers, etc. can only be grouped artificially and it is impossible to put one genotype in one group. This is because these characters are generally regulated by several genes in interaction with the environment. Despite the fact that the alleles of the genes taking part in the formation of these characters obey the laws of heredity when being transferred to the progeny, the course of inheritance cannot be followed in most cases. If the number of genes is not too great, it may be possible to self-pollinate a large number of F_2 s and trace back the genotypes of the various F_2 individuals from the characters of their progeny. This will then disclose the course of heredity for the character in question. This procedure is a good way of eliminating the disturbing effect of the environment and can be used to give an approximate idea of the degree of heterozygosity in the parents and the relative value of their genotypes. If a relatively large number of genes determine the character, the only way to estimate the number of freely combining genes, the average relative effect of the alleles of the individual genes (dominance) and the interaction of the alleles of different genes (epistasis), as well as their interaction with the environment, is to apply more complex biometrical methods.

3.4.5 Luxuriance and depression

It is a general phenomenon in the F_1 plants of interspecific and intergeneric crosses that some or all of their organs develop more intensively than those of the parents. This is usually a question of enhanced vegetative growth, referred to as luxuriance. The leaves are larger and flower development is also more abundant. Gigantic growth was already experienced by the well-known American breeder BURBANK (1914) in the F_1 of the interspecific crosses *Junglans nigra* × *J. californica* and *J. regia* × *J. nigra*. According to KARPECHENKO (1928) the first generations of *Raphanus sativus* × *Brassica oleracea* also developed more intensively, the plants growing to a height of 2.5 m and producing an abundance of flowers, although the parents only measured 70–90 cm in height. Similarly intense growth was reported by RENNER (1929) in interspecific hybrids of *Nicotiana*. In addition to their more intense growth, luxuriant plants often developed more rapidly and matured earlier, only rarely having a longer vegetation period. Such luxuriance was observed by WETTSTEIN (1933) in the F_1 of *Populus* species hybrids, where the plants again surpassed the parent species in

plant height and in the excessive growth observed in various phases of development.

Less frequently, all or some of the organs of the F_1 plants are found to be dwarf or poorly developed. The viability of such plants is also unsatisfactory, as observed in several hybrids of *Gramineae*, *Gossypium* (BROWN-MENZEL, 1952), *Nicotiana* (KEHR, 1951), *Epilobium* (RENNER, 1929), *Fragaria*, etc. The majority of these plants die off at an early stage and can only be raised using special cultivation techniques.

In interspecific crosses of wheat (*Triticum*), too, plant height sometimes exhibits genetic**, and more often economic* luxuriance; this represents the highest value of the heritability index. The greatest extent of luxuriance for plant height can be observed in tri- and pentaploid hybrids, such as ssp. *carthlicum* ($2n=28$) $\times$ *T. monococcum* ($2n=14$), *T. timopheevii* ($2n=28$) $\times$ *T. monococcum* ($2n=14$), *T. turgidum* ($2n=28$) $\times$ *T. aestivum* ($2n=42$) or *T. timopheevii* ($2n=28$) $\times$ *T. aestivum* ($2n=42$) (BELEA, 1964). This is graphically illustrated in Fig. 31, which depicts the percentage deviation of the F_1 hybrids from the mean value (100%)* of the two parents. Depression, i.e. a value lower than the average of the two parents, was primarily observed in the F_1 hybrids of diploid $\times$ hexaploid crosses (*T. aestivum* $\times$ *T. monococcum*, ssp. *spelta* $\times$ *T. monococcum*). Similar observations were made by GUTTENMACHER (1960), HMELEV

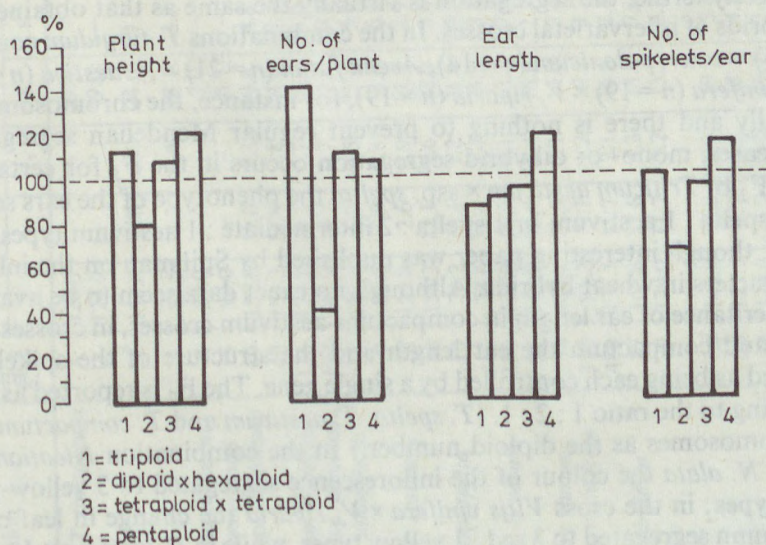


Fig. 31. Percentage deviation from the mean value (100%) of the two parents for quantitative characters of interspecific *Triticum* hybrids in the F_1 (BELEA, 1964)

* economic luxuriance = a value greater than that of the parent with the higher value.

** genetic luxuriance = a value greater than the average of the two parents.

*** the standard curve of the graph (100%) indicates the genetic luxuriance.

(1952), LELLEY (1953), SCHIEMANN-STAUDT (1958), etc. STARZYCZKI-WAS (1960) found the plant height of the first generation to be intermediate.

Productive tillering (the number of shoots per plant which produce ears) and plant height had approximately the same values in tri- ($2x \times 4x$) and pentaploid ($4x \times 6x$) hybrids, and in interspecific crosses within the tetraploid series, though the number of ears per plant is more strongly influenced by external climatic factors than other quantitative characters (Table 27).

3.5 Morphology of the F_2 and later generations

In the F_2 generations of interspecific and intergeneric hybrids the plants exhibit various types of segregation as regards morphological traits depending on the parental species. When crossing parental species differing in a large number of traits, hybrid derivatives with extremely varied phenotypes are reported in the literature (PERCIVAL, 1948; KANIEWSKI, 1948; BELL et al., 1955, etc.).

As the degree of relationship becomes less close, so the appearance of forms, shapes and even species differing completely from the parents becomes more frequent, a fact which may be of great significance from the point of view of evolution.

If parents with homologous genomes are crossed and the first generation is completely fertile, the segregation is virtually the same as that obtained for the F_2 hybrids of intervarietal crosses. In the combinations *T. turgidum* conv. *durum* ($n=14$) $\times$ conv. *polonicum* ($n=14$), *Avena fatua* ($n=21$) $\times$ *A. aestiva* ($n=21$) and *Vitis vinifera* ($n=19$) $\times$ *V. riparia* ($n=19$), for instance, the chromosomes divide normally and there is nothing to prevent regular Mendelian segregation. In many cases, mono- or dihybrid segregation occurs in the F_2 for certain traits. In the F_2 of *Triticum aestivum* $\times$ ssp. *spelta*, the phenotype of the ears segregates into 3 *spelta* : 1 *aestivum* or 1 *spelta* : 2 intermediate : 1 *aestivum* types. In 1901 a brief, though interesting paper was published by Spillman on the inheritance of characters in wheat hybrids. Although no exact data seem to be available on the inheritance of ear length in compactum-aestivum crosses, in crosses between *spelta* and compactum the ear length and the structure of the spikelets were reported as being each controlled by a single gene. The F_2 is reported as splitting according to the ratio 1 : 2 : 1. (*T. spelta*, *T. aestivum* and *T. compactum* all have 42 chromosomes as the diploid number.) In the combination *Nicotiana langsdorffii* $\times$ *N. alata* the colour of the inflorescence segregated to 3 yellow-green : 1 white types; in the cross *Vitis vinifera* $\times$ *V. riparia* the change in leaf colour in the autumn segregated to 3 red : 1 yellow types, while in *V. vinifera* $\times$ *V. rupestris* this character showed a segregation of 1 red : 2 slightly red : 1 yellow types, though branching and the arrangement of the growing tip exhibited dihybrid segregation.

When the parents differ from each other with respect to a large number of morphological traits, segregation is extremely varied and can hardly be fath-

Table 27.

Quantitative characters in the first generations of interspecific *Triticum* hybrids

Combination	Plant no.	Plant height		Ears/plant		Ear length		Spikelets/ear		D-value	
		$\bar{x}$	s	$s_{\bar{x}}$	$\bar{x}$	s	$s_{\bar{x}}$	$\bar{x}$	s	$\bar{x}$	$s_{\bar{x}}$
<i>T. monococcum</i> × <i>T. timopheevii</i> reciprocal	4	120.0	—	—	29.4	—	—	25.3	—	40.8	—
<i>ssp. carthlicum</i> × <i>T. monococcum</i> reciprocal	2	124.0	—	—	49.0	—	—	24.1	—	31.7	—
<i>ssp. carthlicum</i> × <i>T. monococcum</i> reciprocal	16	130.0	5.7	0.6	24.0	9.2	1.1	32.1	3.1	31.3	2.1
<i>T. aestivum</i> × <i>T. monococcum</i> reciprocal	7	86.5	4.2	0.4	18.1	3.8	0.7	31.8	2.6	52.1	1.6
<i>ssp. spelta</i> × <i>T. monococcum</i> reciprocal	4	89.0	—	—	3.0	—	—	12.0	—	17.1	—
<i>T. timopheevii</i> × <i>ssp. carthlicum</i> reciprocal	5	90.0	—	—	6.1	—	—	17.2	—	14.6	—
<i>T. timopheevii</i> × <i>ssp. dicoccum</i> reciprocal	69	157.0	11.0	1.3	14.8	4.8	1.1	21.4	1.5	21.9	2.9
<i>ssp. carthlicum</i> × <i>ssp. dicoccum</i> reciprocal	49	153.3	13.6	2.8	24.0	7.1	2.3	20.5	1.4	19.7	1.4
<i>conv. durum</i> × <i>T. timopheevii</i> reciprocal	136	124.2	8.3	0.7	18.2	4.6	1.3	18.0	1.6	24.4	4.1
<i>conv. durum</i> × <i>T. timopheevii</i> reciprocal	138	143.9	4.7	0.7	17.2	3.6	0.5	20.9	2.3	19.1	2.3
<i>T. timopheevii</i> × <i>T. aestivum</i> reciprocal	8	126.6	6.7	0.5	23.2	5.9	2.3	18.3	1.3	23.7	3.9
<i>T. timopheevii</i> × <i>T. aestivum</i> reciprocal	9	80.8	7.9	0.8	8.6	6.1	2.2	16.8	1.5	25.8	4.1
<i>T. timopheevii</i> × <i>ssp. spelta</i> reciprocal	28	124.8	2.6	0.9	11.8	2.9	0.7	26.8	2.3	23.0	3.9
<i>T. timopheevii</i> × <i>ssp. spelta</i> reciprocal	30	158.2	12.1	2.6	12.0	3.4	1.1	20.6	4.1	18.2	4.2
<i>T. aestivum</i> × <i>ssp. dicoccum</i> reciprocal	10	70.2	6.1	1.2	21.0	4.6	0.8	30.1	1.8	40.1	6.8
<i>T. aestivum</i> × <i>ssp. dicoccum</i> reciprocal	15	74.6	11.4	3.1	5.8	3.5	0.9	17.5	2.3	25.4	3.0
<i>T. aestivum</i> × <i>conv. durum</i> reciprocal	130	163.2	16.3	4.1	13.1	7.6	1.9	21.5	1.3	17.2	0.8
<i>T. aestivum</i> × <i>ssp. carthlicum</i> reciprocal	25	137.0	16.8	5.4	16.6	1.9	0.6	20.1	6.5	16.5	2.5
<i>T. aestivum</i> × <i>ssp. carthlicum</i> reciprocal	34	105.2	11.5	2.1	10.0	3.4	0.9	21.5	3.5	22.3	2.1
<i>T. aestivum</i> × <i>ssp. carthlicum</i> reciprocal	120	91.2	9.1	1.2	14.2	1.9	0.2	15.2	4.9	16.4	2.2
<i>T. aestivum</i> × <i>T. turgidum</i> reciprocal	480	136.1	11.7	2.1	16.8	2.1	0.3	16.7	3.6	13.1	1.8
<i>T. aestivum</i> × <i>T. turgidum</i> reciprocal	27	167.8	12.6	4.3	18.0	7.6	2.1	22.4	2.8	15.6	2.1
<i>T. aestivum</i> × <i>T. turgidum</i> reciprocal	20	129.0	11.7	3.2	13.2	4.2	1.7	25.0	1.6	18.5	2.4
<i>Parental species</i>											
<i>T. monococcum</i>	20	143.0	5.8	0.3	19.6	5.8	0.6	40.8	1.8	42.0	1.4
<i>T. timopheevii</i>	20	127.5	6.7	3.8	18.5	4.1	0.5	21.1	1.4	24.4	3.8
<i>ssp. carthlicum</i>	24	120.0	8.2	2.2	16.7	3.4	0.3	20.9	1.9	16.8	1.2
<i>ssp. dicoccum</i>	20	134.6	7.9	2.1	26.8	3.1	0.1	20.5	3.2	21.1	1.9
<i>T. aestivum</i>	30	119.0	6.8	1.9	12.1	2.9	1.1	18.1	2.9	20.8	2.3
<i>conv. durum</i>	25	131.0	9.8	2.1	6.1	2.7	0.9	18.0	2.8	21.1	2.2

omed on the basis of the Mendelian laws. If for any purpose a large number of F_2 hybrid plants are raised, hardly any two of the population are alike, the plants ranging from the more frequent intermediates to the rarer or completely missing parental types, as observed, for example, in crosses of *Dianthus*, *Antirrhinum*, etc. This phenomenon is of great importance for practical breeders, since it gives rise to numerous new types, combinations and transgressions (*Triticum*, *Nicotiana*, *Brassica*, etc.).

In interspecific hybrids of wheat, too, the appearance in the F_2 of segregation types quite different from the parents or the intermediates is extremely frequent even if the species crosses have identical numbers of chromosomes, and especially if they have different genomes. In the second generation of the ssp. *carthlicum* (AB) $\times$ *T. timopheevii* (AG) cross, for instance, plants with ears which are branching, compact, or thin like those of two-row barley are to be found, as are those with compact ears with awned glumes like those of ssp. *carthlicum*, or with ears reminiscent of *T. timopheevii*, which again have awned glumes; plants with twin or branched ears (*T. turgidum* v. *mirabile*) can also be observed. In the F_2 of this combination, the $K\chi^2$ value (7.28) calculated on the basis of the 3:1 segregation ratio for the stalk, leaf and auricle hairiness of *T. timopheevii* and the leaf downiness of ssp. *carthlicum* was greater than the 3.84 value of $K\chi^2$ given in the table at the $P=5\%$ level of significance. Of the 1030 F_2 individuals, 28.7% were haired. These plants exhibited the downiness of ssp. *carthlicum*, a character which was retained in later generations.

In this crossing direction these two morphological traits did not follow the 3:1 course of inheritance at the $P=5\%$ level of significance. The intense hairiness of *T. timopheevii* could be observed on 29.3% of the 71.3% F_2 plants with hairy leaves. 42% of the hybrids were less hairy than the parent in question.

In the reciprocal cross the segregation ratio for leaf and auricle hairiness was 3.15:1 ($K\chi^2=3.31$; $P=5\%$). In this crossing direction the calculated $K\chi^2$ value was within the $P=5\%$ limit, so a segregation ratio of 3:1 could be accepted.

Among the varied forms found in the F_2 of conv. *durum* $\times$ *T. timopheevii*, types similar to the species *T. monococcum* and ssp. *carthlicum* segregated out. Extremely varied forms were observed in the F_2 and later generations of *T. timopheevii* $\times$ ssp. *dicoccum* and ssp. *carthlicum* $\times$ ssp. *dicoccum*. In the F_3 generation, individuals with the ear type of conv. *durum* var. *leucomelan*, which have the *dicoccum* fragility, those of the compact *T. aestivum* var. *nigroturcicum* type and of others resembling the ear type of ssp. *dicoccum* frequently appeared.

The F_2 segregation is considerably more complicated if crosses are made between species with different numbers of chromosomes. In the cross ssp. *spelta* ($2n=42$, ABD) $\times$ ssp. *carthlicum* ($2n=28$, AB), plants with compact ears reminiscent of ssp. *dicoccum*, others with the loose or squarehead ears (loose in the lower part and compact above) characteristic of countless *T. aestivum* varieties and, with greater or less frequency, distorted forms all segregated. In addition, constant *aestivum*-type plants could be found, corresponding in all respects

(morphological, genetic, cytological, immunological, etc.) to cultivated wheat, which, when crossed with the latter, gave seed setting similar to that obtained in variety crosses and produced completely fertile progeny (BELEA, 1964, 1971). These data bear evolutionary importance. They can be used to prove that common wheat (*T. aestivum*) could have originated polyphyletically, rather than monophyletically. Pyramidal, awnless ears, becoming suddenly pointed at the top, are also to be found, while in crosses between ssp. *dicoccum* and *T. aestivum*, speltoid types arise, and in the trigeneric F_2 generation of this combination with *T. monococcum* some of the spikelets are completely open (Fig. 32). *Dicoccum*-*aestivum* crosses made by the same investigator likewise gave a 1 : 2 : 1 ratio for the inheritance of ear length, with *dicoccum* segregants having a diploid chromosome number of 28. The fact that the results of awn inheritance are an awnless F_1 and a 3 : 1 awnless-awned ratio in the F_2 was first determined by BIFFEN (1905) and has since been repeatedly confirmed by the work of some fourteen investigators. In the *T. aestivum* $\times$ ssp. *carthlicum* combination, in addition to awnless ears, compound ears of the ssp. *vavilovii* type also appear. The long, extended glumes can also be regarded as types which are quite different from these parents.

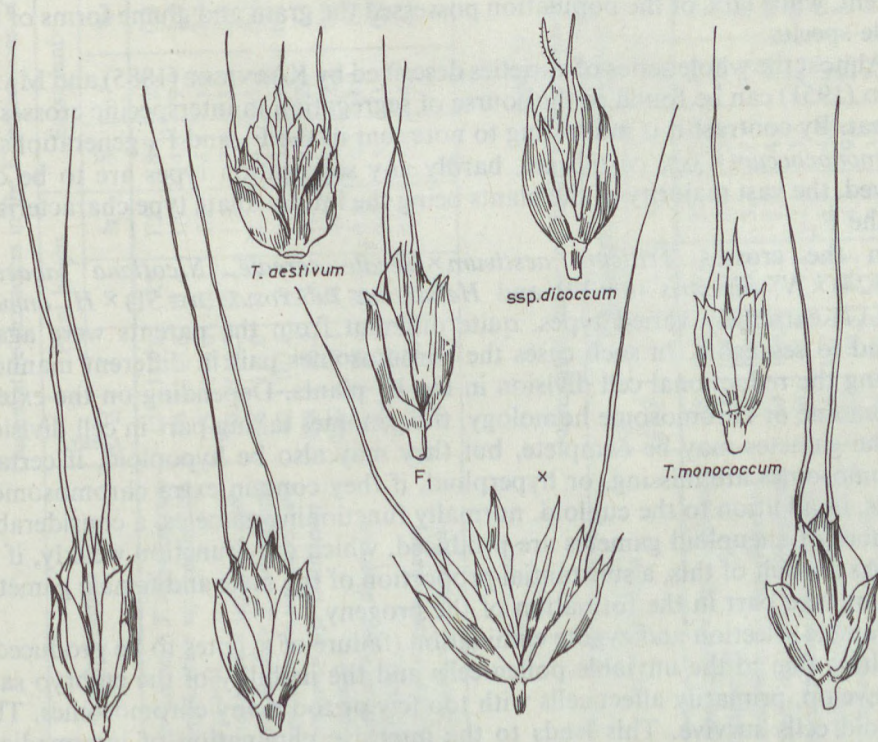


Fig. 32. Spikelet forms of the F_1 and F_2 of the trigeneric combination (*Triticum aestivum* $\times$ ssp. *dicoccum*) $\times$ *T. monococcum* and of the parental species (BELEA, 1976)

In the F_2 and F_3 generations of the crosses *conv. polonicum* $\times$ *T. aestivum* and *ssp. sphaerococcum* $\times$ *conv. durum*, polonicoid, speltoid, vavilovoid and square-head ear types were observed. In the latter combination the largest proportion of plants (72.2%) had *turanicum* glumes, but were sterile. The remainder of the segregating forms resembled one of the two parents or were intermediate. In this combination 8.9% of the ears were awnless, despite the fact that both parental species were awned. In addition to the types mentioned, a small number of hexaploids with the awned glumes characteristic of *ssp. carthlicum* also segregated, as did a few plants with the grain shape of *conv. polonicum* and others with the *dicoccum* fragility and glume fitting.

Exact investigations into the inheritance of brown glume colour were first carried out by NILSSON-EHLE in 1908, the F_2 ratio usually being found to be 3 : 1, though it was sometimes 15 : 1. Similarly, LOVE-CRAIG (1919) found a 15 : 1 ratio between a brown *aestivum* and a yellow *durum*, thus indicating the presence of two genes for brown glume colour.

In the F_3 generation, *aestivum*, plants with awned glumes, the fragility or spikelet arrangement of *spelta* or *dicoccum*, or with long-shouldered and beaked glumes again segregated from the above combination. In the F_3 of *ssp. sphaerococcum* $\times$ *T. aestivum*, 29.5% of the plants had the round grains of the female parent, while 60% of the population possessed the grain and glume forms of the male species.

Almost the whole series of varieties described by KÖRNICKE (1885) and MANSFELD (1951) can be found in the course of segregation in interspecific crosses of wheat. By contrast it is interesting to note that in the F_2 and F_3 generations of *T. monococcum* $\times$ *ssp. carthlicum*, hardly any segregation types are to be observed, the vast majority of the plants being the intermediate type characteristic of the F_1 .

In the crosses *Triticum aestivum* $\times$ *Secale cereale*, *Nicotiana tabacum* ($n=24$) $\times$ *N. silvestris* ($n=12$) and *Helianthus tuberosus* ($n=51$) $\times$ *H. annuus* ($n=17$) extremely varied types, quite different from the parents were again found to segregate. In such cases the chromosomes pair in different manners during the reductional cell division in the F_1 plants. Depending on the extent of genome or chromosome homology, the genomes taking part in cell division in the gametes may be complete, but they may also be hypoploid, if certain chromosomes are missing, or hyperploid, if they contain extra chromosomes. Thus, in addition to the euploid, normally functioning gametes, a considerable number of aneuploid gametes are produced, which only function weakly, if at all. As a result of this, a substantial proportion of the male and female gametes do not take part in the formation of the progeny.

Gamete selection and zygote elimination (failure of zygotes to be produced), resulting due to the unviable pollen cells and the inability of the embryo sacs to develop, primarily affect cells with too few or too many chromosomes. The euploid cells survive. This leads to the intensive elimination of intermediate types and other aneuploid forms in the F_2 and later generations and the

Table 28.
Quantitative characters in the F₂ generations of interspecific *Triticum* hybrids

Combination	Plant no.	Plant height			Ears/plant			Ear length			Spikelets/ear			D-value		
		$\bar{x}$	s	$s_{\bar{x}}$	$\bar{x}$	s	$s_{\bar{x}}$	$\bar{x}$	s	$s_{\bar{x}}$	$\bar{x}$	s	$s_{\bar{x}}$	$\bar{x}$	s	$s_{\bar{x}}$
<i>ssp. carthlicum</i> × <i>T. monococcum</i>	18	115.6	7.5	1.5	8.7	2.5	0.4	8.7	0.3	0.1	18.2	1.8	0.9	21.0	1.4	0.7
<i>T. timopheevii</i> × <i>ssp. carthlicum</i>	99	115.0	11.4	1.2	14.6	9.9	1.0	7.9	1.3	0.1	18.7	2.8	0.3	23.7	4.3	0.4
reciprocal	15	115.0	14.2	4.2	16.4	5.4	2.1	7.6	1.7	0.6	17.8	2.3	0.9	20.6	5.3	0.2
<i>T. timopheevii</i> × <i>ssp. dicoccum</i>	97	110.3	19.3	1.9	7.6	3.4	0.3	8.3	3.2	0.3	18.2	1.1	0.1	22.2	3.3	0.4
<i>conv. durum</i> × <i>T. timopheevii</i>	36	111.0	11.4	2.3	6.1	3.4	0.3	8.4	2.5	0.5	16.8	4.4	0.9	19.8	2.6	0.2
<i>ssp. carthlicum</i> × <i>ssp. dicoccum</i>	62	107.8	3.4	0.4	3.0	1.5	0.2	10.3	1.0	0.0	18.7	1.7	0.6	18.7	1.8	0.2
<i>T. aestivum</i> × <i>ssp. carthlicum</i>	148	98.2	12.7	2.5	10.2	9.7	2.1	12.2	0.2	0.1	19.8	0.3	0.0	16.1	0.1	0.1
reciprocal	132	85.1	14.5	3.1	8.2	2.5	0.2	8.2	1.8	0.2	17.6	3.7	0.2	21.4	4.8	0.6
<i>T. aestivum</i> × <i>ssp. dicoccum</i>	95	89.6	21.4	6.8	4.2	8.1	1.2	9.1	2.1	0.6	16.4	1.5	0.3	11.3	4.5	0.3
reciprocal	12	95.7	29.1	9.7	5.1	1.5	0.6	7.8	2.1	0.7	14.9	3.1	1.1	20.6	6.8	2.7
<i>T. aestivum</i> × <i>conv. durum</i>	94	78.0	26.4	7.3	5.4	6.2	2.1	9.3	2.9	0.8	17.2	2.8	0.4	11.3	4.8	0.3
<i>T. turgidum</i> × <i>T. aestivum</i>	86	—	—	—	—	—	—	11.8	1.1	0.1	18.8	1.0	0.1	16.1	1.1	0.1

Table 29.
Quantitative characters in the F₃ generations of interspecific *Triticum* hybrids

Combination	Plant no.	Plant height			Ears/plant			Ear length			Spikelets/ear			D-value		
		$\bar{x}$	s	$s_{\bar{x}}$	$\bar{x}$	s	$s_{\bar{x}}$	$\bar{x}$	s	$s_{\bar{x}}$	$\bar{x}$	s	$s_{\bar{x}}$	$\bar{x}$	s	$s_{\bar{x}}$
<i>T. timopheevii</i> × <i>ssp. carthlicum</i>	38	110.3	19.6	3.1	3.1	4.4	0.4	8.4	1.4	0.2	18.3	4.9	0.7	21.7	3.9	0.7
reciprocal	34	114.9	30.8	0.9	5.8	0.6	0.1	8.9	1.7	0.2	18.5	3.1	0.5	21.8	2.9	0.3
<i>T. timopheevii</i> × <i>ssp. dicoccum</i>	60	108.2	19.5	3.2	7.4	3.8	0.2	6.9	4.7	1.2	19.8	2.1	0.2	28.6	2.8	0.4
<i>conv. durum</i> × <i>T. timopheevii</i>	60	89.6	14.6	2.8	4.7	3.9	0.4	7.4	3.8	1.4	17.7	4.6	0.5	23.9	2.9	0.5
<i>ssp. carthlicum</i> × <i>ssp. dicoccum</i>	110	81.0	9.8	2.3	5.5	3.1	0.9	7.2	1.3	0.3	16.2	6.8	0.9	22.5	2.4	0.3
<i>T. aestivum</i> × <i>ssp. carthlicum</i>	26	127.5	7.1	1.9	4.1	1.2	0.4	9.1	1.2	0.1	17.1	1.3	0.4	19.0	2.4	0.5
reciprocal	186	94.3	15.2	4.1	9.0	2.6	0.7	9.0	4.6	1.3	18.9	2.9	0.3	21.4	2.6	0.5
<i>ssp. dicoccum</i> × <i>T. aestivum</i>	26	91.0	28.5	9.7	3.9	2.1	0.3	10.0	2.6	0.3	17.3	3.5	0.4	17.3	2.9	0.8
reciprocal	19	79.9	22.4	6.9	5.6	8.4	2.1	12.1	3.2	0.4	16.0	1.7	0.3	13.2	2.1	0.4

Table 30.
Correlation coefficients for the first generation of interspecific *Triticum* hybrids averaged over many years

Combination	Ear length Spikelets/ ear	Grain length Glume length	Grain width Glume width	Spikelets/ ear D-value	Grain length Grain width	Glume length Glume width	Ear length D-value	Plant height Ears/plant
<i>ssp. spelta</i> × <i>ssp. carthlicum</i>	0.73	—	0.0	0.38	0.0	0.0	0.40	0.40
<i>T. aestivum</i> × <i>ssp. carthlicum</i>	0.29	—	—	0.63	—	—	0.98	0.13
<i>T. turgidum</i> × <i>T. aestivum</i>	0.23	—	—	0.57	—	—	0.99	0.87
<i>ssp. carthlicum</i> × <i>T. timopheevii</i>	0.41	0.65	0.0	0.44	0.0	0.0	0.30	0.16
<i>ssp. dicoccum</i> × <i>T. aestivum</i>	0.32	0.71	0.0	0.30	0.0	0.0	0.32	0.62
<i>ssp. carthlicum</i> × <i>T. monoccum</i>	0.40	—	—	0.62	—	—	0.58	0.90
<i>T. timopheevii</i> × <i>ssp. carthlicum</i>	0.44	0.81	0.0	0.50	0.1	0.0	0.62	0.10
<i>ssp. carthlicum</i> × <i>ssp. dicoccum</i>	0.31	0.70	0.0	0.91	0.0	0.0	0.25	0.52
<i>T. timopheevii</i> × <i>ssp. dicoccum</i>	0.21	—	—	0.51	0.0	0.0	0.89	0.51
<i>T. timopheevii</i> × <i>ssp. durum</i>	0.18	—	—	0.43	—	—	0.71	0.44
average of $r =$	0.35			0.53			0.60	0.47

predominance in the population of euploid plants having the same chromosome numbers as the parents.

When crossing species with different chromosome numbers or differences in genome quality, in which case a high degree of sterility will be observed even in the F_1 , there is a steep decline in the segregation ratio in the F_2 and later generations. In practical breeding it is often the eliminated intermediate types, or the plants with an excessive number of chromosomes (tri- or tetrasomes) which would be of most use, for instance in breeding for disease resistance. For instance, when breeding for resistance to the disease *Phytophthora infestans*, which causes root and tuber rotting, the valuable resistance gene is often lost when susceptible cultivated potato varieties are crossed with resistant wild potatoes due to the elimination of the tetrasomic chromosomes on which the gene transferring resistance is located. This is why it is difficult to transfer disease resistance from wild species to cultivated species. Luckily, however, practical breeders are assisted by the fact that, in the F_2 , plants arise which have the same chromosome numbers as the parents but do not correspond entirely with the parents in their characters. Since in the course of reductional cell division whole homologous chromosomes or chromosome sections are exchanged, new gene connections come about, as the result of which new types and forms may segregate. Great practical significance is attached to gene combinations arising in this way from interspecific crosses, because they facilitate the fixing in the desired species of characters which cannot be transferred through intervarietal crosses. If favourable results are to be obtained, there must be complete or partial homology between the combined genomes of the two parental species.

In the case of extremely sterile interspecific and intergeneric hybrids, where the majority of combinational types are lost in the F_2 as the consequence of intense gamete selection and zygote elimination, practical results can nevertheless be achieved if a large enough number of plants are raised.

When comparing the quantitative characters of the F_2 and later generations with the similar values in F_1 hybrids it has been found that the luxuriance in wheat plant height, for example, is retained in later generations, but to a lesser extent compared to the average of the two parents (Tables 28 and 29). Productive tillering, on the other hand, had a much lower value than in the first generation.

When studying the correlations between quantitative characters, SCHEIBE (1951), ISENBECK-ROSENSTIEL (1950) and BELEA (1964) found that the strongest positive correlations were generally found between the number of wheat spikelets per ear and the ear length, the number of spikelets per ear and the ear compactness (D value), the grain length and the glume length, and the plant height and the productive tillering (Table 30). The correlation between ear length and D value was less strong. This is understandable, since the vast majority of the hybrids included in the table are different combinations of *T. timopheevii* and ssp. *dicoccum*, where the relatively short but compact ear (D value) of the parental species is also expressed in the progeny.

4. Sterility, fertility and cytology of interspecific and intergeneric hybrids

Even before the time of Mendel, during the first half of the last century, it was common knowledge that interspecific, and particularly intergeneric hybrids often had reduced yield potential or were completely sterile, producing no yield at all. Other plants, such as *Salix* and *Epilobium*, do not even produce flowers, while tobacco sheds its flowers at an early stage.

NÄGELI (1866) mentions the fact that since species hybrids are frequently fertile, while the individuals of pure species are not infrequently infertile, the perfect or imperfect structure of the sex organs is not decisive in determining the nature of an organism. The sterility of the male and female organs does not necessarily indicate that they are hybrids, while fertility is not always indicative of pure origin. LEWIS (1961) reported the fact that Mendel produced two different specimens of *H. auricula* × *H. aurantium*, one of which was sterile, while the other produced a single seed.

In the majority of cases, the reason for this sterility is the fact that disturbances arise especially in the course of reductional cell division, in the development of the cell nucleus in flowers with normal external development. These disturbances can be attributed to genetic, physiological or biochemical causes, quite independently of external climatic factors (temperature, moisture, humidity, etc.). Countless examples are to be found in the literature in this connection. In the case of maize (CLARK, 1940), tobacco (GOODSPEED-AVERY, 1939), cotton (BEASLEY-BROWN, 1942), peas (HÄKANSSON, 1936), cabbage (ATTIA-MUNGER, 1950), wheat (BELEA, 1976), etc. factors may arise which influence the distribution and frequency of chiasma formation or produce anomalies in spindle and cell formation.

FOCKE (1881) concluded that hybrids between different species form a more limited number of pollen grains in their anthers and a more limited number of normal seeds in their fruits than plants of pure origin. They frequently produce neither pollen nor seeds. With hybrids of nearly related biotypes this weakening of the capacity for sexual reproduction is not generally present. The flowers of infertile or barely fertile hybrids remain fresh for a long time as a rule. Fertility must be restored if the novel lineage is to spread to other sites. The probability of a new lineage establishing itself is a function not only of its physical isolation from its progenitors, but also of its genetic isolation, because if hybridisation is possible, a minority element may be "hybridised" out of existence, since a

larger proportion of its progeny will be hybrids than will those of a majority element, such as one of the parental taxa (LEWIS, 1961).

Mention is also made in the literature of the fact that the zygote elimination arising in fully developed plants, and factors inhibiting normal chromosome pairing (genes inducing asynapsis) may also cause pollen anomalies, as a consequence of which the plants will be sterile. Disturbances in reductional cell division may also be caused by genetic factors (differences in chromosome number or genome quality). A more detailed discussion of these will be presented below.

Sterility may also arise in interspecific and intergeneric hybrids if only part of the viable embryo sac is fertilised. It has been suggested that the alien pollen may induce the metabolic processes to proceed too rapidly or too slowly and that this may be the cause of sterility.

4.1 Pollen sterility and fertility

For the reasons described above, the pollen mother cell in normally developed flowers develops irregularly and produces inviable (sterile) pollen. It is worth noting that even hereditarily well-balanced species, or even varieties, do not produce 100% viable (fertile) pollen, despite the fact that they are normally fertilised. As can be seen from Table 31, cultivar B 1201 of common wheat (*T. aestivum*) only produces 74.4% fertile pollen suitable for pollination. The anthers dehisce if they contain more than 30% fertile pollen. The swelling of these pollen grains causes the anthers to burst open. Regularly shaped pollen grains which stain well with carmine acetic acid are regarded as fertile.

The ratio of fertile to sterile pollen also depends on which species is used as pollinator. It often happens that the development of the endosperm ceases 8–10 days after the growth of the pollen tube and the embryo dies for lack of nutrients. In other cases, plants developing from shrivelled grain die off shortly prior to full development due to late-acting lethality.

Table 31.
Pollen fertility of *Triticum L.* species

Triticum species	No. of plants tested	Fertile pollen	
		Deviation	Mean %
<i>T. monococcum</i>	20	62.09–98.50	89.3
ssp. <i>dicoccum</i>	15	81.40–93.42	86.9
ssp. <i>carthlicum</i>	23	69.08–95.33	85.9
<i>T. timopheevii</i>	34	57.35–92.74	80.7
<i>T. turgidum</i>	18	53.40–89.62	78.6
<i>T. aestivum</i> (B. 1201)	25	58.00–90.59	74.4
<i>T. aestivum</i> (F 481)	18	68.62–82.27	78.7
<i>T. aestivum</i> (Bezostaya 1)	10	74.85–89.63	81.6

Differences in pollen fertility may be observed from one ear or flower to another, or even within the same ear or inflorescence. Similar plants may produce anthers containing pollen with different degrees of fertility.

Pollen sterility is still more conspicuous when the plant species crossed are only distantly related to each other. In wheat, for example, the pollen of the first generation in various combinations involving *T. monococcum* is almost completely sterile (Table 32). Since the anthers do not dehisce, plants which are incapable of self-fertilisation are easily recognised during the flowering period. As the flowers are not fertilised, they remain open for a long time. In the same manner, a high degree of pollen sterility is experienced in the first generation

Table 32.

Pollen fertility and sterility in the first generation of interspecific *Triticum* hybrids

Combination	No. of plants	No. of pollen grains	Fertile pollen	Percentage of	
				sterile	fertile
				pollen	
<i>T. timopheevii</i> × <i>T. monococcum</i>	9	680	0.0–1.3	99.4	0.6
ssp. <i>carthlicum</i> × <i>T. monococcum</i>	8	464	0.0–2.4	99.0	1.0
<i>T. timopheevii</i> × ssp. <i>carthlicum</i>	22	9431	0.0–10.7	94.5	5.1
reciprocal	8	3013	0.0–8.9	96.8	3.2
<i>T. timopheevii</i> × conv. <i>durum</i>	25	8790	1.2–8.8	96.3	3.7
reciprocal	12	4310	0.0–7.2	97.7	2.3
<i>T. timopheevii</i> × ssp. <i>dicoccum</i>	14	5012	0.0–1.9	99.2	0.8
ssp. <i>carthlicum</i> × ssp. <i>dicoccum</i> ('Khapli')	9	3122	20.9–65.1	55.4	44.6
ssp. <i>carthlicum</i> × ssp. <i>dicoccum</i> ('Vernal')	21	7761	41.2–98.7	14.4	85.6
tetraploid × diploid				99.2	0.8
diploid × tetraploid				99.0	1.0
<i>T. timopheevii</i> × tetraploid				96.8	3.2
tetraploid × <i>T. timopheevii</i>				97.3	2.7
tetraploid × tetraploid				34.9	65.1
<i>T. aestivum</i> × <i>T. timopheevii</i>	22	8328	0.2–15.1	97.9	1.2
reciprocal	21	7873	0.0–3.8	98.6	1.4
<i>T. aestivum</i> × ssp. <i>carthlicum</i>	15	4672	52.4–97.3	17.9	82.1
reciprocal	12	3444	37.1–89.1	34.9	65.5
<i>T. aestivum</i> × ssp. <i>dicoccum</i>	11	4075	43.7–95.1	14.0	86.0
reciprocal	9	3048	18.6–83.4	30.3	69.7
<i>T. turgidum</i> × <i>T. aestivum</i> ('B 1201')	16	5610	5.2–60.3	73.2	26.8
reciprocal	14	5226	48.1–92.7	29.8	70.2
<i>T. turgidum</i> × <i>T. aestivum</i> ('Mp 706')	10	3114	61.6–99.2	14.2	85.8
reciprocal	11	5237	47.6–58.7	64.3	35.7
hexaploid × tetraploid				31.5	68.5
tetraploid × hexaploid				38.2	61.2

Table 33.

Pollen and seed fertility of the F_1 hybrid and amphiploid of *Solanum indicum* $\times$ *S. melongena* (PRAKKEN-SWAMINATHAN, 1952)

Combination	Seed fertility		Pollen fertility
	Deviation	Mean	
<i>Solanum indicum</i>	33-61	44.7 ± 5.9	98.3 ± 2.45
<i>Solanum melongena</i>	845-2209	1380.0 ± 28.9	96.9 ± 0.05
<i>S. indicum</i> $\times$ <i>S. melongena</i> F_1	14-16	29.9 ± 5.5	41.5 ± 1.80
amphiploid	no seeds		35.05

of crosses involving *T. timopheevii*. By contrast, ssp. *carthlicum* $\times$ *dicoccum* proved to be fully fertile in practice, as did various combinations of *T. aestivum*, especially if it was crossed with species having the same number of chromosomes. Differences are also found between cultivars, depending on which cultivars are used in the crosses. When the wheat cultivar B 1201 was crossed with *T. turgidum*, for instance, there was 26.8% fertile pollen in the F_1 , while this figure was 85.8% when the cultivar Mp 706 was used.

In pentaploid ($2n=35$) hybrids originating from interspecific crosses of wheat, there is a greater degree of pollen sterility if the species with the higher chromosome number is used as the female parent (41.3%). In this crossing direction, as mentioned above, the seed setting is also lower, but germination is better. In the reciprocal cross, however, there was a slight reduction in pollen sterility (33.5%).

Considerable deviations in pollen sterility are also experienced between the individual F_1 plants of the same combination (Table 32). In the *T. timopheevii* $\times$ *T. aestivum* cross, for example, the percentage of viable pollen formed in various individuals of the first generation fluctuated from 0.2-15.1%. Even greater variation can be observed in the F_2 and F_3 generations. Types segregating in the second generation of this cross contained 0-93% fertile pollen. In this way, it is possible, even in early generations, to select plants producing a relatively large quantity of viable pollen, despite the fact that species hybrid are characterised by a high degree of pollen sterility. The extent to which flowers become fertilised in these plants is substantially better than average. The pollen fertility of F_1 hybrids of *Solanum indicum* $\times$ *S. melongena* was 41.5%, while that of the amphiploids was 35.05% (Table 33).

4.2 Fertility and cytology of F_1 hybrids

4.2.1 Genome homology

As was mentioned previously, it is possible to cross species with different chromosome numbers and to raise viable progeny generations from them. In the same way, it is possible to combine species in which the quality of the

genomes differs. During the development of the embryo and endosperm it would seem that differences in the quality of the chromosomes plays an even greater role than differences in their quantity, a fact which is of primary importance in interspecific and intergeneric crosses. The genome complexes formed cause developmental anomalies if they are not homologous with the genomes of the maternal ovary tissue. This phenomenon can be traced very clearly by means of cytological analyses.

In the course of chromosome pairing only homologous chromosomes or chromosome sections can pair and mutually exchange material, i.e. only chromosomes in which the individual genes are located in a similar order. If all the chromosomes of a male chromosome set or genome are homologous with those of the female, all the parental chromosomes can pair during the reductional cell division taking place in the first generation. If, however, one or more, or even all, of the chromosomes of the parental species have different structures i.e. only certain genes are the same, while others are different, only the homologous chromosomes or sections are able to pair. Since the homologous parts of the chromosomes themselves consist of homologous and non-homologous sections, so that mutual exchange cannot take place, they are referred to as semihomologous or homoeologous. It is impossible to determine from the form of the paired chromosomes whether they are completely homologous or only homoeologous. If, however, pairing proceeds abnormally and the two chromosomes only conjugate in some of the cells, it can be assumed that pairing is homoeologous or semihomologous. If there are serious differences in the gene orders of all the parental chromosomes, i.e. there is no homology, pairing does not generally occur.

More than half of all the species of angiosperms, as will be discussed in detail below, are polyploid, i.e. they have several genomes. Species which contain several identical genomes (AA) are called autopolyploids, as opposed to those which contain non-homologous genomes and are known as allopolyploids (genome formula = AB). In addition, species exist which contain homoeologous genomes (AA¹), designated by STEBBINS (1947) as segmental allopolyploids. Species with a higher level of ploidy (hexa-, octo-, decaploids, etc.) may have genomes which are completely homologous, homoeologous or non-homologous.

4.2.2 Allo- and autosyndesis

If both parents contain only one genome, e.g. A and A¹, and all chromosomes pair, it can be assumed that the chromosomes of genomes A and A¹ are homologous. If, on the other hand, one or both of the parents have several genomes (e.g. AB and A¹B¹) and only some of the chromosomes pair, it may be that the chromosomes of genomes A and B pair with those of A¹ and B¹, but it may also happen that pairing occurs between chromosomes of the A or A¹ genomes and those of the B or B¹ genomes. If parents with different genomes

are crossed, i.e. chromosomes bearing differing types of inheritance enter the hybrid from the two parents due to chromosome pairing, this process is referred to as allosyndesis; if, however, pairing takes place between species with the same genomes, it is known as autosyndesis. The failure of chromosome pairing to take place is called asyndesis.

4.2.3 Chromosome pairing in interspecific and intergeneric hybrids

From a cytological point of view, interspecific hybrids can be divided into groups according to their chromosome or genome numbers and quality. Many of the species which can be crossed with each other have the same chromosome number, but their genomes are not homologous. Another group of hybridisable species have different chromosome numbers but identical genome quality (homologues). Depending on the homology of the genomes and the number of chromosomes, chromosome pairing can take place in various ways (Table 34).

1. It is fairly general for the species which are crossed to have the same chromosome number and homologous genomes. In this case, all the chromosomes pair, cell division takes place normally and the same number of chromosomes will be found in each gamete. In the cross *T. turgidum* conv. *polonicum* ($n = 14$; genomes AB) $\times$ conv. *durum* ($n = 14$; genomes AB), for example, as the result of regular cell division, the hybrid has $2n = 28$ chromosomes forming 14 bivalents (14^{II})*; in the cross *T. aestivum* ssp. *spelta* ($n = 21$; genomes ABD) $\times$ *T. aestivum* ($n = 21$; genomes ABD) the hybrid has $2n = 42$ chromosomes and forms 21 bivalents in meiosis; the hybrid of *Vitis vinifera* ($n = 19$) $\times$ *V. riparia* ($n = 19$) has $2n = 38$ chromosomes and forms 19^{II} (NEGRUL, 1930); in *Nicotiana paniculata* ($n = 12$) $\times$ *N. benavidesii* ($n = 12$) the $2n = 24$ chromosome hybrid forms 12^{II} (GOODSPEED, 1945); while in the first generation of *Gossypium barbadense* ($n = 26$) $\times$ *G. tomentosum* ($n = 26$), which has $2n = 52$ chromosomes, the plants form 26^{II} .

Cytologically these species are closely connected with each other and can be regarded as near relations; on the basis of other criteria, however, they are mostly treated by taxonomists as separate species. In some genera, however, as in the case of *Triticum*, it may happen that the new classification treats a substantial portion of the species as sub-species, for the very reason of the ease with which they can be hybridised and the normal course of cell division. Since it has been proved that the *Aegilops* species played a role in the evolution of wheat, and are closely related to it, the *Aegilops* species, which were previously classified as an independent genus, have recently been included in the *Triticum* genus and been renamed.

* The Roman numerals in the superscript designate the chromosome connections which may arise in the course of reductional cell division: I = univalent, II = bivalent, III = trivalent, IV = quadrivalent etc.

Table 34.

Chromosome pairing and chromosome distribution in interspecific and intergeneric hybrids (OEHLER, 1956)

Homology of genomes		Chromosome number of the parents	Chromosome connection	Genome formula of parents	Genome formula of F_1	Chromosome pairing in F_1	Chromosome number of F_1 gametes	Fertility
between the genomes of the two parents	between the genomes of a single parent							
All completely homologous	Homologous	same	allosyndesis	$AA \times AA$	AA	a^{II}	a	Fertile
	Non-homologous	same	allosyndesis	same	AA	a^{II}	a	Weakly fertile
		same	allosyndesis	same	AA	a^{II}	a	Weakly fertile
Some genomes completely homologous	Homologous	different	allosyndesis	$AAA \times AAAA$	AAAA	$2a^{II}$	$2a; a + (0 - 3a)$	Sterile
	Non-homologous	different	allosyndesis	$AA \times AAAA$	AAAA	$(a + b + c)^{II}$	$a + b + c$	Fertile
		different	allosyndesis	$AA \times AAAA$	AAAA	a^{II}	$a + (0 - a)$	Weakly fertile
Remaining completely homologous	Homologous	different	allosyndesis	$AA \times AABBBB$	AABB	$2a^{II}$	$2a; a + (0 - 3a)$	Weakly fertile
	Non-homologous	different	allosyndesis	$AA \times AABBBB$	AABB	$a^{II} + b^{II}$	a + b	Fertile
		different	allosyndesis	$AA \times AABBBB$	AABB	$a^{II} + b^{II}$	a + b	Fertile
Remaining homologous	Non-homologous	same	allosyndesis	$AACC \times AAC^1C^1$	AAC^1C^1	$a^{II} + c^{II}$	$a + (0 - c) -$	Weakly fertile
Remaining non-homologous	Homologous	same	allosyndesis	$AADD \times AAA^1D$	AAA^1D	$a^{II} + II + I$	$a + (0 - a)^1$	Weakly fertile
	Non-homologous	same	allosyndesis	$AABB \times AADD$	AABD	$a^{II} + b + d$	$a + (0 - b)$	Weakly fertile
		different	allosyndesis	$AA \times A^1A^1$	AA^1	$a^{II} + I$	$(0 - a) + (0 - a)$	Sterile
		same	allosyndesis	$AA \times AABBB$	AAB	$a^{II} + b$	$a + (0 - b)$	Weakly fertile

Table 34. (continued)

Homology of genomes		Chromosome number of the parents	Chromosome connection	Genome formula of parents	Genome formula of F_1	Chromosome pairing in F_1	Chromosome number of F_1 gametes	Fertility
between the genomes of the two parents	between the genomes of a single parent							
All homoeologous	Homologous	different	autosomes allosyndesis	$AA \times A^1A^1A^1A^1$	AA^1A^1	$a(III + II + I)$	$(0 - a) + (0 - 2a)$	Sterile
	Remaining genomes homologous Non-homologous	same different	allosyndesis allosyndesis	$AABB \times A^1A^1BD$ $AA \times A^1A^1BB$	AA^1BD AA^1B	$a(II + I)$ $a(II + I)$	$(0 - a)(0 - a^1) + (0 - b) + (0 - d^1)$ $(0 - a) + (0 - a^1)$	Almost sterile Sterile
Non-homologous	Homologous	same different	autosomes autosomes	$AAAA \times CCDD$ $AAAA \times EE$	$AACD$ AAE	$a^{II} + c^1 + d^1$ $a^{II} + c^1$	$a + (0 - c) + (0 - d)$ $a + (0 - c)$	Weakly fertile Weakly fertile
	Homoeologous	same different	autosomes autosomes	$AAA^1A^1 \times CCDD$ $AAA^1A^1 \times EE$	AA^1CD AA^1E	$a(II + I)$ $a(II + I) + E^1$	$(0 - a) + (0 - a^1) + (0 - d)$ $(0 - a) + (a - a^1) + (0 - E)$	Sterile Sterile
Non-homologous	same	same	asynesis	$AA \times RR$	AR	$a^1 + I^1$	$(0 - a) + (0 - r)$	Sterile
	different	same	asynesis	$AABB \times RRSS$	$ABRS$	$a^1 + b^1 + r^1 + S^1$	$(0 - a) + (0 - b) + (0 - r) + (0 - s)$	Sterile
Non-homologous	different	different	asynesis	$AABB \times RR$	ABR	$a^1 + b^1 + r^1$	$(0 - a) + (0 - b) + (0 - r)$	Sterile

It also frequently happens that subspecies or cultivars that are classified in the same species behave when crossed as if they were independent species. An example of this is the Indian cultivar 'Khapli', which belongs taxonomically to the *nudiglume* variety of *T. turgidum* ssp. *dicoccum* but is difficult to cross even at the same polyploid level, anomalous chromosome pairing being observed in meiosis. In the cross *T. turgidum* conv. *ispahanicum* ($n=14$; genomes AB) $\times$ Khapli ($n=14$; genomes AB), for example, where the F_1 had a chromosome number of $2n=28$, the most frequent chromosome pairing during meiosis was $11^{II}6^I$ or $8^{II}+11^I$ (Table 35). A high sterility is the consequence of anomalous cell division. The extreme genetic isolation of this cultivar is probably caused by differences in the cytoplasm.

2. In other pairs of species, the genomes are homologous, but they have different chromosome numbers. Crosses are often made between the diploid original species and its autotetraploid form ($AA \times A$), when only trivalents should be obtained if the homologous chromosomes paired regularly. It is often observed, however, that in some cells there are only trivalents, but in other cells bi- and univalents also occur. This was found by BELEA (1976) in a cross between diploid *T. monococcum* ($n=7$; genome A) and an artificially produced autotetraploid *T. monococcum* ($n=14$; genomes AA), where bi- and univalents were discovered in some of the cells. Similar observations were made by other authors. In the F_1 of *Lolium loliaceum* ($n=7$) $\times$ *L. rigidum* (non-reduced gamete with 14 chromosomes), which had a chromosome number of $2n=21$, only 7^{III} were formed in some of the cells (JENKIN-THOMAS, 1939); in the first generation of *Fragaria vesca* ($n=7$) $\times$ *F. orientalis* ($n=14$) in addition to $1-4^{III}$, the most frequent chromosome pairing was $7^{II}+7^I$ (STANDT, 1951). The hybrid of *Petunia hybrida* ($n=14$) $\times$ *P. axillaris* ($n=7$) also has $2n=21$ chromosomes, which form the expected 7^{III} .

If diploid or tetraploid plant species are crossed with species at a higher polyploid level, multi-, bi- and univalents are often formed, though in many cases only bivalent chromosomes appear in the course of cell division. In such cases all the chromosomes of the parental species with the lower chromosome number pair allosyndesically with the similar chromosomes of the species at the higher polyploid level, while the remaining chromosomes pair with each other by means of autosyndesis (Digitalis type).

The first generation of *Fragaria vesca* ($n=7$) $\times$ *F. moschata* ($n=21$) has $2n=28$ chromosomes and forms 14^{II} (SCHIEMANN, 1951); the $2n=32$ chromosome F_1 of *Prunus domestica* ($n=24$) $\times$ *P. cerasifera* ($n=8$) usually forms 16^{II} or $1-5^{III}+6-16^{II}+0-3^I$ (DARLINGTON, 1928); the $2n=48$ chromosome hybrid of the cross *Solanum demissum* ($n=36$) $\times$ *S. verrucosum* ($n=12$) forms partly 24^{II} and partly $1-6^{IV}+1-3^{III}+9-23^{II}+1-7^I$ (PROPACH, 1938); while the F_1 of *Agropyron ferganense* $\times$ *A. patagonicus* formed $2-22^I+3-13^{II}+0-2^{III}$ (Table 36). *Glycine max* and wild perennial *Glycine* species were crossed (NEWELL et al., 1987) in 390 genotype combinations. Sixteen F_1 interspecific hybrids representing 12 genotype combinations were obtained by embryo culture and grown to matu-

Table 36.

Chromosome pairing in meiosis in *Agropyron ferganense* and its F₁ hybrids (after DEWEY, 1981)

Species and combination	No. of cells	Chromosome number	Metaphase I							
			Chromosome pairing							
			I		II		III		IV	
<i>A. ferganense</i>	204	14	0-2	0.04	6-7	6.98				
<i>A. ferganense</i> × <i>A. spicatum</i>	346	14	0-6	0.87	3-7	6.21	0-2	0.09	0-1	0.11
<i>A. ferganense</i> × <i>A. libanoticum</i>	185	14	0-8	2.72	3-7	5.45	0-1	0.09	0-1	0.03
<i>A. ferganense</i> × <i>A. dasystachyum</i>	174	21	4-9	6.74	4-8	6.40	0-2	0.49		
<i>A. ferganense</i> × <i>A. caninum</i>	241	21	2-15	8.25	2-8	5.50	0-4	0.56	0-1	0.02
<i>A. ferganense</i> × <i>A. hystrix</i>	199	21	5-15	8.70	3-8	6.00	0-2	0.10		
<i>A. ferganense</i> × <i>A. patagonicus</i>	204	28	2-22	12.76	3-13	6.89	0-2	0.42	0-1	0.05

rity, 7 of them being *G. max* ($2n=40$) × *G. tomentella* ($2n=78$), 3 being reciprocals of this cross and 2 being *G. canescens* ($2n=40$) × *G. max*. The F₁ hybrids differed morphologically according to the genotype combination involved and showed varying degrees of anther development, hybrids with wild *Glycine* as the female parent being best in this respect. As expected, the chromosome numbers for the *G. tomentella* and *G. canescens* hybrids were $2n=59$ and $2n=40$, respectively. The F₁ hybrids showed low chromosome pairing and abnormal meiosis and were sterile.

If, in the course of reductional cell division, only bivalents are formed, the chromosomes divide normally and each cell contains the same number of chromosomes. If, however, in addition to bivalents, multi- and univalents are also formed, the cells will contain differing numbers of chromosomes due to the irregular distribution of the chromosomes.

An intermediate stage is represented by those interspecific hybrids which arise by means of auto- and allopolyploidy. If the genomes of the species with the lower chromosome number are homologues of the genomes of the parent with the higher chromosome number, and the remaining genomes of the species with the higher chromosome number are homologous with each other, all the chromosomes are able to pair. In this case, chromosome pairing is allosyndesic when the chromosomes originate from both parents, and autosyndesic for the residual chromosomes of the parent with the higher level of polyploidy.

The hybrid of *Helianthus tuberosus* ($n=51$; genomes AAB) × *H. annuus* ($n=17$; genome B) has $2n=68$ chromosomes and forms 34^{II} (17A_tA_t + 17B_aB_a); the F₁ of the cross *Phleum nodosum* ($n=7$; genome B) × *Ph. pratense* ($n=21$;

genomes AAB) has $2n = 28$ chromosomes and forms 14^{II} ($7A_pA_p + 7B_pB_n$) (NORDENSKÖLD, 1937).

3. It is found extremely frequently that the parental species in the cross have more than one completely homologous genome, while the remaining genome(s) is/are only homologous in part, if at all. The chromosome numbers of the parents may be the same or, as is frequently the case, different. The chromosomes which are homologous with each other pair and divide normally, while the non-paired chromosomes remain as univalents. In the course of reductional division, the univalents split into two lengthwise during the first and second phases of division. In rare cases the univalents divide twice. In many instances they do not reach the daughter cells and form micronuclei. This means that the cells will have different numbers of chromosomes. Numerous interspecific hybrids from the genera *Avena* (NISHIYAMA, 1934), *Triticum* (BELEA, 1976), *Brassica* (MORINAGA, 1929), *Gossypium* (SKOVSTAD, 1935), *Rosa* (TÄCKHOLM, 1922), *Chrysanthemum* (SHIMOTOMAI, 1933), *Viola* (CLAUSEN, 1931) and various grasses belong in this group. In triploid plants of *Avena* (e.g. *A. canariensis* $\times$ *A. maroccana*), too, very few bivalents are formed (Table 37).

In the most general case, all the genomes of the parental species with the lower chromosome number are homologous with those of the parent with the higher chromosome number. The hybrids form as many bivalents as possible using the chromosomes of the species at the lower level of polyploidy (Drosera type).

The $2n = 27$ chromosome hybrid of *Setaria faberii* ($n = 18$; genomes AB) $\times$ *S. italica* ($n = 9$; genome A) forms $9^{II} + 9^I$, while the F_1 of *Nicotiana rustica* ($n = 24$) $\times$ *N. paniculata* ($n = 12$) has $2n = 36$ chromosomes and forms $12^{II} + 12^I$ (GOODSPEED et al., 1926). In a similar manner, the $2n = 29$ chromosome F_1 of *Brassica napella* ($n = 19$) $\times$ *B. napa* ($n = 10$) forms $10^{II} + 9^I$ (MORINAGA, 1929) and the first generation of *Gossypium hirsutum* ($n = 26$) $\times$ *G. thuroeri* ($n = 13$), which has $2n = 39$ chromosomes, forms $13^{II} + 13^I$ (WEBBER, 1939).

BELEA (1976) observed that although the genome (M) of *Aegilops mutica* was different, in a cross with *T. turgidum* ssp. *carthlicum* ($n = 14$; genomes AB) the majority of the $2n = 21$ chromosome F_1 s formed $7^{II} + 7^I$ (Table 38). These chromosome pairing data suggest that the M genome of *Ae. mutica* is homo-

Table 37.

Chromosome pairing in meiosis in interspecific *Avena* hybrids (after LEGGETT, 1980)

Combination	No. of cells examined	Chromosome pairing								
		I	II	III	IV	V	VI	VII	VIII	IX
<i>A. postrata</i> $\times$ <i>A. canariensis</i>	100	0.43	0.12	1.61	0.02	—	0.07	—	—	—
<i>Av</i> 939 $\times$ <i>A. maroccana</i>	50	0.84	8.02	0.98	1.54	0.14	0.08	—	0.08	0.02
<i>A. prostrata</i> $\times$ <i>A. maroccana</i>	100	12.72	4.81	1.72	0.08	0.01	0.01	0.01	—	—
<i>A. carainensis</i> $\times$ <i>A. maroccana</i>	150	12.33	2.98	0.84	0.06	0.006	—	—	—	—
<i>A. canariensis</i> $\times$ <i>A. maroccana</i>	200	14.71	2.87	0.15	0.015	0.005	—	—	—	—
<i>Av</i> 2203										

Table 38.

Chromosome pairing in meiosis in various triploid and tetraploid *Aegilops* × *Triticum* F₁ hybrids

Configuration	Chromosome number	Combination							
		<i>Ae. ovata</i> × <i>boeoticum</i>		<i>sp. carthlicum</i> × <i>Ae. mutica</i>		<i>Ae. ovata</i> × <i>dicoccum</i>		<i>Ae. triuncialis</i> × <i>turgidum</i>	
		No.	%	No.	%	No.	%	No.	%
9 ^{II} + 3 ^I	21			1					
8 ^{II} + 5 ^I	21			3					
7 ^{II} + 7 ^I	21			52					
6 ^{II} + 9 ^I	21			15					
5 ^{II} + 11 ^I	21			2					
3 ^{II} + 15 ^I	21	1							
2 ^{II} + 17 ^I	21	8							
1 ^{II} + 19 ^I	21	15							
21 ^I	21	9							
1 ^{III} + 5 ^{II} + 8 ^I	21	1	94.4	1					
2 ^{III} + 4 ^{II} + 7 ^I	21			2					
1 ^{IV} + 6 ^{II} + 5	21			3					
1 ^{IV} + 5 ^{II} + 7 ^I	21			1	100				
1 ^{III} + 3 ^{II} + 13 ^I	22	1	2.8						
3 ^{II} + 17 ^I	23	1	2.8						
2 ^{II} + 23 ^I	27					1	3.4		
2 ^{II} + 25 ^I	29					2	6.9		
1 ^{II} + 26 ^I	28					6		1	
28 ^I	28					20	89.7	15	100
No. of cells examined		36	100.0	80	100.0	29	100.0	16	100.0

genomes C^uM^b) and hexaploid wheat (*T. aestivum* ssp. *vavilovii*, $n = 21$; genomes ABD) result in chromosome pairing of 7^{II} + 21^I in the F₁ (Table 40), which means that the cells contain 7 + (0–21) chromosomes.

If, in the parental species, homoeologous genomes are present in addition to the completely homologous genomes, the most frequent form of pairing is multivalent (chiefly tri- and quadrivalents). The hybrid of *Avena barbata* ($n = 14$; genomes AB) × *A. strigosa* ($n = 7$; genome A) usually forms 7^{II} + 7^I, but up to as many as 5 trivalent chromosome conjugations may arise due to the homoeology of the A and B genomes (NISHIYAMA, 1934). In the cross *T. timopheevii* ($n = 14$; genomes AG) × *T. aestivum* ($n = 21$; genomes ABD) the most frequent chromosome pairing was 10^{II} + 15^I and 1^{III} + 9^{II} + 14^I (Table 41).

4. Cases where the parental species only have one or more homoeologous genomes and no homologous genomes are also fairly frequent; the chromosome numbers may be the same or different. In hybrids the homoeologous connections only become apparent if there are no genuine homologous connections. In general, homoeologous chromosomes only pair loosely, and divide more or less normally. If, in addition to bivalents, multi- and univalents also appear, the

Table 39.

Chromosome pairing in meiosis in the triploid *T. turgidum* conv. *polonicum* $\times$ *T. monococcum* F_1 hybrid

Configuration	Chromosome number	No.	%
$9^{II} + 3^I$	21	44	
$8^{II} + 5^I$	21	11	
$7^{II} + 7^I$	21	52	
$5^{II} + 11^I$	21	6	
$1^{III} + 6^{II} + 6^I$	21	8	
$1^{III} + 5^{II} + 8^I$	21	3	
$2^{III} + 5^{II} + 5^I$	21	3	
$1^{IV} + 1^{III} + 4^{II} + 6^I$	21	2	
$1^{IV} + 5^{II} + 7^I$	21	8	
$1^V + 4^{II} + 8^I$	21	2	84.8
$8^{II} + 4^I$	20	1	
$7^{II} + 6^I$	20	2	
$6^{II} + 8^I$	20	4	
$5^{II} + 10^I$	20	1	
$1^{III} + 6^{II} + 5^I$	20	3	
$1^{IV} + 5^{II} + 6^I$	20	3	
$2^{IV} + 3^{II} + 6^I$	20	1	9.1
$6^{II} + 7^I$	19	2	1.2
$8^{II} + 7^I$	22	2	
$1^{IV} + 5^{II} + 8^I$	22	4	3.7
18^{II}	36	1	0.6
$20^{II} + 1^{II}$	41	1	0.6
No. of cells examined		164	100.0

cells will have different chromosome numbers. This group is characterised by the fact that various types of chromosomal pairing are possible. The number of chromosomes which pair may also vary considerably, depending on the species or varieties used as crossing partners.

EMESWELLER-JONES (1935) observed 8^{II} in 72% of the cells in the first generation of a cross between *Allium cepa* ($n=8$) originating from Japan and *A. fistulosum* ($n=8$). When LEVAN (1941) produced the same hybrid using a variety of European origin, normal pairing was only observed in 2% of the cells due to a high degree of abnormality in cell division.

In the F_1 of crosses between *Aegilops speltoides* ($n=7$; genome S) $\times$ *Ae. longissima* ($n=7$; genome S¹) and *Ae. caudata* ($n=7$; genome C) $\times$ *Ae. umbellulata* ($n=7$; genome C^u) the pairing is again slightly abnormal. In the latter combination the $2n=14$ chromosomes formed 3–6^{II}.

Similar disturbances in chromosome pairing were experienced in the *Helianthus annuus* ($n=17$) $\times$ *H. petiolaris* ($n=17$) cross. In the first generation chromosome rings were observed in metaphase I and chromatid bridges in anaphase I, while the number of bivalents was 7–11.

Table 40.
Chromosome pairing in meiosis in various *Aegilops* × *Triticum* pentaploid F₁ hybrids

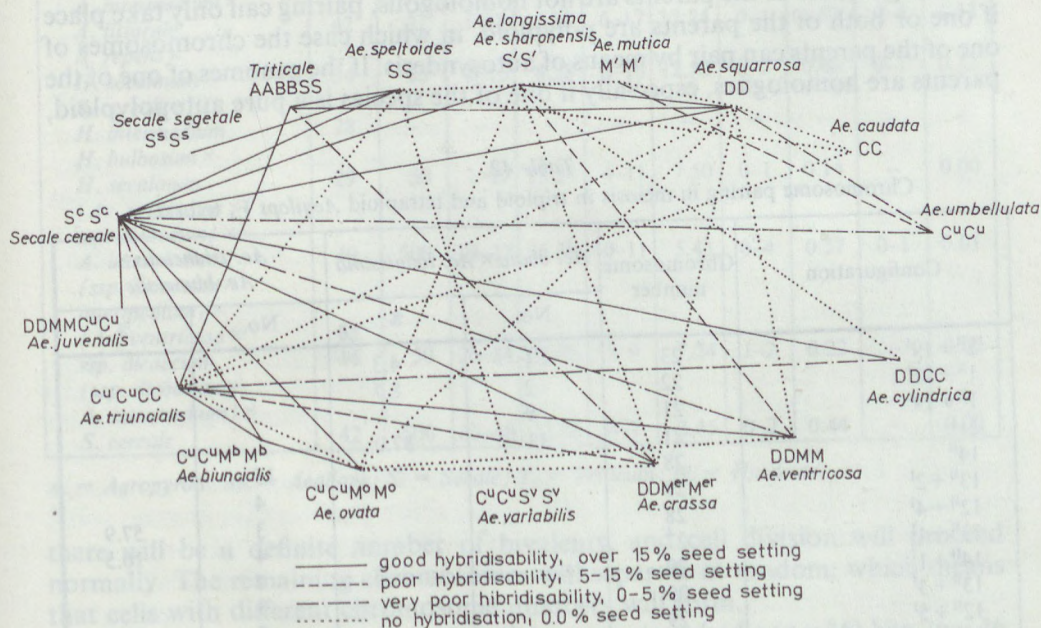
Combination	No. of cells examined	Chromosome number	As a % of total cells	15 ^{II} + 5 ^I	13 ^{II} + 9 ^I	11 ^{II} + 13 ^I	10 ^{II} + 15 ^I	9 ^{II} + 17 ^I	8 ^{II} + 19 ^I	7 ^{II} + 21 ^I	6 ^{II} + 23 ^I	5 ^{II} + 25 ^I	4 ^{II} + 27 ^I	3 ^{II} + 29 ^I	1 ^{II} + 33 ^I	1 ^{III} + 14 ^{II} + 4 ^I	1 ^{III} + 10 ^{II} + 12 ^I	1 ^{III} + 9 ^{II} + 14 ^I	1 ^{III} + 8 ^{II} + 16 ^I	7 ^{II} + 20 ^I	2 ^{IV} + 1 ^{III} + 8 ^{II} + 7 ^I	3 ^{III} + 6 ^{II} + 14 ^I	1 ^V + 1 ^{IV} + 1 ^{III} + 6 ^{II} + 11 ^I	1 ^V + 1 ^{IV} + 1 ^{III} + 5 ^{II} + 11 ^I	
<i>Ae. cylindrica</i> × <i>aestivum</i>	97	35		2	2	13	15	3	4	14						1	4	3	9						
<i>Ae. biuncialis</i> × <i>aestivum</i>	83	35					3	6		15	11	5	4	2	1		1		4	4	8	4	5	1	1
<i>Ae. triuncialis</i> × <i>aestivum</i>	171	35		4	5	2	3	4	2	6	1	2	1			2	6	2	10	3	4	11	6	2	
<i>Ae. cylindrica</i> × <i>vavilovii</i>	31	35	100	3	2	7	8			10							1								
<i>Ae. ventricosa</i> × <i>aestivum</i>	75	35	100									2	9	35	46				1						
Combination	No. of cells examined		Chromosome number	As a % of total cells	Chromosome number	As a % of total cells	1 ^{IV} + 10 ^{III} + 11 ^I	1 ^{IV} + 1 ^{III} + 7 ^{II} + 14 ^I	2 ^{IV} + 1 ^{III} + 9 ^{II} + 6 ^I	12 ^{II} + 12 ^I	6 ^{II} + 24 ^I	4 ^{II} + 28 ^I	1 ^{IV} + 1 ^{III} + 11 ^{II} + 6 ^I	2 ^{III} + 10 ^I + 10 ^{II}	1 ^{III} + 10 ^{II} + 13 ^I	9 ^{II} + 19 ^I	1 ^{III} + 7 ^{II} + 20 ^I	6 ^{II} + 25 ^I	9 ^{II} + 16 ^I	7 ^{II} + 20 ^I	2 ^{IV} + 1 ^{III} + 8 ^{II} + 7 ^I	3 ^{III} + 6 ^{II} + 14 ^I	1 ^V + 1 ^{IV} + 1 ^{III} + 6 ^{II} + 11 ^I	1 ^V + 1 ^{IV} + 1 ^{III} + 5 ^{II} + 11 ^I	
<i>Ae. cylindrica</i> × <i>aestivum</i>	97	35	83.5	5					1	2	2	1		2		4	1								
	97	36	7.2																						
	97	37	7.2																						
	97	34	2.1																						
<i>Ae. biuncialis</i> × <i>aestivum</i>	83	35	92.8					1																	
	83	36	6.0																						
	83	37	1.2																						
<i>Ae. triuncialis</i> × <i>aestivum</i>	171	35	84.8	24				28	9	1							1								
	171	36	7.6																						
	171	37	2.9																						
	171	34	4.7																						

Table 41.

Chromosome pairing in meiosis in various pentaploid *Triticum* F₁ hybrids

Combination	No. of cells examined	Chromosome number	As a % of total cells	12 ^{II} + 11 ^I	11 ^{II} + 13 ^I	10 ^{II} + 15 ^I	9 ^{II} + 17 ^I	8 ^{II} + 19 ^I	1 ^{III} + 12 ^{II} + 8 ^I	1 ^{III} + 10 ^{II} + 12 ^I	1 ^{III} + 9 ^{II} + 14 ^I	2 ^{III} + 9 ^{II} + 11 ^I	2 ^{III} + 8 ^{II} + 13 ^I	10 ^{IV} + 8 ^I + 1 ^{IV} + 1 ^{III}
<i>T. timopheevii</i> × <i>T. aestivum</i>	67	35	100	8	5	15	5	1	7	8	13	1	2	2
<i>ssp. spelta</i> × <i>T. timopheevii</i>	47	35	100	4	3	8	6	2	6	6	8	3	1	—

Within the tetraploid level, even greater disturbances are found during meiosis in crosses involving certain *Aegilops* species, e.g. *Ae. ovata* (C^uM^o), *Ae. triuncialis* (C^uC) and *Ae. biuncialis* (C^uM^b) (Fig. 34). The low frequency of bivalents in meiosis would appear to indicate that the C^u genomes of these species are not completely homologous but rather homoeologous. Only in the case of *Ae. triuncialis* (C^uM^b) × *Ae. biuncialis* (C^uC) did chromosome pairing proceed normally (Table 42).

Fig. 34. Hybridisability of *Aegilops* and *Secale* species with different chromosome numbers and genomes (BELEA, 1976)

Despite agreement in the chromosome number, anomalies in cell division can be observed in other interspecific crosses if there are deviations in genome homology. In the F_1 of *Triticum timopheevii* ($n=14$; genomes AG) $\times$ ssp. *carthlicum* ($n=14$; genomes AB), for instance, in addition to bivalents, the most frequent formation was $12^{II}+4^I$ or $11^{II}+6^I$ (Table 35). In this cross there was a somewhat higher degree of ear fertilisation than in the combination conv. *durum* ($n=14$; genomes AB) $\times$ *T. timopheevii* ($n=14$; genomes AG). GOODSPEED (1945) found $3-10^{II}$ in the F_1 of *Nicotiana corymbosa* ($n=12$) $\times$ *N. petunioides* ($n=12$), while WEBBER (1939) observed $7-13^{II}+2-12^I$ in the F_1 of *Gossypium sanguineum* ($n=13$) $\times$ *G. anomalum* ($n=13$).

Great difficulties are encountered in meiotic cell division if the crossing partners have different chromosome numbers, even if one or two genomes are of identical quality. In an F_1 hybrid of *Triticum turgidum* ssp. *dicoccum* ($n=14$; genomes AB) $\times$ *T. monococcum* ($n=7$; genome A), for example, BELEA (1976) observed chromosome pairing of $0-1^{IV}+0-3^{III}+3-7^{II}+6-15^I$; these hybrids were also extremely sterile.

In the meiosis of F_1 hybrids of *Aegilops caudata* ($n=7$; genome C) $\times$ *T. aestivum* ($n=21$; genomes ABD), too, some of the chromosomes remained in the form of univalents (7^I). Pairing only took place between the A and B genomes. In theory, the appearance of a higher proportion of balanced forms if possible through the formation of new types of genomes. In addition to the parental types, types AACC, BBCC and DDCC may also occur.

If the genomes of the parents are not homologous, pairing can only take place if one or both of the parents are polyploid, in which case the chromosomes of one of the parents can pair by means of autosyndesis. If the genomes of one of the parents are homologues, especially if one of the species is a pure autopolyploid,

Table 42.

Chromosome pairing in meiosis in triploid and tetraploid *Aegilops* F_1 hybrids

Configuration	Chromosome number	<i>Ae. ovata</i> $\times$ <i>Ae. longissima</i>		<i>Ae. triuncialis</i> $\times$ <i>Ae. biuncialis</i>	
		No.	%	No.	%
$2^{II}+19^I$	23	1	4.3		
$1^{II}+22^I$	22	2	8.7		
$1^{II}+19^I$	21	9			
21^I	21	11	87.0		
14^{II}	28			15	
$13^{II}+2^I$	28			4	
$12^{II}+4^I$	28			3	57.9
$13^{II}+1^I$	27			4	10.5
$14^{II}+1^I$	29			4	
$13^{II}+3^I$	29			3	
$12^{II}+5^I$	29			5	31.6
No. of cells examined		23	100.0	38	100.0

Table 43.

Meiotic chromosome pairing in interspecific and intergeneric hybrids in the Hordeae family
(after CAUDERON - SAIGNA, 1961)

Combination	2n	No. of cells examined	Meiotic chromosome pairing							
			I		II		III		IV	
				Mean		Mean		Mean		Mean
<i>A. junceum boreo-atlanticum</i> × <i>A. elongatum</i>	21	100	0-7	3.40	0-9	4.50	0-7	2.76	0-1	0.08
<i>A. junceum boreo-atlanticum</i> × <i>A. repens</i>	35	206	5-29	15.30	3-15	9.70	0-2	0.09	0-1	0.00
<i>A. junceum mediterraneum</i> × <i>A. littorale</i>	42	12	2-16	9.83	9-14	11.17	1-4	2.17	0-3	0.83
<i>A. junceum mediterraneum</i> × <i>A. intermedium</i>	42	47	1-13	6.80	5-13	8.40	0-8	4.34	0-3	0.98
<i>A. junceum mediterraneum</i> × <i>A. campestre</i>	49	44	4-10	5.57	13-22	18.75	0-3	1.02	0-3	0.57
<i>A. campestre</i> × <i>A. repens</i>	49	21	11-24	17.66	8-19	13.66	0-2	0.38	0-2	0.71
<i>A. campestre</i> × <i>A. intermedium</i>	49	28	4-13	9-14	8-19	14.18	0-5	1.64	0-3	1.32
<i>A. intermedium</i> × <i>A. littorale</i>	42	21	1-10	5.38	6-17	12.24	0-4	1.62	0-4	1.33
<i>A. repens</i> × <i>H. secalinum</i>	34	25	3-15	8.28	8-16	12.52	0-2	0.40	0-1	0.12
<i>S. cereale</i> × <i>H. intermedium</i>	28	-	-	-	-	-	-	-	-	-
<i>H. bulbosum</i> × <i>H. secalinum</i>	29	50	7-19	13.58	4-11	7.50	0-1	0.14	-	0.00
(<i>Ae. ventricosa</i> × <i>ssp. dicoccum</i>) × <i>A. intermedium</i>	49	500	19-47	36.38	0-11	5.43	0-4	0.57	0-1	0.01
(<i>ssp. dicoccum</i> × <i>intermedium</i>) × (<i>Ae. ventricosa</i> × <i>ssp. dicoccum</i>)	63 44	50	26-34	28.86	5-9	7.24	1-2	0.22	-	0.00
(<i>ssp. dicoccum</i> × <i>A. intermedium</i>) × <i>S. cereale</i>	42	500	25-40	33.78	0-7	3.45	0-2	0.44	-	0.00

A. = *Agropyron*; *Ae.* = *Aegilops*; *S.* = *Secale*; *T.* = *Triticum*; *H.* = *Hordeum*

there will be a definite number of bivalents, and cell division will proceed normally. The remaining chromosomes will separate at random, which means that cells with different chromosome numbers will form.

The hybrid of *Zea mays* ($n=10$) × *Tripsacum dactyloides* ($n=36$) has $2n=46$ chromosomes and forms 18^{II} (*Tripsacum*) + 10^{I} (*Zea*) (MANGELSDORF - REEVES,

Table 44.

Chromosome pairing in meiosis in F_1 hybrids of *Agropyron*, *Sitanion* and *Elymus* (after DEWEY, 1981)

Combination	Chromosome number	Chromosome pairing					
		I	II	III	IV	V	VI
<i>A. libanoticum</i> × <i>A. spicatum</i>	14	0.53	6.71	0.02	—	—	—
<i>A. ferganense</i> × <i>A. spicatum</i>	14	0.87	6.21	0.09	0.11	—	—
<i>A. ferganense</i> × <i>A. libanoticum</i>	14	2.72	5.45	0.09	0.03	—	—
<i>A. spicatum</i> × <i>A. dasystachyum</i>	21	6.84	6.95	0.08	—	—	—
<i>A. libanoticum</i> × <i>A. dasystachyum</i>	21	6.08	5.96	0.98	0.02	—	—
<i>A. spicatum</i> × <i>A. caninum</i>	21	7.66	5.87	0.03	0.38	—	—
<i>A. ferganense</i> × <i>A. caninum</i>	21	8.25	5.50	0.56	0.01	0.004	—
<i>A. spicatum</i> × <i>S. hystris</i>	21	7.18	6.84	0.05	—	—	—
<i>A. libanoticum</i> × <i>S. hystris</i>	21	8.34	6.03	0.20	—	—	—
<i>A. ferganense</i> × <i>S. hystris</i>	21	8.70	6.00	0.10	—	—	—
<i>A. spicatum</i> × <i>E. patagonicus</i>	28	5.27	10.75	0.24	0.07	0.01	0.03
<i>A. libanoticum</i> × <i>E. patagonicus</i>	28	14.15	6.68	0.17	—	—	—
<i>A. ferganense</i> × <i>E. patagonicus</i>	28	12.76	6.89	0.42	0.05	—	—

A. = *Agropyron*; *S.* = *Sitanion*; *E.* = *Elymus*

1931). The $2n = 35$ chromosome hybrid of *Iris korolkowii* ($n = 11$) × *I. macrantha* ($n = 24$) forms 12^{II} (*I. macrantha*) + 11^{II} (*I. korolkowii*), while the chromosome pairing in the first generation of *Beta vulgaris* ($n = 9$) × *B. trigyna* ($n = 27$), which has $2n = 36$ chromosomes, is 9^{III} (*B. trigyna*) + 9^I (*B. vulgaris*) (BLEIER, 1936).

CAUDERON-SAIGNA (1961) crossed various species of *Agropyron* and observed the greatest frequency of univalents in the meiosis of the F_1 hybrids of *Agropyron campestre* × *A. repens* and *A. ferganense* × *A. caninum* (Tables 43 and 44). Among the triple hybrids, a high frequency of univalents was found in the meiosis of the F_1 of the combination *Aegilops ventricosa* × ssp. *dicoccum* × *Agropyron intermedium* (36 or 38^I on average).

As mentioned above, if the genomes of the parent species are only homoeologous, the bivalents are only loosely connected and at higher levels of polyploidy varying quantities of multi- and univalents also appear. In such cases the distribution of the chromosomes is irregular and the cells will have different chromosome numbers. In the F_1 of the cross *Aegilops ventricosa* ($n = 14$; genomes DM^v) × conv. *durum* ($n = 14$; genomes AB) the $2n = 28$ chromosomes form $0-3^{II} + 22-28^I$ (KATAYAMA, 1931), while this same *Aegilops* species, when pollinated with *T. aestivum* ($n = 21$; genomes ABD), gives a $2n = 35$ chromosome F_1 hybrid which most frequently forms $1^{II} + 33^I$ (Table 40). The $2n = 28$ chromosomes of *Triticum aestivum* ($n = 21$; genomes ABD) × *Secale cereale* ($n = 7$; genome R) form $0-1^{III} + 0-3^{II} + 22-28^I$ (BLEIER, 1934). In this case autosyndesis occurs between the parental genomes.

Table 45.

Chromosome pairing in meiosis in *Aegilops crassa* (*T. crassum*) $\times$ *Hordeum vulgare* F_1 hybrids (after FEDAK-NAKAMURA, 1981)

Genotype	Chromosome pairing				No. of cells examined
	I	II	III	IV	
<i>Aegilops crassa</i> $\times$ <i>Hordeum vulgare</i>	19.13	3.87	0.36	0.01	230
<i>Aegilops crassa</i> $\times$ <i>Hordeum vulgare</i>	17.71	4.56	0.37	0.02	130
Average of two hybrid lines	18.62	4.12	0.36	0.01	360
<i>Aegilops crassa</i> polyhaploid	10.47	4.81	0.28	0.02	184
<i>Hordeum vulgare</i> haploid	6.90	0.04	—	—	589
Total haploids	17.37	4.85	0.28	0.02	773

In the meiosis of F_1 hybrids of *Aegilops crassa* $\times$ *Hordeum vulgare* (BOMI), the chromosome pairing was roughly equivalent to the polyhaploids of *Aegilops crassa* (Table 45). In the pentaploid hybrids of *Agropyron tsukushiense* ($6x$) $\times$ *Hordeum bulbosum* ($4x$), chromosome conjugation of $4^{II} + 27^I$ was found in 12, and $5^{II} + 25^I$ in 17 of the 51 cells examined (SHINGENOBU-SAKAMOTO, 1981). The percentage chromosome pairing was 23.5 and 33.3%, respectively (Table 46).

If no homology or homoeology (semi-homology) whatsoever exists between the genomes of the two parents, the chromosomes remain as univalents in the course of cell division and the cells will have different chromosome numbers (Pygaera type). In the cross *Aegilops umbellulata* ($n=7$) $\times$ *Haynaldia villosa* ($n=7$) all the cells of the $2n=14$ chromosome F_1 contain 14^I (v. BERG, 1937). Similarly, the $2n=18$ chromosomes of *Raphanus sativus* ($n=9$) $\times$ *Brassica oleracea*

Table 46.

Chromosome pairing in meiosis in *Agropyron tsukushiense* ($6x$) and *Hordeum bulbosum* ($4x$) hybrids (after SHINGENOBU-SAKAMOTO, 1981)

Combination	No. of cells examined	Chromosome pairing		Frequency, %
		I	II	
<i>Agropyron tsukushiense</i> ST-1 $\times$ <i>Hordeum bulbosum</i> HB-7 ($2n=35$)	1	33	1	2.0
	1	31	2	2.0
	8	29	3	15.7
	17	27	4	33.3
	12	25	5	23.5
	7	23	6	13.7
	3	21	7	5.8
	1	19	8	2.0
	1	17	9	2.0
Total	51			100.0

Table 47.

Chromosome pairing in meiosis (meta-I) in a *T. turgidum* conv. *durum* (Nordum) $\times$ *Agropyron distichum* F₁ hybrid (after PIENAAR, 1980)

No. of cells examined	Chromosome pairing in metaphase I								Chiasma frequency
	univalent	bivalent			multivalent				
		fragment	ring	complete	III	IV	V	VI	
200	14.12 (6-26)	3.55 (0-7)	1.26 (0-4)	4.81 (1-9)	0.375 (0-2)	0.75 (0-2)	0.01 (0-1)	0.01 (0-1)	9.17 (1-14)

cea ($n=9$) form 18¹ (KARPECHENKO, 1928), the $2n=40$ chromosomes of *Nicotiana bigelovii* ($n=24$) $\times$ *N. suaveolens* ($n=16$) form 40¹ in the F₁ (GOODSPEED et al., 1927), and the $2n=36$ chromosomes in the first generation of *Oryza sativa* ($n=12$; genome A) $\times$ *O. minuta* ($n=24$; genomes BC) form 36¹ (MORINAGA, 1940). The meiosis in the F₁ of *Aegilops triuncialis* ($n=14$; genomes C^uC) $\times$ *T. turgidum* ($n=14$; genomes AB) also produced only univalents (28¹) (Table 38).

In the F₁ meiosis of *T. turgidum* conv. *durum* $\times$ *Agropyron distichum*, PIENAAR (1980) reported chromosome pairing frequencies of 14.12¹ + 4.81¹¹ + 1.145 multivalents (Table 47). SHARMA-GILL (1981) used *Agropyron* species (*A. smithii* and *A. ciliare*) not previously used for crossing in combinations with *T. aestivum* and found that the first generations ($2n=35$) gave univalent frequencies of 33.11¹ and 26.18¹ respectively (Table 48).

Table 48.

Chromosome pairing in meiosis in *Agropyron* $\times$ *Triticum* F₁ hybrids (after SHARMA-GILL, 1981)

Combination	Chromosome number	No. of cells examined	Univalent		Bivalent		complete	Chiasma frequency
			mean	deviation	fragment	ring		
<i>Agropyron smithii</i> $\times$ <i>Triticum aestivum</i>	26	1	26		0	0	0	0
	30	11	27.33	24-30	0.82	0.18	1.0	1.2
	31	3	27.67	25-31	1.67	0	1.67	1.7
	32	3	29.30	28-30	1.00	0.33	1.33	1.7
	34	4	32.00	30-34	0	1.00	1.00	1.7
	35	9	33.11	24-35	0.44	0.11	0.56	0.7
	36	1	32		1	1	2	3
	38	1	34		2	0	2	2
<i>Agropyron ciliare</i> $\times$ <i>Triticum aestivum</i>	35	130	26.18	14-35	3.84	0.41	4.29	4.9

4.2.4 Formation of non-reduced cells

The presence of non-paired chromosomes usually interferes with the normal course of reductional cell division. In interspecific hybrids where a large number of univalents occur with only a few bivalents, the chromosomes are often incapable of moving towards the poles (due to this interference). In such cases, instead of two daughter cells, only one cell is often produced in the first phase of division, and this contains all the chromosomes, which means that non-reduced cells are formed (*Aegilops* × *Triticum*, *Triticum* × *Secale*, *Raphanus* × *Brassica* hybrids, etc.). In these instances, the nucleus was referred to by Rosenberg as a restitution nucleus, while KIHARA (1951) and KATAYAMA (1933) defined the phenomenon as regression.

During the second phase of cell division, the process of division proceeds normally, with diads being produced instead of tetrads. A similar phenomenon can be observed if the two nuclear spindles merge during the second phase of cell division, as is found in the case of *Salix* (HÄKANSSON, 1929), *Galeopsis* (MÜNTZING, 1930) and *Nicotiana* (BRIEGER, 1928). Another possibility is that, during the first phase of cell division, the univalent chromosomes split in half lengthways and daughter cells fail to form in the second phase (e.g. *Triticum turgidum* × *Haynaldia villosa*). It may also happen that both divisions fail to occur and tetraploid giant pollen grains are formed, as observed by KIHARA-LILIENFELD (1936) in *Aegilops caudata* × *Ae. speltoides* and by THOMPSON (1940) in *Lactuca spicata* × *L. indica*.

Knowledge on the structures participating in meiotic pairing, and in fact on the whole process, is still very deficient. In recent years, however, a certain amount of progress has been made with respect to the pairing of homologous and homoeologous chromosomes. It is a well-known fact that during the meiosis of hexaploid ($2n=42$) wheat, the pairing of homologous chromosomes leads to the formation of 21 bivalents, while in the 21-chromosome haploids the formation of one or two, or in rare cases four, bivalents can be observed. Thus, in the case of *T. aestivum*, homoeologous pairing does not take place even if there are no homologous chromosomes. Quite independently of each other, both OKAMOTO (1957) and RILEY (1958) discovered the fact that the pairing of homoeologous chromosomes is inhibited, or influenced, by a gene on the long arm ($5B^L$) of chromosome 5B. These authors crossed a mono-5B line of *T. aestivum* with other wheat species. On analysing the F_1 meiosis they found that when the 5B chromosome was missing, there were considerably fewer univalents, with a proportionate rise in the frequency of bi- and quadrivalents. When chromosome 5B was present, on the other hand, the frequency of univalent chromosomes rose. RILEY-EWART (1960) treated the 5B ditelosomic line of Chinese Spring with the mutagen ethyl-methane-sulphonate (EMS) and obtained mutants, which were then fixed in the homozygotic state and which facilitated homologous pairing in wheat × rye crosses. The mutant allele was found to be recessive compared to the normal dominant allele. FELDMANN (1966) raised the dose of the asynaptic gene on $5B^L$ to six times the original

strength and found that even the pairing of homologous chromosomes failed to take place, though a few homoeologous chromosomes paired. The reason for this is that the more intense asynaptic effect of the 5B chromosome ($2n=42$) causes the chromosomes to move a few micrometres away from each other, as the result of which the chromosomes take up random positions during cell division. One or two homoeologous chromosomes may thus come together and pair. In the F_1 meiosis of the cross mono-5B Courtot ($ABD-1D$) $\times$ *Aegilops*

Table 49.

Chromosome pairing in meiosis in a *Triticum aestivum* $\times$ *Aegilops ventricosa* F_1 hybrid due to the effect of chromosome 5B (after DOSBA, 1974)

Designation	Chromosome number	No. of cells examined	Univalent	Bivalent			Trivalent	Quadri-valent	Multi-valent
				Complete	Open	Closed			
Mono-5B	41	106	1.20	19.90	1.36	18.54	—	—	—
'Courtot' mono-5B			1-5	18-20	0-5	15-20	—	—	—
'Courtot' $\times$ <i>Ae. ventricosa</i>	34	200	12.84	6.90	2.78	4.12	1.70	0.50	0.04
			5-21	3-11	0-7	0-7	0-6	0-3	0-1
<i>Ae. ventricosa</i>	28	50	0.0	14.00	2.02	11.98	—	—	—
			—	—	0-6	8-14	—	—	—
'Chinese Spring' nulli-5B tetra-5Dx			14.24	7.16	2.80	4.36	1.22	0.44	—
<i>Ae. ventricosa</i>	34	50	9-20	3-10	0-6	2-7	0-3	0-2	—
	35	147	12.28	6.92	2.98	3.94	1.87	0.77	—
			7-19	2-11	0-7	1-7	0-5	0-1	—
			0.47	19.19	3.49	15.70	0.24	0.59	—
'Chinese Spring' nulli-5B tetra-5D	42	90	0-3	15-21	0-8	8-19	0-1	0-4	—

ventricosa ($n=14$; genomes DM^V), too, the presence of chromosome 5B reduced the frequency of bivalents. There was a rise in bivalent frequency (7.16^{II}) in the F_1 of Chinese Spring nulli-5B tetra-5Dx *Ae. ventricosa*. In this case the effect of the suppressor gene on chromosome $5B^L$ was counteracted to some extent by chromosome 5D (Table 49). Later research proved that, in addition to $5B^L$, factors present on the long or short arms of other chromosomes (2A, 3A, 3D and 3B) also inhibited the pairing of homoeologous chromosomes, while genes located on other chromosomes ($5A^L$, $5B^S$, $5D^S$ and especially $5D^L$) stimulated this pairing. Naturally, systems inhibiting or stimulating chromosome pairing may occur not only in wheat, but also in other plant species.

4.2.5 Ability of gametes to function

If normal chromosome pairing and chromosome distribution take place, well developed gametes capable of functioning are generally formed. Hybrids obtained from plant species which contain only homologous genomes are often just as fertile as the parents. In the case of hybrids from parents with differing chromosome numbers, however, sterile gametes are often found, which may be formed in various ways. It can be assumed that the parents of such hybrids differ only in small structural changes in certain parts of the chromosomes, which are so slight as to allow reductional cell division to proceed normally.

In certain genera of the *Gramineae* family (*Triticum*, *Aegilops*, *Hordeum*, *Secale*), fertility is generally expressed as number of grains per ear or per spikelet. The fertility of other plants is determined on the basis of the number of seeds found in the berries or gourds. BELEA (1964, 1976) obtained sterile F_1 plants in the combinations *T. aestivum* ($n=21$, genomes ABD) $\times$ *T. monococcum* ($n=7$, genome A), ssp. *spelta* ($n=21$, genomes ABD) $\times$ *T. monococcum* ($n=7$), ssp. *carthlicum* ($n=14$, genomes AB) $\times$ *T. monococcum* ($n=7$), *T. timopheevii* ($n=14$, genomes AG) $\times$ *T. monococcum* ($n=7$) and *T. timopheevii* ($n=14$) $\times$ ssp. *spelta* ($n=21$). Slightly better fertility in terms of number of grains per ear and per spikelet was observed in the first generation of conv. *durum* ($n=14$, genomes AB) $\times$ *T. timopheevii* ($n=14$) (Table 50).

A level of fertility acceptable in practice was found in the F_1 plants of *T. turgidum* ($n=14$, genomes AB) $\times$ *T. aestivum* ($n=21$) and ssp. *dicoccum* ($n=14$, genomes AB) $\times$ *T. aestivum* ($n=21$), and in the reciprocal crosses of these combinations.

Different levels of fertility were also observed in F_1 hybrids produced using different cultivars of various species. For instance, in the first generation of the cross ssp. *dicoccum* $\times$ *T. aestivum* the number of grains/ear was 1.5 if cultivar B 1201 was used, while this value was as high as 31.9 if the cultivar Fortunato was used, as seen in Table 47. Similarly large differences in fertility were found in the F_1 plants when the cultivars F 481 (1.4 grains per ear) or B 1201 (0.3 grains per ear) were crossed with *T. monococcum*.

A high degree of sterility was observed both within the *Aegilops* genus and in the first generation of *Aegilops* $\times$ *Triticum* crosses (Fig. 35), especially within the diploid *Aegilops* series and in triploid ($2x \times 4x$) *Aegilops* hybrids.

Similar results were obtained in crosses between diploid *Avena* species, particularly for *A. prostrata* and *A. longiglumis*, and for other oat species (Fig. 36).

If different numbers of chromosomes are found in the gametes of interspecific hybrids, not all the gametes will be capable of developing. The fertility of such interspecific hybrids is greatly reduced. The more abnormal the reductional cell division, the more likely fertility is to be affected.

In *Triticum* interspecific hybrids which contain a small number of univalent chromosomes in addition to the constant number of bivalents (e.g. $14^{II} + 7^I$), the chromosome numbers of the gametes fluctuate between specific limits ($14 + 0 - 7$).

Table 50.

Fertility in the first generation of interspecific *Triticum* L. hybrids

Combination	Plant number	Grains/ plant	Grains/ear		
			$\bar{x}$	s	$s_{\bar{x}}$
<i>T. monococcum</i> × <i>T. timopheevii</i>	14	0.0	0.0	—	—
reciprocal	12	0.0	0.0	—	—
<i>T. monococcum</i> × ssp. <i>carthlicum</i>	10	0.0	0.0	—	—
reciprocal	45	1.3	0.0	0.0	0.0
<i>T. aestivum</i> (B1201) × <i>T. monococcum</i>	4	9.0	0.3	0.0	0.0
<i>T. aestivum</i> (F481) × <i>T. monococcum</i>	3	21.4	1.4	0.0	0.0
ssp. <i>spelta</i> × <i>T. monococcum</i>	3	0.0	0.0	0.0	0.0
<i>T. timopheevii</i> × ssp. <i>carthlicum</i>	69	26.6	2.6	2.8	0.6
reciprocal	48	33.6	1.4	0.6	0.2
<i>T. timopheevii</i> × ssp. <i>dicoccum</i>	136	1.8	0.1	1.2	0.1
reciprocal	12	2.6	1.4	1.3	0.2
ssp. <i>carthlicum</i> × ssp. <i>dicoccum</i>	138	625.1	36.4	18.3	2.3
<i>T. aestivum</i> × <i>T. timopheevii</i>	30	1.2	0.1	0.0	0.0
reciprocal	29	8.3	0.7	0.9	0.3
<i>T. aestivum</i> × ssp. <i>dicoccum</i>	130	318.3	24.3	5.3	1.1
reciprocal (B1201)	25	257.3	15.5	8.2	2.5
reciprocal (F481)	13	628.4	31.9	10.9	2.4
<i>T. aestivum</i> × conv. <i>durum</i>	34	256.0	25.6	4.9	1.9
<i>T. aestivum</i> × ssp. <i>carthlicum</i>	75	702.7	29.4	6.4	0.2
reciprocal	30	556.7	23.1	5.9	0.4
<i>T. aestivum</i> × <i>T. turgidum</i>	27	603.0	33.5	6.9	2.1
reciprocal	20	372.2	28.2	5.7	1.9
ssp. <i>spelta</i> × ssp. <i>carthlicum</i>	50	316.4	37.3	1.9	0.4

14 to 21, in practice gametes with slightly different chromosome numbers are obtained. This is due partly to the lagging of univalents during reductional cell division, and partly to the fact that the remaining univalents migrate to the poles in groups rather than at random.

Only embryo sacs containing 14 or 21 chromosomes are able to develop, and pollen mother cells with 14 or 21 chromosomes are also much more viable than those with an intermediate number of chromosomes. Among the euploids, those with 21 chromosomes function much more efficiently than those with 14 chromosomes, which contain only the chromosomes of the AB genomes.

If an interspecific hybrid contains only a small, varying number of bivalents and a large quantity of univalents, intense fluctuations will occur in the chromosome numbers of the genomes. In general, gametes which contain all the chromosomes of a genome are capable of development, while the intermediate types die off. In two-genome hybrids, viable gametes occur with a frequency of only 0.024% (KIHARA, 1938). Non-reduced gametes are also well able to develop. In many interspecific and intergeneric hybrids, the gametes are the only cells capable of further development.

As mentioned above, there is a close correlation between the dehiscence of the anthers and the ratio of sterile/fertile pollen grains they contain. In the case

	Diploids								tetraploids				hexaploids					
	<i>A. pilosa</i>	<i>A. ventricosa</i>	<i>A. prostrata</i>	<i>A. damascena</i>	<i>A. longiglumis</i>	<i>A. canariensis</i>	<i>A. wiestii</i>	<i>A. hirtula</i>	<i>A. strigosa</i>	<i>A. barbata</i>	<i>A. vaviloviana</i>	<i>A. abyssinica</i>	<i>A. magna</i>	<i>A. murphyi</i>	<i>A. fatua</i>	<i>A. sterilis</i>	<i>A. byzantina</i>	<i>A. sativa</i>
<i>A. clauda</i>	F	S		—				—	—	—			—					
<i>A. pilosa</i>		S		—	—			—	—	—	—	—	—					S
<i>A. ventricosa</i>					—			—	—	—	—	—	—					S
<i>A. prostrata</i>				S	S	S		S	S				S	S				S
<i>A. damascena</i>					—			—	—				S					
<i>A. longiglumis</i>							S	S	S	S	S	S	S	S				S
<i>A. canariensis</i>																		S
<i>A. wiestii</i>								F	F	S	S	S						
<i>A. hirtula</i>									F	S	S	S	S					S
<i>A. strigosa</i>										S	S	S		S				S
<i>A. barbata</i>										F	F	S	S	S	S	S	S	S
<i>A. vaviloviana</i>											F							S
<i>A. abyssinica</i>												S				S	S	S
<i>A. magna</i>													S	S		S	S	S
<i>A. murphyi</i>														S		S		S
<i>A. fatua</i>																F	F	F
<i>A. sterilis</i>																	F	F
<i>A. byzantina</i>																		F

— = crosses attempted and failed

S = sterile

F = fertile

S = amphiploid with moderate to good fertility

S = amphiploid with low fertility (note: some seed-set in prostrata x longiglumis hybrids)

Fig. 36. Fertility of F_1 hybrids in interspecific *Avena* crosses (RAJHÁTHY-THOMAS, 1974)

of interspecific hybrids in wheat, at least 30% of the pollen must be fertile if the pollen grains are to swell sufficiently to split the anthers. Although the majority of interspecific hybrids (*Triticinae*, *Nicotiana*, *Brassica*, *Gossypium*, etc.) are pollen sterile, some of the plants have viable embryo sacs. This figure is 0.33% on average for *Aegilops* x *Triticum* hybrids, 0.08% for *Triticum* x *Haynaldia* hybrids and 0.06% for *Triticum* x *Secale* hybrids.

Several authors have dealt with the correlation between percentage seed setting, pollen fertility, the number of univalents and the fertility of the F_1 hybrids. When carrying out interspecific hybridisation in *Triticum*, BELEA (1964) investigated the correlations between seed setting percentage, the pollen fertility of the F_1 hybrids, the frequency of univalents in reductional cell division and the number of grains/ear, and found the greatest positive correlation between seed setting and pollen fertility and between seed setting and the fertility of the

Table 51.

Correlation between certain characters in interspecific *Triticum* hybrids

Combination	Seed setting %	Pollen fertility %	Univalent frequency %	Grains/ear No.
<i>T. timopheevii</i> × <i>T. monococcum</i>	1.9	0.6	100.0	0.0
ssp. <i>carthlicum</i> × <i>T. monococcum</i>	13.1	1.0	100.0	0.5
<i>T. timopheevii</i> × ssp. <i>carthlicum</i>	11.0	5.1	78.9	2.6
<i>T. timopheevii</i> × ssp. <i>dicoccum</i>	17.2	0.8	85.7	0.1
<i>T. timopheevii</i> × ssp. <i>dicoccum</i> ('Vernal')	23.6	85.6	9.8	36.4
ssp. <i>carthlicum</i> × ssp. <i>dicoccum</i> ('Khapli')	17.9	44.6	12.6	29.1
<i>T. aestivum</i> × <i>T. timopheevii</i>	1.5	1.9	100.0	0.1
reciprocal	3.9	1.5	100.0	0.1
<i>T. aestivum</i> × ssp. <i>carthlicum</i>	31.3	82.1	100.0	19.3
reciprocal	37.4	65.5	100.0	28.6
<i>T. aestivum</i> × ssp. <i>dicoccum</i>	21.6	86.0	100.0	24.3
<i>T. turgidum</i> × <i>T. aestivum</i> ('Mp 706')	55.4	85.8	100.0	28.2

seed setting – pollen fertility $r=0.8$ seed setting – no. of univalents $r=0.19$ seed setting – no. of grains/ear $r=0.75$ pollen fertility – no. of univalents $r=0.078$ pollen fertility – no. of grains/ear $r=0.92$ no. of univalents – no. of grains/ear $r=0.34$

F_1 plants (Table 51). The better the seed setting, which basically depends on the number of fertile pollen grains, the greater the fertility of the F_1 hybrids. It follows from this that there is a negative correlation between the number of univalents and the fertility of the F_1 plants. In practice, there is no direct correlation between pollen fertility and the number of univalents.

The same can be observed as a function of crossing direction, when the pollen fertility in pentaploid hybrids is lower (31.5%) in hexaploid × tetraploid crosses than in the reciprocals (38.2%). It may also happen, of course, that higher seed setting is obtained in the case of low pollen fertility. In general, ear productivity rises parallel to the percentage of viable pollen.

The presence of a large number of univalent chromosomes as the consequence of abnormal cell division leads to lower fertility. This correlation is not particularly close, however. Cases are frequently found where this correlation does not apply: low fertility when there are only a few univalent chromosomes, or relatively good fertility combined with a univalent frequency of 100% (mainly in pentaploid hybrids). This can probably be put down to the fact that genome homology has a greater effect on fertility than differences in the number of chromosomes.

Sterility can be caused by genes in the cell nucleus and the cytoplasm alike. If chromosome pairing is prevented in meiosis by the inhomology of the chromosomes of the two parents, it is referred to as chromosomal sterility. In this case the univalents are either distributed at random between the two poles

during the first meiotic division, or split into chromatids. In both cases, as the result of the second division, gametes with differing chromosome numbers are formed.

Not only the cell nucleus, or the chromosomes they contain, take part in the transfer of characters. In addition, there is a system of plasmagenes associated with the cytoplasmic structures. The ovum is known to donate the majority of the cytoplasm to the cell arising when the gametes unite, since there is virtually no cytoplasm in the male gamete. For this reason, characters transferred by cytoplasmic inheritance from generation to generation are passed on by the female parent. Physiological processes only take place normally in intact cells where the external and internal conditions required for these processes are met. The cell nucleus is in close, complex relation to the cytoplasm, which not only supplies the nucleus with nutrients, but, quite apart from the independent role of the cytoplasm in inheritance, also plays a decisive part in determining the priority of gene functioning. In the case of *Paramecium aurelia*, for example, Sonneborn demonstrated the fact that each animal has a large number of genes, each of which controls the formation of a specific cilium antigen. However, only one antigen is ever produced in any quantity. Which of the antigens will be produced in preponderance will be determined by the cytoplasm, interestingly enough by means of the interaction between the cytoplasm and the environment. For example, harsh environmental effects, such as the presence of alien substances or changes in salt concentrations, will determine which antigen the animal will synthesise, though this can only be one for which it contains a suitable gene. The cytoplasm thus plays a decisive and interesting role in controlling the alternative and exclusive priorities of gene functioning.

Cytoplasmic factors inducing pollen infertility have been found in a number of plant species. This phenomenon is widely used in the production of hybrid seeds. The genetics of cytoplasmic male sterility has been investigated in the greatest detail for maize. The appearance of sterility is connected with plasmagenes, but its manifestation depends on genotypic conditions. Restorer genes (S) have been discovered which counteract the phenotypic sterility. Normal pollen may develop even in cytoplasmically male sterile plants if they also contain genes capable of restoring fertility. Therefore, sterility is only observed in the absence of these genes, in plants with the ss genotype. The S gene does not, however, alter the plasmagenes in the cytoplasm which are responsible for sterility. In order to maintain cytoplasmic male sterility, a plant of type A, which is pistillate (having viable ovules and sterile pollen), should be pollinated with pollen from a plant of type B. If seeds with high yield potential are to be produced, two lines are crossed, one of which possesses cytoplasmic male sterility, while the other contains the S gene.

FRANKEL (1947) demonstrated the fact that the cytoplasmic male sterility of petunias can also be transferred by grafting. The fertile plant was grafted onto the sterile plant, with the result that the grafted plant also became cytoplasmically male sterile.

A characteristic example of cytoplasmic inheritance is the experiment

carried out by MICHAELIS (1937) on *Epilobium* (willow-herb). The *E. hirsutum* × *E. luteum* hybrid is male sterile. Meiosis proceeds normally, but in later stages the young pollen grains degenerate. The hybrid has tiny leaves and is female fertile, as it produces seed when back-crossed to the parent species. When back-crossing was carried out with the species *E. luteum*, the anomalies observed in the fertility of the F_1 plants were even more pronounced. The F_1 of the next back-cross dies off in the germ stage. It can thus be seen that the higher the proportion of *E. luteum* chromosomes in the progeny, the greater their sterility. In the reciprocal cross (*E. luteum* × *E. hirsutum*) there is a smaller degree of inhibition in development (large-leaved) and the F_1 has extremely good pollen fertility. When back-crossed to *E. hirsutum* the plants were entirely of the *E. hirsutum* type by BC²⁵. In spite of this, it was possible to prove the retention of the *E. luteum* cytoplasm type (inheritance of large leaves), which was inherited quite independently of the cell nucleus.

The existence of this inheritance was proved in a number of experiments by RHOADES (1933), who replaced each of the 10 chromosomes of maize separately without causing any change in the inheritance of sterility. This series of experiments indicates the different levels of interaction between the cytoplasm and the cell nucleus. The effect of the cytoplasm cannot be manifested without the nucleus.

This phenomenon is of economic importance, since it means that for numerous crops (sorghum, maize, sugar beet, flax, etc.) male sterile lines can be used in producing hybrid seed, thus making it unnecessary to castrate the female parent (detasselling in maize). When cytoplasmic sterile plants are crossed with normal individuals, the progeny obtained are sterile. This technique substantially reduces the costs of producing hybrid seed.

The discovery of a new, cytoplasmically male sterile source is also reported by WHELAN (1981) in sunflower: the nucleus ($2n = 34$) of cultivated sunflower (*Helianthus annuus*) was introduced into the cytoplasm of the perennial *H. giganteus* and a completely male sterile line was produced after four back-crosses. JOHNSON (1958) produced male sterile cabbages through substitution with the cytoplasm of a radish cultivar (Early Scarlet Globber). Male sterile plants were selected after interspecific crossing in Savoy cabbage by NIENUHOF (1961) and in broccoli by COLS (1957).

In the late sixties rapid progress was made in the breeding of hybrid wheat on the basis of cytoplasmic male sterility. This was facilitated by the work of KIHARA (1951, 1954), who found male sterile individuals in hybrids from the combination *T. aestivum* × *Ae. caudata* back-crossed to *T. aestivum*. Later, FUKASAWA (1958) selected male sterile lines from the combination *Aegilotriticum* × conv. *durum* after back-crossing to conv. *durum* and from the hybrids of *Aegilotriticum* × ssp. *dicoccum*. This author mentions that when *Ae. ovata* was used as the female parent there was a gradual increase in pollen fertility. In the reciprocal cross (conv. *durum* × *Ae. ovata*), male sterile lines with a completely *durum*-type cytoplasm were obtained after several back-crosses (BC³) (Fig. 37).

The breeding of hybrid wheat received especially great impetus world-wide

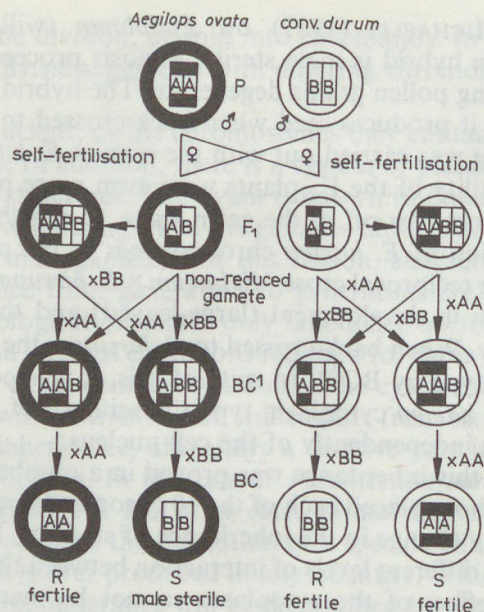


Fig. 37. Genome restoration diagram for a substitution between *Aegilops ovata* and *T. turgidum* conv. durum. A and B represent the haploid chromosome sets of *Aegilops ovata* and conv. durum and the black rectangle the cytoplasm of *Aegilops ovata* (FUKASAWA, 1958)

after B. L. JOHNSON (1967) found cytoplasmically male sterile plants among *T. timopheevii* × *T. aestivum* hybrids. For a long time these formed the initial stock for work in this field. Nowadays, a considerable number of cytoplasmic male sterile sources are available, obtained by means of interspecific crossing, particularly by MANN-LUCKEN (1971). For this purpose, the large pollen grains of *Aegilops*, *Secale* and *Haynaldia* species are also used. Since *Secale* and *Haynaldia* are difficult to cross with wheat, *Aegilops* species are used as intermediates in the production of male sterile sources.

Considerable advantages stem from the fact that the cytoplasm effect is not entirely independent of the functioning of various genes located on the chromosomes. Some lines are able to restore fertility (restorer, Rf lines) and if the stigma of a male sterile plant is pollinated with pollen from such plants, the next generation will produce fertile pollen. ROGERS-EDWARDSON (1952) were the first to report on maize lines which were able to overcome cytoplasmic sterility. Normal pollen may develop even in cytoplasmically male sterile plants if they contain fertility restoring genes. This means that sterility is only manifested in the absence of such genes.

In recent years, research on hybrid wheat breeding on the basis of cytoplasmic male sterility has lost momentum due to the difficulties encountered (cumbersome nature of the method, etc.). It would seem that the application of gametocides will be more successful. The F₁ and F₂ lines of hybrid wheat produced at Martonvásár using the Shell compound WL 84811 were entered in national variety trials in 1989 (verbal communication).

4.3 Fertility and cytology of the F_2 and later generations

4.3.1 Progeny of fertile F_1 generations

The populations employed in crosses may be at various stages in the process of species formation, so the fertility of the hybrids will differ due to differing extents of genetic isolation.

As mentioned earlier in the chapter entitled "Morphology of interspecific and intergeneric hybrids", the phenotype of fertile F_1 plants from parents with homologous genomes is virtually equivalent to that of intervarietal hybrids. Segregation obeys the Mendelian laws. If there are substantial deviations between the morphological traits of the parents, the types segregating in the F_2 will be extremely varied. In many cases the variability will be so great that it is impossible to find two identical plants, which means that classification is also impossible. This makes gene analysis extremely difficult. The majority of the plants are intermediates; forms reminiscent of the F_1 occur with the greatest frequency, while very few types resemble the parents. The pure parental forms are often completely missing. By contrast, the appearance of new types, transgressions, is frequent. In general, the F_2 and the later generations are completely fertile.

If the parents contain a few homologous genomes, euploid, fertile plants begin to appear in the F_4 or F_5 . In the case of parents with completely different genomes, cytologically well-balanced, fertile individuals cannot be found until much later, in the F_7 – F_9 generations.

4.3.2 Progeny of F_1 hybrids with poorer fertility

Some hybrids produce a large number of sterile gametes in the F_1 despite the fact that they stem from parents with identical chromosome numbers and genomes, where chromosome pairing proceeds normally. One such combination is *Phaseolus vulgaris* $\times$ *Ph. coccineus*, where the loss of the coccineus chromosomes in the F_2 frequently causes the formation of sterile gametes. In this combination a great many sterile or semi-sterile plants are found, together with very few fertile ones. The various morphological traits (stalk branching, leaf shape and size, structure of the inflorescence, flower colour and seed shape) combine freely with each other. In all plants bearing traits characteristic of the coccineus type, the stigma going down the outside of the style (hypogeic cotyledon) is generally sterile. In the reciprocal cross (*coccineus* $\times$ *vulgaris*) no plants of the *vulgaris* type can be found (epigeic cotyledon, stigma going down the inside of the style). So far, it has proved impossible to transfer these distinctive interspecific traits from one species to the other since they are associated with gamete or zygote sterility, which means that the plants are sterile.

The progeny of the F_1 hybrids of autopolyploid species develop in various ways depending on the reductional cell division in the first generation. If only bivalents are formed in the F_1 , the chromosome number of the F_2 plants will be uniform and constant. All the characters which are located in chromosomes which pair by means of auto- or allosyndesis are inherited according to the Mendelian laws.

The chromosome number of the second generation of the *Fragaria niponica* $\times$ *F. moschata* (LILIENFELD, 1933) and *F. vesca* $\times$ *F. moschata* (SCHIE-MANN, 1951) crosses is $2n=28$, as in the F_1 , and the chromosomes generally form 14^{II} ; these hybrids have good fertility. Segregation for foliage colour, tendrill formation, leaf shape and habit occurs according to the Mendelian laws.

If, in addition to bivalents, multi- and univalents are also formed in the F_1 , among the progeny the fertility of plants with different chromosome numbers will vary substantially. In the F_2 of *Solanum chaucha* ($n=18$) $\times$ *S. stenotomum* ($n=12$) the plants had chromosome numbers of $2n=24-29$, while in the second generation of the cross *S. chaucha* ($n=18$) $\times$ *S. tuberosum* ($n=24$) plants with $2n=39-48$ chromosomes were observed. The greatest proportion of the plants contained $2n=45-46$ chromosomes. The second generation of *Fragaria orientalis* ($n=14$) $\times$ *F. moschata* ($n=21$) consisted of plants with $2n=28-42$ chromosomes. Individuals with $2n=28$ chromosomes resembled *F. orientalis*, while those with $2n=42$ chromosomes were reminiscent of *F. moschata*. Among the $2n=11$ chromosome F_2 plants of *Vicia amphicarpa* $\times$ *V. obovata* a few were found which had $2n=16-17$ chromosomes (Fig. 38).

The progeny of hybrids where the parents contained both homologous and non-homologous genomes, so that the F_1 gametes possess x bivalents and $0+y$

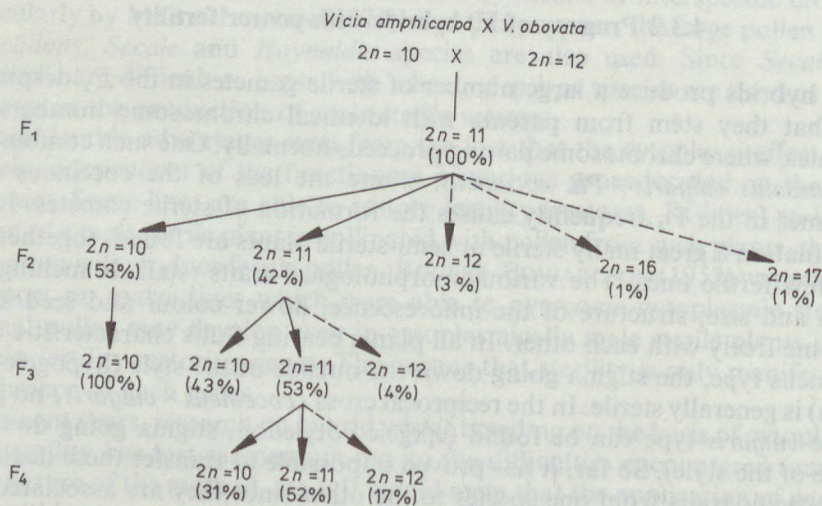


Fig. 38. Chromosome numbers in the F_1 and later generations of a cross between *Vicia amphicarpa* and *V. obovata* (METTIN, 1962)

univalent chromosomes, will contain $2x + (0...2y)$ chromosomes in the F_2 after self-fertilisation (OEHLER, 1956). SAPEHIN (1930), KIHARA-MATSUMURA (1940), etc. made detailed studies on the cytology of pentaploid *Triticum* hybrids. In theory the triploid interspecific hybrids of the *Triticinae* (KIHARA, 1940; BELEA, 1976) and interspecific hybrids of *Avena* (NISHIYAMA, 1934), *Allium* (LEVAN, 1936) and *Petunia* (LEVAN, 1937) behave similarly.

The chromosome number of pentaploid *Triticum* species hybrids is $2n = 35$, in which case the AABBDD genomes consist of either ABD from the male and AB from the female parent, or the reciprocal case. If sufficient plants are available, as in the case of ssp. *carthlicum* ($n = 14$; genomes AB) $\times$ *T. aestivum* ($n = 21$; genomes ABD) or ssp. *spelta* ($n = 21$; genomes ABD) $\times$ ssp. *dicoccum* ($n = 14$; genomes AB), extremely varied plants with chromosome numbers of $2n = 28-42$ arise from the zygotes. Their frequency follows a random distribution curve (KIHARA, 1924).

If pollination is carried out with a plentiful supply of pollen, strong competition arises between pollen grains with different chromosome numbers. In wheat, not only gametes with 14 or 21 chromosomes, but also those with 18 or 20 chromosomes have an advantage over the others. Due to the elimination of the univalents, two peaks can be observed on the curve of chromosome number distribution in the F_2 . What is more, when ovules with a lower chromosome number are fertilised by pollen with a higher chromosome number, the development of the endosperm is deficient and there will be a reduction in the viability of the developing seeds.

The progeny plants will be fertile or sterile depending on the chromosome combinations. Among the fertile combinations, plants with more or less than $2n = 35$ chromosomes can be distinguished. The first group contains plants with $2n = 28-34$ chromosomes, which possess all the chromosomes of the A and B genomes and 1-7 of the chromosomes from genome D. After a few generations the univalent chromosomes of the D genome are eliminated. The members of the second group have $2n = 36-42$ chromosomes. In addition to all the chromosomes of genomes A and B, they contain one complete D genome and 1-7 chromosomes from a second D genome. In later generations the duplicated D genome may arise again, since in each plant, as the result of gamete selection and zygote elimination, only fertile combinations arise with the same or a higher number of chromosomes. The plants of sterile chromosome combinations are weakly fertile or completely sterile. Plants with a low number of chromosomes only contain 1-3 pairs of chromosomes from genome D, while those with higher chromosome numbers lack some of the second set of D chromosomes (Table 52).

Among the plants with low chromosome numbers, fertility increases as the number of univalents drops; in the same way, individuals with a larger number of chromosomes show an improvement in fertility as the number of bivalents increases. Plants with $2n = 42$ chromosomes are just as fertile as the hexaploid parent, while those with $2n = 28$ chromosomes have somewhat weaker fertility than the tetraploid parent. The lowest fertility was observed for aneuploid

Table 52.

Chromosome pairing in the F_2 generations of pentaploid *Triticum* hybrids in plants with various chromosome numbers

Chromosome number		Chromosome pairing in fertile combinations	Chromosome pairing in sterile combinations		
F ₁	F ₂	I	II	III	IV
35	28	14 ^{II}			
	29	14 ^{II} + 1 ^I			
	30	14 ^{II} + 2 ^I	15 ^{II}		
	31	14 ^{II} + 3 ^I	15 ^{II} + 1 ^I		
	32	14 ^{II} + 4 ^I	15 ^{II} + 2 ^I	16 ^{II}	
	33	14 ^{II} + 5 ^I	15 ^{II} + 3 ^I	16 ^{II} + 1 ^I	
	34	14 ^{II} + 6 ^I	15 ^{II} + 4 ^I	16 ^{II} + 2 ^I	17 ^{II}
	35	14 ^{II} + 7 ^I	15 ^{II} + 5 ^I	16 ^{II} + 3 ^I	17 ^{II} + 1 ^I
	36	15 ^{II} + 6 ^I	16 ^{II} + 4 ^I	17 ^{II} + 2 ^I	18 ^{II}
	37	16 ^{II} + 5 ^I	17 ^{II} + 3 ^I	18 ^{II} + 1 ^I	
	38	17 ^{II} + 4 ^I	18 ^{II} + 2 ^I	19 ^{II}	
	39	18 ^{II} + 3 ^I	19 ^{II} + 1 ^I		
	40	19 ^{II} + 2 ^I	20 ^{II}		
	41	20 ^{II} + 1 ^I			
	42	21 ^{II}			

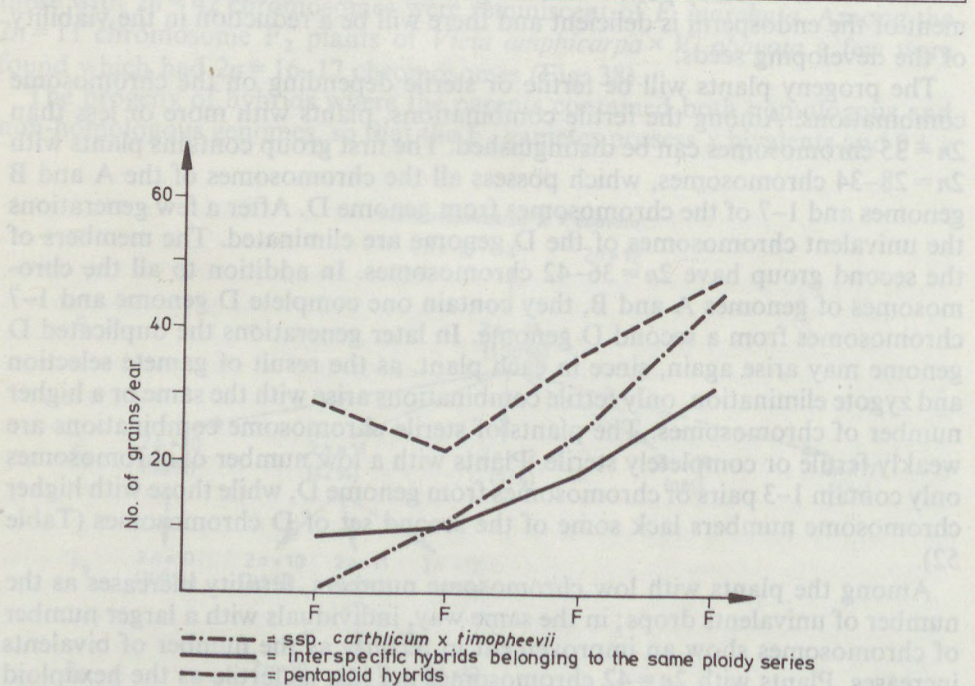


Fig. 39. Mean fertility of interspecific wheat hybrids belonging to the same or different polyploidy levels (BELEA, 1976)

plants with a chromosome number of $2n=33$. In the majority of cases, although the embryo sac is capable of development, only part of it is fertilised: this explains the temporary drop in fertility experienced in the F_2 (Fig. 39). Within the same level of polyploidy, however, even in the combination ssp. *carthlicum* ($2n=28$; genomes AB) $\times$ *T. timopheevii* ($2n=28$; genomes AG), where the genomes are not identical, BELEA (1976) found an increase in the number of grains per ear.

Due to the chromosome segregation outlined above, the progeny generations are completely fertile. They consist of plants with chromosome numbers concurring with those of the parents and are cytologically and genetically constant. In general, due to the urge to regain the euploid state, constant aneuploid plants can only be observed if, in place of the missing chromosomes, the plants contain other chromosomes capable of pairing.

Among the progeny of pentaploid *Triticum* hybrids, dwarf plants with weak fertility and a chromosome number of $2n=40$ were also observed; these form 20^{II} . One chromosome pair from the D genome is missing from these plants (nullisome). In later generations of these plants, individuals were found which had normal growth, full fertility and a chromosome number of $2n=42$. In the course of chromosome pairing the formation of $19^{II} + 1^{IV}$ was observed. According to SEARS (1944), chromosome 2D can be substituted by 2B. Plants which contain nulli-2D-tetra-2B chromosomes (i.e. 2B is present four times) are viable and fertile, despite the fact that the two chromosomes are not homologous. With regard to both chromosomes the monosomic plants form $20^{II} + 2^I$.

The hairiness or downiness of the nodes and glumes and the length and colour of the glumes have a segregation ratio of 3 : 1. Plants with a chromosome number of $2n=28$ resemble the parent with the lower chromosome number with respect to ear type, ear density and the pith content of the straw (*durum* type: closely packed ear, pithy straw), while plants with $2n=42$ chromosomes are of the *aestivum* type (loosely packed ear, hollow straw). In the group with higher chromosome numbers the *aestivum* type is more frequent and there is a drop in the number of plants exhibiting *durum* traits, while in the group containing fewer chromosomes the number of *durum* types rises.

It often happens that plants which have the same chromosome number as one of the parents do not all resemble the parent in question. This can be attributed to the fact that, in the course of cell division, certain homologous chromosomes or chromosome sections of genomes A and B have changed places. Plants with $2n=28$ chromosomes may be of the *aestivum* type, while $2n=42$ plants may bear *durum* traits. If the genotype of *durum* is $A_dA_dB_dB_d$ and that of *aestivum* is $A_aA_aB_aB_aDD$, many mixed types: $A_aA_aB_aB_a$ and $A_dA_dB_dB_dDD$, will also appear.

In the F_3 generation of *T. turgidum* conv. *polonicum* $\times$ *T. aestivum*, too, fertility is inherited together with certain morphological traits. For the sum total of the genotypes the fertile: sterile ratio was 287 : 93, which is approximately equal to the 3 : 1 Mendelian segregation. A considerable proportion (38.6%) of the sterile plants in this combination were intermediate, or had a glume shape

Table 53.

Fertility of the F₂ and F₃ generations of interspecific *Triticum* L. hybrids

Combination	F ₂					F ₃				
	Plant no.	Grains/plant	Grains/ear			Plant no.	Grains/plant	Grains/ear		
			$\bar{x}$	s	s $\bar{x}$			$\bar{x}$	s	s $\bar{x}$
<i>ssp. carthlicum</i> × <i>T. monococcum</i>	8	7.4	0.06	0.0	0.0	—	—	—	—	—
<i>T. timopheevii</i> × <i>ssp. carthlicum</i>	99	40.1	11.9	0.1	0.0	38	73.1	24.4	9.2	4.1
reciprocal	15	37.2	10.9	9.9	3.1	34	42.2	7.4	9.8	4.2
<i>T. timopheevii</i> × <i>ssp. dicoccum</i>	97	12.6	2.1	3.6	0.2	60	68.5	8.7	5.7	0.6
conv. <i>durum</i> × <i>T. timopheevii</i>	36	14.1	2.4	3.7	0.4	60	79.4	16.9	6.1	1.2
<i>ssp. carthlicum</i> × <i>ssp. dicoccum</i>	62	126.1	26.4	13.2	1.7	110	102.7	37.9	9.9	2.5
<i>T. aestivum</i> × <i>ssp. dicoccum</i>	95	70.1	16.7	7.4	2.5	19	190.5	23.3	9.6	2.5
reciprocal ('B 1201')	17	121.2	7.3	5.5	2.1	26	29.7	7.6	7.4	0.6
reciprocal ('Fortunato')	12	116.4	25.1	15.2	2.4	18	85.4	41.6	8.9	2.8
<i>T. aestivum</i> × conv. <i>durum</i>	95	112.3	30.5	8.1	2.7	—	—	—	—	—
<i>T. aestivum</i> × <i>ssp. carthlicum</i>	110	224.6	12.7	2.1	1.1	140	267.1	30.1	9.8	2.1
reciprocal	48	135.7	16.7	9.7	1.2	82	135.8	27.8	9.7	3.2
<i>T. aestivum</i> × <i>T. turgidum</i>	53	542.3	36.1	15.4	1.1	94	781.9	57.8	9.6	3.2
reciprocal	76	297.4	22.3	9.7	2.1	84	270.1	46.7	8.9	2.6
<i>ssp. spelta</i> × <i>ssp. carthlicum</i>	61	341.8	31.3	11.4	2.4	72	236.4	39.4	5.9	2.0
average for pentaploid hybrids			22.0					34.3		

and spikelet arrangement similar to that of conv. *polonicum* (45.6%). Only 18.2% belonged to the *T. aestivum* type, while a small proportion belonged to the *ssp. spelta* (2.5%), *ssp. dicoccum* (3.9%) and *T. timopheevii* (1.3%) types (BELEA, 1976).

There are wide variations in fertility between the hybrid plants of the F₁, and even more so in the F₂ and F₃. An analysis of fertility in the F₁–F₃ hybrids of the combination *ssp. carthlicum* × *T. timopheevii*, for example, indicates that in the first generation the fertility of the plants in terms of number of grains per ear ranged from 0 to 7.4, while in the F₂ this value was 0.3–3. In the third generation individuals producing as many as 37 grains per ear could be found (Table 53).

In the F₂ of *Nicotiana tabacum* (2n=48) × *N. sylvestris* (2n=24), similarly to the *Triticum* hybrids, plants with 2n=24–48 chromosomes were found. Plants

with $2n=24-25$ chromosomes resembled the *N. sylvestris* parent, those with around $2n=40$ were intermediate, while those with $2n=46-48$ chromosomes resembled *N. tabacum*. The parental types were fertile, while the intermediates were sterile. In the interspecific cross *N. paniculata* ($2n=24$) $\times$ *N. rustica* ($2n=48$) a very large number of combinations are possible as regards the morphological traits of the parent with the higher chromosome number (*N. rustica*). As the result of gamete and zygote elimination, there is a great likelihood of asymmetric distribution. The only cells capable of functioning are those which are entirely parental types or which contain a preponderance of *N. rustica* chromosomes and very few from *N. paniculata*. Those cells which are unable to function contain few chromosomes from *N. rustica* and a great many from *N. paniculata*.

Considering the potential of hybridisation to alter the genetic composition of populations, it is important to recognise the relative paucity of recombination products from species crosses. ANDERSON (1939) demonstrated that in crosses between *Nicotiana langsdorfii* and *N. alata* the hindrance to recombination was attributed to gametic elimination, zygotic elimination, pleiotropism and linkage. The restrictive effect of linkage on recombination was found to be severe. However, the tight coherences present in F_2 and F_3 *Nicotiana* hybrids may be broken to release variation in later generations, as shown in crosses between *N. langsdorfii* and *N. sanderae* and in interracial hybrids within *Potentilla*, *Madia*, *Antirrhinum*, etc.

The restricted recombination in species crosses is also expressed in the large proportion of subvital and inviable segregates in the F_2 population. STEPHENS (1979) found that the viable fraction of the F_2 hybrids of *Gossypium hirsutum* $\times$ *G. barbadense* consisted primarily of plants resembling the parental species or the F_1 hybrid. In several other plant genera (*Lycopersicum*, *Tragopogon*, *Phaseolus*, *Rubus*, etc.) the frequency distributions of the phenotypes in the F_2 and later generations are shifted towards a parental type.

4.3.3 Progeny generations of back- and top-crosses

4.3.3.1 Back-crossing to the parents

The back-crossing method elaborated by BRIGGS-ALLARD (1953) and RUDORF (1956) for use in variety crosses can also be generally applied in interspecific and intergeneric crossing. With the exception of somatic hybridisation and polyploidisation, which will be discussed later, this is the only way in which hybrid grains can be obtained and progeny raised from sterile F_1 hybrids. The method is also used in cytogenetics for the production of aneuploids.

In many cases back-crossing can be successfully carried out to both parents, as in the case of *Nicotiana* species. In other cases back-crossing is more success-

Table 54.

Effect of repeated back-crossing (BC) on the fertility of interspecific *Triticum* hybrids

Combination	Plant no.	Grains/ plant	Grains/ ear	Grains/ spikelet
			mean	
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × ssp. <i>dicoccum</i> BC ₁ ^{1*}	10		21.6	1.3
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × ssp. <i>dicoccum</i> BC ₁ ²	16		27.6	1.4
<i>T. aestivum</i> (F481) × ssp. <i>dicoccum</i> ('Vernal') F ₁	130	420.5	24.6	1.3
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × <i>T. aestivum</i> BC ₁ ¹	81		16.3	0.9
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × <i>T. aestivum</i> BC ₂ ¹	230		33.3	2.1
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × <i>T. aestivum</i>				
Mean for the same cultivars BC ₁ ²	123	313.0	25.1	1.9
(<i>T. aestivum</i> × ssp. <i>dicoccum</i>) × <i>T. aestivum</i>				
Mean for different cultivars BC ₁ ²	260	683.0	31.1	2.0
(<i>T. aestivum</i> × <i>T. turgidum</i>) × <i>T. aestivum</i> BC ₂ ¹	209		47.7	2.8
<i>T. aestivum</i> × <i>T. turgidum</i> F ₁	27	603.0	33.5	1.4
(<i>T. aestivum</i> × ssp. <i>carthlicum</i>) × <i>T. aestivum</i> BC ₁ ¹	23	197.0	20.7	1.2
(<i>T. aestivum</i> × ssp. <i>carthlicum</i>) × <i>T. aestivum</i> BC ₁ ²	32	96.0	22.0	1.3
(<i>T. aestivum</i> × ssp. <i>carthlicum</i>) × <i>T. aestivum</i> BC ₁ ³	69	114.2	24.6	1.4
(<i>T. aestivum</i> × ssp. <i>carthlicum</i>) × <i>T. aestivum</i> BC ₂ ¹	38	180.7	34.6	1.9
(<i>T. aestivum</i> × ssp. <i>carthlicum</i>) × <i>T. aestivum</i> BC ₂ ²	29	185.7	39.1	2.2
<i>T. aestivum</i> × ssp. <i>carthlicum</i> F ₁	25	469.0	29.4	1.3

* upper index: number of back-crosses (BC)

lower index: number of generations (F)

ful to one crossing partner (*Triticum* × *Secale* × *Triticum*) than to the other (*Triticum* × *Secale* × *Secale*). It also happens quite frequently that hybrid seeds are only obtained in back-crosses to one of the parents, as in the case of *Raphanus* × *Brassica*, where only back-crosses to *Raphanus* produce satisfactory results, no hybrid seed being obtained in back-crosses to *Brassica* (KARPECHENKO, 1928). The success of crossing depends primarily on the quantity of F₁ ovules capable of development. If embryo sacs with different chromosome numbers are all viable, the F₂ segregates into types which differ cytologically and morphologically, the plants being intermediate between the F₁ and the parental species used in back-crossing.

When studying fertility relations, BELEA (1964) observed a temporary reduction in fertility in back-crosses of the first generation of *T. aestivum* × *T. turgidum* ssp. *carthlicum* to both parents. There was a considerable rise in fertility in the F₂, when an average 30.0 grains per ear were obtained in the second back-cross to common wheat (Table 54).

When *T. aestivum* × *T. turgidum* was back-crossed to various cultivars of *T. aestivum*, individuals with high productivity could be selected even in BC¹ (43.9 grains per ear on average). In several combinations the temporary reduction in fertility occurring as the result of the first back-cross was counteracted by a rise in the thousand grain mass. In the BC¹ of (*T. aestivum* × ssp. *dicoc-*

cum) $\times$ *T. aestivum*, for example, the number of grains per ear was 16.3 and the thousand grain mass 47.2 g, compared to 24.6 grains/ear and a grain mass of 42.0 g in the direct cross. Naturally, cases were also observed where both yield components rose in the early generations of certain combinations as the result of selection.

In the BC_2^{1*} of (*Triticum* $\times$ *Secale*) $\times$ *Triticum* the plants are morphologically intermediate between the first generation and *Triticum*, while there are no plants which resemble rye. The reverse is true in the combination (*Triticum* $\times$ *Secale*) $\times$ *Secale*, where the plants resemble the F_1 and rye, and no wheat types can be found. If the F_1 plant is fertile, the plants of the F_2 population can already be grouped, in the case of cereals, for example, on the basis of ear type, awnedness, glume colour, rachis fragility, straw length, etc., and these plants can be included in further experiments in bulk. In the latter combination the $2n=28$ chromosome plants of the progeny possess 2 wheat and 2 rye genomes, while the 28-chromosome progeny of (*Triticum* $\times$ *Secale*) $\times$ *Triticum* have 4 wheat genomes (LEBEDEFF, 1932). Plants with $2n=49$ chromosomes contain 42 wheat and 7 rye chromosomes ($21^{II} + 7^I$). In the later generations the rye chromosomes are eliminated. OHLENDORF (1957) obtained balanced, constant individuals in the combination (*Triticum aestivum* $\times$ *Agropyron intermedium*) $\times$ *T. aestivum*, where the $2n=56$ chromosomes consisted of 42 wheat and 14 *Agropyron* chromosomes.

In the BC_2^1 of (*Aegilops ovata* $\times$ *T. aestivum*) $\times$ *T. aestivum*, too, the plants are intermediate morphologically between the first generation and *T. aestivum*. In the reciprocal cross, however, the progeny bore more resemblance to the *Aegilops* parent.

Balanced, constant plants with a chromosome number of $2n=48$, forming $12^{III} + 12^I$, are also found in the BC_2^1 of (*Nicotiana tabacum* $\times$ *N. rusbyi*) $\times$ *N. rusbyi*. In the BC_2^1 of (*N. rustica* $\times$ *N. paniculata*) $\times$ *N. rustica* some of the hybrid plants contained $2n = 38-48$ chromosomes, while the viable ovum contained 14-24 chromosomes.

The $2n=27$ chromosome plants of (*Raphanus sativus* $\times$ *Brassica oleracea*) $\times$ *Raphanus sativus* have 9^{II} (*Raphanus*) + 9^I (*Brassica*). The *Brassica* chromosomes are rapidly eliminated, since only plants with 9R and few B gametes are viable, while those with a large number of *Brassica* chromosomes die off (KARPECHENKO, 1928).

In back-cross progeny of *Gossypium hirsutum* $\times$ (*G. hirsutum* $\times$ *G. barbadense*), STEPHENS (1979) found significant elimination of the donor germ-plasm through both male and female gametes. Selective elimination can be detected by the significant distortion of specific monofactorial segregations and also by the cumulative tendency for the recurrent parent genotype to be recovered more rapidly than expected as a result of random segregation and

* the lower index indicates the number of generations and the upper index the number of back-crosses

recombination. Stephens stated that of four loci which showed selective elimination, two were suspected on independent grounds of being carried on structurally differentiated chromosomes.

RICK (1963) reported that back-crosses of the F_1 hybrid of *Lycopersicum esculentum* $\times$ *L. chilense* to *L. esculentum* contained an excess of *L. esculentum* markers, while back-crosses to *L. chilense* were deficient in such markers. The back-crossing of maize $\times$ *Tripsacum* hybrids to maize is accompanied by the rapid elimination of maize genomes contaminated through crossing-over with *Tripsacum* (MANGELSDORF, 1951), although there is evidence that inbred lines of maize may be modified and improved by the receipt of certain *Tripsacum* genes. Back-crosses of *Phaseolus vulgaris* $\times$ *P. coccinea* F_1 s to both parents show a highly significant deviation from the expected 1 : 1 ratio when the donor allele is transmitted through the pollen but not through the ovum. RICK (1969) obtained hybrids between *Solanum pennellii* and *Lycopersicum esculentum* that were successively back-crossed to the latter, but the monogenic ratios departed from 1 : 1, the deficiency of *esculentum* alleles (the recurrent parent) being the most frequent. This trend is contrary to the majority of observations in species hybrids, as exemplified in back-crosses of F_1 *Gossypium barbadense* $\times$ *G. hirsutum* (STEPHENS, 1979).

As the result of back-crosses to the parents in generations later than F_2 , plants with the same chromosome numbers as the parents are obtained. Very frequently, however, these plants differ in nature from the parents. The crossing over of chromosome sections can be expected if the species crossed contain homologous (or homoeologous) genomes. If, however, the parent species do not contain homologous or homoeologous genomes, only plants of purely parental type appear in the progeny generations. If one or both of the parents are polyploid, cytologically balanced forms may appear in the progeny, which do not contain all the genomes of the parents. In the combinations $(ABD \times R) \times ABD$ or $(ABD \times R) \times R$, in addition to the AABBDD and RR parental types, the types AABRRR, AADRRR, BBDDRR, AARR, BBRR, DDRR, AABB, AA, BB and DD may also theoretically appear, giving plants which are balanced, fertile and constant as regards their genomes.

4.3.3.2 Repeated back-crossing

Pollen-sterile interspecific hybrids can be back-crossed to one of the parents in several successive generations. If the back-cross is carried out to the species used as female parent in the original cross, e.g. $(A \times B) \times A \times A$, etc., after a few generations the plants will contain exclusively female genomes, while the male chromosomes are lost. If the genomes of the parents are homologous or homoeologous, types bearing characters derived from both parents will be found in the population due to chromosome exchange (*Nicotiana*, *Triticum*). If there is no homology between the parental genomes, only pure female forms will arise. If back-crossing is carried out to the species originally used as the male parent,

Table 55.

Effect of repeated back-crossing and of selection in various generations on the fertility of the combination (*T. aestivum* × *T. turgidum*) × *T. aestivum*

Repeated back-crossing	Generation			Average
	F ₁	F ₂	F ₃	
BC ¹	21.6	39.6	47.4	36.2
BC ²	42.2	49.6	59.0	50.2
BC ³	40.4	41.7	54.6	45.6
Average	34.7	46.9	53.7	

Table 56.

Effect of top-crossing with a third species and of selection in various generations on the fertility of the combination (*T. turgidum* × conv. *durum*) × *T. aestivum*

Repeated back-crossing after top-crossing	Generation				Average
	F ₁	F ₂	F ₃	F ₄	
BC ¹	26.5	43.7	49.5	57.2	44.2
BC ²	21.3	46.3	68.0	65.3	50.2
BC ³	26.0	40.6	65.5	—	44.0
Average	24.6	43.5	61.0	61.2	

e.g. (A × B) × B × B, etc., the progeny will contain only male genomes; these genomes, however, are situated within the female cytoplasm, which means that the cell nucleus of one species can be transferred to the cytoplasm of another species.

When the *Aegilops caudata* × *Triticum aestivum* combination is repeatedly back-crossed to wheat, plants resembling wheat are obtained, with gametes containing $n=21$ chromosomes, but in a cytoplasm stemming from *Aegilops caudata*. These plants show some differences in morphology, e.g. the ears are erect, as in *Aegilops caudata*, and have black glumes.

If triticale (wheat × rye allopolyploid) is repeatedly back-crossed to rye, the progeny are reminiscent of rye and contain rye chromosomes in a wheat cytoplasm. This alloplasmic rye differs in many respects from the original rye.

In certain combinations, selection for ear productivity causes a greater increase in fertility than repeated back-crossing. This is confirmed by the data in Table 55, where the fertility in the combination (*T. aestivum* × *T. turgidum*) × *T. aestivum* exhibits linear growth in the F₂ and later generations compared to the first generation. This consistent increase in productivity is far from certain to occur as the result of repeated back-crosses. The BC₃² hybrids were the most fertile. A similar situation was observed in triple hybrids of (*T. turgidum* × conv. *durum*) × *T. aestivum* (Fig. 40), where productivity was particularly good in generation BC₃² and BC₃³ (Table 56).

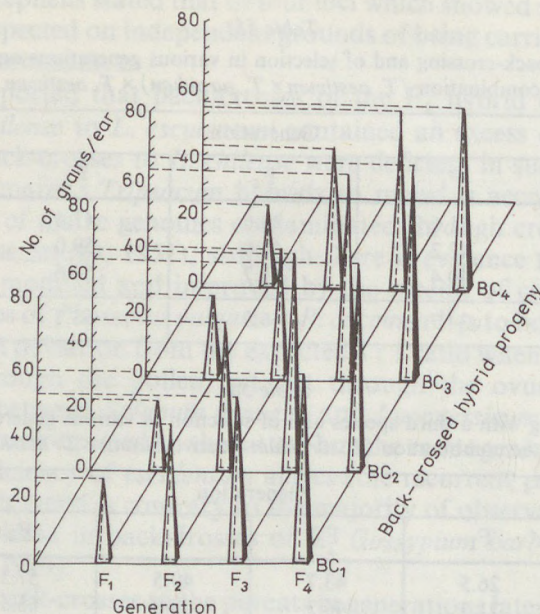


Fig. 40. Effect of repeated back-crossing (BC) and selection in various generations on the fertility of the (*T. turgidum* × conv. *durum*) × *T. aestivum* combination (BELEA, 1976)

4.3.3.3 Top-crossing with a third species

Top-crossing with a third species also plays an important role in the restoration of fertility. Examples of this are (*Triticum turgidum* × *Secale cereale*) × *T. aestivum* (NAKAJIMA, 1951), (*Aegilops ovata* × ssp. *carthlicum*) × *Triticum aestivum* (BELEA, 1976), (*Nicotiana tabacum* × *N. rusbyi*) × *N. silvestris* (BEISSER, 1934), etc. This possibility is of particular significance in cases where the cross can only be carried out with great difficulty, if at all, without the use of an intermediary variety, e.g. *Aegilops umbellulata* × ssp. *dicoccum* × *T. aestivum* (SEARS, 1956b), *Gossypium hirsutum* × *G. herbaceum* × *G. harknessii* (BROWN-MENZEL, 1950), *Triticum turgidum* × *Secale cereale* × *Agropyron elongatum* (KISS, verbal communication), *Raphanus sativus* × *Brassica oleracea* × *B. carinata* (KARPECHENKO, 1929), *Triticum monococcum* × ssp. *carthlicum* × *T. aestivum* (BELEA, 1976), etc. In this way, triple hybrids provide a relatively easy technique for uniting in a single plant genomes from parent species which cannot be crossed directly.

If the species used in top-crossing possesses genomes which are homologous with those of one of the parents, well-balanced forms may appear, as in back-crossing, e.g. *T. turgidum* × conv. *durum* × *T. aestivum*. The number of genetically constant types obviously varies depending on the different gene complements of the species.

A cytologically unbalanced hybrid generation will be obtained if the species used for top-crossing not only has non-homologous genomes, but also a different chromosome number. Examples of this are when the combinations *T. timopheevii* ($n=14$; genomes AG) $\times$ *ssp. carthlicum* ($n=14$; genomes AB) and *T. turgidum* ($n=14$; genomes AB) $\times$ *T. timopheevii* ($n=14$; genomes AG) are top-crossed with *T. aestivum* ($n=21$; genomes ABD). In triple hybrids of *Aegilops caudata* ($n=7$; genome C) $\times$ *ssp. dicoccum* ($n=14$; genomes AB) $\times$ *T. aestivum* ($n=21$; genomes ABD), the D genome does not pair with the C genome, so the chromosomes of both remain as univalents. In theory it is possible for balanced combinations to come about through the incorporation of new genomes. In addition to the parental types, AABB, AABBDD and CC, plants with the genomes AABBCC, AACC, BBCC and DDCC may also appear. Completely fertile euploid plants can easily be obtained if repeated back-crossing is carried out to the species used in top-crossing.

As in the case of back-crossing, a temporary reduction in the fertility of the F_1 hybrids was observed by BELEA (1965) after the first top-cross with a third species, but the fertility rose perceptibly as the result of BC^2 . In interspecific crosses of wheat, the number of grains per ear in these generations equalled or surpassed the fertility of hybrids originating from direct crosses in the majority of combinations (Table 57).

The hybrid of (*Triticum turgidum* $\times$ *Secale cereale*) $\times$ *Agropyron elongatum* was a completely sterile perennial plant. It tillered strongly and produced 80–100 ears each year, but the flowers set no seed. The triple hybrids died off in 1964 after a period of 8 years (Kiss, verbal communication).

Table 57.

Effect of top-crossing with a third species on the fertility of interspecific *Triticum* L. hybrids

Combination	Plant no.	Grains/ plant	Grains/ ear	Grains/ spikelet
			mean	
(<i>T. aestivum</i> $\times$ <i>ssp. dicoccum</i>) $\times$ <i>conv. durum</i> F_1	11		15.9	1.0
(<i>T. aestivum</i> $\times$ <i>ssp. dicoccum</i>) $\times$ <i>conv. durum</i> BC_1^2	15		28.2	1.8
(<i>T. aestivum</i> $\times$ <i>ssp. dicoccum</i>) $\times$ <i>ssp. carthlicum</i> F_1	10		16.7	1.2
(<i>T. aestivum</i> $\times$ <i>ssp. dicoccum</i>) $\times$ <i>ssp. carthlicum</i> BC_1^2	12		25.0	1.4
(<i>T. turgidum</i> $\times$ <i>conv. durum</i>) $\times$ <i>T. aestivum</i> F_1	17	256.1	26.5	1.5
(<i>T. turgidum</i> $\times$ <i>conv. durum</i>) $\times$ <i>T. aestivum</i> BC_1^2	186	223.7	21.3	1.2
(<i>T. turgidum</i> $\times$ <i>conv. durum</i>) $\times$ <i>T. aestivum</i> BC_1^3	38	247.7	26.0	1.4
(<i>T. turgidum</i> $\times$ <i>conv. durum</i>) $\times$ <i>T. aestivum</i> F_2	40		43.7	2.1
(<i>T. turgidum</i> $\times$ <i>conv. durum</i>) $\times$ <i>T. aestivum</i> BC_2^2	35		46.3	2.2
(<i>T. turgidum</i> $\times$ <i>conv. durum</i>) $\times$ <i>T. aestivum</i> BC_2^3	71		40.6	2.3
(<i>T. turgidum</i> $\times$ <i>conv. durum</i>) $\times$ <i>T. aestivum</i> F_3	34		49.5	2.7
(<i>T. turgidum</i> $\times$ <i>conv. durum</i>) $\times$ <i>T. aestivum</i> BC_2^3	27		68.0	3.2
(<i>T. turgidum</i> $\times$ <i>conv. durum</i>) $\times$ <i>T. aestivum</i> BC_3^3	37		65.5	3.3
(<i>T. turgidum</i> $\times$ <i>conv. durum</i>) $\times$ <i>T. aestivum</i> BC_4^2	77		61.2	3.1
(<i>T. turgidum</i> $\times$ <i>conv. durum</i>) $\times$ <i>T. aestivum</i> F_4	38		57.2	3.0

4.4 Somatic hybridisation between species

The technique of somatic cell fusion makes it possible to combine distant forms which cannot be crossed at present by sexual means. With protoplasts which have been deprived of their cell walls and are surrounded only by a membrane, it is far easier to isolate cell organelles, such as cell nuclei or chloroplasts, which thus facilitates cell fusion.

The thought that hybridisation might be possible not only through the merging of gametes, but also through the fusion of non-differentiated (somatic) cells, had already been raised by the beginning of the century.

The earliest attempt of this nature is attributed to Winkler (in DUDITS, 1982), who hoped to fuse the cells of *Lycopersicon esculentum* and *Solanum nigrum* by grafting shoots together. KÜSTER, (1909) based his suggestion that somatic cells could be hybridised on the fact that spontaneous fusion was observed between plant protoplasts. These efforts did not arouse a great deal of interest at the time, since they were unsuccessful, due to lack of a suitable method. Once the technique of fusion was perfected and knowledge of genetic laws broadened, work advanced at a rapid pace. The technique of protoplast fusion enables various animal or plant cells or protoplasts to be fused, the cell nuclei being united in a single cell. The fact that these are heterokaryons can be checked cytologically. If identical protoplasts are fused, homokaryons arise. In these multinuclear cells, cell division may take place in several ways. During the first cell division, mitosis may take place in only one of the parental cell nuclei; as the result of this asynchronous mitosis, the cell nucleus of the other parent becomes separated and is eventually lost. It may also happen that mitosis takes place in both cell nuclei of the heterokaryon, in which case synkaryons are produced. This happens only rarely. Most frequently the chromosomes of one of the plants are lost after fusion (soya – tobacco, horse beans – petunia, etc.).

Protoplast fusion widens the range of plant genera and species which can be hybridised and is thus of enormous importance in increasing genetic variability. New hybrid combinations possessing as yet unknown properties may be produced. Another great advantage of this method is the fact that colchicine treatment is not required to overcome the hybrid sterility arising during sexual crossing. Factors which obstruct fertilisation or inhibit the development of the endosperm can also be eliminated, as can factors inducing incompatibility, etc.

Using this method, not only the species of plant genera, but also mammal – plant, insect – plant, etc. protoplasts can be fused, since it has been proved that after fusion DNA synthesis is able to continue in the cell nuclei of both parents and the fused cells are capable of division (DUDITS, 1982).

To obtain efficient fusion it is necessary to work with a large number of viable protoplasts. Fusion is generally induced by incubation in a high concentration of polyethylene glycol (PEG), a high concentration of Ca^{2+} and a relatively high pH. This treatment is necessary to remove the negative charge on the protoplasts. Electrofusion has become popular in recent years. After somatic hybridisation the biggest problem is to select the somatic hybrids from the cell population.

Table 58.

Hybrids produced by protoplast fusion between plant species within a single genus

Combination	Author
<i>Daucus carota</i> × <i>D. capillifolius</i>	DUDITS et al., 1977
<i>Datura innoxia</i> × <i>D. candida</i>	SCHIEDER, 1978
<i>Datura innoxia</i> × <i>D. discolor</i>	SCHIEDER, 1978a
<i>Datura innoxia</i> × <i>D. sanguinea</i>	SCHIEDER, 1978
<i>Datura innoxia</i> × <i>D. stramonium</i>	SCHIEDER, 1978a
<i>Nicotiana glauca</i> × <i>N. langsdorffii</i>	CARLSON et al., 1972
<i>Nicotiana knightiana</i> × <i>N. sylvestris</i>	MALIGA et al., 1977
<i>Nicotiana tabacum</i> × <i>N. debneyi</i>	GLEBA-HOFFMANN 1979
<i>Nicotiana tabacum</i> × <i>N. glauca</i>	EVANS et al., 1980
<i>Nicotiana tabacum</i> × <i>N. knightiana</i>	MALIGA et al., 1978
<i>Nicotiana tabacum</i> × <i>N. nesophila</i>	EVANS et al., 1980
<i>Nicotiana tabacum</i> × <i>N. stocktonii</i>	EVANS et al., 1980
<i>Nicotiana tabacum</i> × <i>sylvestris</i>	MELCHERS, 1977
<i>Petunia hybrida</i> × <i>P. axillaris</i>	IZHAR-POWER, 1979
<i>Petunia hybrida</i> × <i>P. parodii</i>	POWER et al., 1976
<i>Petunia parodii</i> × <i>P. inflata</i>	POWER et al., 1979
<i>Petunia parodii</i> × <i>P. paryflora</i>	POWER et al., 1980
<i>Solanum nigrum</i> × <i>S. tuberosum</i>	BINDING et al., 1982

The first successful attempt at producing hybrid plants by means of protoplast fusion was reported by CARLSON et al. (1972). Later, numerous cases of somatic hybridisation became known, especially in the *Solanaceae* family (Table 58). The fact that somatic hybridisation has been successful between *Solanum tuberosum* and *Lycopersicon lycopersicum*, between *Brassica* and *Arabidopsis* and between *Daucus carota* and *Aegopodium podagria* shows that even inter-generic hybridisations are possible. This is of especial interest since these hybrids are impossible to obtain by sexual means (PIERIK, 1987). Somatic hybridisation is interesting from an agricultural point of view, especially for important crops where it is possible to regenerate complete functional plants from protoplasts. In general, after fusion the characters of both parents reach expression in the hybrids, so they give the impression of being intermediate types. In the case of somatic cell fusion, the female effect is not manifested, since the chloroplasts and mitochondria of both parents are included in the fused cell. It is also possible to produce fused cells without cell nuclei, containing only cytoplasmic genes. These are known as cybrids, and are of great significance in the transfer of cytoplasmic male sterility.

Cell hybridisation between genera which are only distantly related to each other leads to the formation of hybrid cell lines. After somatic cell fusion between soya and tobacco, KAO (1977) selected cell lines in which the presence of tobacco characters could be proved using cytological and isoenzymatic analyses even after several years, despite the fact that the tobacco chromosomes were lost. Cell lines of this type have also been produced for other genera (Table 59).

Table 59.

Hybrid cell lines produced by somatic protoplast fusion between species belonging to different genera

Combination	Author
I. Intergeneric somatic hybrid plants	
<i>Arabidopsis thaliana</i> × <i>Brassica campestris</i>	GLEBA-HOFFMANN, 1979
<i>Datura innoxia</i> × <i>Atropa belladonna</i>	KRUMBIEGEL-SCHIEDER, 1979
<i>Solanum tuberosum</i> × <i>Lycopersicon esculentum</i>	MELCHERS et al., 1978
<i>Nicotiana tabacum</i> × <i>Petunia hybrida</i>	HUANG et al., 1983
<i>Nicotiana tabacum</i> × <i>Hordeum vulgare</i>	SOMMERS et al. 1986
II. Intergeneric fusion products observed to undergo division but not plantlet regeneration	
<i>Glycine soja</i> × <i>Nicotiana glauca</i>	KAO, 1977
<i>Petunia hybrida</i> × <i>Vicia faba</i>	BINDING-NEHLS, 1978
<i>Atropa belladonna</i> × <i>Nicotiana chinensis</i>	GLEBA et al., 1982
<i>Daucus carota</i> × <i>Hordeum vulgare</i>	DUDITS et al., 1979
<i>Daucus carota</i> × <i>Petunia hybrida</i>	REINERT-GOSCH, 1976
<i>Glycine max</i> × <i>Brassica napus</i>	KARTHA et al., 1974
<i>Glycine max</i> × <i>Caragana arborescens</i>	CONSTABEL et al., 1975b
<i>Glycine max</i> × <i>Colchicum autumnale</i>	CONSTABEL et al., 1975
<i>Glycine max</i> × <i>Hordeum vulgare</i>	KAO and MICHAYLUK, 1974
<i>Glycine max</i> × <i>Melilotus</i> sp.	CONSTABEL et al., 1975
<i>Glycine max</i> × <i>Medicago sativa</i>	CONSTABEL et al., 1975
<i>Glycine max</i> × <i>Nicotiana glauca</i>	CONSTABEL et al., 1975
<i>Glycine max</i> × <i>Nicotiana langsdorffii</i>	CONSTABEL et al., 1975
<i>Glycine max</i> × <i>Nicotiana rustica</i>	CONSTABEL et al., 1975
<i>Glycine max</i> × <i>Nicotiana tabacum</i>	CONSTABEL et al., 1975
<i>Glycine max</i> × <i>Pisum sativum</i>	KAO-MICHAYLUK, 1974
<i>Glycine max</i> × <i>Vicia hajastana</i>	KAO-MICHAYLUK, 1974
<i>Glycine max</i> × <i>Zea mays</i>	KAO-MICHAYLUK, 1974
<i>Nicotiana tabacum</i> × <i>Hyoscyamus muticus</i>	POTRYKUS-HOFFMANN, 1973
<i>Brassica napus</i> × <i>Raphanus sativus</i>	GLIMELIUS et al., 1986
<i>Petunia hybrida</i> × <i>Parthenocissus tricuspidata</i>	POWER et al., 1976
<i>Petunia hybrida</i> × <i>Solanum nigrum</i>	BINDING-NEHLS, 1978
<i>Petunia hybrida</i> × <i>Vicia faba</i>	BINDING and NEHLS, 1978
<i>Vicia hajastana</i> × <i>Pisum sativum</i>	KAO-MICHAYLUK, 1974
<i>Citrus sinensis</i> × <i>Poncirus trifoliata</i>	GROSSER, 1988b
<i>Citrus sinensis</i> × <i>Severinia disticha</i>	GROSSER, 1988a
<i>Triticum monococcum</i> × <i>Penisetum americanum</i>	VASIL et al., 1988
<i>Saccharum officinarum</i> × <i>Pennisetum americanum</i>	TABAIZADEH et al., 1987
III. Hybrids which lose one of the parental genomes after somatic protoplast fusion	
<i>Daucus carota</i> × <i>Aegopodium podgraria</i>	DUDITS et al., 1979
<i>Daucus carota</i> × <i>Petroselinum</i>	DUDIST et al., 1980

Great advances have been made in this field of science since the first successful protoplast fusion was carried out. The possibility of producing cybrids was previously completely unknown, but now provides a way of transferring male sterility. This method also facilitated the protoplast fusion and breeding of potato and tomato (MELCHERS et al., 1978).

4.5 Changes in chromosome number

The constant chromosome number generally characteristic of the species may be changed by abnormalities occurring in the course of meiotic or mitotic cell division. If the gametes arise without meiosis taking place, they will contain unreduced sets of chromosomes, resulting after fertilisation in polyploid cells consisting of three or four sets. If the chromosomes fail to migrate to the poles in the course of mitosis, the diploid cell will again give rise to a polyploid (tetraploid) cell.

The anomalous separation may be confined to a single chromosome. It may happen that during anaphase all the chromosomes split and are divided between the two poles with the exception of one which fail to separate. This chromosome may join one of the progeny cells or may be eliminated. In either case the chromosome number will be one greater or smaller (aneuploidy).

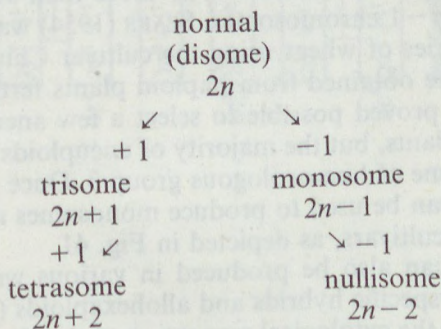
Aneuploidy and polyploidy cause changes not only in the chromosome number, but also in the number of genes, and this may make its effect felt in both the phenotype and in the course of heredity.

The full haploid chromosome set is designated by n . Euploids are tissues which contain balanced, complete sets of chromosomes, irrespective of the chromosome number. Aneuploids, on the other hand, are plants which have unbalanced chromosome numbers differing from those of the euploid organism.

4.5.1 Aneuploidy

In the cells of higher plants the diploid chromosome number generally comprises homologous male and female chromosomes. Thus, each chromosome is present twice (disome). If some of the chromosomes deviate from this general rule, it is a case of aneuploidy, as mentioned above.

If each cell contains 3 homologous chromosomes instead of two, the cell is a trisome; if it contains 4 chromosomes it is a tetrasome. If one of the homologous pair is missing, we speak of a monosome, while if both are lost, it is a nullisome:



In the case of nullisomes and tetrasomes it is important to note that the numerical deviation refers to the same homologous chromosome. If the chromosomes are designated by letters, the same letters referring to homologous chromosomes, the following cases can be distinguished:

AABBCCDD	normal disome
ABBCDD ($2n-2$)	not a nullisome, but a double (A, C) monosome
AABBDD ($2n-2$)	C-nullisome
AAABCCDD ($2n$)	B-monomosome, A-trisome

The chromosome set of double trisomic types ($2n+1+1$) contains three each of two non-homologous chromosomes.

In the majority of diploid plants, of all the possible types, only the normal (disome) type is viable. Viability decreases in the following order: disome – trisome – monosome – tetrasome – nullisome.

Among the aneuploids, trisomic organisms are formed most frequently. The first trisomic chromosome set was observed by Bridges and Morgan in the fruit fly *Drosophila melanogaster*. Later, in plants, BLAKESLEE–AVERY (1937) was the first to produce trisomes in *Datura stramonium*. All the 12 types obtained by this author contained 25 chromosomes and caused phenotypical changes in the yield. Since then, trisomic series have been produced for numerous crops of economic importance (wheat, maize, tomato, tobacco, etc.). These not only assist in locating individual genes, but can be used as initial stock in chromosome manipulations for breeding purposes.

If one of the chromosomes of a trisomic cell or organism is an isochromosome, it is referred to as a secondary trisome. By contrast to normal, or primary, trisomes, secondary trisomes contain certain genes in a quadruple dose, while others are only present twice. With the aid of secondary trisomes it is possible to locate genes on the various arms (isochromosomes) of the chromosome.

In the majority of monosomic diploid organisms, the lack of a single chromosome ($2n-1$) is lethal. In species of polyploid origin, such as wheat or tobacco, the loss of a single chromosome is less serious. In the course of meiosis, cell division takes place normally. Since the univalent chromosome migrates to neither pole, it is frequently eliminated, so more than 50% of the gametes of monosomes possess $n-1$ chromosomes. SEARS (1954) was the first to produce a full monosomic series of wheat using the cultivar Chinese Spring. The first monosomic lines were obtained from haploid plants fertilised with the pollen of normal plants. It proved possible to select a few aneuploid lines from the progeny of triploid plants, but the majority of aneuploids were produced using the asynaptic nullisome of homoeologous group 3. Once a monosomic variety has been formed, it can be used to produce monosomes and substitution lines in other species and cultivars, as depicted in Fig. 41.

Monosomic lines can also be produced in various ways with the help of intergeneric and interspecific hybrids and allohexaploids (Figs. 42, 43 and 44). Another possibility is the cytological separation of the chromosomes belonging

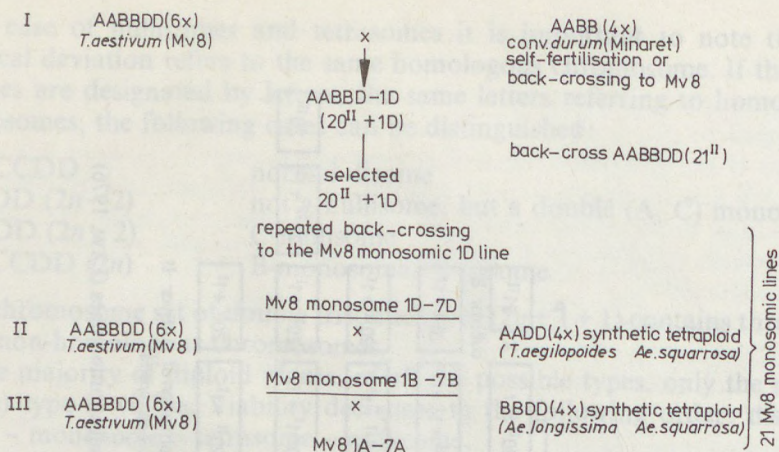


Fig. 42. Outline of the production of monosomic lines with the aid of intergeneric and interspecific hybrids and allohexaploids (SIDDIQUI, 1972)

to the G genome, say, of *T. timopheevii*, or of some other wheat species, after which the artificially produced allopolyploid ($n=21$; genomes AAG) of *T. timopheevii* ($n=14$; genomes AG) $\times$ *T. monococcum* ($n=7$; genome A) can be compared with the chromosomes of the naturally occurring species *T. zhukovskyi* (AAG) (Fig. 45). Likewise, the chromosomes belonging to the D genome of hexaploid wheat can be cytologically separated through the artificial allopolyploidisation of *Aegilops squarrosa* $\times$ *conv. durum* (Fig. 46).

The phenomenon of nullisomy is extremely rare; in this case a homologous pair of chromosomes is completely missing ($2n-2$). Nullisomes can usually be produced only from plant species of polyploid origin (bread wheat) through the

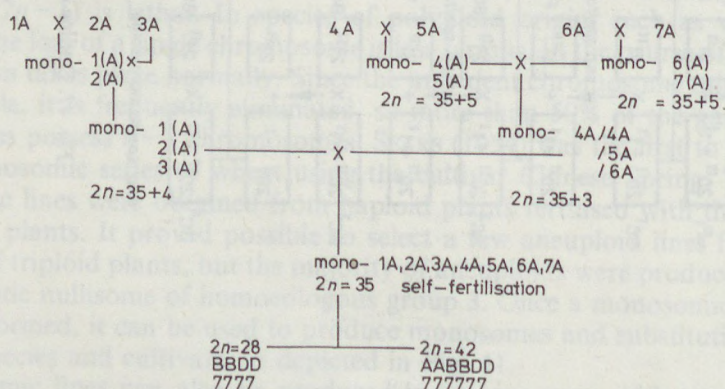


Fig. 43. Outline of the production of the tetraploid components of allohexaploid Triticum using the monosomic method (SIDDIQUI, 1972)

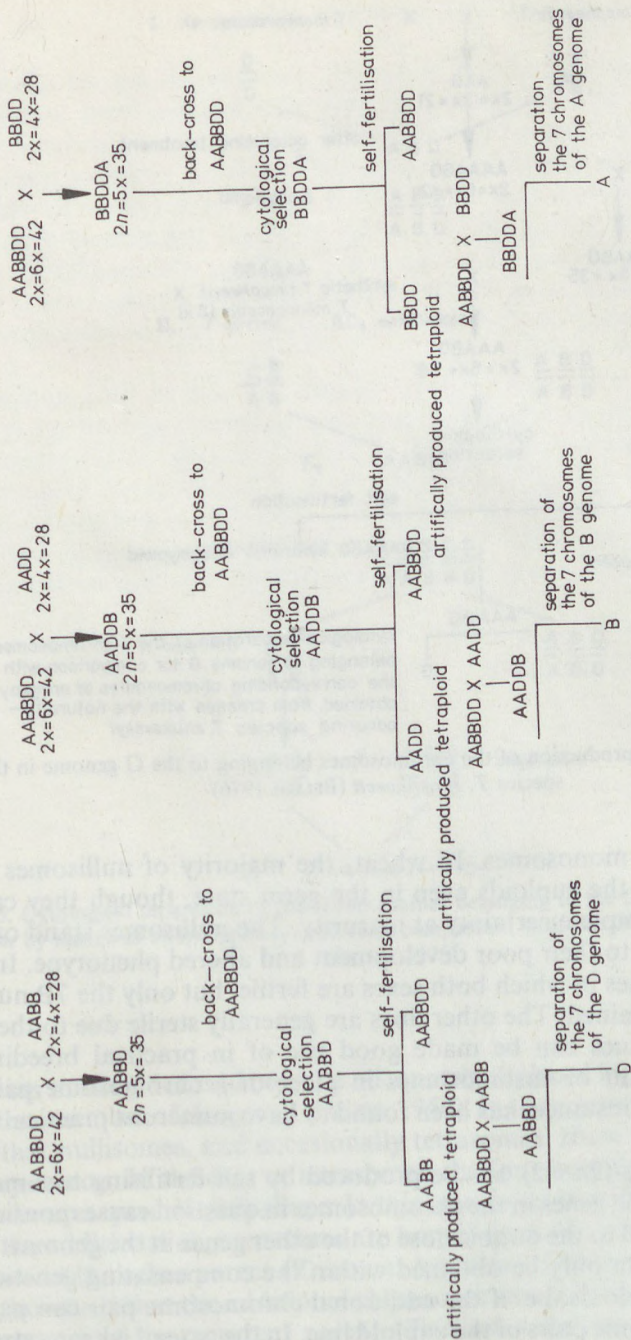


Fig. 44. Outline of the production of monosomic lines with the aid of intergeneric and interspecific hybrids and allohexaploids (Siddiqui, 1972)

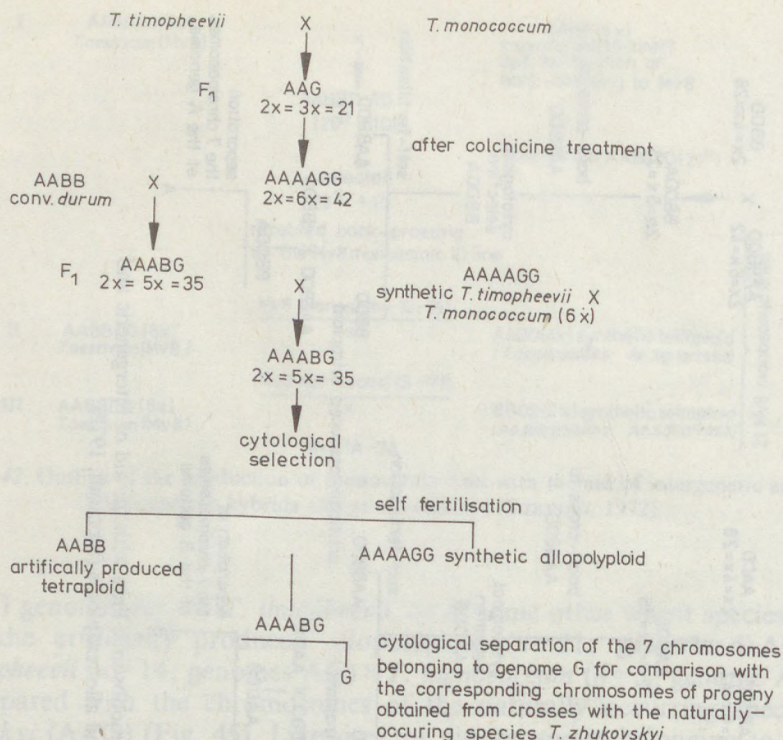


Fig. 45. Outline of the production of the chromosomes belonging to the G genome in the wheat species *T. timopheevii* (BELEA, 1976)

self-fertilisation of monosomes. In wheat, the majority of nullisomes can be distinguished from the euploids even in the germ state, though they can only be selected with complete certainty at maturity. The nullisomes stand out from the population due to their poor development and altered phenotype. In wheat there are 9 nullisomes in which both sexes are fertile, but only the 7B nullisome can be stably maintained. The other lines are generally sterile due to their poor viability. Certain lines can be made good use of in practical breeding: the substitution of a pair of chromosomes in place of a chromosome pair from another species, for instance, has been found to have numerous practical advantages (see below).

Tetrasomic plants ($2n+2$) can be produced by self-fertilising trisomes. The quadruple dose of the genes in the chromosomes in question causes considerable difficulties compared to the double dose of the other genes in the genome. Viable tetrasomic plants can only be obtained within the compensating genetic background of the polyploids, i.e. if the additional chromosome pair can pair with one of the chromosome pairs of the euploid line. In the case of wheat, tetrasomic plants can be used with great success in the identification of homoeologous chromosomes, since it was found that if one member of the homoeologous

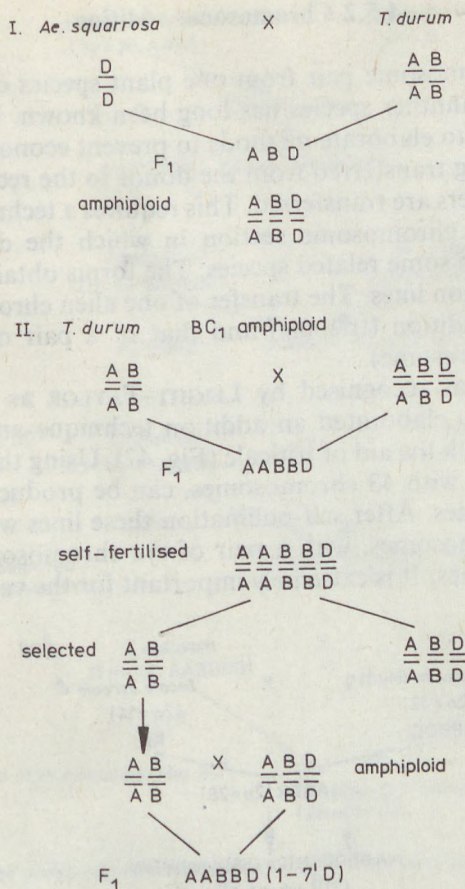


Fig. 46. Cytological separation of the chromosomes belonging to the D genome of *Aegilops squarrosa* by means of allopolyploidy, and their comparison with the D genome of *T. aestivum* (BELEA, 1976)

group was missing, it could be quite adequately replaced by the tetrasomic form of another member of the group (SEARS, 1954). In the course of meiosis it is often found that nullisomes, and occasionally tetrasomes, show no abnormality, for this very reason. In the case of tetrasomes, the four homologous chromosomes often take up a quadrivalent shape. In this case, it is a true instance of tetrasomy, where the additional chromosomes are homologues of the corresponding chromosomes in the other parent (*Triticum*, *Nicotiana*, *Gossypium*, etc.). It is often found, however, that the additional chromosomes are not homologous with the chromosomes of the recurrent parent (*Triticum* × *Agropyron*).

4.5.2 Chromosome addition

The fact that a chromosome pair from one plant species can be added to the chromosome set of another species has long been known. Plant breeders have always endeavoured to elaborate methods to prevent economically undesirable characters from being transferred from the donor to the recipient species when certain given characters are transferred. This requires a technique by which only the chromosome or chromosome section in which the desired character is located is added from some related species. The forms obtained in this way are known as alien addition lines. The transfer of one alien chromosome is referred to as monosomic addition (trisome) and that of a pair of chromosomes as disomic addition (tetrasome).

This possibility was recognised by LEIGHT-TAYLOR as long ago as 1927, while O'MARA (1938) elaborated an addition technique and added rye chromosomes to wheat with the aid of triticale (Fig. 47). Using this programme, two different plants, each with 43 chromosomes, can be produced, containing different rye chromosomes. After self-pollination these lines will give plants containing $2n=44$ chromosomes, with a pair of rye chromosomes in addition to the wheat chromosomes. It is extremely important for the various characters of

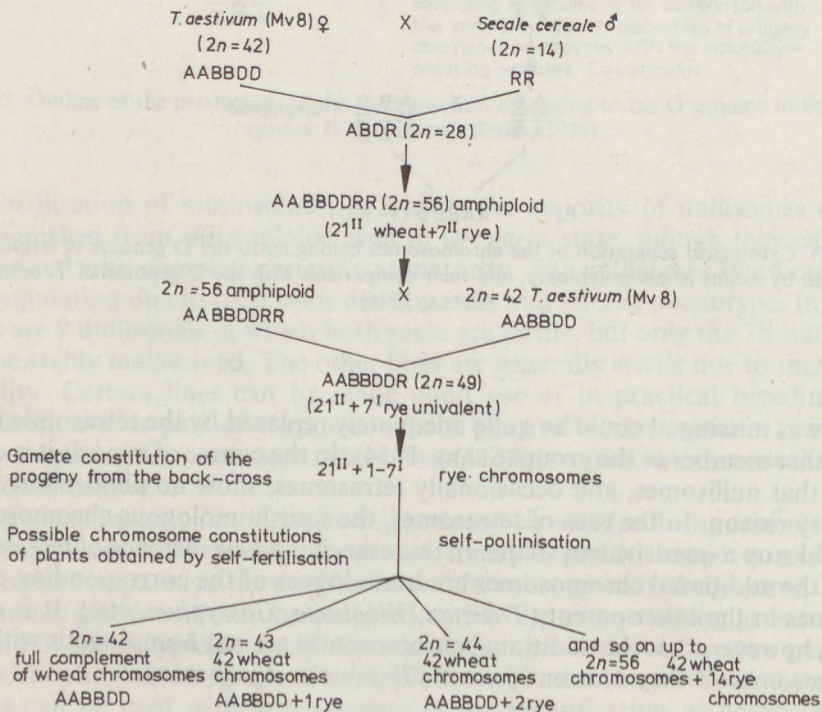


Fig. 47. Addition of rye chromosomes to wheat species (WILLIAMS, 1964)

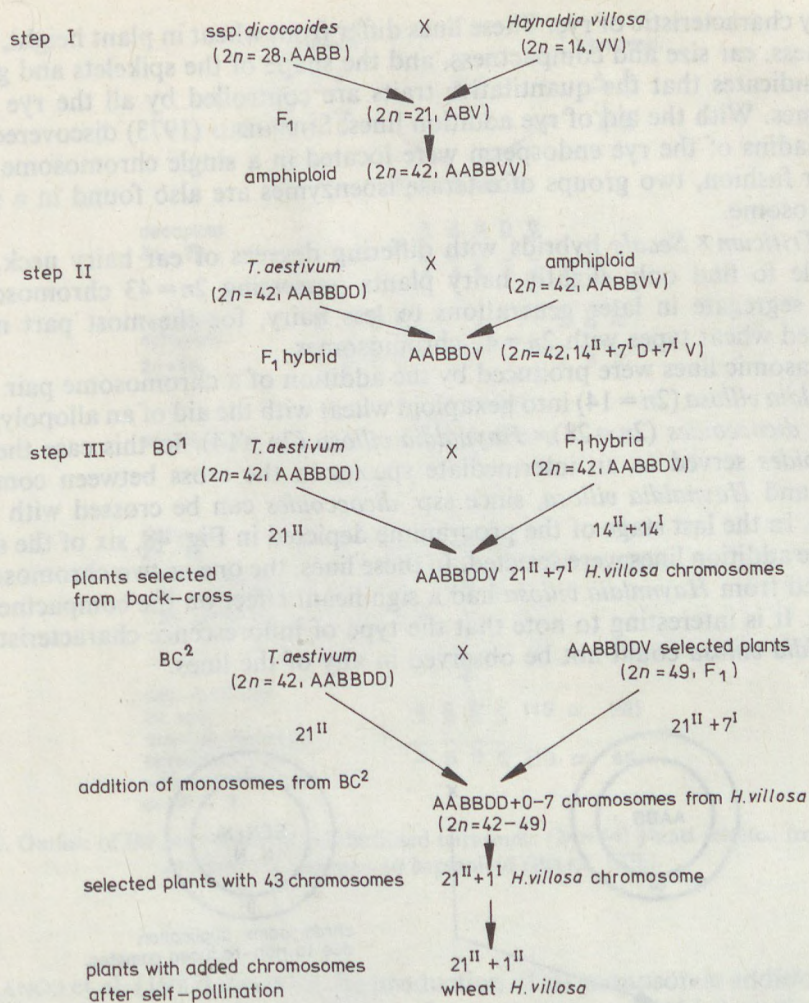


Fig. 48. Addition of *Haynaldia villosa* chromosomes to cultivated wheat (WILLIAMS, 1964)

rye to be present in the aneuploids chosen for self-pollination at the end of the programme. Undesirable lines of rye can be removed by selection. Due to the frequent lack of conjugation, $2n=44$ lines formed by the addition of a chromosome pair from rye are often less fertile than wheat. RILEY (1960) observed anomalies in meiotic cell division, often leading to the elimination of the rye chromosomes from triticale. This is due to the fact that asynapsis is characteristic of inbred lines of rye. The lack of conjugation can thus be put down, in all probability, to inbreeding. RILEY-EWART (1960), DRISCOLL-SEARS (1971) and SCHLEGEL (1982) made further improvements in O'Mara's method in order to produce rye-wheat addition lines with the aid of polyhaploids ($n=28$). In the addition lines the quantitative characters and some of the quality traits are

mainly characteristic of rye. These lines differ from wheat in plant height, straw thickness, ear size and compactness, and the shape of the spikelets and grains. This indicates that the quantitative traits are controlled by all the rye chromosomes. With the aid of rye addition lines, SHEPHERD (1973) discovered that the gliadins of the rye endosperm were located in a single chromosome. In a similar fashion, two groups of esterase isoenzymes are also found in a single chromosome.

In *Triticum* $\times$ *Secale* hybrids with differing degrees of ear hairy neck, it is possible to find only slightly hairy plants possessing $2n=43$ chromosomes, which segregate in later generations to less hairy, for the most part naked stemmed wheat types with $2n=42$ chromosomes.

Tetrasomic lines were produced by the addition of a chromosome pair from *Haynaldia villosa* ($2n=14$) into hexaploid wheat with the aid of an allopolyploid of ssp. *dicoccoides* ($2n=28$) $\times$ *Haynaldia villosa* ($2n=14$). In this case the ssp. *dicoccoides* served as an intermediate species in the cross between common wheat and *Haynaldia villosa*, since ssp. *dicoccoides* can be crossed with both species. In the last stage of the programme depicted in Fig. 48, six of the seven possible addition lines were selected. In these lines, the one or two chromosomes inherited from *Haynaldia villosa* had a significant effect on the compactness of the ear. It is interesting to note that the type of inflorescence characteristic of *Haynaldia villosa* could not be observed in any of the lines.

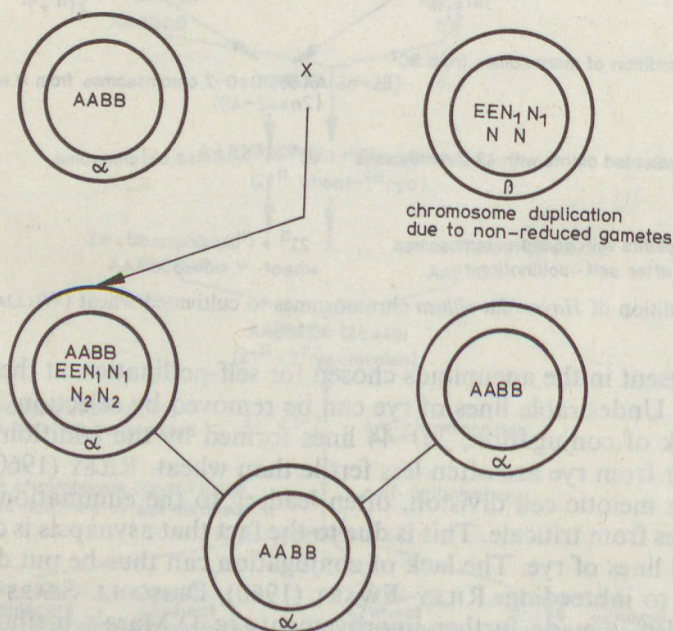


Fig. 49. Addition of *Agropyron elongatum* chromosomes to the species *T. turgidum* conv. *durum* with the aid of non-reduced gametes (SCHULZ-SCHAEFFER-McNEAL, 1977)

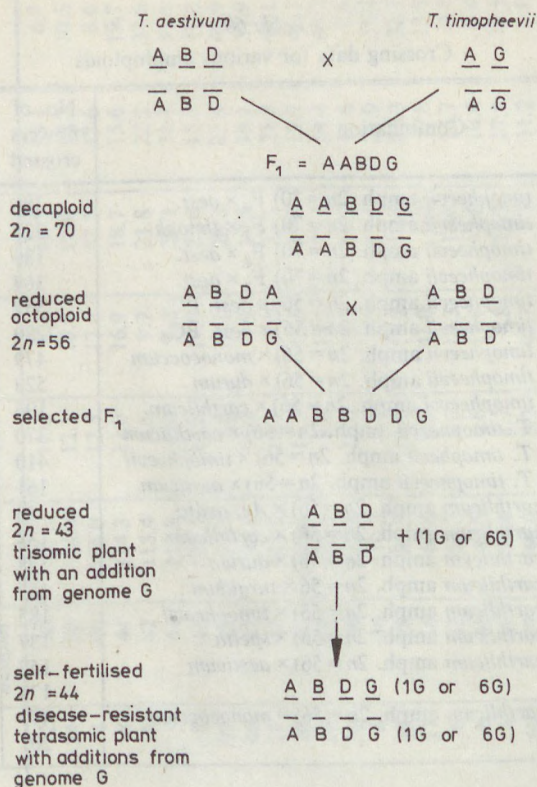


Fig. 50. Outline of the production of self-fertilized tetrasomic (2n=44) plants selected from a *T. aestivum* × *T. timopheevii* heptaploid (BELEA, 1976)

BLANCO et al. (1987) reported the production of six monosomic addition lines in which different *Dasypyrum villosum* chromosomes were added to *T. durum*.

SEARS (1956b) added the leaf rust resistance of *Aegilops umbellulata* to common wheat by top-crossing the allopolyploid *Ae. umbellulata* × ssp. *dicoccoides* with *T. aestivum*. In this way he isolated two monosomic and disomic addition lines. Later, KIMBER (1967) produced a first generation of *Ae. umbellulata* × *T. aestivum* in an embryo culture, obtaining six mono- and disomic lines. MAKINO (1976) added chromosomes from this same species to conv. *durum*. DVORAK-KNOTT (1974) added a chromosome of *Agropyron elongatum* to *T. aestivum* (Fig. 49). Other authors report the introduction of a chromosome from *Avena barbata* into *A. wiestii* (NISHIYAMA, 1981).

In later generations (F₅–F₇) of the *T. aestivum* × *T. timopheevii* allopolyploid (2n=70) mentioned above, BELEA (1976) selected disease resistant addition lines with 2n=44 chromosomes. These contained the 1G chromosome pair of *T. timopheevii* (Fig. 50).

Table 60.
Crossing data for various amphiploids

Combination	No. of flowers crossed	No. of seeds obtained	Seed setting %
(<i>T. aestivum</i> × <i>T. timopheevii</i> amph. $2n=70$) F_1 × <i>aest.</i>	386	0	0.0
(<i>T. aestivum</i> × <i>T. timopheevii</i> amph. $2n=70$) F_1 × <i>timoph.</i>	320	0	0.0
(<i>T. aestivum</i> × <i>T. timopheevii</i> amph. $2n=70$) F_2 × <i>aest.</i>	189	12	6.3
(<i>T. aestivum</i> × <i>T. timopheevii</i> amph. $2n=70$) F_3 × <i>aest.</i>	364	14	3.8
(<i>T. aestivum</i> × <i>T. timopheevii</i> amph. $2n=56$) × <i>aest.</i> BC_1	552	29	5.3
(<i>T. aestivum</i> × <i>T. timopheevii</i> amph. $2n=56$) × <i>aest.</i> BC_2	2280	274	12.0
(<i>T. aestivum</i> × <i>T. timopheevii</i> amph. $2n=56$) × <i>monococcum</i>	479	13	2.7
(<i>T. aestivum</i> × <i>T. timopheevii</i> amph. $2n=56$) × <i>durum</i>	528	3	0.6
(<i>T. aestivum</i> × <i>T. timopheevii</i> amph. $2n=56$) × <i>carthlicum</i>	196	0	0.0
(<i>ssp. carthlicum</i> × <i>T. timopheevii</i> amph. $2n=56$) × <i>carthlicum</i>	370	26	7.0
(<i>ssp. carthlicum</i> × <i>T. timopheevii</i> amph. $2n=56$) × <i>timopheevii</i>	410	18	4.4
(<i>ssp. carthlicum</i> × <i>T. timopheevii</i> amph. $2n=56$) × <i>aestivum</i>	161	11	9.5
(<i>Ae. ovata</i> × <i>ssp. carthlicum</i> amph. $2n=56$) × <i>Ae. ovata</i>	56	4	7.1
(<i>Ae. ovata</i> × <i>ssp. carthlicum</i> amph. $2n=56$) × <i>carthlicum</i>	138	13	9.4
(<i>Ae. ovata</i> × <i>ssp. carthlicum</i> amph. $2n=56$) × <i>durum</i>	528	3	0.6
(<i>Ae. ovata</i> × <i>ssp. carthlicum</i> amph. $2n=56$) × <i>turgidum</i>	157	0	0.0
(<i>Ae. ovata</i> × <i>ssp. carthlicum</i> amph. $2n=56$) × <i>timopheevii</i>	185	0	0.0
(<i>Ae. ovata</i> × <i>ssp. carthlicum</i> amph. $2n=56$) × <i>spelta</i>	137	1	0.7
(<i>Ae. ovata</i> × <i>ssp. carthlicum</i> amph. $2n=56$) × <i>aestivum</i>	152	4	2.6
reciprocal	174	2	1.2
(<i>Ae. ovata</i> × <i>ssp. carthlicum</i> amph. $2n=56$) × <i>monococcum</i>	479	9	1.8
reciprocal	201	0	0.0

In later generations of this allopolyploid, some of the plants with a chromosome number reduced to $2n=56$ were back-crossed to various cultivars of *T. aestivum* (Table 60). Observation showed that the reduced allooctoploids were much easier to cross with cultivars of common wheat than the original $2n=70$ chromosome plants. If the allopolyploid *ssp. carthlicum* × *T. timopheevii* was back-crossed to one of the parents, fewer hybrid grains were obtained (7.0–4.4% seed setting) than after top-crossing with a third species. The octoploid *Ae. ovata* × *ssp. carthlicum*, however, could be easily crossed with both parental species.

Morphologically, plants of the species *T. aestivum* which contain an additional chromosome pair from *T. timopheevii* differ somewhat from the recipient species. They are similar to trisomic plants in that the leaves are broader, pendant, darker green and slightly hairy. Plants with additional chromosomes differed most noticeably from common wheat in the number of ears per plant (tillering) and the number of grains per ear (fertility) (Table 61).

Using *T. turgidum* as an intermediate species, RILEY (1966) added the complex disease resistance of *Aegilops ventricosa*, KERBER-DYCK (1969) the leaf rust resistance of *Ae. squarrosa*, and BELEA (1976) the stem rust resistance of *Ae. ovata* to common wheat (Fig. 51). This latter combination, where the plants

Table 61.

Major quantitative characters in plants after addition, substitution and back-crossing

Combination	N	Chromosome number	Plant height	Ear length	Ears plant	Spikelets ear	D-value	Grains ear
<i>T. aestivum</i> × <i>T. timopheevii</i> amphiploid F ₁	22	70	85.2	11.3	7.8	18.5	16.4	6.7
<i>T. aestivum</i> × <i>T. timopheevii</i> amphiploid F ₃	24	56	118.0	12.1	10.9	19.0	15.7	10.5
<i>T. aestivum</i> × <i>T. timopheevii</i> amphiploid F ₆	4	46	135.0	12.5	17.0	17.5	12.6	8.6
<i>T. aestivum</i> × <i>T. timopheevii</i> amphiploid F ₆	8	44	114.3	12.0	16.9	18.7	15.6	19.7
<i>T. aestivum</i> × <i>T. timopheevii</i> amphiploid F ₆	6	42	115.4	9.8	9.7	21.8	22.2	37.6
<i>T. aestivum</i> × <i>T. timopheevii</i> amphiploid F ₆	5	44	112.8	9.6	8.2	20.3	21.1	31.8
(<i>T. aestivum</i> × <i>T. timopheevii</i> amph.) × <i>T. aest.</i> BC ₁ ²	8	42	118.5	13.7	17.0	21.0	15.3	48.0
(<i>T. aestivum</i> × <i>T. timopheevii</i>) × <i>T. aest.</i> BC ₁ ² subs.	97	42	97.2	9.5	12.1	20.3	21.4	49.9
(<i>T. aestivum</i> × <i>T. timopheevii</i>) × Eryth. 3201 × F 293	46	42	96.1	10.2	4.9	19.5	19.1	37.9
(<i>T. aestivum</i> × <i>T. timopheevii</i>) × Arnaut de St.	17	42	111.9	10.3	5.3	22.1	21.5	44.1
(<i>T. aestivum</i> × <i>T. timopheevii</i>) × Eryth. 3201 × <i>T. turg.</i>	20	42	110.8	11.2	15.5	19.8	17.7	46.1
<i>T. aestivum</i> (F 481)	20	28	127.5	8.6	18.5	21.1	24.4	49.7
<i>T. timopheevii</i>	30	56	123.8	10.0	3.5	19.7	18.6	8.8
ssp. <i>carthlicum</i> × <i>T. timopheevii</i> octoploid	4	44	110.2	8.7	5.3	19.1	21.9	35.4
ssp. <i>carthlicum</i> × <i>T. timopheevii</i> octoploid × <i>T. aest.</i> BC ₁	45	28	83.5	10.2	11.2	17.6	17.3	32.1
ssp. <i>carthlicum</i>	27	56	66.0	6.3	41.0	6.2	9.8	13.8
<i>Ae. ovata</i> × ssp. <i>carthlicum</i> octoploid F ₁	6	52	58.3	9.0	13.3	15.0	16.7	3.7
<i>Ae. ovata</i> × ssp. <i>carthlicum</i> octoploid F ₄	8	46	40.5	6.6	17.9	7.0	10.6	6.4
<i>Ae. ovata</i> × ssp. <i>carthlicum</i> octoploid F ₄	4	44	73.4	8.7	4.8	15.3	17.6	28.9
<i>Ae. ovata</i> × ssp. <i>carthlicum</i> octoploid × <i>T. aest.</i> BC ₁	50	28	46.0	3.3	43.3	3.7	11.2	5.0
<i>Ae. ovata</i>	25	42	86.0	9.6	4.6	19.2	21.3	46.8
<i>T. aestivum</i> (Kavkaz)								

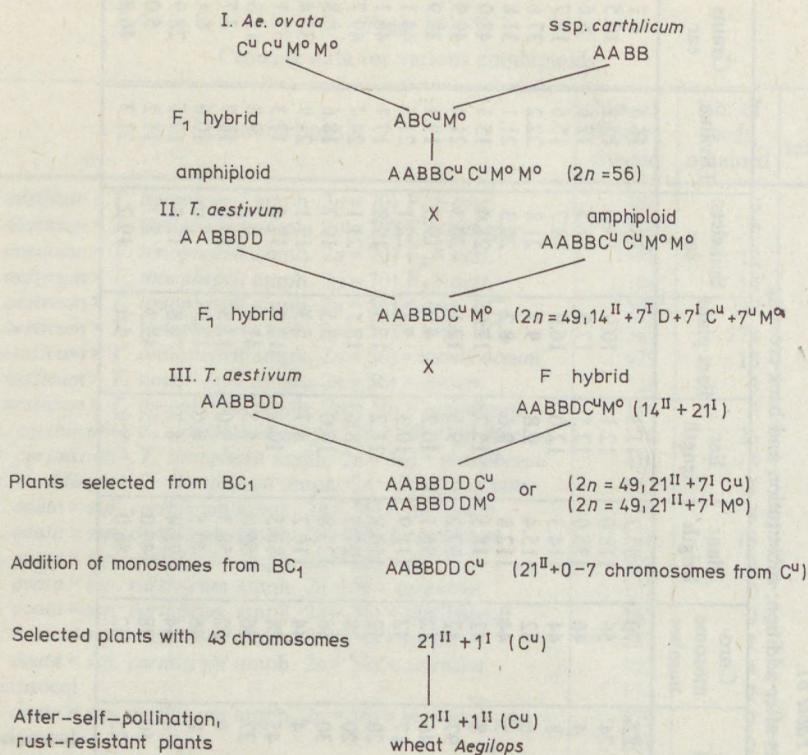


Fig. 51. Outline of the production of a self-fertilised tetrasomic ($2n=44$) plants by means of selection from the combination (*Aegilops ovata* $\times$ *ssp. carthlicum* allopolyploid) $\times$ *T. aestivum* (BELEA, 1976)

gained the $1C^u$ chromosome of *Ae. ovata*, differed from the recipient (*T. aestivum*) species in their slight downiness, somewhat harder glumes and more fragile ear rachis.

Abnormalities in cell division can mostly be observed in monosomic addition lines. Aneuploid lines of this sort are often not constant, segregating into disomic and monosomic plants after self-fertilisation, the former type being predominant. Reduced plants ($2n=56$) of the allopolyploid *T. aestivum* $\times$ *T. timopheevii*, for instance, were still not completely balanced cytologically even in the F_5 . On average, univalents were found in 96.5% of the plants examined. The number of univalents was two in 31.1% of cases, four in 35.6%, six in 17.2% and 8–10 in 10% (BELEA, 1976). Abnormalities in cell division were observed far less frequently in plants with the addition of the $1G$ or $6G$ chromosomes of *T. timopheevii*. This can probably be attributed to the fact that these chromosomes are homologous with one of the chromosomes of common wheat.

4.5.3 Chromosome substitution

This term is used when one or more chromosomes are exchanged for a similar number of chromosomes from the recipient species (alien substitution lines). In this case, the chromosome number does not change. Geneticists are familiar with this phenomenon since the work of KATTERMANN (1936), who replaced the 5A chromosome responsible for the speltoid character of wheat by a rye chromosome carrying a gene for hairy neck. O'MARA (1974) also noted that in the progeny of certain $2n=44$ addition lines, where weak asynapsis was observed, a pair of wheat chromosomes was lost. Consequently, in these plants a pair of wheat chromosomes was exchanged for a pair of rye chromosomes (the 6B chromosome of wheat). Plants which were nullisomes for the 6B chromosome exhibited complete male sterility and partial female fertility. By contrast, the substitution lines were completely fertile and viable, which means that the rye chromosomes were able to take over some of the functions of the missing pair of wheat chromosomes. In addition to the gene responsible for the hairiness characteristic of rye, a gene for dwarfness was also located on this chromosome. In experiments carried out by JONES-JENSEN (1954) fertile plants with normal straw length and hairy straw also segregated; in these plants only the chromosome section responsible for hairiness was substituted, not that bearing the gene for dwarfness.

HOLMES (1938) substituted the chromosome coding super-sensitivity to the tobacco mosaic virus from *Nicotiana glutinosa* into *N. tabacum* by back-crossing the allopolyploid of the two species to various cultivars of *N. tabacum*. The super-sensitive response determines resistance to the virus, leading to the destruction of the virus. After repeated back-crossing of the super-sensitive phenotypes to *N. tabacum*, constant homozygotic forms with 48 chromosomes were obtained, which were identical to the recipient species in every respect, except for their response to the tobacco mosaic virus.

Chromosome substitution lines are likely to be of use in interspecific crosses where the parental species possess valuable economic characters and the loss of undesirable linked characters is not particularly difficult to achieve.

Since the work of Kattermann, a large number of substitution lines have been produced containing valuable economic characters from some related or alien species. RILEY et al. (1968) substituted the 2M chromosome of *Aegilops comosa*, responsible for resistance to yellow rust, for the 2A, 2B and 2D chromosomes of mono-Chinese Spring. These plants were viable and fertile, only differing from the recipient species in grain size and ear type. SEARS (1974, 1977) substituted the 3Ag chromosome of *Agropyron elongatum* for the 7D chromosome of common wheat. By means of chromosome exchange, the leaf rust resistance of *Ag. elongatum* into *T. aestivum* was introduced. BAKSHI-SCHLEHUBER (1958), KNOTT (1964). As regards their viability and fertility, these plants were equivalent to wheat. Similarly valuable lines were obtained when transferring favourable properties of the species *Nicotiana glutinosa* and *N. plumbiginifolia* into *N. tabacum* by means of substitution.

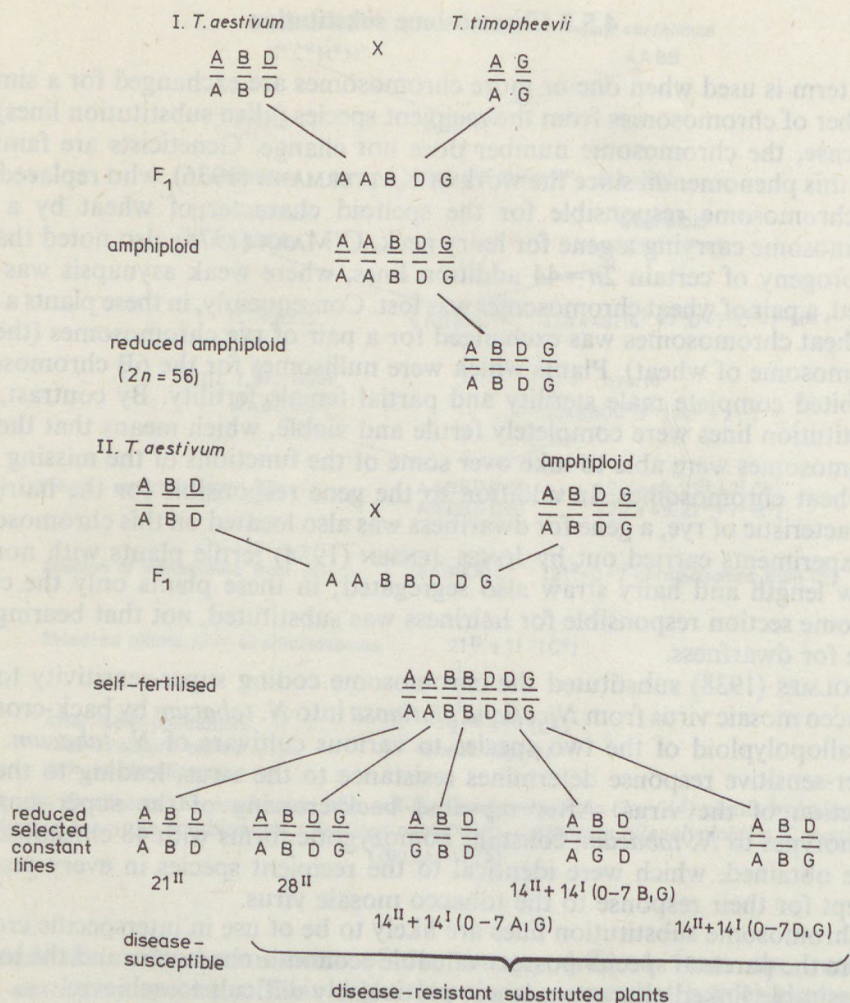


Fig. 52. Outline of the production of substituted plants by means of selection from the combination (*T. aestivum* $\times$ *T. timopheevii* allopolyploid) $\times$ *T. aestivum* (BELEA, 1976)

After back-crossing reduced ($2n = 56$) allooctoploid lines of *T. aestivum* $\times$ *T. timopheevii* to *T. aestivum*, followed by self-fertilisation, BELEA (1976) selected disomic substitution plants which were disease resistant (Fig. 52). These plants, too, were only slightly different from the recipient species. The presence of the alien chromosome was primarily indicated, as a phenotypic marker trait, by the disease resistance. This is due to the fact that the 1G chromosome of *T. timopheevii*, as mentioned previously, is able to take over several of the functions of the missing chromosome from common wheat. The results can only be regarded as completely satisfactory if the recipient species

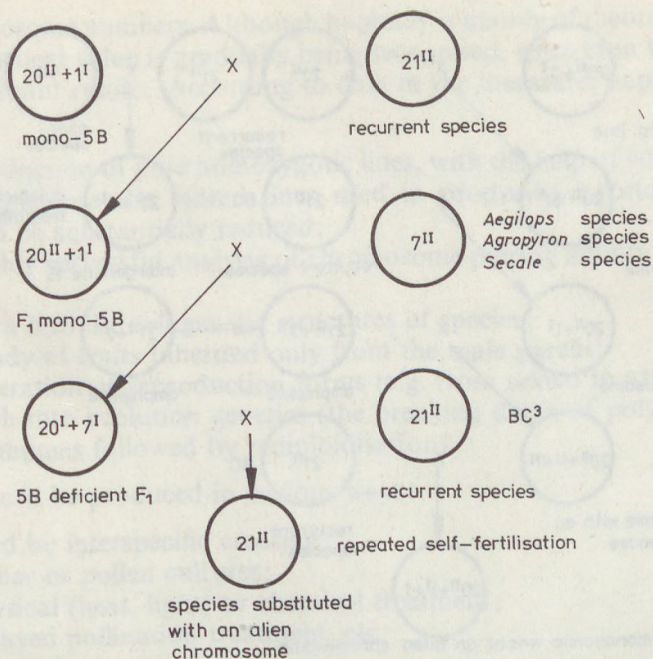


Fig. 53. Substitution of an alien chromosome with the aid of mono-5B (BHOWAL, 1979)

gains a new character without any disturbances in meiotic cell division. Due to the relatively weak asynapsis and the segregation of the univalents, gametes containing 21 chromosomes were formed, in which case the chromosome pairing was 20 (*T. aestivum*) + 1 (*T. timopheevii*). After fertilisation of these gametes with the 21 chromosome *T. aestivum* species, alien monosomic substitution lines were found among the progeny (20^{II} *T. aestivum* + 1^I *T. timopheevii*). Among the progeny, only the disease resistant plants were back-crossed, as a result of which disease resistant wheat lines were obtained. These plants contained the 1G or 6G chromosomes of *T. timopheevii* in place of the 2D or 6B chromosome pair of *T. aestivum*.

The alien chromosome is generally exchanged for a specific chromosome. This is understandable, since very few wheat chromosomes are in such close relationship with their homoeologous partners that two extra doses of one can completely make up for the loss of the other. In some cases the alien chromosome can be replaced not by all the members of the genome group, but only by one or two of the chromosomes.

Polyploidy, alien chromosome addition and substitution, and induced translocation and recombination are all suitable for the transfer of major economic characters from the wild species of the related genera (*Aegilops*, *Agropyron*, *Secale*, *Haynaldia*, *Elymus*) of the *Triticinae* family into cultivated species. Using an improved method, BHOWAL (1979) promoted the substitution and

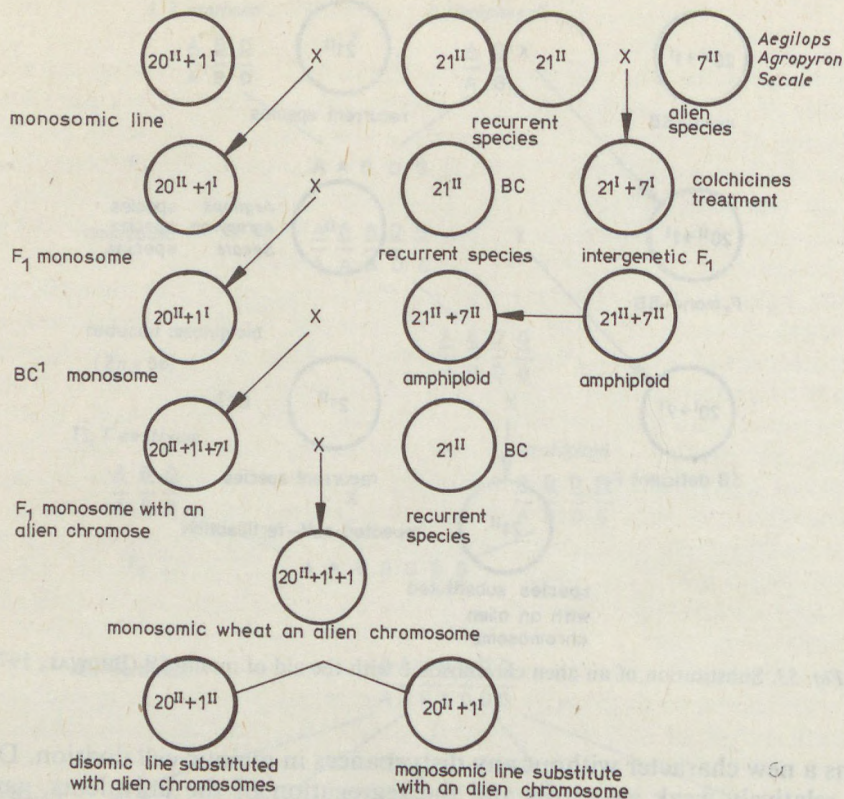


Fig. 54. Substitution of chromosomes from an alien species with the aid of monosomic lines and polyploidy (BHOWAL, 1979)

recombination of alien chromosomes through the use of mono-5B Chinese Spring (Fig. 53) and by means of polyploidy (Fig. 54).

The substitution of alien chromosomes may also facilitate crossing-over between two homologous chromatids. The genes involved may be useful markers in the compiling of chromosome maps. Aneuploid lines created artificially or occurring spontaneously in nature may play an important role in increasing the variability of evolution.

4.5.4 Haploidy

In nature, plants with monoploid chromosome sets are found extremely rarely. In such cases the chromosome set consists of a single genome (complete haploid gene set). In plant organisms of this type, meiosis is irregular, because there are no homologous chromosomes. This means that the gametes formed have dif-

ferent chromosome numbers. Although haploidy is mainly of theoretical importance, its practical value is gradually being recognised, since even today it may lead to significant results. According to data in the literature, haploidy can be used for:

(a) the production of pure homozygotic lines, with the help of which the time required to produce the inbred lines used in producing hybrid maize, for example, can be substantially reduced;

(b) the highly successful analysis of chromosome pairing affinity in polyploid plants;

(c) research into the cell genetic structures of species;

(d) the study of traits inherited only from the male parent;

(e) the alteration of reproduction forms (e.g. from sexual to asexual, etc.);

(f) research into evolution genetics (the breaking down of polyploid plants into basic genomes followed by rediploidisation).

Haploids can be produced in various ways:

(a) induced by interspecific crossing;

(b) in anther or pollen cultures;

(c) by physical (heat, light) or chemical treatment;

(d) by delayed pollination treatment, etc.

In the present case, only haploid plants produced through interspecific and intergeneric crosses will be discussed.

Haploid plants have been successfully produced by means of interspecific and intergeneric crosses in a considerable number of plant genera (*Datura*, *Nico-*

Table 62.

Outline of the production of haploid plants from the cross *Hordeum vulgare* × *Hordeum bulbosum* (SYMKO, 1969)

No. of days after castration	<i>Hordeum vulgare</i> ♀ $2n = 2x = 14$ Castration	<i>Hordeum bulbosum</i> ♂ $2n = 2x = 14$ Application of fresh pollen
2	Pollination	with fresh pollen
3-5	GA ₃ treatment: one drop of 75 ppm GA ₃ on the flower every 2-3 days	
14-16	Excision; raising in in vitro embryo culture in the dark at max. 22°C	
22-28	Transfer of individual embryos to 12-hour illumination at max. 22°C	
40-50	Treatment of young seedlings (in the 2-3 leaf state) with 0.1% colchicine solution for 5 hours; planting out to growing site	

Table 63.

Production of haploids in crosses between *Hordeum* and other plant species by means of chromosome elimination

Plant species and polyploidy level	Type of progeny obtained	Frequency	Authors
<i>H. leporinum</i> (4x) × <i>H. vulgare</i> (2x)	<i>H. leporinum</i> (4x) <i>H. vulgare</i> (2x)		SUBRACHNAMYAM, 1979
<i>H. bulbosum</i> (4x) × <i>H. secalicum</i> (4x)	hybrids with <i>H. bulbosum</i> (2x)		CAUDERON-CAUDERON, 1956
<i>H. arizonicum</i> (6x) × <i>H. bulbosum</i> (2x)	<i>H. arizonicum</i> (3x)		ISLAM-SPARROW, 1974
<i>H. arizonicum</i> (6x) × <i>H. vulgare</i> (2x)	<i>H. arizonicum</i> (3x) hybrids (4x)		ISLAM-SPARROW, 1974
<i>H. lechleri</i> (6x) × <i>H. vulgare</i> (2x)	<i>H. lechleri</i> (3x) hybrids (4x)	18	RAJHÁTHY-SYMKO, 1963
<i>H. jubatum</i> (4x) × <i>H. bulbosum</i> (2x)	<i>H. jubatum</i> (2x)	24	RAJHÁTHY-SYMKO, 1963
<i>H. vulgare</i> (2x) × <i>Secale cereale</i> (2x)	<i>H. vulgare</i> (x) hybrids (2x)	1 2	KRUSE, 1967
<i>H. brachyantherum</i> (4x) × <i>H. vulgare</i> (2x)		2	
<i>H. depressum</i> (4x) × <i>H. bulbosum</i> (2x-4x)		1-4	SUBRACHNAMYAM, 1979
<i>H. depressum</i> (4x) × <i>H. vulgare</i> (2x)		2	SHIGENOBU-SAKAMOTO, 1981
<i>Ae. crassa</i> (4x) × <i>H. bulbosum</i> (2x)		1	NAKAMURA et al., 1981

tiana, *Oryza*, *Hordeum*, *Zea*, *Triticum*, etc.). This is primarily of importance in the production of basic stock for the restoration of combining ability and fertility. JÖRGENSEN (1928) was probably the first to produce a haploid using this method in a cross between *Solanum nigrum* and *S. luteum*. Later, in the *Solanaceae* family, a polyhaploid of *S. tuberosum* was produced by pollinating with pollen from the diploid *S. phuraja*. YERK-PELOGUIN (1987) used callus cultures taken from wild *Solanum* species to carry out numerous crosses between *S. tuberosum* haploid and wild *Solanum* species for the purpose of germ plasm transfer. PISSAREV-VINOGRADOVA (1945) obtained monoploid barley from a combination of *Hordeum vulgare* and *Elymus arenareus*. DAVIES (1958) used an in vitro technique to raise dihaploid plants of *Hordeum bulbosum* (4x) and *H. vulgare* (Table 62).

A cross between these latter barley species was first made in 1934 by KUCKUCK. Later, a very high frequency (90-100%) of haploid plants was obtained in this combination. Numerous researchers, including KAO-KASHA (1969), KASHA-KAO (1970), LANGE (1971), JENSEN (1972), SYMKO (1969), etc., produced haploid cultivated barley through the elimination of the *H. bulbosum* chromosomes (Fig. 55) using the method described in Table 62. Fired by this success, researchers later selected haploids from crosses between species from other plant genera and other *Hordeum* species (Table 63).

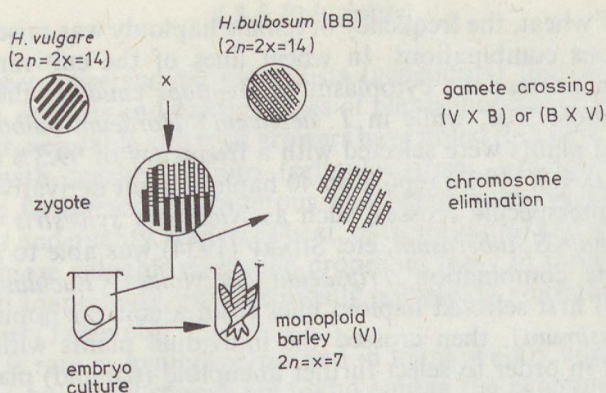


Fig. 55. Outline of the production of haploid barley by means of chromosome elimination with the aid of embryo cultures (JENSEN, 1972)

Table 64.

Production of haploid Triticum plants from various *Triticum* × *Hordeum* crosses (FINCH-BENNETT, 1982)

Female parent	Male parent	Plant number%*		Authors
<i>T. aestivum</i> 6x	<i>H. vulgare</i> 2x	2	0.0	ISLAM et al., 1976
		5	0.0	FEDAK, 1980
		20	15.0	ISLAM et al., 1981
		27	9.1	
<i>T. aestivum</i> 6x	<i>H. bulbosum</i> 2x <i>H. bulbosum</i> 4x <i>H. bulbosum</i> 2x + 4x	11	100.0	BARCLAY, 1975
		59	100.0	BARCLAY, 1975
		223	99.1	MILLER-CHAPMAN, 1976
		293	99.3	
conv. <i>durum</i> 4x <i>T. timopheevii</i> 4x <i>H. vulgare</i> 2x	<i>H. vulgare</i> 2x <i>H. bogdanii</i> 2x <i>T. aestivum</i> 6x	2	100.0	SHEPHERD-ISLAM, 1981
		1	0.0	KIMBER-SALLEE, 1976
		75	0.0	CLAUSS, 1980
		67	0.0	ISLAM et al., 1976
		21	0.0	KRUSE, 1973
		8	0.0	MUJEEB et al., 1980
		1	0.0	THOMAS et al., 1977
		15	6.7	FEDAK, 1980
		187	0.1	
<i>H. vulgare</i> 2x	conv. <i>durum</i> 4x <i>T. timopheevii</i> 4x ssp. <i>dicoccum</i> 4x <i>T. monococcum</i> 2x	6	0.0	THOMAS et al., 1977
		1	0.0	CAUDERON et al., 1978
		6	0.0	KRUSE, 1973
		1	0.0	KRUSE, 1973
<i>H. chilense</i> 2x	<i>T. aestivum</i> 6x conv. <i>durum</i> 4x	16	0.0	MARTIN-LAGUNA, 1980
		11	0.0	MARTIN-LAGUNA, 1980
<i>H. pusillum</i> 2x	<i>T. aestivum</i> 6x	2	0.0	FINCH-BENNETT, 1980

* where 100% is the number of pollinated stigmata

In the case of wheat, the frequency of female haploidy was raised to 30–100% in certain species combinations. In wheat lines of the cultivar Salmon, for example, which possess the cytoplasm of *Aegilops caudata*, the haploid frequency was almost 50%, while in *T. aestivum* × *Hordeum bulbosum* (2x–4x) crosses, haploid plants were selected with a frequency of 99.3% (Table 64).

MAGOON-KHANNA (1963) report on 40 haploid plant derivatives originating from various interspecific crosses, such as *Nicotiana sylvestris* × *N. tabacum*, *Solanum chaucha* × *S. tuberosum*, etc. SHARP (1934) was able to select haploid plants from the combination *Tripsacum dactyloides* × *Euchlaena mexicana*. MURRAY (1980) first selected haploid lines from a cultivar population of flax (*Linum usitatissimum*), then crossed the individual plants with the original diploid cultivar in order to select further aneuploid (triploid) plants.

According to observations made by MARTIN-CHAPMAN (1977), chromosome pairing was better in the F₁ hybrid of *Hordeum chilense* × *Triticum aestivum* than in the haploid Chinese Spring cultivar. In the hybrids, 5^{II} + 1^{III} were observed during meiosis (Table 65). In the haploid plants a low frequency of bivalents (0.24 on average) was found.

By means of chromosome mapping it became possible to determine the chromosomal location of several characters in a number of plants (e.g. maize, barley, wheat, etc.). In wheat, chromosome mapping can be carried out fairly easily with the aid of a telocentric series of chromosomes. If the centromere is used as a marker, it is possible to determine the distance from the centromere.

Table 65.

Chromosome pairing in meiosis in *Hordeum chilense* × *T. aestivum* and haploid Chinese Spring (after MARTIN-CHAPMAN, 1977)

Designation	No. of cells	Univalent	Bivalent	Trivalent
		chromosomes		
<i>H. chilense</i> × <i>T. aestivum</i> hybrid	60	23.67 (17–28)	1.97 (0–5)	0.13 (0–1)
Haploid Chinese Spring	240	20.52 (17–21)	0.24 (0–2)	

Interspecific hybrids and allopolyploids are extremely useful in determining the chromosomal location of various characters. ROWLAND-KERBER (1974) used the synthetic hexaploid Tetra Canthatch × *Aegilops squarrosa* (AABBDD) and telocentric Chinese Spring wheat lines to locate brown glume colour (Rg2) on the 1D chromosome, waxiness (W2) on the 2D, red coleoptile colour (Rc3) on the 7D, leaf rust resistance (Lr21) on the 1D and the leaf rust resistance of the mature plant (Lr22) on the 2D chromosome.

4.5.5 Polyploidy

It has long been observed by naturalists (geneticists) that in the course of domestication, animals and various types of plants increase in size. In a similar manner, flower, vegetable and fruit growers have noted that new, long-flowering ornamentals with dazzling colours (primulas, irises, hyacinths, etc.), better-looking, more flavoursome pomiferous and berry fruits, vegetables with improved flavour and quality, cereals (wheat, oats, sorghum) and grasses, etc. with substantially more valuable economic properties (easy to thresh, greater yield potential, high adaptability, etc.) are mostly polyploids, since they form natural polyploid series (Table 66).

Polyploidy is rare in gymnosperms and in many woody angiosperms. Considerably more polyploid species are found among the perennial soft-stemmed angiosperms, while they are most frequent among the algae, where organisms with the highest polyploid levels are to be found. Roughly a quarter to a third of flowering plant species are polyploids, i.e. they contain several genomes.

According to KOSTOFF (1943), there are far more species with 40 or more chromosomes among the cultivated plants than among the wild species. This would seem to indicate that polyploidy has a favourable effect in the formation of valuable characters in cultivated plants. In the 30 major crops used for human

Table 66.
Polyploidy series of some major crops (after OEHLER, 1956)

Basic chromosome number Poly- ploidy level	Genus				
	Poa	Bromus	Prunus	Rubus	Fragaria
	$n=7$	$n=7$	$n=8$	$n=7$	$n=7$
Diploid	<i>P. trivialis</i> <i>P. Chalixi</i>	<i>B. sterilis</i> <i>B. tectorum</i> <i>B. arvensis</i>	<i>P. persica</i> <i>P. mahalab</i> <i>P. avium</i> <i>P. armeniaca</i> <i>P. amygdalus</i>	<i>R. odoratus</i> <i>R. idaeus</i> <i>R. xanthocarpus</i> <i>R. Ulmifolius</i>	<i>F. vesca</i> <i>F. colliana</i> <i>F. californica</i>
Triploid	<i>P. palustris</i>		<i>P. avium nana</i> <i>P. spinosa</i>	<i>R. recurvans</i> <i>R. canadensis</i>	
Tetraploid	<i>P. palustris</i> <i>P. nemoralis</i>	<i>B. maximus</i> <i>B. secalius</i>	<i>P. padus</i> <i>P. cerasus</i> <i>P. fruticosa</i> <i>P. spinosa</i>	<i>R. caesius</i> <i>R. loganobaccus</i> <i>R. laciniatus</i>	<i>F. orientalis</i>
Pentaploid	<i>P. compressa</i>		<i>P. spinosa</i>	<i>R. loganobaccus</i>	
Hexaploid	<i>P. nemoralis</i>	<i>B. erectus</i>	<i>P. spinosa</i>	<i>R. macropetalus</i>	<i>F. elatior</i>
Heptaploid	<i>P. compressa</i>				
Octoploid		<i>B. inermis</i> <i>B. carinatus</i> <i>B. ciliatus</i>	<i>P. triloba</i>		<i>F. virginiana</i> <i>F. chiloensis</i> <i>F. grandiflora</i>
Polyploid	<i>P. glauca</i> <i>P. pratensis</i>		<i>P. laurocerasus</i> $2\pi=84$	<i>R. macropetalus</i> $2\pi=84$	<i>F. glauca</i> <i>F. indica</i> $2\pi=84$

Table 66. (continued)

Poly- ploidy level	Basic chromo- some num- ber	Genus				
		Agrostis	Alopecurus	Malus	Solanum	Vaccinium
		<i>n</i> = 7	<i>n</i> = 7	<i>n</i> = 17	<i>n</i> = 12	<i>n</i> = 12
Diploid		<i>A. Biebersteiniana</i>	<i>A. aequalis</i>	<i>M. amurensis</i>	<i>S. chacoense</i>	<i>V. myritillus</i>
Triploid		<i>A. elegans</i>	<i>A. utriculatus</i>	<i>M. baccata</i>	<i>S. polyadenium</i>	<i>V. vitis-idaea</i>
		<i>A. interrupta</i>	<i>A. amurensis</i>	<i>M. floribunda</i>	<i>S. ajannuiri</i> , etc.	
				<i>M. pumila</i>	<i>S. maglia</i>	
				<i>M. bracteata</i>	<i>S. tenuifilamentum</i>	
Tetraploid				<i>M. lancifolia</i>	<i>S. mamilliferum</i> , etc.	
		<i>A. alba</i>	<i>A. pratensis</i>	<i>M. coronaria</i>	<i>S. tuberosum</i>	<i>V. uliginosum</i>
		<i>A. vulgaris</i>	<i>A. ventricosus</i>	<i>M. glabrata</i>	<i>S. andigenum</i> , etc.	<i>f. genuina</i>
Hexaploid		<i>A. verticillata</i>	<i>A. mucronatus</i>	<i>M. tirongo</i>		<i>f. Corymbosum</i>
		<i>A. planifolia</i>			<i>S. demissum</i>	<i>V. hirsutum</i>
		<i>A. hissaira</i>				<i>V. virgatum</i>
Heptaploid		<i>A. gigantea</i>				<i>V. pallidum</i>
		—	—	—	—	—
Octoploid		<i>A. borealis</i>	<i>A. vaginatus</i>			
Polyploid			<i>A. textilis</i>			
			<i>A. glacialis</i>			
			<i>A. borealis</i>			
			<i>A. alpinus</i>			

consumption and animal feeding, there is a substantial increase in the carbohydrate, fat, vitamin and protein contents as the level of polyploidy rises. These naturally occurring polyploids drew the attention of breeders to the fact that plants of similar value could perhaps be produced artificially. In nature, new species are still being formed by polyploidisation as the result of external climatic factors.

It was also noted that the diploid species were adapted to a specific environment. Allopolyploids, on the other hand, which contained genomes from species with various ecological requirements, were much more adaptable. STEBBINS (1947) attributed this phenomenon, which provides plentiful opportunities for selection, to the increased size of the organism, others to the larger number of genes. If a population finds itself in completely new environmental and ecological conditions, only the most vital individuals will survive, while the rest die off.

VIDA (1974), too, considers polyploidy to be one of the most significant events in chromosome evolution and raises the question of whether polyploidy is only of importance in the formation of lower taxa (sub-species, species, perhaps genera), or whether it may also have played a role in macro- or even mega-evolu-

tion. Despite the fact that, from the phylogenetic point of view, it played an important role in the origin of species, there does not seem to be any direct correlation between the level of phylogenesis and the frequency of polyploidy. The artificial production of new allopolyploids and autopolyploids also makes it possible for new species to be formed.

4.5.5.1 Induction of polyploids

When these facts were recognised, there was a substantial rise in the number of breeders attempting to use this method and the number of geneticists dealing with evolution research, and they have applied numerous techniques and chemicals to create polyploid plants. One method of inducing polyploidy, which was previously the most widespread, was a sudden change in the temperature. In nature, too, this is a factor which generally causes polyploidy. MICHAELIS (in GYÖRFFY, 1939) prevented meiosis from taking place in *Epilobium* and *Oenothera* by applying a temperature of -4°C . STOW (in GYÖRFFY, 1939) observed abnormalities in cell division in *Solanum tuberosum* at $27-30^{\circ}\text{C}$, when diploid pollen is formed in place of the normal haploids due to the failure of the homologous chromosomes to pair.

Sudden changes in temperature from cold to hot or vice versa proved to be more effective in doubling the genomes than constant cold or hot treatment. When treating bulbs of *Tulipa* and *Narcissus* in this way a fairly high percentage of diploid, tetraploid and sterile pollen was obtained (the ratio of polyploid pollen was often greater than 25%). In *Petunia violacea* MATSUDA (1936) observed an increase in the number of giant pollen grains if the budded shoots were kept at $10-13^{\circ}\text{C}$ prior to treatment at 40°C . According to BRIEGER, (1929) the meiosis of *Nicotiana* could only be influenced by extreme changes in temperature ($2-35^{\circ}\text{C}$).

Temperature fluctuations occurring in nature may also induce the formation of giant pollen, as experienced by Stow (in GYÖRFFY, 1939) in *Solanum tuberosum*.

Considerably greater importance is attached to the doubling of the chromosome sets in the cells of the meristem, the dividing cells of the plant, from which tetraploid shoots develop. This can be achieved most reliably by carrying out treatment on the proembryo, during the first division after fertilisation. RANDOLPH (1932) placed the ears (spadix) of maize in water at $43-45^{\circ}\text{C}$ 30 hours after pollination, thus inhibiting the normal process of proembryonic division. In this way, tetraploid forms were produced. In a similar manner, DORSEY (1936) obtained amphiploids in wheat-rye hybrids. These methods result in tetraploid seeds in plants where both fertilisation and the first somatic cell division producing the proembryo take place relatively quickly.

In plants with good regeneration ability, the formation of polyploid organisms may easily be initiated from scar tissue forming on cut stems (*Solanum* genus). JÖRGENSEN (1928) was able to obtain tetraploid shoots, in addition to

normal shoots, from the callus tissue of cut stems with absolute certainty. A classical example of polyploidy induced by regeneration was described by WETTSTEIN (1933) in the case of bryum.

Polyploidy can also be achieved using chemicals. Treatment with chloral hydrate, for example, was used by NEMEC as long ago as 1940 to disturb the normal process of cell division. With the exception of mosses, however, this chemical only resulted in partial tetraploidy (so-called chimeras). KOSTOFF (1933) demonstrated the presence of tetraploidy in plants suffering from viral diseases, and WIPF-COOPER (1938) in plant tumours. This is probably induced by changes in viscosity due to alterations in the metabolism or possibly to the formation of special biochemical substances, preventing the chromosomes from migrating to the two poles. Numerous other compounds are also employed, including dinitrogen oxide, acenaphthene, phenyl urethane, cyanide, azide, etc., of which the latter inhibits oxidation, while others obstruct the processes supplying energy for mitosis. They thus prevent mitosis from taking place, but do not influence chromosome duplication.

Substances which inhibit mitosis and meiosis are generally referred to as mitotic poisons. Those chemicals which also occur in tissues under natural conditions are endogens, while those which are introduced from outside are exogens.

Mitotic poisons can be classified according to their chemical structures, their effects and their possible action mechanisms. The chemical may inhibit one particular phase of mitosis or the whole mechanism of mitosis. It may affect one or more mitotic mechanisms, such as the cell membrane cycle, chromosome spiralisation, the operation of the centromere, the formation of the spindle, the movement and duplication of the chromosomes, the protein metabolism or the processes supplying energy for mitosis and meiosis.

Although many methods and chemicals are known for the induction of polyploidy, as a result of which polyploid plants have been produced, often with a frequency of over 30%, even the best of the previously applied methods was uncertain due to the clumsiness of the treatment, and did not become widespread. Great changes were brought about by the introduction into general practice of a new chemical, colchicine. This compound, an alkaloid found in the plant *Colchicum autumnale*, was first applied in 1934 by DUSTIN and HAVAS (in CHODKOWSKI, 1937) in mammal genetics. The method was later perfected by BLAKESLEE-AVERY (1937). These authors were the first to prove that colchicine also induced significant changes in the process of plant cell division (DUSTIN et al., 1937). Colchicine treatment can be carried out on seeds, seedlings or older plants. Dry seeds can be germinated in a 0.02–0.05% solution. Since colchicine intensely inhibits growth, the growth of the radicle is also greatly inhibited and 60–70% of the plants are generally destroyed. Depending on the plant species to be treated, a 0.2–2.0% concentration of colchicine can be dripped onto the growing tip or injected into the tissues close to the growing tip. The compound can also be used in the form of an ointment, causing the cells of the vegetative tip to turn polyploid.

Treatment is more effective if the colchicine solution is combined with 10 mg/dm³ gibberellin, in which case the growth-inhibiting effect of colchicine is counteracted by the GA₃, so that a higher percentage of the population survives. This is particularly important if the solution is used in higher concentrations. A rise in temperature promotes polyploidisation.

Another way of improving efficiency is to dip the tips of young seedlings into the solution when the first leaves begin to appear. In many plants the cotyledonous stage lasts for a long time, the initiation of shoot growth being very sluggish. In the same way, any intensely developing branch of the mature plant can be dipped in colchicine solution. The effectiveness of the treatment can be improved if, prior to dipping, the side branches and some of the leaves are removed, so that growth is concentrated in the treated branch. By keeping shoots of *Portulaca* in a 0.025% solution for a day, BLAKESLEE-AVERY (1937) obtained tetraploid tissue. A polyploid effect can also be induced if only the growing tip is treated with colchicine solution. To this end, young, densely packed leaves are cut open to reveal the growing tip and this is treated with drops of a solution varying in concentration depending on the plant species. In some plants, such as flax, one or two drops are sufficient, while in others treatment may have to be repeated, possibly for several days. In the case of stiff, woody branches, a glass tube filled with agar containing colchicine can be pulled onto the branch, or the cooled agar can be dripped onto the growing tip before it solidifies. The growing tip of the shoot can be spread with a lanoline paste containing colchicine, though this has the disadvantage that the colchicine diffuses out of the paste with difficulty and it is impossible to know what concentration is acting.

Polyploidy may cause phenotypic changes affecting either the whole plant or only part of it. The most characteristic morphological, physiological, histological and cytological changes are as follows:

DUSTIN et al. (1937) reported that at low concentrations (0.000 025%) seedlings developed more intensely, while higher concentrations (0.0005%) caused slower root growth, shorter roots and hypertrophic swellings on the root tip. The younger the plant, the more pronounced this hypertrophy is. If the root is put into water, tumour formation ceases, but if it is put into colchicine again, a new tumour forms. If this alternation is continued, the root will eventually look like a string of beads.

One characteristic change in seedlings after treatment is the swelling of the stem below the cotyledon (the hypocotyl). This is a sure sign that polyploidy has been induced. If the concentration is too high, the plant ceases to develop and finally dies off. The percentage destruction can be reduced by after-treatment with heteroauxin.

Since it is very rarely possible to turn the whole of the growing tip into a tetraploid, the plant will generally be a mixochimera, very varied, often distorted in form due to the fact that the tissues have different chromosome numbers. The leaves are often thicker, with a rough surface (*Petunia*, *Hyoscyamus*), shinier (*Capsicum*) or, as in young leaves of flax, intensely swollen around the

growing tip, so that after a few days the treated growing tip resembles a houseleek (*Sempervivum*). The diploid and tetraploid tissues of chimera-type leaves can also be distinguished by the size of the stomata.

Often the side shoots also contain diploid-tetraploid chromosome numbers. It is advisable to remove non-polyploid branches, so that the plant is forced to develop the polyploid branches more intensively. Gigantic growth can frequently be observed, with thickened stems and often larger flowers, too. The individual flowers of *Vicia* and *Antirrhinum* are closer to each other due to a shortening of the internodes. Anomalies may also occur in the meiosis of tetraploid pollen mother cells, leading to the creation of hypo- and hyperdiploid or even haploid pollen grains. Great changes are also observed in the size and shape of the pollen.

Colchicine may prevent the normal course of several consecutive cell divisions, in which case polyploid cells with $4n$, $8n$ or $16n$ chromosomes may arise. The formation of octoploid ($8n$) cells is extremely frequent.

Several researchers have investigated the action mechanism of colchicine. This compound modifies the life cycle of the cells in the M phase of metaphase by preventing cytokinesis, i.e. the formation of the spindle, or by disturbing the functioning of the spindle. This effect is known as C-mitosis, since the majority of polyploid plants are produced using colchicine. The effect of colchicine on the nuclear spindle leads to various degrees of obstruction to the division of the chromosomes in metaphase and anaphase. Since it does not harm chromosome duplication, it can be used to produce polyploids. In some cases multi-polar spindles, the destruction of progeny cell nuclei or aneuploidy may be induced. Despite the C-effect, the chromosomes continue their spiralisation cycle and the two chromatids may shorten and repel each other, but the centromeres remain connected to each other. Thus, if treatment is to be successful, it is important to know what state the cells are in during treatment. The time required for the cell cycle, which differs in different plant species, can be determined experimentally. In wheat, for example, the minimum length of the M phase of the cell cycle, until the first telophase of meiosis, is five times as long as in the root meristem (12.5 h). Similarly, the premeiotic DNA synthesis takes four times as long (15 h) as the S phase in the cells of the root tip (3.8 h).

Properly synchronised systems may be useful in various physiological, biochemical and genetic analyses, not to mention the production of induced polyploids and mutants. It is very important for as many cells as possible to enter the mitosis stage during colchicine treatment. In the case of an adequately synchronised system the vast majority of the cells in the treated tissues will be at the same polyploid level, thus increasing the efficiency of polyploid production. Cell division can be synchronised by means of various chemicals, e.g. 5-aminouracyl. This work will be successful if the conditions before and after treatment are suitable for rapid, continuous growth.

Twelve hours after colchicine treatment the cell cycle enters its first phase, and then the second and third phases. Forty-eight hours later abnormal mitosis may be observed among the scattered chromosomes in metaphase. Normal cell

division is not restored for three days. As the result of colchicine treatment, chromosomes in metaphase can be found scattered round the cell. This is followed by the merging of certain chromosomes, resulting in the formation of micronuclei which later merge. At this stage the cells are multinuclear. This is often followed by abnormal mitosis with a partially inactive spindle. In the end, mitosis ceases completely. In the case of higher concentrations or a longer treatment time, normal mitosis is not restored at all: the chromosomes are dissolved and appear in the cytoplasm in the form of intensely staining nucleic acid drops. The disappearance of the nucleic acid leads to the destruction of the cells. If the whole plant is exposed to colchicine treatment for a lengthy period, the plant will be destroyed. It is a general observation that there is an inverse correlation between colchicine concentration and treatment time (EIGSTI, 1938). Better results are obtained when lower concentrations are applied for a longer period, than when high concentrations are used for a short period, since in the latter case a larger percentage of the plants are destroyed.

4.5.5.2 Types of polyploids

Polyploids are cells (organisms) in which the cell nuclei contain 3 or more genomes. A genome is the genetic material of a chromosome set with the basic chromosome number characteristic of a group of related species, and is denoted by x . Polyploids are euploid plants with a larger number of complete genomes. Diploid organisms thus contain two identical genomes (AA), autotriploids three (AAA), autotetraploids four (AAAA), etc. From a physiological point of view the chromosome number is denoted as n , $2n$, $3n$, $4n$, etc. and from a phylogenetic point of view as x , $2x$, $3x$, $4x$, etc. as follows:

monoploid	$n = x = 7$
diploid	$2n = 2x = 14$
triploid	$2n = 3x = 21$
tetraploid	$2n = 4x = 28$
pentaploid	$2n = 5x = 35$
hexaploid	$2n = 6x = 42$
heptaploid	$2n = 7x = 49$
octoploid	$2n = 8x = 56$, etc.

The symbols n and $2n$ indicate the chromosome numbers of the reduced (gamete) haploid and the double-diploid organism. The majority of plant organisms have different basic chromosome numbers. Rye, wheat, oats and peas have an n value of 7, for instance; hyacinths 8; fodder and sugar beet and chrysanthemums 9; maize and sorrel 10; potatoes, tomatoes and tulips 12, etc. In some genera there are two or more basic chromosome numbers, each of which has a corresponding diploid and often a polyploid series. Examples of this are *Vicia*: $x = 6, 7$ ($2x = 12, 14$); *Allium*: $x = 7, 8$ ($2x = 14, 16$, $4x = 28, 32$, $6x = 42$, 48 , $8x = 64$); *Nicotiana*: $x = 8, 9, 12$. The haploid chromosome number of *Crepis*

may be 3, 4, 5, 6, 7, 8 or 9, while in *Iris* the basic series range from 8–24, with the corresponding diploid numbers.

A multiplication of the chromosome number may lead to the origin of polyploids which are extremely varied from the point of view of genetics and cytology. Depending on whether the genomes are identical or different, organisms arising due to the multiplication of the chromosome number are referred to as auto- or allopolyploids. *Autopolyploids* are the polyploid progeny of individuals with identical genomes. In this case the organism contains only one type of genome. This type of polyploid may originate through the duplication of the chromosome sets of somatic tissues as the result of inhibited cytokinesis or through the formation of gametes without a reduction in the chromosome number. Thus, the doubling or multiplication of the chromosome number occurs within the chromosome set of the same plant (e.g. *T. monococcum*: $2n=14$; genome A, and autotetraploid *T. monococcum*: $2n=28$; genomes AA).

Autotetraploids can be produced relatively simply by inhibiting the formation of the mitotic spindle during anaphase (e.g. using colchicine). These plants usually have more intense development, but they are less fertile than the original diploid forms. This was found, for example, by BELEA (1969b) in the case of an autotetraploid of *T. monococcum* ($2n=28$). These plants could be crossed with common wheat far more readily than diploid *T. monococcum*, making it possible to transfer the disease resistance of this species into cultivated wheat. Similar results were reported for other plants. In crosses between diploid *Solanum polyadenium* ($2n=24$) or *S. chacoense* ($2n=24$) and *S. tuberosum* ($2n=48$), for example, little or no seed setting was obtained (1.2 seeds per fruit), whereas the autotetraploids of the former two *Solanum* species could be crossed far more successfully with *S. tuberosum* (30.6 seeds per fruit). Crossing was also more successful in the case of dihaploid ($2n=24$) and tetraploid ($2n=48$) potato species, or when the autotetraploid form of *Lycopersicon esculentum* was used in crosses with *L. peruvianum* instead of diploid *L. esculentum*. It proved possible to select virus-resistant, high-yielding lines from the former combination (KLEINHEMPEL–THEMANN, 1987). This phenomenon may also occur in nature, when spontaneous hybrids arise through crosses with autotetraploid species, in cases where they could not have been formed with the original diploid form.

If autotetraploids are duplicated they give rise to autooctoploid cells, which are rarely viable. If the autotetraploid plant is crossed with the initial diploid form, autotriploids are obtained (e.g. triploid water melons). In autotriploid plants, meiotic cell division is irregular, since the associations of the three doses of homologous chromosomes will not be equally distributed in meiosis. This leads to the formation of gametes with different chromosome numbers, most of which are unviable, and the plant may be completely sterile.

The polyploids of hybrids arising from interspecific and intergeneric crosses are known as allopolyploids or amphiploids. These plants are produced when the species involved in the cross have two different sets of chromosomes (A and B). Even the diploid hybrids contain genomes AB, and have chromosome numbers different to those of the parents. A distinction is made between the

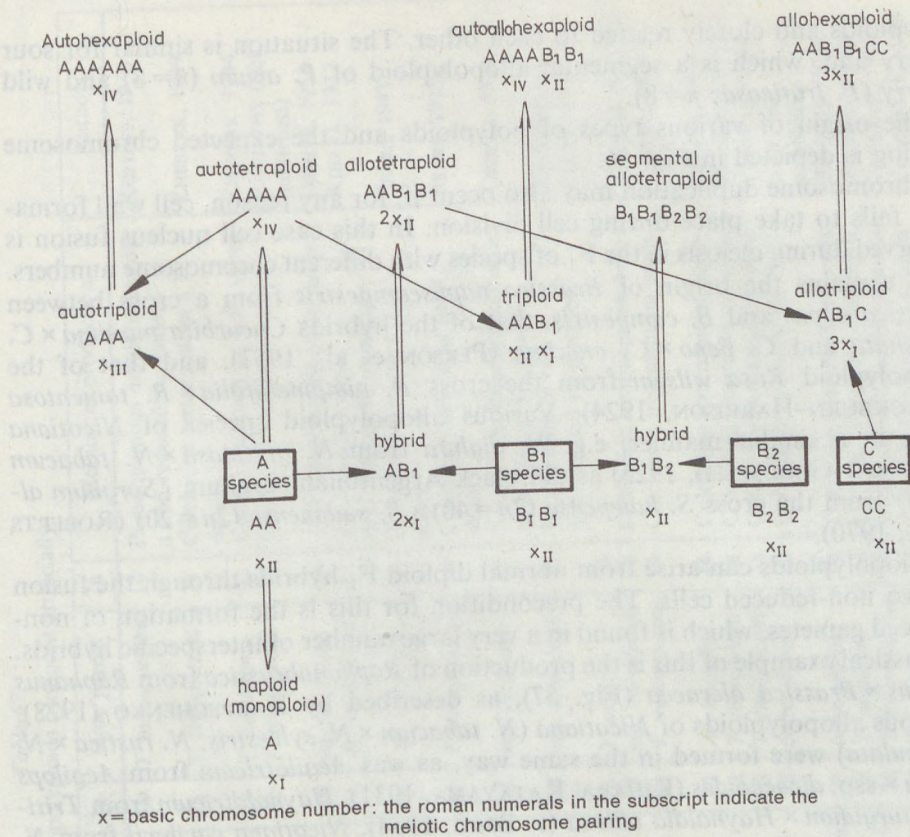


Fig. 56. Outline of the production of various polyploids (VIDA, 1981)

allopolyploids of interspecific hybrids with the same chromosome numbers and genomes, and those of interspecific or intergeneric hybrids with different chromosome numbers and genomes. These latter plants are usually stable and the progeny generation do not segregate into the parental types. This can be observed in the triticale (rye-wheat hybrid) produced by RIMPAU in 1891, which still has the same habit as that described by RIMPAU. The closer the relationship between the two parents, the greater the segregation in the progeny and the more frequently the chromosome number is reduced.

Since, in nature, the genomes become different from each other as the result of gradual evolutionary selection, any degree of transition is possible between auto- and allopolyploidy. These transitional forms are known as *autoallopolyploids*. Certain polyploid plants which were previously thought to be autopolyploids later turned out to be segmental allopolyploids. One example of this is cultivated potato (*Solanum tuberosum*), which is now regarded as the hybrid of two species (*S. stenotomum* and *S. sparsipilum*), both of which are

polyploids and closely related to each other. The situation is similar for sour cherry and, which is a segmental allopolyploid of *P. avium* ($n=8$) and wild cherry (*P. fruticosa*; $n=8$).

The origin of various types of polyploids and the expected chromosome pairing is depicted in Fig. 56.

Chromosome duplication may also occur if, for any reason, cell wall formation fails to take place during cell division. In this case cell nucleus fusion is observed during meiosis in the F_1 of species with different chromosome numbers. This explains the origin of *Brassica napuscampestris* from a cross between *Brassica napus* and *B. campestris*, that of the hybrids *Cucurbita maxima* $\times$ *C. moschata* and *C. pepo* $\times$ *C. maxima* (PERSON et al., 1951), and that of the allopolyploid *Rosa wilsoni* from the cross *R. pimpinellifolia* $\times$ *R. tomentosa* (BLACKBURN-HARRISON, 1924). Various allopolyploid species of *Nicotiana* arose in a similar manner, e.g. *N. digluta* from *N. glutinosa* $\times$ *N. tabacum* (CLAUSEN-GOODSPEED, 1925) as did black Argentinian sorghum (*Sorghum al-mum*) from the cross *S. halepense* ($2n=40$) $\times$ *S. sudanense* ($2n=20$) (ROBERTS et al., 1970).

Allopolyploids can arise from normal diploid F_1 hybrids through the fusion of two non-reduced cells. The precondition for this is the formation of non-reduced gametes, which is found in a very large number of interspecific hybrids. A classical example of this is the production of *Raphanobrassica* from *Raphanus sativus* $\times$ *Brassica oleracea* (Fig. 57), as described by KARPECHENKO (1928). Various allopolyploids of *Nicotiana* (*N. tabacum* $\times$ *N. sylvestris*, *N. rustica* $\times$ *N. paniculata*) were formed in the same way, as was *Aegilotriticum* from *Aegilops ovata* $\times$ ssp. *dicoccoides* (KIHARA-KATAYAMA, 1931), *Haynaldtricum* from *Triticum turgidum* $\times$ *Haynaldia villosa* (v. BERG, 1934), *Nicotiana vavilovii* from *N.*

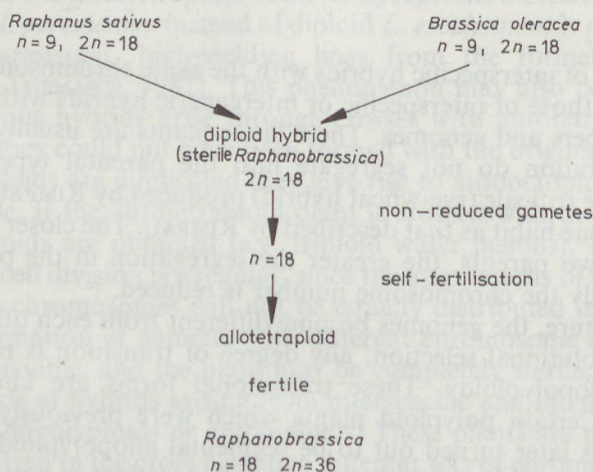


Fig. 57. Outline of the production of a *Raphanus sativus* $\times$ *Brassica oleracea* allopolyploid (*Raphanobrassica*) (KARPECHENKO, 1928)

Table 67.
Major allopolyploids produced artificially

Designation	2n	Female parent	2n	Male parent	2n	Method of production	Authors
<i>Triticum timococcum</i>	42	<i>T. timopheevii</i>	28	<i>T. monococcum</i>	14	Pseudogamous development of a non-reduced F ₁ gamete	KOSTOFF, 1936
<i>T. duro-timopheevii</i>	56	conv. durum	28	<i>T. timopheevii</i>	28	Colchicine treatment on a F ₁ shoot	ZHEBRAK, 1939
<i>T. durum-aestivum</i>	70	conv. durum	28	<i>T. aestivum</i>	42	Colch. treatment on a F ₁ shoot	ZHEBRAK, 1944
<i>T. aestivo-timopheevii</i>	70	<i>T. aestivum</i>	42	<i>T. timopheevii</i>	28	Colchicine treatment on stem	RAJHATHY (not published)
<i>T. aestivum-dicoccum</i>	56	<i>T. aestivum</i>	42	ssp. dicoccum	28	Colchicine treatment on seeds	OEHLE, 1958
<i>Aegilops speltoides-umbellulata</i>	28	<i>Ae. speltoides</i>	14	<i>Ae. umbellulata</i>	14	Fertilisation of two non-reduced F ₁ gametes	KIHARA, 1937
<i>Aegilops caudata-uniaristata</i>	28	<i>Ae. caudata</i>	14	<i>Ae. uniaristata</i>	14	Colchicine treatment on F ₁ shoot	SEARS, 1941
<i>Aegilotriticum speltoides-monococcum</i>	28	<i>Ae. speltoides</i>	14	<i>T. monococcum</i>	14	Colchicine treatment on F ₁ shoot	SEARS, 1941
<i>Aegilotriticum caudata-dicoccum</i>	42	<i>Ae. caudata</i>	14	ssp. dicoccum	28	Apogamous development of a non-reduced F ₁ gamete	OEHLE, 1934
<i>Aegilotriticum ovata-dicoccoides</i>	56	<i>Ae. ovata</i>	28	ssp. dicoccoides	28	Fertilisation of two non-reduced F ₁ gametes	TSCHERMAK-BLEIER, 1926
<i>T. tauschourarticum</i>	28	<i>T. tauschii</i>	14	<i>T. urartu</i>	14	Colchicine treatment on seeds	BELEA et al., 1974
<i>Aegilotriticum ovata-carthlicum</i>	56	<i>Ae. ovata</i>	28	ssp. carthlicum	28	Colchicine treatment on seeds	OEHLE, 1934
<i>Aegilotriticum ventricosum-monococcum</i>	42	<i>Ae. ventricosa</i>	28	<i>T. monococcum</i>	14	Colchicine treatment on seeds	OEHLE, 1934
<i>Aegilotriticum aestivum-kotschyi</i>	56	<i>T. aestivum</i>	42	<i>Ae. kotschyi</i>	14	Colchicine treatment on seeds	ZHUKOVSKY, 1928
<i>Triticum fungicidum</i>	56	ssp. carthlicum	28	<i>T. timopheevii</i>	28	Colchicine treatment on seeds	ZHEBRAK, 1944
<i>Triticum sovieticum</i>	56	conv. durum	28	<i>T. timopheevii</i>	28	Colchicine treatment on seeds	KISS (not published)
<i>T. timopheevii-durum</i>	56	<i>T. timopheevii</i>	28	conv. durum	28	Colchicine treatment on seeds	ZHEBRAK, 1944
<i>T. polonicum-durum</i>	56	conv. polonicum	28	conv. durum	28	Colchicine treatment on seeds	ZHEBRAK, 1944
<i>T. borisovii</i>	70	conv. durum	28	<i>T. aestivum</i>	42	Colchicine treatment on seeds	ZHEBRAK, 1944
<i>T. edwardii</i>	42	conv. durum	28	<i>T. monococcum</i>	14	Colchicine treatment on seeds	GANDILIAN, 1986
<i>T. monoccourarticum</i>	28	<i>T. monococcum</i>	14	<i>T. urartu</i>	14	Colchicine treatment on seeds	GANDILIAN, 1986
<i>T. sinskourarticum</i>	28	<i>T. sinskajee</i>	14	ssp. boeoticum	14	Colchicine treatment on seeds	

Table 67. (continued)

Designation	2n	Female parent	2n	Male parent	2n	Method of production	Authors
<i>Aegilotricum dicoccoides</i>	42	ssp. <i>dicoccoides</i>	28	<i>Ae. speltoides</i>	14	Colchicine treatment on seeds	McFADDEN-SEARS, 1946
<i>Ae. speltoides</i>							
<i>Aegilotricum dicoccoides</i>	42	ssp. <i>dicoccoides</i>	28	<i>Ae. umbellulata</i>	14	Colchicine treatment on seeds	McFADDEN-SEARS, 1947
<i>Ae. umbellulata</i>							
<i>Aegilotricum carthlicum</i>	42	ssp. <i>carthlicum</i>	28	<i>Ae. sharonensis</i>	14	Colchicine treatment on a young F ₁ shoot	McFADDEN-SEARS, 1947
<i>Ae. sharonensis</i>							
<i>Aegilotricum timopheevii</i>	42	<i>T. timopheevii</i>	28	<i>Ae. caudata</i>	14	Colchicine treatment on a young F ₁ shoot	McFADDEN-SEARS, 1947
<i>Ae. caudata</i>							
<i>Aegilotricum speltoides</i>	42	<i>Ae. speltoides</i>	14	<i>T. timopheevii</i>	28	Colchicine treatment on seeds	McFADDEN-SEARS, 1947
<i>T. timopheevii</i>							
" <i>T. spelta</i> "							
" <i>T. spelta</i> "							
<i>Aegilotricum ovata</i>	42	ssp. <i>dicoccoides</i>	28	<i>Ae. squarrosa</i>	14	Colchicine treatment on seeds	McFADDEN-SEARS, 1946
ssp. <i>dicoccum</i>							
<i>Aegilotricum ovata</i>	42	ssp. <i>dicoccum</i>	28	<i>Ae. squarrosa</i>	14	Colchicine treatment on seeds	KIHARA-LILIENFELD, 1949
conv. <i>durum</i>							
<i>Aegilotricum ventricosa durum</i>	56	<i>Ae. ovata</i>	28	ssp. <i>dicoccum</i>	28	Colchicine treatment on seeds	TSCHERMAK, 1929
<i>Aegilotricum ventricosa durum</i>	56	<i>Ae. ovata</i>	28	conv. <i>durum</i>	28	Colchicine treatment on seeds	TSCHERMAK, 1929
<i>Aegilotricum cylindrica durum</i>	56	<i>Ae. ventricosa</i>	28	conv. <i>durum</i>	28	Chromosome duplication in an F ₁ zygote	SZOROKINA, 1938
<i>Aegilotricum cylindrica durum</i>	56	<i>Ae. cylindrica</i>	28	conv. <i>durum</i>	28	Colchicine treatment on F ₁ plant	SEARS, 1944
<i>Aegilotricum dicoccum cylindrica</i>	56	ssp. <i>dicoccum</i>	28	<i>Ae. cylindrica</i>	28	Colchicine treatment on seeds	BERG-SEARS, 1941
<i>Aegilotricum triuncialis dicoccoides</i>	56	<i>Ae. triuncialis</i>	28	ssp. <i>dicoccoides</i>	28	Chromosome duplication in an F ₁ zygote	McFADDEN-SEARS, 1947
<i>Aegilotricum ovata dicoccoides</i>	56	<i>Ae. ovata</i>	28	ssp. <i>dicoccoides</i>	28	Chromosome duplication in an F ₁ zygote	TSCHERMAK-BLEIER, 1926

Table 67. (continued)

Designation	2n	Female parent	2n	Male parent	2n	Method of production	Authors
<i>Aegilotriticum ovata turgidum</i>	56	<i>Ae. ovata</i>	28	<i>T. turgidum</i>	28	Colchicine treatment on F ₁ plant	PERCIVAL, 1930
<i>Aegilotriticum triaristata aestivum</i>	70	<i>Ae. triaristata</i>	28	<i>T. aestivum</i>	42	Colchicine treatment on F ₁ shoot	OEHLER, 1934
<i>Aegilotriticum timopheevii bicornis</i>	42	<i>T. timopheevii</i>	28	<i>Ae. bicornis</i>	14	Colchicine treatment on seeds	McFADDEN-SEARS, 1947
<i>Aegilotriticum timopheevii uniaristata</i>	42	<i>T. timopheevii</i>	28	<i>Ae. uniaristata</i>	14	Colchicine treatment on seeds	McFADDEN-SEARS, 1947
<i>Aegilotriticum longissima durum</i>	42	<i>Ae. longissima</i>	14	conv. <i>durum</i>	28	Chromosome duplication in an F ₁ zygote	KASCHIRI, 1974
<i>Aegilotriticum timopheevii squarrosa</i>	42	<i>T. timopheevii</i>	28	<i>Ae. squarrosa</i>	14	Chromosome duplication in an F ₁ zygote	McFADDEN-SEARS, 1947
<i>Triticale durum-montanum</i>	42	conv. <i>durum</i>	28	<i>S. montanum</i>	14	Colchicine treatment on seeds	SEARS, 1947
<i>Triticale aestivum-cereale Rimpau</i>	56	<i>T. aestivum</i>	42	<i>S. cereale</i>	14	Possibly segregation from F ₁ × <i>Triticum</i>	RIMPAU, 1877
<i>Triticale aestivum-cereale</i>	56	<i>T. aestivum</i>	42	<i>S. cereale</i>	14	Colchicine treatment on seeds	KISS, 1956
<i>Haynaldtricum turgidovillosum</i>	42	<i>Haynaldia vill.</i>	14	<i>T. turgidum</i>	28	Possibly chromosome duplication in the somatic cell	V. BERG, 1934
<i>Aegilaldia umbellulata-villosa</i>	28	<i>Ae. umbellulata</i>	14	<i>H. villosa</i>	14	Colchicine treatment on F ₁ shoot	SEARS, 1941
<i>Agroticum durum-intermedium</i>	70	conv. <i>durum</i>	28	<i>Agr. intermedium</i>	42	Heat-shock treatment on the zygote	KHIZNIAK, 1937
<i>Agroticum aestivum-intermedium</i>	84	<i>T. aestivum</i>	42	<i>Agr. intermedium</i>	42	Fertilisation of two non-reduced gametes	PETO, 1938
<i>Agroticum aestivum-distichum</i>	70	<i>T. aestivum</i>	42	<i>Agr. distichum</i>	28	Colchicine treatment on seeds	PIENAAR, 1980
<i>Agroticum durum-distichum</i>	56	conv. <i>durum</i>	28	<i>Agr. distichum</i>	28	Colchicine treatment on seeds	PIENAAR, 1979
<i>Agroticum durum-elongatum</i>	42	conv. <i>durum</i>	28	<i>Agr. elongatum</i>	14	Colchicine treatment on seeds	PIENAAR, 1979
<i>T. timopheevii-bogdanii</i>	42	<i>T. timopheevii</i>	28	<i>Hordeum bogdanii</i>	14	Colchicine treatment on seeds	KIMBER, 1983
<i>H. chilense-polonicum</i>	42	<i>Hordeum chilense</i>	14	conv. <i>polonicum</i>	28	Colchicine treatment on seeds	PADILLA-MARTIN, 1983
<i>H. chilense-georgicum</i>	42	<i>Hordeum chilense</i>	14	ssp. <i>georgicum</i>	28	Colchicine treatment on seeds	PADILLA-MARTIN, 1983
<i>H. chilense-aestivum</i>	56	<i>Hordeum chilense</i>	14	<i>T. aestivum</i>	42	Colchicine treatment on seeds	CHAPMAN, 1978

Table 67. (continued)

Designation	2n	Female parent	2n	Male parent	2n	Method of production	Authors
<i>Bromus carinatus-Trini</i>	98	<i>B. carinatus</i>	56	<i>B. Trini</i>	42	Colchicine treatment on F ₁ plant	STEBBINS-- MILLER, 1950
<i>Brassica chinensis-carinata</i>	54	<i>B. chinensis</i>	20	<i>B. carinata</i>	34	Colchicine treatment on F ₁ plant	HOWARD, 1942
<i>Agrotriticum intermediodurum</i>	70	conv. <i>durum</i>	28	<i>Agr. intermedium</i>	42	Colchicine treatment on F ₁ shoot	SCHULZ-SCHAEFFER-HALLER, 1987
<i>Agrotriticum</i>	70	conv. <i>durum</i>	28	<i>Agr. triphorum</i>	42	Colchicine treatment on F ₁ shoot	POPE-LOVE, 1952
<i>Brassica napo-campestris</i>	58	<i>B. napus</i>	38	<i>B. campestris</i>	20	Chromosome duplication in an F ₁ zygote	FRANDSEN, 1947
<i>Raphanobrassica sativo-oleracea</i>	36	<i>R. sativus</i>	18	<i>B. oleracea</i>	18	Fertilisation of two non-reduced F ₁ gametes	KARPECHENKO, 1928
<i>Rosa wilsoni</i>	42	<i>R. pimpinellifolia</i>	28	<i>R. tumetosa</i>	14	Chromosome duplication in an F ₁ zygote	OECHLER, 1958
<i>Fragaria vesca-chiloensis</i>	70	<i>F. vesca</i>	14	<i>F. chiloensis</i>	56	Chromosome duplication in an F ₁ zygote	SCHIEHMANN, 1943
<i>Rubus "Nessberry"</i>	28	<i>R. trivialis</i>	14	<i>R. strigosus</i>	14	Colchicine treatment on F ₁ shoot	STRAATHOF-GOLDY, 1987
<i>Gossypium arboreum-thurberi</i>	52	<i>G. arboreum</i>	26	<i>G. thurberi</i>	26	Colchicine treatment on F ₁ shoot	BEASLEY, 1940
<i>Gossypium hirsutum-herbaceum</i>	78	<i>G. hirsutum</i>	52	<i>G. herbaceum</i>	26	Colchicine treatment on F ₁ shoot	BEASLEY, 1940
<i>Gossypium hirsutum-barbadense</i>	104	<i>G. hirsutum</i>	52	<i>G. barbadense</i>	52	Colchicine treatment on F ₁ shoot	BEASLEY, 1940
<i>Primula Kewensis</i>	36	<i>P. floribunda</i>	18	<i>P. verticillata</i>	18	Colchicine treatment on F ₁ shoot	PELLEW, 1927
<i>Nicotiana alata-plumbaginifolia</i>	38	<i>N. alata</i>	18	<i>N. plumbaginifolia</i>	20	Colchicine treatment on F ₁ shoot	FARDY-HITTIER, 1945
<i>Nicotiana glauca-plumbaginifolia</i>	44	<i>N. glauca</i>	24	<i>N. plumbaginifolia</i>	20	Colchicine treatment on seeds	KEHR-SMITH, 1952
<i>Nicotiana glutinosa-glauca</i>	48	<i>N. glutinosa</i>	24	<i>N. glauca</i>	24	Colchicine treatment on F ₁ shoot	SMITH, 1939
<i>Nicotiana suaveoleus-glauca</i>	56	<i>N. suaveoleus</i>	32	<i>N. glauca</i>	24	Colchicine treatment on F ₁ shoot	IZARD, 1950

Table 67. (continued)

Designation	2n	Female parent	2n	Male parent	2n	Method of production	Authors
<i>Nicotiana debneyi-plumbaginifolia</i>	68	<i>N. debneyi</i>	48	<i>N. plumbaginifolia</i>	20	Colchicine treatment on seeds	KEHR-SMITH, 1952
<i>Nicotiana digluta</i>	72	<i>N. glutinosa</i>	24	<i>N. tabacum</i>	48	Chromosome duplication in an F ₁ zygote	CLAUSEN-GOOD-SPEED, 1925
<i>Nicotiana rustica-suaveoleus</i>	80	<i>N. rustica</i>	48	<i>N. suaveoleus</i>	32	Colchicine treatment on F ₁ plant	IZARD, 1950
<i>Nicotiana rustica-tabacum</i>	96	<i>N. rustica</i>	48	<i>N. tabacum</i>	48	Seed centrifugation	KOSTOFF, 1937
<i>Solanum nigrumlutem</i>	120	<i>S. nigrum</i>	72	<i>S. luteum</i>	48	Regeneration of cut stem from callus	JÖRGENSEN, 1928
<i>Lycopersican pimpinellifolium-esculentum</i>	48	<i>L. pimpinellifolium</i>	24	<i>L. esculentum</i>	24	Regeneration of cut stem from callus	LINDSTROM, 1935
<i>Digitalis maritonensis</i>	112	<i>D. ambigua</i>	56	<i>D. purpurea</i>	56	Fertilisation of two non-reduced F ₁ gametes	BUXTON-DARLINGTON, 1931
<i>Lactuca indicata</i>	52	<i>L. spicata</i>	34	<i>L. indica</i>	18	Fertilisation of two non-reduced F ₁ gametes	THOMPSON, 1940

glauca × *N. langersdorfii* (KOSTOFF, 1938) and a synthetic rape species from *Brassica rapa* × *B. oleracea* (RUDORF, 1950).

Allopolyploids may also be formed in later stages of development. The species *Primula kewensis*, for example, was produced from a fertile tetraploid shoot of the F_1 of *P. floribunda* × *P. verticillata*. As the result of heat shock, certain shoots and flowers of *Nicotiana* species hybrids may also turn into allopolyploids (KOSTOFF, 1938). JÖRGENSEN (1928) obtained allopolyploids of *Solanum nigrum* × *S. luteum* from the cellus of decapitated shoots.

Allopolyploids may also segregate in the BC_3^1 due to the random distribution of chromosomes. In later generations of *Brassica rapa* × *B. oleracea* back-crossed to *B. rapa*, plants containing $2n=38$ chromosomes and reminiscent of rape segregated (RUDORF, 1950). Within a single sub-tribe MÜNTZING (1939) back-crossed primary F_1 hybrids to existing polyploids and produced a new allopolyploid of *Triticum aestivum* × *Secale cereale* ($2n=56$; genomes AABBDDRR) when back-crossing F_1 s with a non-reduced ovum to triticales. *Nicotiana rupa* also originates from selection in progeny generations of a back-cross of the F_1 hybrid ($2n=36$) of *N. rustica* ($2n=48$) × *N. paniculata* ($2n=24$) to *N. rustica*.

If the diploid species are first autotetraploidised using colchicine treatment, then crossed with each other, the F_1 plants are allopolyploids with respect to the original species. A new *Raphanobrassica* (MCNUGHTON, 1973) arose from a cross between autotetraploid *Raphanus sativus* and *Brassica oleracea*, while a cross between autotetraploid *Brassica oleracea* and *B. rapa* ssp. *rapifera* resulted in an allopolyploid very similar to the male parent, but with a higher chromosome number (OLSSON et al., 1955).

Some of the more important artificially produced allopolyploids are listed in Table 67.

4.5.5.3 Analysis of polyploids

Like pure species, allopolyploids can be easily crossed and back-crossed with each other within the same sub-tribe, often not only with the parental species, but with other species, too. *Haynaldtricum (turgo-villosum)* is easily crossed with all the cultivars of *T. aestivum*, *T. turgidum*, *Secale cereale* and *Triticale*. The *T. timopheevii* × *Hordeum bogdanii* allopolyploid crosses particularly well with the female parent (Table 68). In the meiosis of the F_1 of this hybrid there were 20^{II} , and only 13.90^{II} in the reciprocal cross. Chromosome pairing of $24.54^I + 1.58^{II} + 0.10^{III}$ was observed in meiosis in the F_1 of the allopolyploid × *Secale cereale*.

In many cases, back-crosses to the parents can only be carried out with difficulty, if at all. Although the *Digitalis purpurea-ambigua* allopolyploid can be back-crossed to the parents, the progeny are sterile (BUXTON-DARLINGTON, 1931). *Raphanobrassica* can only be crossed with tetraploid and octoploid species of *Brassica* and not with the diploid. In this case, the *Raphanus* chro-

Table 68.

Chromosome pairing in meiosis in a *Triticum timopheevii* × *Hordeum bogdanii* amphiploid and in trigenic F₁ hybrids with *Secale cereale* (after KIMBER-SALLEE, 1979)

Designation	Uni-valent	Bivalent			Trivalent	No. of cells examined
		fragment	ring	complete		
<i>T. timopheevii</i> ×	19.05	0.95	0.01	0.96	0.01	100
<i>H. bogdanii</i> F ₁	13–21	0–4	0–1	0–4	0–1	–
<i>T. timopheevii</i> ×	0.10	1.80	19.15	20.95	–	20
<i>H. bogdanii</i> amphiploid	0–2	0–4	16–21	20–21	–	–
Amphiploid ×	6.90	0.85	13.05	13.90	0.10	20
<i>T. timopheevii</i>	6–7	0–4	10–14	11–14	0–1	–
Amphiploid ×	24.54	1.56	0.02	1.58	0.10	50
<i>Secale cereale</i>	19–28	0–4	0–1	0–4	0–1	–

mosomes are eliminated and pure *Brassica* species are obtained (SHAHAVIN-SKAYA, 1937). When back-crossed to *Raphanus* the *Brassica* chromosomes are lost and pure *Raphanus* plants are obtained. This allopolyploid also crosses easily with the species *B. carinata*, *B. napus*, *B. pekinensis* and *B. campestris*, whereas it can only be crossed with the original parents with great difficulty (KARPECHENKO, 1929). *Nicotiana alata* is difficult to cross with *N. tabacum*, but the allopolyploid *N. debneyi* × *N. tabacum* is easy to cross with *N. alata*, giving fertile progeny (KEHR-SMITH, 1952). These crossing data help to illustrate the fact that in this way it is possible to create genome connections which would otherwise be virtually inconceivable.

Those allopolyploids which arise due to the duplication of the chromosomes in somatic cells, rather than through the fertilisation of non-reduced F₁ gametes or through apogamous development, are generally constant. The genomes of these parents are not homologous with each other, i.e. they are not related to each other. If, however, homology exists between one or more of the parental chromosomes or genomes, chromosome pairing will be multivalent, leading to the formation of cells with different chromosome numbers. Numerous examples of this can be cited, such as *Agropyron* × *Triticum* (POPE-LOVE, 1952), *Nicotiana* (KOSTOFF, 1938) or *Primula kewensis* (PELLEW, 1927). Within the *Agropyron* genus, the chromosome pairing in the F₁ of the allopolyploid *Agropyron curvifolium* × *A. repens* was 6.01^I + 31.36^{II} + 0.17^{III} + 0.19^{IV} (DEWEY, 1981) (Table 69). This leads to varying degrees of fertility and to morphological differences in the progeny.

The allopolyploid *T. aestivum* (ABC) × *T. timopheevii* (AG), where there is a common (A) genome, also has greater fertility than the initial species hybrid due to the chromosome duplication. Fertility was poorer for the *Aegilops ovata* (C^aM^o × ssp. *carthlicum* (AB) allopolyploid, where there are no common genomes, and this fertility continued to drop in later generations, particularly in the F₂ (Table 70).

Table 69.

Chromosome pairing in meiosis in *Agropyron curvifolium*, *A. repens*, their F_1 hybrid and the allopolyploid (after DEWEY, 1980)

Combination	Plant number	Chromosome number	Chromosome pairing							
			I		II		III		IV	
			devia- tion	mean	devia- tion	mean	devia- tion	mean	devia- tion	mean
<i>A. curvifolium</i>	10	28	0-2	0.03	10-14	13.76	0-1	0.003	0-2	0.11
<i>A. repens</i>	3	42	0-4	0.24	17-21	20.31	0-1	0.01	0-2	0.28
F_1 hybrid	12	35	7-23	14-82	5-14	9.73	0-2	0.20	0-1	0.03
C_3 allopolyploid	1	70	0-20	6.02	25-35	31.36	0-2	0.17	0-2	0.19

Allopolyploidisation can also be used to transfer favourable economic characters from wild species into cultivated species. It was with this end in view that ZSEBRAK (1944) and TAVRIN (1964) produced the allopolyploid of *T. aestivum* $\times$ *T. timopheevii*, which they named *T. borisovii*. In this way they hoped to transfer the disease resistance of *T. timopheevii* into common wheat. After colchicine treatment and back-crossing to *T. aestivum*, sesquidiploid plants, containing the full chromosome set (ABD) of common wheat and the A genome of *T. timopheevii*, were selected with a frequency of 40% from the $2n=70$ plants (CARENYA-NIKOLSKII, 1966).

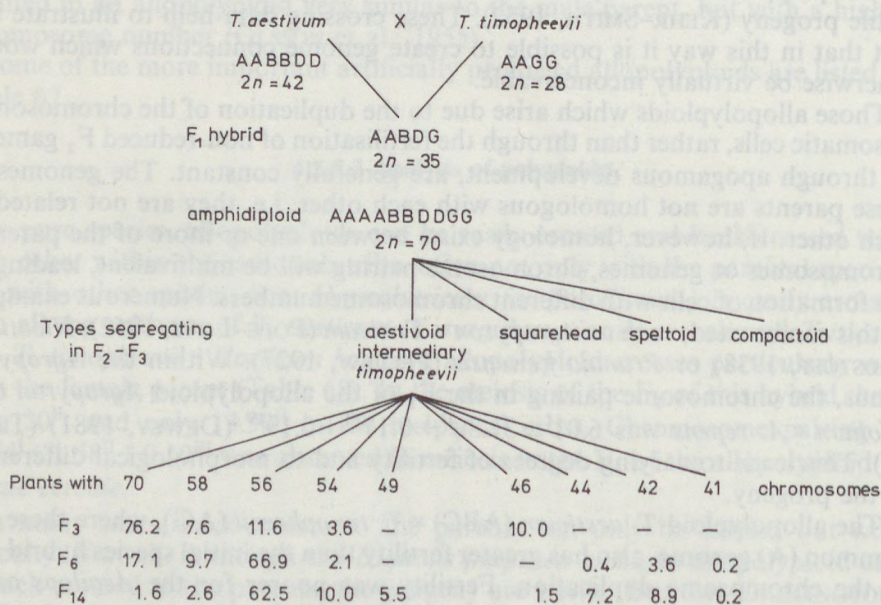


Fig. 58. Reduction of the chromosome number in the *T. aestivum* $\times$ *T. timopheevii* allopolyploid (BELEA, 1976)

Table 70.
Major quantitative characters of the *Aegilops ovata* × ssp. *carthlicum* allopolyploid

Generation	Plant no.	Chromo-some number	Plant height			Ear length			Ears/plant			Grains/ear		
			$\bar{x}$	s	$S_{\bar{x}}$	$\bar{x}$	s	$S_{\bar{x}}$	$\bar{x}$	s	$S_{\bar{x}}$	$\bar{x}$	s	$S_{\bar{x}}$
F ₁ F ₂ F ₃ F ₄ F ₅	27	56	66.0	2.3	1.2	6.3	3.3	0.7	41.0	4.8	1.9	13.8	4.3	1.7
	51	56	57.5	1.2	0.0	6.5	0.2	0.0	16.2	2.2	0.6	5.0	2.8	2.0
	49	56	52.8	9.9	3.0	5.9	0.9	0.0	14.1	3.7	1.3	6.1	1.2	0.4
	11	56	45.0	7.7	2.7	6.7	0.8	0.3	15.9	2.9	1.4	6.7	1.3	0.5
	27	56	40.1	0.8	0.3	6.6	1.0	0.4	17.9	5.1	1.9	8.0	3.8	0.9
<i>Ae. ovata</i> ssp. <i>carthlicum</i>	50	28	46.0	2.0	1.0	3.3	2.6	0.6	43.3	7.3	2.8	5.0	2.7	1.5
	45	28	83.5	2.3	0.5	10.2	1.9	0.6	11.2	2.8	0.4	32.1	8.1	2.6

Sesquidiploid plants may arise if non-reduced gametes also take part accidentally in pollination. These often differ phenotypically from the diploid parents. The parental chromosome number and gene quality leaves its mark on their habit, since the hybrids have an extra set of male chromosomes.

The allopolyploids *T. aestivum* × *T. timopheevii*, produced in Hungary by Rajháthy, and *Aegilops ovata* × ssp. *carthlicum* (AABB^CC^MM^O), obtained by Belea using colchicine treatment, were employed by BELEA (1976) as sources of disease resistance (leaf and stem rust, powdery mildew). In the second and third generations of the first combination mentioned, in addition to intermediate plants, compactoid, squarehead, speltoid, etc. types also appeared. These types were sterile. The vast majority of the original allopolyploids, which contained $2n=70$ chromosomes, became reduced to octoploids with $2n=56$ chromosomes. A few plants were reduced to even lower chromosome numbers in later generations (BELEA, 1976; BELEA-FEJÉR, 1981; Fig. 58).

This allopolyploid also facilitated the study of the genetic background of disease resistance. The appearance of such a large proportion of plants with $2n=56$ chromosomes made it possible for the first time to determine whether a full genome was lost, or whether chromosomes were eliminated at random. Traditional karyotypic analysis indicated that the chromosomes belonging to the A or G genomes of *T. timopheevii* were the first to be eliminated (Fig. 59). Later, chromosomes belonging to other genomes were lost in the course of reduction. Thus, elimination does not affect whole genomes, but involves random chromosomes (FEJÉR-BELEA, 1978b).

This finding was confirmed by electrophoretic isoenzymatic analyses. It is a well-known fact that structural genes coding the isoenzyme alcohol dehydrogenase (ADH) are located on the chromosomes of the 4th homoeologous group of wheat (HART, 1970). Taking this into consideration, it can be seen from the ADH zymograms that it was the chromosomes of homoeologous group 4, belonging to genomes A and G of *T. timopheevii*, that were missing from plants with $2n=56$ chromosomes. By contrast, in $2n=44$ addition lines, chromosomes 4A and 4G were absent. In the two parent plants a phenotypically distinctive ADH triplet characteristic of tetra- and hexaploid species is present. The ADH spectrum of the $2n=56$ allooctoploid is identical to that of *T. timopheevii*, while the $2n=44$ plants exhibited the phenotype of common wheat (Fig. 60). Esterase (EI) analyses, in agreement with the karyotypic analysis, indicated the lack of the 3A, 3G, 6A and 6G chromosomes of *T. timopheevii* in plants with $2n=56$ chromosomes.

SCHULZ-SCHAEFFER-HALLER (1987) observed after the amphiploidisation ($2n=70$) of conv. *durum* ($2n=28$) × *Agropyron intermedium* ($2n=42$) that hybrids with a chromosome number of $2n=56$ appeared more frequently. Principally the chromosomes of the male parent were lost.

The random elimination of chromosomes was observed by BELEA and co-workers (1974) in the octoploid *Aegilops ovata* × ssp. *carthlicum* ($2n=56$), too. In lines reduced to a chromosome number of $2n=49$, marker chromosomes were used to identify the chromosomes. In the case of *Ae. ovata* these were

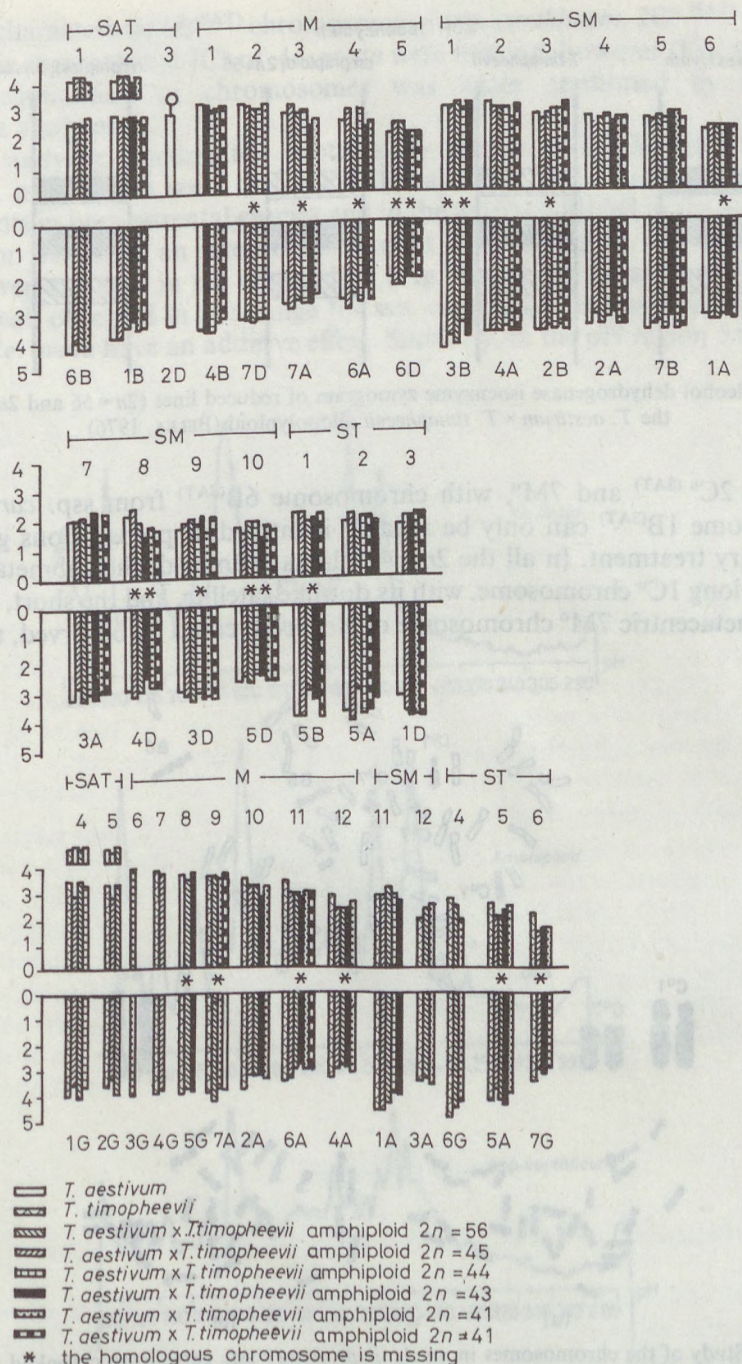


Fig. 59. Study on the reduction of the *T. aestivum* x *T. timopheevii* allopolyploid with the aid of karyotype analysis (BELEA, 1976)

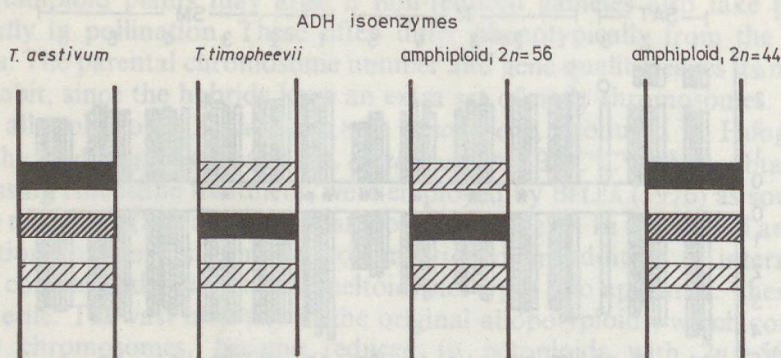


Fig. 60. Alcohol dehydrogenase isoenzyme zymogram of reduced lines ($2n=56$ and $2n=44$) of the *T. aestivum* $\times$ *T. timopheevii* allopolyploid (BELEA, 1976)

$1C^{u(SAT)}$, $2C^{u(SAT)}$ and $7M^o$, with chromosome $6B^{(SAT)}$ from ssp. *carthlicum*. Chromosome $1B^{(SAT)}$ can only be reliably identified in preparations given no preliminary treatment. In all the $2n=49$ plants examined, the submetacentric, relatively long $1C^{u(SAT)}$ chromosome, with its dot-like satellite, and the short, approximately metacentric $7M^o$ chromosome of *Ae. ovata* could be observed, as could



Fig. 61. Study of the chromosomes in an *Aegilops ovata* $\times$ ssp. *carthlicum* octoploid with a chromosome number reduced to $2n=49$, with the aid of karyotype analysis (a) *Ae. ovata*, (b) ssp. *carthlicum* parental chromosomes (BELEA et al., 1974)

the long, characteristic 6B^(SAT) chromosome of *ssp. carthlicum*. 2C^u (SAT) and the acrocentric chromosome 7C^u of *Ae. ovata* were missing, however (Fig. 61). The random elimination of chromosomes was again confirmed by esterase isoenzyme analyses.

When studying fractionated proteins by means of isoelectric focussing (IEFPG), it could be seen that the IEP values of the majority of protein components in both parental species and in the amphiploid fell in the acidic pH range. For *Ae. ovata* an intense peak could be observed at pH 4.80, which became even stronger in the amphiploid (Fig. 62). It can be assumed that the smaller peak observed in this range for *ssp. carthlicum* and the corresponding peak of *Ae. ovata* have an additive effect. Similarly, in the pH region 5.05–0.16,

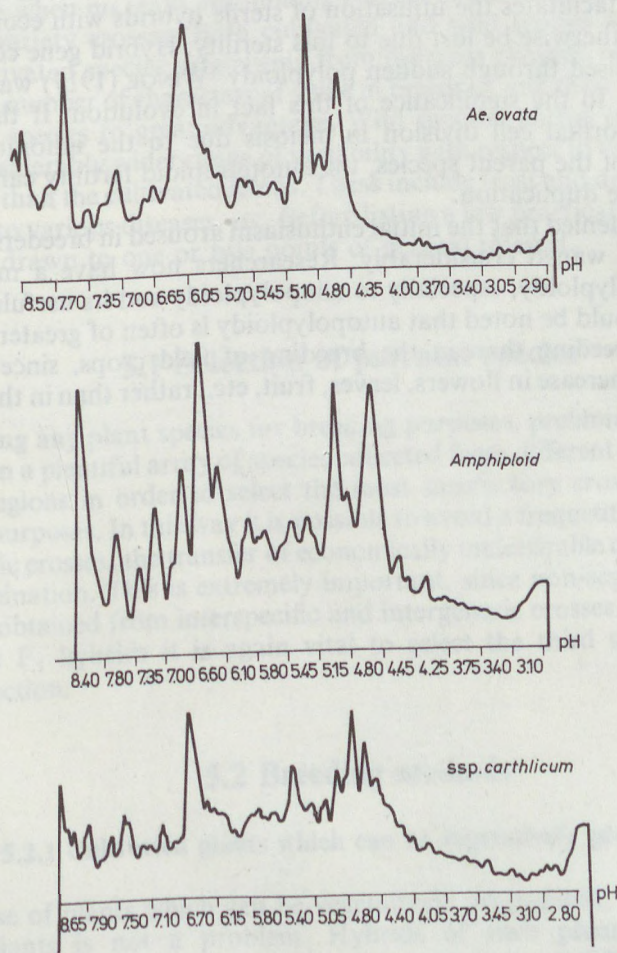


Fig. 62. Densitometer curves of the proteins of the *Aegilops ovata* × *ssp. carthlicum* allopolyploid and the parents after fractionation by means of electrophoresis (FEJÉR et al., 1976).

there is another extremely intensive peak in the amphiploid, which can be explained by codominance.

In general, the F_1 plants of allopolyploids are uniform. In later generations, depending on the degree of relationship between the parental partners, types differing from the intermediate type appear with greater or lesser frequency. In the F_3 generation of the allopolyploid *Ae. ovata* $\times$ ssp. *carthlicum*, for example, plants reminiscent of *Ae. ovata* but, unlike the female parent, easily threshed and awnless, are to be found among the plants, which are mostly of the compact ear type. A characteristic feature is the extremely large grain, which is slightly pointed at each end. The crease is deep and the germ lies at an angle of less than 45° .

One great advantage of polyploidy, apart from the creation of new forms, is the fact that it facilitates the utilisation of sterile hybrids with economic value, which would otherwise be lost due to this sterility. Hybrid gene complexes are generally stabilised through sudden polyploidy. WINGE (1917) was the first to draw attention to the significance of this fact in evolution. If the sterility is caused by abnormal cell division in meiosis due to the inhomology of the chromosomes of the parent species, the autotetraploid fertility can be restored by chromosome duplication.

It cannot be denied that the initial enthusiasm aroused in breeders by artificial polyploidy has waned considerably. Researchers now have a more realistic approach to polyploidy, especially to allopolyploidy and its usefulness in plant breeding. It should be noted that autopolyploidy is often of greater significance in vegetable breeding than in the breeding of field crops, since the aim of breeding is an increase in flowers, leaves, fruit, etc., rather than in the grain yield (e.g. cereals).

5. Practical results and future prospects

Interspecific and intergeneric crosses were carried out for practical purposes even before the time of Mendel, but real interest in this field was not expressed until a time when no really resounding success could be achieved any more by means of variety crosses. Both cultivated and wild species were used in this work. Cultivated species originating from different climatic regions often possess a large number of characters of value in breeding, and these can be combined with other species to great advantage. Wild species, on the other hand, often have a considerably wider range of variability with respect to valuable economic characters than the cultivated forms. These include frost and drought resistance, resistance to various diseases, etc. Before listing a few practical results, attention should be drawn to one or two points of general interest.

5.1 Selection of parental species

Before using any plant species for breeding purposes, preliminary studies must be made on a plentiful array of species collected from different geographical and climatic regions in order to select the most satisfactory crossing partners for breeding purposes. In this way it is possible to avoid a frequent error threatening interspecific crosses: the transfer of economically undersirable characters into the new combination. This is extremely important, since non-segregating progeny are often obtained from interspecific and intergeneric crosses. When top-crossing sterile F_1 hybrids it is again vital to select the third species with great circumspection.

5.2 Breeding methods

5.2.1 Cultivated plants which can be vegetatively propagated

In the case of plants which can be vegetatively propagated, the sterility of the hybrid plants is not a problem. Hybrids of such plants can be further propagated without any difficulty even if the parents have differing chromosome numbers and genome quality. If success is achieved with a single cross, rather

than selecting desirable individuals from a segregating population, new lines, chiefly the hybrids of allopolyploid cultivated plants, can be propagated directly using vegetative techniques.

If the progeny are raised from seed, the segregating types may be sterile or fertile, homozygotic or heterozygotic, cytologically balanced or unbalanced, having different chromosome numbers. By vegetative means, these plants, too, can be further propagated. Naturally, the majority of these continue to segregate when they are sown from seed again. Every single progeny may lead to a new cultivar, if they satisfy breeding and production requirements. In such cases it does not matter whether they are cytologically balanced or not. In this way, countless valuable cultivars have been born, for instance in the *Iris* genus, where a multitude of triploid, pentaploid and aneuploid forms are to be found among the forms grown in gardens. The majority of *Saccharum* cultivars (BREMER, 1931) are aneuploid, as are various garden ornamentals, such as *Crocus* (PROPACH, 1938) and *Hyacinthus* (DE MOL, 1928).

The so-called secondarily balanced species provide a good illustration of the significance of aneuploidy in the formation of new, valuable cultivated plants. A particularly good example of this is the Pomoideae family, which comprises

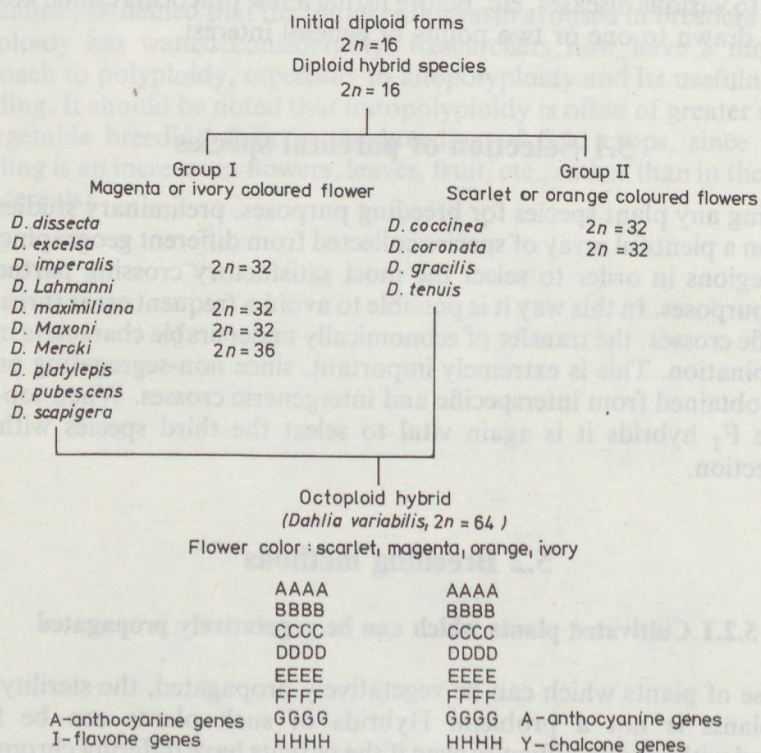


Fig. 63. Outline of the origin and constitution of dahlias (CRANE-LAWRENCE, 1952)

such fruit species as apples, pears and quinces. These all developed from a basic genome containing seven chromosomes, which now exist in the forms $AA_1BB_1B_2CC_1C_2DD_1EE_1FF_1GG_1$. Some of the species are tetraploids, others hexaploids. In these plants, aneuploidy has led to the creation of aneuploid chromosome combinations which effectively promote the formation of high-yielding cultivated plants. Among the ornamentals, numerous valuable cultivars of tulips, daffodils, hyacinths, irises, etc. are aneuploid, indicating the fact that aneuploidy may play an important role, particularly in the case of plants which can be vegetatively propagated.

A great many spontaneous autotetraploid cultivars of pear (Diel, Pap), raspberry and grape, various ornamentals, such as certain primulas (*Primula sinensis* and *P. malacoides*), dahlias (*Dahlia variabilis*; Fig. 63) and hyacinths (*Hyacinthus orientalis*), the Tetra cultivar of Antirrhinum and certain cultivars of red clover (*Trifolium pratense*) and late turnips have all originated in this manner. The artificially produced autotetraploid cultivar of tomato produces more ascorbic acid even in the shade than diploid tomatoes matured in the sun. The leaves and tendrils of autotetraploid water melons are broader and more resistant to diseases caused by *Collectrichum*. Cultivated strawberry (*Fragaria ananassa*) is also an artificially autotetraploidised plant. The different variants of this are vegetatively propagated hybrid clones originating from a cross between two octoploid species (*F. chiloensis* and *F. virginiana*). Later, the genome of yet another octoploid species (*F. cuneifolia*) enriched the genome reserves of strawberries. The strawberry cultivar Vescana, which has $2n=70$ chromosomes, is derived from a back-cross of the non-reduced F_1 of *F. ananassa* $\times$ *F. vesca* to *F. ananassa* (Fig. 64).

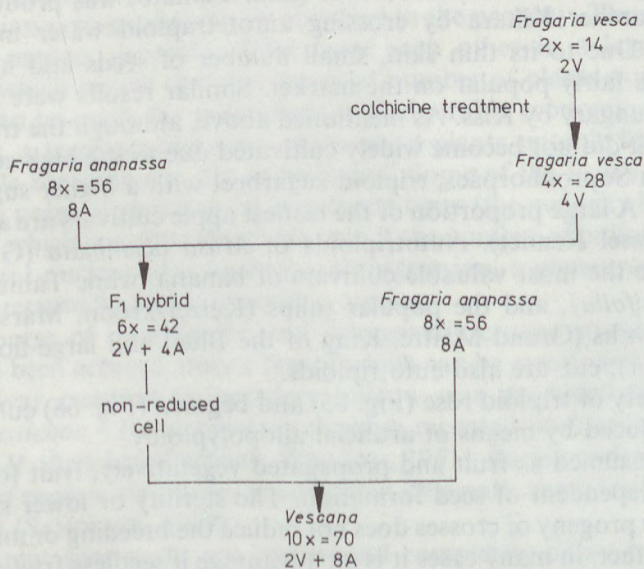


Fig. 64. Outline of the production of the strawberry cultivar Vescana (KUCKUCK, 1979)

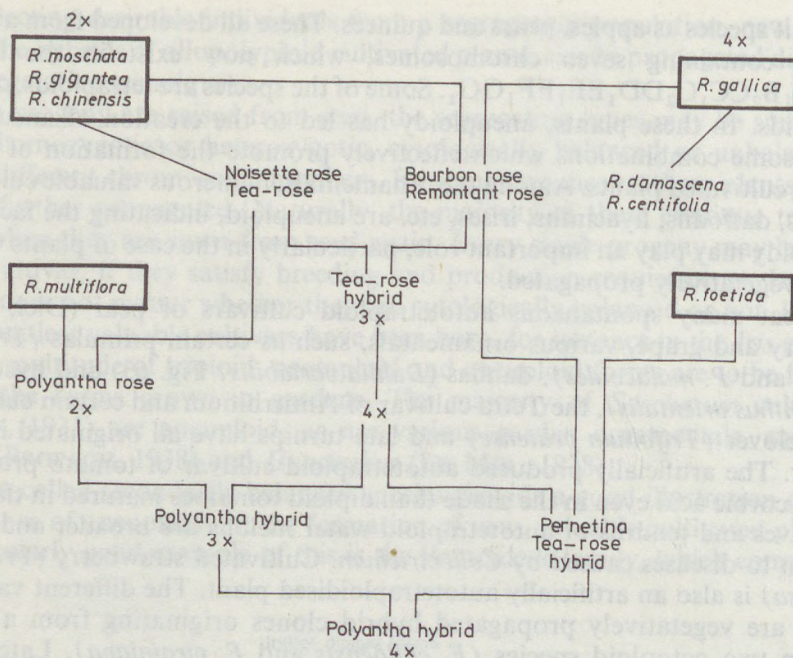


Fig. 65. Outline of the production of various rose hybrids (KUCKUCK, 1979)

The first triploid water melon cultivar (Shin-Yamato) was produced by the Japanese researcher Kihara by crossing autotetraploid water melon to its diploid form. Due to its thin skin, small number of seeds and higher sugar content, it was fairly popular on the market. Similar results were achieved in Kecskemét, Hungary by Kiss. As mentioned above, although the triploid form was valuable, it did not become widely cultivated due to the high costs of seed production. In Sopronhorpács, triploid sugarbeet with a higher sugar content was produced. A large proportion of the tastiest apple cultivars are also triploid (Boskoop, Kassel Rennet). Autotriploids of *Musa acuminata* (Gros Michel Cavendish) are the most valuable cultivars of banana, while Tahitian lemons (*Citrus aurantifolia*), and the popular tulips (Keizer-kroon, Marsenet, Pink, Beauty), hyacinths (Grand Maitre, King of the Blue) and large-flowered daffodils (Emperor), etc. are also autotriploids.

A great variety of triploid rose (Fig. 65) and begonia (Fig. 66) cultivars have also been produced by means of artificial allopolyploidy.

In plants consumed as fruit and propagated vegetatively, fruit formation is often quite independent of seed formation. The sterility or lower seed setting observed in the progeny of crosses does not reduce the breeding or market value of the fruit. In fact, in many cases it is an advantage if seedless fruit are formed (e. g. triploid water melon, grapes, apples, etc.)

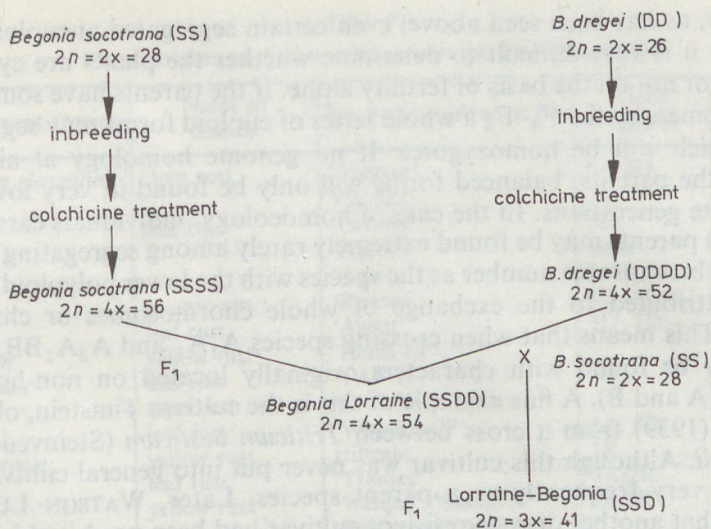


Fig. 66. Outline of the production of Lorraine-Begonia (KUCKUCK, 1979)

5.2.2 Cultivated plants which can be sexually propagated

Any cultivated plant which is grown for its vegetative organs or seeds can be propagated sexually. As mentioned above, if the parents have identical chromosome numbers and homologous genomes, the first generation will be fertile and Mendelian segregation can be observed in the progeny. The only difficulty is that the parents generally differ from each other in a large number of characters, which means that a substantial number of plants must be raised if selection is to be made for individuals with desirable economic characters. In other words, a large population is necessary if plants suitable for the theoretically possible breeding aim are to be found. Some of the forms of value from the breeding point of view consist of extreme types (the majority being recessive characters), which are often sought in vain if the number of individuals is small. A larger plant number also facilitates transgression, a phenomenon often observed in interspecific and intergeneric crosses.

In the course of interspecific and intergeneric crosses numerous practical results have been achieved, only a few of which can be mentioned here. A spring barley cultivar resistant to powdery mildew was produced from the cross *Hordeum distichon* × *H. spontaneum* through repeated back-crossing of the F₁ progeny to *H. distichon* (RUDOLF-WIENHUS, 1951). Barley varieties resistant to barley dwarf mosaic virus were produced in Denmark using triploid and aneuploid forms (SANDFAER, 1979).

If the parent species do not correspond completely either in chromosome number or in genome quality, breeding is complicated by loss of fertility.

Naturally, as has been seen above, even certain segregated aneuploids may be fertile, so it is very difficult to determine whether the plants are cytologically balanced or not on the basis of fertility alone. If the parents have some homologous genomes, by the F_4 - F_5 a whole series of euploid forms may segregate, not all of which will be homozygotes. If no genome homology at all is found between the parents, balanced forms will only be found in very low numbers in very late generations. In the case of homoeology, individuals carrying traits from both parents may be found extremely rarely among segregating types with the same chromosome number as the species with the lower polyploid level. This can be attributed to the exchange of whole chromosomes or chromosome sections. This means that when crossing species A_1A_1 and A_2A_2BB , combinations may be found with characters originally located on non-homologous genomes (A and B). A fine example of this is the cultivar Timstein, obtained by PRIDHAM (1939) from a cross between *Triticum aestivum* (Steinvedel) and *T. timopheevii*. Although this cultivar was never put into general cultivation, it is still used very frequently as a parent species. Later, WATSON-LUIG (1958) reported that another disease-resistant cultivar had been produced in Australia from this same combination. This was marketed under the name Timvera. HEYNE-JONSTON (1954) and KUSPIRA-UNRAU (1957) used these two cultivars to produce several disease-resistant cultivars. RUDORF (1956) mentions the fact that the disease-resistant cultivar Newthatch also inherited this character indirectly from *T. timopheevii*. BRIGGLE-REITZ (1963) and SUNESON (1947) give the origin of the disease-resistant wheat cultivars Ideal 59, Ace, Georgia 1123 and Bladsoe as a cross between *T. timopheevii* and *T. aestivum*, as does AFIFI (1953) in the case of the cultivar Tousson.

The cultivars Hope and H_{44} , which are again disease-resistant, were selected by MCFADDEN (1930) from the progeny generation of a cross between the Russian cultivar Emmer (ssp. *dicoccum*) and the Canadian cultivar Marquis (*T. aestivum*). These were then used to produce the cultivars Apex, Vesta, Rival and Mercury. According to FRASEN-PETERSON (1954) the cultivars Pilot, Renown, Regent, Stewart and Carleton all originated from interspecific crossing, the last two having been selected from the combination Marquis $\times$ Jumillo (conv. *durum*). In the Institute of Breeding and Genetics in Odessa, the cultivars Sarrubra, Sarrosa and Blanza were again produced using conv. *durum*. The stem rust resistant cultivars Lutescens 3632, Erythrospermum 8303, Erythrospermum 7801, Candicans 76/10, Kamelinka E-223 and Caesium 94/1453 were also derived from interspecific crosses.

The Italian researcher RUSMINI (1959) produced the wheat cultivar Capelli from the combination (*T. turgidum* $\times$ conv. *durum*) $\times$ conv. *durum*, while Strampelli made a cross between Duro di Puglia (conv. *durum*) and Akagomughi (*T. aestivum*), which resulted in the strong-stemmed dwarf cultivar Balilla, later used as a parent species in producing numerous cultivars (San Pastore, Fortunato, Valino, Turano, etc.). Certain sources of disease resistance which can be used to improve the resistance of common wheat are listed in Table 71.

When studying the protein and lysine contents of wheat cultivars and inter-

Table 71.

Major sources of disease resistance in the *Triticae* subtribe

Donor parent species	Name of disease	Recurrent cultivar or line	Gene symbol	Authors
<i>Agropyron elongatum</i>	stem rust	'Thatcer' PW 327	6A 6D,	ZELLER, FISCHBEK, 1974
	leaf rust	'Pawnee'	3D	
		'Agrus'	Lr19	
		'Agatha'	Lr19	
	mosaic virus	'Rescue'	5D, 6D	
	leaf rust	'Agent'	3D, 7D	
<i>Agropyron intermedium</i>	yellow rust	'Heine IV'		
	leaf rust	'TAF 1'		
	stem rust	'TAF 2'		
<i>Secale cereale</i>	leaf rust	'Vilmorin 27'	3A, 7D	
	yellow rust	tritiale	1R	CAUDERON, 1983 LELLEY, 1976
	leaf rust	'Transec'	4A/2R	
	yellow rust	'Weique', 'Sanno', 'Feldkrone', 'Hamlet', 'Linos', 'Kavkaz', 'Aurora', 'Lovrin 10', 'Lovrin 12', 'Lovrin 13', 'Winetou', 'Clement', 'Disponent', 'Persue', 'Zorba', 'Salzmünder', 'Orlando', 'Saladin', 'Neuzucht', 'Wentzel', St. 2153/63, 'Imperial', 'Holdfast', 'Riebasel'	1B/1R	
<i>Aegilops umbellulata</i>	leaf rust	'Chinese Spring'	A/6C ^u /	
	leaf rust	'Transfer'	Lr9	
<i>Aegilops comosa</i>	yellow rust	Chinese Spring	2M	
	yellow rust	'Compair'	2D/2M	
<i>Aegilops ventricosa</i>	yellow rust	'Roazon'		
<i>Triticum timopheevii</i>	stem rust	'Hope', H 44,	Sr18	
	powdery mildow	'Khapstein', 'Lee', 'Timgalen', 'Timvera', 'Timstein', 'Versntein', 'Pawnee', 'Transfer', 'Gabo', 'Lee'	Sr7/a Sr5, 99 Sr11 Lr3, Lr10 Lr14a	
	leaf rust	'Hope', 'H 44'	Sr21	
	powdery mildow		Sr3	
<i>Triticum monococcum</i>	stem rust	'Marquillo', 'Jumillo'		
<i>T. turgidum</i> conv. <i>durum</i>				
<i>T. turgidum</i> ssp. <i>dicoccum</i>	powdery mildow	'Khapli'	Pm4	
<i>T. monococcum</i> ssp. <i>boeoticum</i>	stem rust	'Spelmar', 'Mindum'	Sr22	

specific hybrids, BELEA-SÁGI (1978) found that the negative correlation experienced in variety hybrids between the protein and lysine contents was far less pronounced in interspecific hybrids. It is thus considerably easier to select for high protein and lysine contents from interspecific crosses (Table 72).

By repeatedly back-crossing the hybrid of *Lycopersicon esculentum* × *L. pimpinellifolium* to cultivated tomato, RUDOLF (1949) produced a cultivar resistant to wilting disease. In a similar manner, SACCARDO-MONTI (1987) obtained lines resistant to *Verticillium dahliae*, *Fusarium oxysporum*, *Phytophthora infestans* and tobacco mosaic virus from repeated back-crosses of the species wild *Lycopersicon peruvianum*, *L. hirsutum*, *L. pimpinellifolium* and *Solanum pennellii* to various cultivars of cultivated tomato (F_5BC_3). These lines also possessed desirable agronomic traits and high fruit quality.

In 1950, RUDOLF re-synthesised *Brassica napus* ($2n=38$) from a cross between *B. oleracea* ($2n=18$) and *B. campestris* ($2n=20$) and produced cultivars that were better than the high-yielding cultivar Lembke which was generally cultivated at the time.

If the crossing partners have no homologous genomes, results can best be achieved by means of chromosome addition or substitution. In 1958, using this

Table 72.
Protein and lysine contents of interspecific wheat (*Triticum* L.) hybrids

Combination	Protein content		Lysine content	
	%	Deviation from the standard	%	Deviation from the standard
PP-1 3119 standard	18.20	100	2.43	100
Tiszatáj GKI-2	18.10	-0.55	2.78	14.4
<i>T. aestivum</i> × <i>T. timopheevii</i> amphiploid	16.27	-10.61	2.60	7.0
(<i>T. turgidum</i> × <i>Produttore</i>) × <i>Bezostaya</i>	18.82	0.34	2.70	11.1
(<i>Bezostaya</i> × amphiploid) × conv. <i>durum</i>	19.38	6.50	2.70	11.1
(Eryth. 3201 × <i>T. turgidum</i>) × F293	22.47	23.46	2.80	15.2
(Eryth. 3201 × <i>T. turgidum</i>) × F293 BC ²	21.40	17.58	2.90	19.3
<i>T. aestivum</i> × ssp. <i>dicoccoides</i>	21.20	16.48	2.60	7.0
conv. <i>ispahanicum</i> × ssp. <i>dicoccoides</i>	19.81	8.81	2.70	11.1
conv. <i>ispahanicum</i> × ssp. <i>dicoccum</i>	19.70	8.24	2.70	11.1
ssp. <i>carthlicum</i> × ssp. <i>dicoccum</i>	24.70	35.71	2.90	19.3
(ssp. <i>dicoccoides</i> × conv. <i>durum</i>) × <i>T. aestivum</i>	20.06	10.21	2.90	19.3
ssp. <i>dicoccum</i> × conv. <i>durum</i>	19.74	8.46	2.60	7.0
conv. <i>polonicum</i> × <i>T. aestivum</i> (Bezost.)	19.68	8.13	2.60	7.0
(<i>T. monococcum</i> × <i>T. zhukovskyi</i>) × Bezost.	24.96	37.14	2.80	15.2
(<i>Ae. cylindrica</i> × conv. <i>vavilovii</i>) × F293	17.80	2.20	2.80	15.2
conv. <i>durum</i> × <i>T. timopheevii</i>	19.88	9.23	2.80	15.2
(<i>T. timopheevii</i> × ssp. <i>dicoccum</i>) × Bezost.	17.26	-5.17	2.80	15.2
(<i>T. timopheevii</i> × ssp. <i>carthl.</i>) × <i>T. aestivum</i>	18.92	3.95	2.60	7.0
(<i>T. timopheevii</i> × ssp. <i>carthl.</i>) × ssp. <i>dicoccum</i>	22.70	24.72	2.70	11.1
(<i>T. timopheevii</i> × ssp. <i>carthl.</i>) × F293	20.14	10.60	2.85	17.3
(<i>T. timopheevii</i> × ssp. <i>carthl.</i>) × conv. <i>durum</i>	22.64	24.39	2.60	7.0

latter method, the 1B chromosome of wheat was successfully replaced in Kecs-kemét by the 1R chromosome of rye, giving rise to a hairy-necked type of wheat which is still in existence today. The productive wheat cultivars Riebesel, Salzmünder and Orlando contain 20 wheat+2 rye chromosomes. The rust resistance of the wheat cultivar Neuzucht and its derivatives (Aurora, Kavkaz, etc.) is attributed to a chromosome segment pair. In the Mexican hexaploid triticale Armadillo the 2R chromosome pair from rye replaces the 2D chromosome pair of wheat. The lines Transec and Agatha, both used as sources of rust resistance, inherited this favourable property by means of translocation from rye and *Agropyron elongatum*, respectively. The leaf rust resistance of *Aegilops umbellulata* (SEARS, 1956b), the stem rust resistance of *T. timopheevii* (BELEA, 1976) and the mosaic virus resistance of octoploid *Agrotricum* have all been substituted into common wheat. The resistance of *Aegilops ventricosa* to *Septoria* and yellow rust was also transferred in this way into the cultivar Roazon, already generally cultivated in France, using ssp. *carthlicum* as an intermediate species.

DVORAK-KNOTT (1974) transferred the stem rust resistance of *Agropyron elongatum*, RILEY et al. (1968) the yellow rust resistance of *Aegilops comosa* and KIMBER (1967) the resistance of *Ae. ventricosa* to stem rust and foot diseases (*Cercospora*) into wheat by means of addition. The cultivar Compair, produced in this way, is now in general cultivation. LEE-LARTER (1970) added the favourable properties of the wheat cultivar Kharkov to rye.

A classical example of the addition of a whole genome from one species to another is the production of hexa- and octoploid triticale. The primary *octoploid* $\times T. aestivum$ hybrids had a slight advantage over the octoploids, but the real success was achieved with the secondary hexaploid triticale. From the combinations triticale $6x \times$ triticale $8x$ and triticale $6x \times Triticum aestivum$, *Secale cereale*, *T. turgidum* or conv. *durum* it proved possible to produce a new type of constant hexaploid wheat-rye hybrid which, under certain ecological conditions, was able to compete with high-yielding wheats and ryes. It could not compete with rye on poor quality sandy soils, however.

This new synthetic hybrid is of especial interest because, up till now, only a sterile form had been observed in nature. This leads to the conclusion that, from the point of view of breeding, triticale represents a step towards the production of new species or new cultivars, which, through careful, patient selection, could lead to new combinations capable of competing with the cultivated cereals formed several thousand years ago.

Asynchrony was discovered in the triticale genome with respect to the chromosome pairing of the wheat and rye chromosomes, and this was attributed mainly to the doses of the polygenes. None of the wheat genomes contains all the genes capable of cooperating with the rye genome; instead, these are scattered around in wheats and rye with different genotypes. With the aid of widely varying crosses and adequate selection, these can now be combined in a single plant.

Since hexaploid triticale is a completely new plant species, it was not exposed

to natural evolution. This explains its poorer adaptability compared to the parent species. In 1978, Hungarian triticales attained outstanding yield potential in Germany (6–9.55 t/ha, compared with 8.7 t for wheat and 7.5 t for rye per hectare). The year 1984 was extremely favourable for cereals in Hungary. The best types of Hungarian triticale were able to compete in Kecskemét with the highest yielding cultivars of wheat (9–10 t/ha). It is conceivable that they will not achieve their true yield potential every year due to their poorer adaptability, but it is not impossible that they will continue to compete well with wheat and rye.

Experience gained so far indicates that rapid results of value in practice cannot be expected from interspecific and intergeneric crosses. Success will only be achieved through patient, persistent efforts.

As mentioned above, incompatibility is a great obstacle to crosses between plant species. Incompatibility prior to fertilisation can now be overcome by means of cell fusion, while the starvation often caused in sexual crosses by poor development of the endosperm can be eliminated by raising in nutrient medium. Cell fusion between genera which are taxonomically distant from each other may lead to the formation of cell lines with which hybridisability can be expanded in the plant kingdom.

MELCHERS and co-workers (1978) were the first to produce allopolyploid plants containing the chromosome sets of both parents ($2n=48$) by fusing protoplasts isolated from a callus culture of *Lycopersicum esculentum* ($2n=24$) $\times$ *Solanum tuberosum* ($2n=24$). The many previous attempts made at producing this hybrid ended in failure. In Mosonmagyaróvár a grafting approach was applied prior to crossing, but this, too, was unsuccessful. The grafted plants looked fine, with potatoes underneath and tomatoes on the stems, but there were doubts about their practical value.

Allopolyploids were successfully obtained by cell fusion for *Arabidopsis thaliana* $\times$ *Brassica campestris*. These were named *Arabidobrassica*. In this case the degree of relationship was considerably less than in the case of genera within the Solanaceae family.

In the early seventies research into bacteriophage and plasmid genetics led to the elaboration of completely new techniques and methods, known collectively as genetic engineering. The many techniques belonging under this heading include the breaking up of DNA molecules and their reconstruction in a definite manner, and the exploitation of possibilities offered by the existence of "jumping" genes.

With the aid of the new technology, extremely varied genes or gene groups can be linked up and occasionally be made to function. This means that conscious human intervention can produce cells with characters that were not previously known in nature (e.g. bacteria producing human enzymes). Mention should also be made of the importance of Ti plasmids, which, through the application of genetic engineering, make completely controlled breeding pos-

sible. This technique can theoretically be used to incorporate any gene whatsoever into the chromosomes of dicotyledonous plants.

The leap which geneticists were able to make due to the elaboration of molecular hybridisation methods is still difficult to evaluate. It is a fact that, in addition to the classical crosses between distant species, it has opened up possibilities at the DNA molecule level for uniting the genes of different creatures where this seemed quite impossible only a short time ago. These approaches to the molecular genetic reconstruction of cells illustrate the unbounded opportunities offered by genetics to mankind for making changes in living nature. The results achieved so far have served to fire imaginations even more. There can be little doubt that before too long techniques such as gene synthesis or the removal of gene blocks from living cells, the integration of the genome with alien DNA, autoreproduction under artificial conditions, the utilisation of episomes, and many more, will cease to be part of science fiction and will become accepted tools in the large-scale genetic transformation of plant organisms.

Glossary

Addition: addition of a chromosome from one species into the chromosome set of another species during interspecific and intergeneric crossing.

Allele: one of a pair of genes located at corresponding sites on homologous chromosomes.

Allopolyploid: a plant hybrid in which the somatic chromosome sets of two species are present.

Anaphase: the phase of cell division following metaphase, when the chromosomes migrate from the equatorial plane to the two poles.

Androgenesis: elimination of the maternal nucleus from the fertilised ovum, so that only male chromosomes are present in the developing individual.

Aneuploid: plants where the chromosome number is not an exact multiple of the basic chromosome number ($2n + 1$, 2 , 3 = hyperploid, with more than the full chromosome number; $2n - 1$, 2 = hypoploid, with less than the full chromosome number).

Apogamy: the embryo (sporophyte) does not develop from a haploid gamete (ovum) but from a diploid cell or cells of the embryo sac gametophyte.

Apomixis: development of a new individual from an unfertilised ovum without sexual cell nucleus fusion. The ovum may be a normal haploid, or a diploid due to the absence of reductional cell division.

Autogamy: self-fertilisation, self-pollination (within a single plant).

Autopolyploid: a polyploid arising due to the multiplication of the complete chromosome set of a species. An autotetraploid, for instance, has four identical sets of chromosomes.

Back-cross: a cross between a hybrid and one of its parents. The derivatives of such crosses are known as back-cross generations with the symbol BC.

Biotype: a population of individuals with the same genetic constitution. The biotype may be homozygotic or heterozygotic.

Bivalent: a chromosome pair arising due to the conjugation (synapsis) of homologous chromosomes.

C₁, C₂, C₃: the first, second and third generations of individuals produced using colchicine.

Cell fusion: spontaneous or induced fusion of cells delimited by a membrane.

Centromere: the constricted central region of the chromosome strands, which divides the chromosome into two parts.

Chimera: tissue consisting of cells with different genotypes.

Chromatin: a well-staining substance, consisting mainly of DNA, from which the chromosomes are formed in the course of mitosis and meiosis.

Chromosome: well-staining corpuscles forming during cell division as the result of a special arrangement of the chromatin, the basic substance of the cell nucleus. The number of chromosomes, which contain DNA, RNA, histone and non-histone proteins and are the agents of heredity, is species-specific.

Colchicine: the alkaloid of meadow saffron ($C_{22}H_{22}NO_6$) used among other things to induce the multiplication of the chromosome number (polyploidy).

Crossing: partial or complete combination of the genetic material of individuals with different genotypes in a sexual manner (by fertilisation).

Cytoplasm: the part of the protoplasm which surrounds the cell nucleus and is delimited by the external cell membrane alone, or by the cell membrane and the cell wall together.

Cytoplasmic male sterility: an abnormality in pollen development determined by chloroplast or mitochondrial DNA inherited through the female.

Decaploid: ten times (10x) the number of chromosomes in the haploid gamete ($x=n$).

Diakinesis: in the course of reductional cell division, the last phase of the prophase of meiosis, in which the chromosomes become shorter and thicker.

DNA (desoxyribonucleic acid): a compound found chiefly in the chromosomes, which can be regarded as the primary material of the gene and the bearer of genetic information.

Diploid: An organism with a chromosome number equivalent to twice the reduced, haploid chromosome set (e.g. in wheat, $2x=14$, i.e. $2n=14$).

Disome: an organism with the diploid chromosome number.

Dominant: a character or allele which is manifested even in the heterozygotic state and completely suppresses the effect of the other.

Donor: in repeated back-crosses the donor parent is only used in the cross once to transfer a certain character, and selection is consistently made for the transferred (donor) character.

Elimination: the loss of certain alleles in the hybrid population, generally leading to the formation of new variations.

Embryo: a plant organism formed from the zygote after repeated cell division, with rudimentary differentiation, making it possible to recognise the shoot and root poles and the cotyledons.

Endosperm: nutritional tissue surrounding the embryo in certain angiospermous plant species.

Euploid: an organism with a complete chromosome number (n =haploid; $2n$ =diploid; $3n$ =triploid; $4n$ =tetraploid; $5n$ =pentaploid; etc.).

Evolution: lineage, e.g. of a plant species.

F₁: designation of the first progeny generation arising from a cross between two organisms.

F₂, F₃, etc.: second, third, etc. progeny generation originating from self-fertilisation.

Factor: an alternative expression for the word gene.

Female sterility: a form of sterility in plants where the ovum is non-viable but the pollen is fertile.

Fertility: ability to produce progeny.

Fusion: see Cell fusion.

Gamete: male or female reproductive cell capable of carrying out or undergoing fertilisation.

Gene: a section of the chromosome producing a functional product, which may be RNA or a protein, the translational product of RNA.

Gene linkage: the joint inheritance of two or more characters, caused by the location of the genes on the same chromosome.

Genetics: the science which studies the inheritance of characters and the extent to which these resemble or differ from those of the parental organism.

Genetic transformation: the transfer of genetic information by introducing isolated DNA into the cell.

Genome: the haploid chromosome set of an organism; hence, the sum total of the genes contained in this set.

Genotype: the sum total of the genetic information stored in the chromosomal genes of an organism.

Haploid: a cell or organism containing a reduced (gametal) chromosome set.

Heptaploid: an organism with a chromosome number equivalent to seven times the reduced, haploid chromosome set (e.g. in wheat $x=7$, $7x=49$, i.e. $2n=49$).

Heterosis: hybrid vigour; a genetic state in which the hybrids are superior to the parents with respect to a certain character.

Heterozygote: a hybrid having different alleles for one or more genes.

Hexaploid: an organism with a chromosome number equivalent to six times the reduced, haploid chromosome set (e.g. in wheat $6x=42$, i.e. $2n=42$).

Homologous chromosomes: chromosomes containing various alleles of the same genes, which pair in the prophase of meiosis.

Homozygote: an organism containing identical genetic material at all loci.

Hybrid: progeny arising from a cross between individuals with different genotypes.

Hybridisation: see Crossing

Idiogram: a diagrammatic representation of the chromosomes, enabling them to be distinguished by their characteristic shapes and sizes.

Incompatibility: the restriction of either self-fertilisation or cross-fertilisation between non-related plants in order to ensure the selectivity of sexual fertilisation.

Intermediary: an organism where the observable properties are intermediate for one or more characters.

Interphase: the part of the cell cycle in which important metabolic processes take place, involving the synthesis of macromolecules, without any visible signs of division.

Interspecific and intergeneric crossing: sexual crosses between species belonging to the same genus (interspecific crosses) or between species from different genera (intergeneric crosses).

Introgression: introduction of the characters of one species into the genotype of another.

In vitro: cells, organs or tissues are removed from the organism and kept for studying under artificial conditions.

In vivo: an experimental system aimed at studying biological processes as they occur in the living organism.

Isoenzyme: within a single species, proteins which have the same enzyme activity, but different structures.

Isolation mechanisms: in population genetics and evolutionary studies, a method whereby populations can be kept side by side without any drop in frequency. Isolation may be geographical, sexual or genetic. One form of the latter is when changes in the number or shape of the chromosomes leads to the separation of new forms.

Karyotype: the characteristics of the chromosome set, determined by differences in shape and size between the various chromosomes.

Lethality: destruction of the cell or organism.

Macroevolution: population changes arising due to genetic changes and leading to the development of new species.

Meiosis: reductional cell division; a special type of division leading to the formation of gametes and consisting of one reductional and one equational division.

Mentor method: use of perennial plants (fruit trees) as stocks in order to change the characters of hybrid seedlings or varieties grafted onto them.

Mitosis: non-reductional cell division, in the course of which the chromosomes are duplicated, then separate, resulting in the formation of progeny cells with the same number of chromosomes as the mother cell.

Monofactorial segregation: when the parents differ from each other with respect to a single pair of genes, the segregation in the F_2 of the cross will be 3 : 1 or 1 : 2 : 1.

Monosome: a plant containing $2n - 1$ chromosomes.

Multivalent: more than two chromosomes pair in the course of cell division.

Mutagen: physical effects or chemicals inducing mutations.

Mutation: one way in which hereditary changes may arise.

Neocombination: in the segregating generation of a hybrid, an individual with a new type of heredity differing from that of both parents.

Nullisome: an organism in which a pair of chromosomes is missing from the full chromosome complement ($2n - 2$).

Octoploid: an organism with a chromosome number equivalent to eight genomes the reduced, haploid chromosome set (e.g. in wheat $x = 7$, $8x = 56$. i.e. $2n = 56$).

Phenotype: the observable properties of an organism, produced by the interaction between the genotype and the environment.

Pollen: male gametes with a characteristic shape, size and colour, found in the anthers.

Polyploid: organism containing more than two genomes (genetic material).

Primary: the first generation of hybrids produced in interspecific and intergeneric crosses.

Prophase: the first phase of cell division.

Protoplast: a plant, fungus or bacterium cell deprived of its cell wall.

Quadrivalent: pairing of four chromosomes in the first metaphase of cell division.

Recessive: a character or allele which is only manifested in the homozygotic state.

Reciprocal cross: a second cross, similar to the first, but with the sexes of the parents changed.

Recurrent parent: a parent used repeatedly in back-crosses and generally possessing recessive characters.

Restorer: a parent species capable of restoring fertility.

RNA (ribonucleic acid): a polymer built up of ribonucleotides. In the course of transcription ribonucleic acids with complementary base sequences are formed on the DNA template. In living cells, messenger RNA (m-RNA), ribosomal RNA (r-RNA) and transfer RNA (t-RNA) are to be found.

Segregation: separation and re-combination of parental characters in progeny generations.

Selection: in natural populations, the differing chances of various individuals or genotypes of surviving, or differences in the number of progeny they produce. In the course of plant breeding, the selection of individuals with specific characters and the propagation of their progeny.

Somatic: vegetative cells and tissues.

Sterility: inability to produce progeny by sexual means.

Stoma: air or gas exchange openings, through which water vapour leaves the plant and air exchange takes place.

Telophase: the last phase of cell division, when the chromosomes migrate towards the poles.

Tetraploid: an individual with four sets of chromosomes.

Tetrasome: an organism containing two extra chromosomes ($2n + 2$).

Translocation: exchange of sections of two non-homologous chromosomes after breakage.

Triploid: an organism with three sets of chromosomes.

Trisome: an organism containing one extra chromosome ($2n + 1$).

Trivalent: a multivalent consisting of three paired chromosomes.

Univalent: a non-paired chromosome in meiosis, as opposed to the paired bivalents.

Variety cross: crosses between varieties belonging to the same species, but having different types of heredity.

Vegetative hybridisation: combination of the characters of two parental organisms with different genotypes with the elimination of the sexual process (in plants, by means of grafting).

Xenia: appearance of characters originating from the pollinator in the embryonic tissues of the hybrid seed.

Zygote: the cell arising after sexual fertilisation due to the union of two gametes. If the gametes are $n + n$ haploids, the zygote will be diploid ($2n$).

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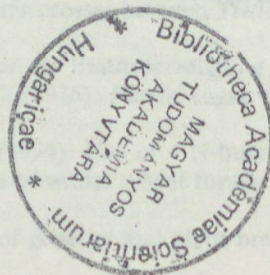
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The possibility of crossing plant species which are only distantly related to each other, the genetic, biochemical and other obstacles which complicate or prevent the production of plant hybrids, and the methods which hold out the promise of success, have always been a fascinating topic for scientists. The new genetic methods (cell fusion, genetic engineering, etc.) which have not yet become general practice make this subject particularly exciting for specialists in this field.

This manual presents a detailed theoretical and practical discussion of interspecific and intergenetic hybrids between gametic plants with particular emphasis on economically valuable horticultural and field crops (fodder, foodstuff, industrial crops) and on plants which deserve special attention.

The book is not only a monograph on some plant species but also a summary of the data and results from numerous related fields.

The aim of the book is to help the work of researchers who wish to employ this method in either theory or practice. Scientists (geneticists, plant breeders) as well as university students in this field will find it a valuable reference book.



AKADÉMIAI KIADÓ,
BUDAPEST

A. BELEA

• **INTERSPECIFIC AND INTERGENERIC
CROSSES IN CULTIVATED PLANTS**

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