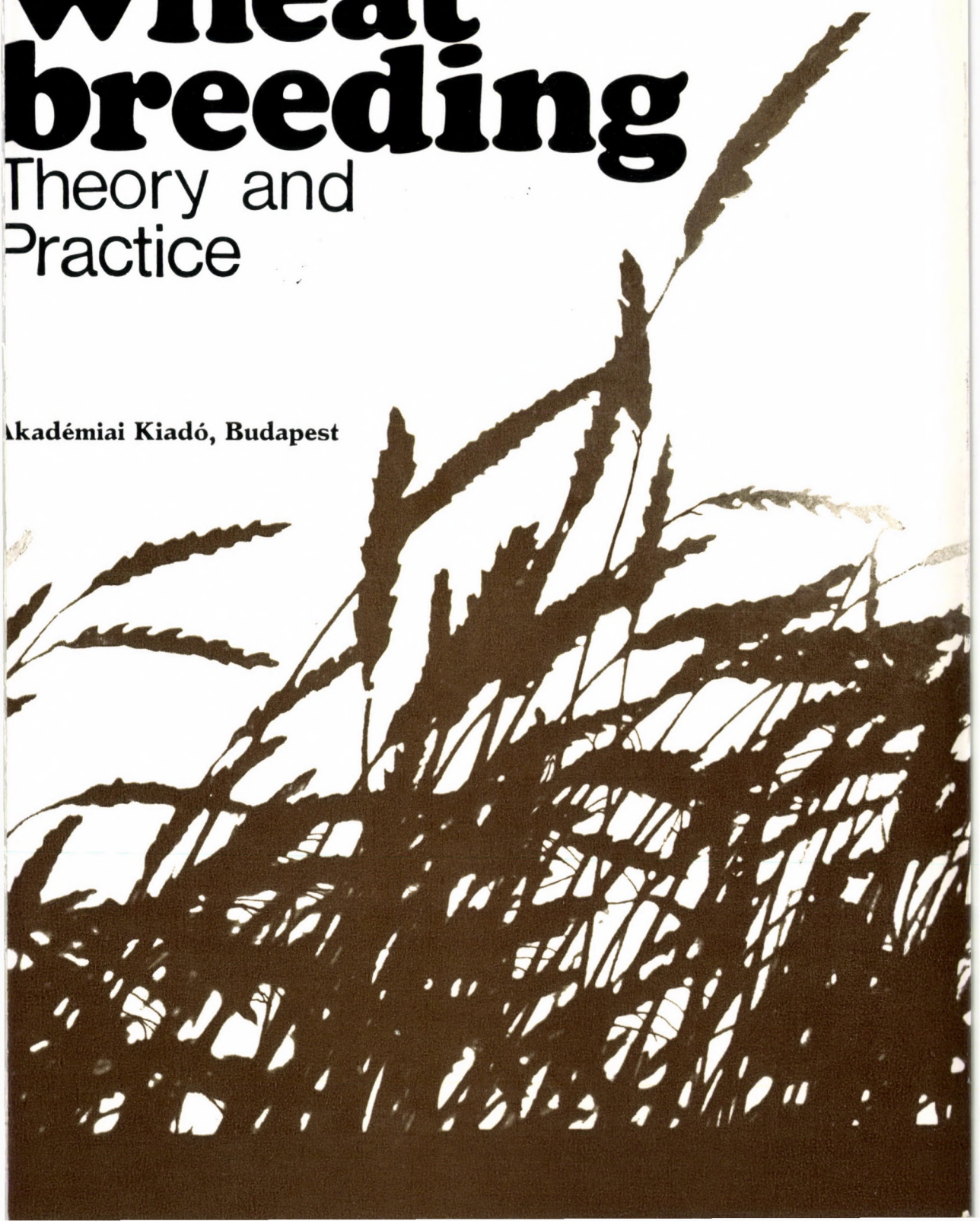
J. Lelley

wheat breeding

Theory and Practice



Akadémiai Kiadó, Budapest

WHEAT BREEDING

János Lelley

On the basis of 25 years of highly active methodological research into wheat breeding the author provides a comprehensive survey of the most important cultivated plants, their breeding and the accompanying research.

While the rigorous treatment of the subject matter prevents the recommendation of the book to the lay-reader, it will be of immense use for wheat breeders and researchers who deal with the genetics and pathology of wheat. It will also be a great benefit to teachers and students of relevant institutions of higher education. It is certain to contribute to the expanding of knowledge of agrarian specialists dealing with seed and wheat growing. The volume assumes at least a basic knowledge of genetics and breeding.

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J. Lelley **WHEAT BREEDING**

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Mrs. E. VIZMATHY

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Chapter 1 Survey of literature

According to archaeological evidence wheat was among the first cultivated plants, and agriculture as a new way of living was mostly founded on the cultivation of the genera *Hordeum* and *Triticum*. Some 8000 years ago these two cereals became the most important sources of energy for the groups of people in Asia Minor who were about to settle down to live a civilized and cultured life. Human care had a decisive effect on the further evolution of the *Triticum* genus from the earliest stages of its cultivation, though, profound intervention began only some 150 years ago with deliberate breeding.

To the best of our knowledge P. Schiriff was the first to breed wheat about 1820 in Haddington, Scotland. The first work on wheat breeding: "The Improvement of Cereals" was written by him. In the 150 years that have passed since a great many scientific papers, text-books, manuals and monographs have been published on wheat breeding and on other investigations supporting the breeders.

The first comprehensive work summarizing the knowledge acquired that far was Hayes and Garber's: Breeding Crop Plants (New York, 1927). In 1942 Hayes and Immer published a new, more comprehensive manual entitled Methods of Plant Breeding. The German Isenbeck and Rosenstiel's Die Züchtung des Weizens, No. 28 of the series Handbuch der Pflanzenzüchtung (ed. Rommer and Rudolf) appeared in 1948. The biology of Wheat by Nosatovsky and Biological Fundamentals of Wheat Growing by Kuperman were published in 1950 in Moscow. Both books were of great importance because at that time genetics, breeding and biology already joined efforts to solve the problems of how to produce improved varieties.

In 1954 Forlani wrote in Pavia his manual: The Wheat in which the main emphasis was laid on the question of breeding. In 1955 Hayes et al. published their Methods of Plant Breeding in which wheat breeding had a leading part. Wheat in the USSR was edited by Zhukovsky in 1957; besides the biology, breeding and growing of wheat, this work gives a survey of the species and varieties grown in the European and Asian wheat growing areas of the Soviet Union, with special regard to some southern parts adjacent to the site of origin of the *Triticum* genus. In the new edition of the series Handbuch der Pflanzenzüchtung published in 1958, the part on wheat breeding was written by Sears et al. Wheat and Wheat Improvement a new handbook on wheat breeding published in 1967 in Madison, USA under the editorship of Quisenberry had been contributed to by well-known experts. Foltyn's monograph The Wheat was published in Prague in 1970.

The wheat production of Hungary played a special role in Europe. The climatic and soil conditions of the Great Hungarian Plain were favourable to produce wheats of a quality unparallelled in the whole continent. Thus it is easy to under-

stand why wheat became the most important cultivated plant in Hungary. The first home work written on wheat was published in 1578 by Melius Horhi P. A pioneer work on wheat breeding: Seed Grain Improvement in Wheat written in Hungarian by Kenessey appeared in 1874. In the following year Mokry published his Wheat Breeding. In 1907 Kosutány wrote a manual on Hungarian Wheat and Hungarian Flour; in 1944 and 1947 a two-volumed work of Villax: Plant Breeding was published with wheat as one of the main subjects. In 1958 Lelley and Rajháthy published a monograph on Wheat and its Breeding. Some five years later a handbook written by Lelley, Mándy and a number of co-authors was again issued on The Wheat.

Since 1958 international symposia on wheat genetics have been organized in every fifth year. The first was held in Winnipeg (Canada), the next one in Lund (Sweden), then in Canberra (Australia) and in Missouri (United States of America). The delivered lectures were in each case published in the form of a book.

Besides books some periodicals report exclusively the results obtained in wheat research, e.g. "Wheat Information Service" (Kyoto, Japan) and "Annual Wheat Newsletter" (ed. Kansas State University and the Canada Department of Agriculture).

In Cambridge, an association the European Wheat Anneuploid Co-operative (EWAC) was established in 1967. This association organized symposia in 1967, 1970 and 1974, and gives information on anneuploid research every year.

The EUCARPIA Cereal and Physiology Section organized a conference in Wageningen between the 24th and 26th of October, 1967. The subjects of the conference were: cereal improvement, hybrid varieties and the aspects of culm shortening. The text of lectures and discussions was published as an extra in the 1968 December number of the Euphytica.

From time to time there are various publications, dealing with wheat research and providing useful information for practical breeding work. A review the World Catalogue of Genetic Stocks, Wheat, edited by the Food and Agricultural Organization of the United Nations (FAO) in Rome, in which the important economic properties of the most outstanding new wheat varieties are categorized. The International Nurseries of Plant Breeding Station (Njoro, Republic of Kenya) reports every year on the leaf and stem rust resistance of the examined varieties. The Agricultural Experiment Station (College of Agriculture, University of Nebraska, Lincoln) has recently organized international comparative variety trials and summarized the results in the Reports of the International Wheat Performance Nursery.

The above-mentioned works clearly indicated that the literature on wheat breeding is very extensive; they comprise, however, only a part of the immense flow of information that deals with the subject of wheat. In scientific reviews of various countries hundreds of papers appear every year. The number of papers and reports published on recent results concerning wheat genetics, breeding and related fields has been at a rough estimate some nine thousand for the last ten years.

The monographs and handbooks mentioned above served the purpose of systematizing and evaluating the continuous flow of information. And since the

quantity of information increases year by year, with the same purpose in mind was the present work written.

The theoretical investigations and practical methods directly connected with wheat breeding will be summarized only after a proper selection. Since a considerable proportion of the papers published in periodicals contains data which either have been known or confirm findings already known. Such data were omitted here, assuming that those who undertake to look into the matter thoroughly are familiar with the earlier literature on wheat breeding and know the respective correlations of biology, genetics, pathology and breeding.

The systematization and grouping of the last ten years of literature reveals at the same time what subjects were most frequently tackled by the researchers. The mass of data for this period gives us information on the most important current tasks of wheat research.

Between 1962 and 1973 the highest number of papers were written on basic research in wheat genetics. This was followed by the subject of wheat quality. The biological value related to the amino acid composition of proteins has inspired many authors mainly in the last five years. Investigations into mutation genetics came into the foreground too. Numerous experiments have recently been carried out with chemical mutegenes.

Winterhardiness passes for a much investigated subject, showing that breeding continues to make efforts to conquer the northern areas, and that not by spring wheats but by winter varieties. Another rapidly developing new subject in the last ten years was the hybrid wheat production. This is quite understandable because work could in essentials start only after 1963 and the prospective results are very promising.

Lodging resistance and in connection with it dwarf growth also belonged to the fashionable subjects in the past years.

The proportion of the literature dealing with the phytopathological resistance clearly reflects the importance of pathogens. The first place is invariably occupied by the research of stem rust resistance, though leaf rust resistance is almost of equal importance. On the other hand, investigations concerning yellow rust resistance are less extensive. Powdery mildew and *Fusarium* have aroused the interest of an increasing number of researchers in the last five years. At the same time, the question of smuts is quite insignificant.

Methodological research though one of the main supports of practical breeding is surprisingly modest. Technical research improving the mechanization of laboratory and field trial operations is likewise very small compared to its significance, notwithstanding that the International Association on Mechanization of Field Experiments (IAMFE) organized international symposia in Vollebekk (1964), Braunschweig (1968) and Brno (1972), where important lectures were delivered on the mechanization of various phases in the course of wheat breeding.

Special place is occupied by the *Triticale* research which made a great progress in the last decades. This subject has by now been so much specialized that it is in fact a separate field of research having its own literature which is but slightly connected with the subject of wheat, and is therefore omitted from this summary.

Chapter 2 **Origin**

In view of a correct taxonomic categorization the evolution of the genus *Triticum* should be carefully studied. It is also useful for genetic research, as well as for practical breeding work, but while tackling the question of origin new correlations concerning human evolution and the prehistory of Europe have been disclosed.

The genera *Triticum* and *Hordeum*, wheat and barley, played a decisive role in human civilization and cultural development. This fact, too, was recognized through investigations into evolution genetics. It has been proved that the site of origin of the European ancient culture and the evolutionary area of the genus *Triticum* coincide. Thus the rate and geographical extension of the evolution of wheat determined the site and time of origin of civilization and culture in Asia Minor (Kuckuck 1959, Braidwood and Howe 1960, Gökgöl 1961, La Baume 1961).

The evolution of the subtribe *Triticinae* began many thousands of years ago, sometime during the Würm glacial age. The genera *Hordeum*, *Aegilops*, *Agropyron*, *Haynaldia*, *Secale* and *Triticum* may have differentiated from a single common ancestor. Nor is it impossible that species which no longer exist also played a role in the evolution (Kimber and Athwal 1972).

It is understandable that ever since the phylogeny of the genus *Triticum* became a timely problem through the findings of Kihara and Lilienfeld (1932) continuous efforts have been made to give a perfect answer to the question.

On the basis of evolution genetic studies, there is no doubt that the tetraploid and hexaploid wheat species are alloploidic and alloplasmic (Suemoto 1968). This finding justifies the division of the *Triticum* genus into groups of species or sections.

T. thaoudar Reut., the most primitive species in the diploid group was identified as the ancestor of genome A (Mettin 1964, Riley 1965*b*). Genome B was traced back to *Aegilops speltoides* Tausch. (Pathak 1940). Later Sears (1956*b*) suggested *Ae. bicornis* to be the donor of genome B. Referring to morphological characters Sarkar and Stebbins (1956) returned, however, to *Ae. speltoides*. On the basis of karyotype analyses and geographical considerations Riley et al. (1969) also supported *Ae. speltoides*. Genome D was supposed to originate from *Ae. squarrosa* (Mc Fadden and Sears 1944, Riley and Chapman 1960, Kerber 1963, Zohary 1963, Galzy 1964, Mettin 1964, Riley 1965*a*).

By the middle of the 1960s the origin of three sections of wheat species was thought to have been clarified since the probable ancestors of the three genomes were known; though during re-synthesis certain difficulties arose. This evolution genetic explanation, however, did not apply to the special position of the tetraploid *T. timopheevi* Zhuk. and the hexaploid *T. zhukovskyi* Men. et Er.

With the improvement of control methods difficulties arose concerning the explanation given on the origin of the tetraploid section. Namely, the examination

of meiosis in the hybrids, the fractioning of proteins, the immune biological analysis and the DNA study did not in certain cases fully confirm the assumed phylogenetic connection. The many thousand years of natural evolution though, gave some explanation to the contradictory experiences, still it could not subdue doubts.

The diploid and two allopolyploid stages of the genus *Triticum* came into existence one after the other during several thousands of years in an area whose climatic and soil conditions have since substantially changed. During that time the components underwent many mutative changes which cannot be perfectly reproduced artificially. During the long period of phylogenesis the genetic structure of the different wild wheat species changed significantly, and after cultivation these changes must certainly have become more intensive. Related species participating as genome donors in the development of the alloploid species changed simultaneously. It is for certain that the genetic and biochemical composition of the now existing species of the hypothetical genome donors in the re-synthesis was not identical with that species contributing to the development of the wheat species groups ten or fifteen thousand years ago. Further, we must reckon with the probability that a few components supposed to have been genome donors have since become extinct.

According to Mac Key (1963) from an evolutionary point of view the genus *Triticum* belongs to the younger genera. He reached this conclusion from the not too great genetical difference between the individual species. In his opinion the processes of hybridization and polyploidization that during the phylogenesis brought about the primitive forms of the individual species groups took place scarcely over ten thousand years ago. The climate of Asia Minor has since changed a great deal, and therefore it is not surprising that one or the other transitional forms or related species no longer exists.

As the investigations became more extensive and the methods more refined, even the less apparent differences could be established. The doubts about the correctness of the explanation of origin grew. The question whether genome A of the tetraploid wheat originated from the diploid wheat, and if so, from which diploid ancestor had to be revised. Whether it was really the *Ae. speltoides*, or perhaps another *Aegilops* species that genome B originated from. It had to be examined whether genome B was not in fact a modified genome A. Since in that case nor is the allopolyploid origin of the tetraploid species group accepted. It had to be examined whether the hexaploid section was of the same origin as the tetraploid; whether the B and A genomes of the hexaploid wheats corresponded to those in the tetraploids or branched off from another line. Finally, it became questionable again, what the origin of genome D was.

Thus, the improvement of the control methods made it – in a paradoxical way – even more difficult to give answer to the above questions. The morphological analysis of chromosomes has not yielded much result in this field, far more has the study of the meiotic irregularities, important in revealing the major genome differences. The increasing preciseness in isolating the protein fractions made the establishment or relationships more reliable, but at the same time disclosed the minor differences too, though it can be supposed that during evolution the different

genetic background and alien plasm in the genomes caused changes that in the electrophoretic examinations make the assumption of a relationship uncertain. Moreover, it should also be considered whether the incessantly improving methods of investigation do not make the details of the evolutionary process so intricate that they might easily lead one astray.

Repeatedly checked examinations have established that in the species of the diploid wheat group the A genome is identical; there is no fundamental genetic difference between these species. In other words, the species of the diploid section are of common origin. There are, however, certain recent findings which cast doubts even on this assumption, because in certain electrophoretic examinations genomes A were not found perfectly identical (Lelley, personal communication) but these investigations have not been completed yet so, for the time being, the common origin of genome A in the diploid section should not be disputed.

Genome A of the species belonging to the tetraploid section is supposed to be also of the same origin as that in the diploid group, accordingly, genome A of the tetraploid species originates from the diploid section (Morris and Sears 1967). Would the above mentioned investigations reveal that even genomes A show differences, than it will have to be decided whether differences exist between the genomes of the tetraploid section, too. This supposition is made probable by the fact that in tetraploid wheats genome A is in an alien plasm, as it has been provide, (Kihara 1966) that in the original spontaneous hybridization producing the tetraploid wheat the partner carrying the genome B was the mother.

The origin of genome B found in the tetraploid and hexaploid sections has become uncertain. On the basis of analyzing the DNA content of the nucleus Rees and Walters (1965) considered the *Ae. speltoides* origin of the genome B to be confirmed, but in 1966 Kimber when studying the meiosis of the genome B concluded that its origin from *Ae. speltoides* is questionable. Again, Chapman (1966) in studying meiosis in the F_1 generation obtained by crossing *Ae. speltoides* with a tetraploid wheat found fewer bivalents than he had expected. Later Sears (1969*b*) pointed out by phenotype examinations too that the *Ae. speltoides* could not be the donor of genome B, because the morphological similarity is not sufficient. The electrophoretic studies performed by Johnson and Hall (1966) also questioned the *Ae. speltoides* origin of genome B. Giorgi and Bozzini (1969*a*, *b*) when examining the chromosomes of a tetraploid wheat synthetized by crossing *Ae. speltoides* with *T. boeoticum* found them morphologically different from those of *T. turgidum*. Kimber and Athwal (1972) proved by crossings that genome B of *Ae. speltoides* was not identical with that of the tetraploid wheat. Rubenstein and Sallee (1973) provided further evidence to the probability of this statement. In spite of all these on the basis of serological tests Aniol (1973) maintains that genome B may originate from *Ae. speltoides* or a closely related species, and Suemoto (1973) too traces back the plasms of tetraploid and hexaploid wheats to *Ae. speltoides*.

By means of the C-banding technique Hadlaczky and Belea (1974) pointed out that in the genome of tetraploid and hexaploid wheats there was always a so-called marker chromosome – probably the 6B or the 1B – on the long arm of which a readily staining heterochromatic spot was observed. In the genome of *Ae.*

speltoides this chromosome could not be seen. This also confirms that genome B is not identical with genome S. Otherwise the *Ae. speltoides* chromosomes stained with the Giemsa technique show a quite different picture than genome B.

Uncertainty concerning the origin of genome B has thus grown. Kimber and Athwal (1972) concluded that for the time being the donor of genome B is unknown. Neither of the *Ae. speltoides* studied by them could be identified with it. They think it likely that *Ae. speltoides* has not even a derivative that could be accepted as donor. At the same time Hillel and Simchen (1973) emphasize that the variability of *Ae. speltoides* is rather low, for otherwise owing to its allogamous nature it could have been more easily crossed. Larsen (1973) calls attention to the fact that the frequency of translocations occurring during the evolution is not uniform in the genomes. Genome D is the least affected in this respect; change is more frequent in the A but the most frequent in genome B. That is why the donor of genome B is so difficult to find today. Kimber and Athwal (1972) do not exclude the possibility that the donor of genome B no longer exists, or was a derivate of a hybrid at that very moment of evolution and cannot therefore be found today. This situation is rather regrettable not only because it makes an important phase in the evolution of the tetra- and hexaploid sections uncertain, but also because, as pointed out by Mac Key (1968), the significance of genome B is underlined by the particularly important role of the 5B chromosome. This genome controls the diploid-like pairing behaviour, and the 1B and 6B satellite chromosomes are supposed to play a special role in the synthesis of RNA.

Thus the origin of genome B has become uncertain. It is likely to originate from the genus *Aegilops*. It may have been introduced into wheat either from a still existing though yet unknown, or from an extinct species. This is an important establishment because the species of the genus *Aegilops* from which genome B is derived must have been a native of the region where the habitat of the diploid wheat, the carrier of genome A was. Otherwise the spontaneous hybridization required for this evolutionary step could not have been realized. Namely, there is archaeological evidence of the existence of *T. dicoccoides* long before cultivation started, and that it had been living in the same territory as *T. monococcum* before man began to cultivate it (Rudorf 1968). Dennel (1973) argues this theory, and he holds the view that *T. dicoccum* is of an earlier origin than *T. dicoccoides*.

Johnson and Hall (1966*a*) and Waines (1971) considered it possible that genome B is perhaps a form of genome A having suffered modification during evolution, and thus tetraploid wheat might be an autopolyploid one. Recent observations of Johnson (1975) implicate *T. urartu* to be the missing B genome donor. In view of the uncertain origin of the B genome this possibility cannot be wholly ruled out but it requires further evidence.

Recently Dover and Riley (1972*a*) investigated the question whether the B genome could be traced back to *Ae. mutica*. Mello–Sampayo (1972) studied *Ae. longissima* as the possible donor of the B genome, but these assumptions require further evidence, too.

There is no uncertainty about the origin of the D genome. It has been repeatedly proved that it derives from *Ae. squarrosa*, as supported by the alpha-amylase isosime tests of Nishikawa (1973), too. The theory that *Ae. ventricosa* might have

been the donor of genome D has been rejected since Siddiqui and Jones (1968, 1969) pointed out that the D genomes of *Ae. squarrosa* and *Ae. ventricosa* were not uniform. The same was proved by the chromosome substitution experiments of Alston (1970). Both in the course of cross-breeding and during mutagene treatments alloploidy was found to be an extremely great advantage from a genetic point of view. It increases the capacity of genetic information storage, the possibility of genetic solutions and the ability of adaptation. Manyfold interactions may exist between the genes, and the action of dosis as well as the possibility of overdominance have become substantially greater (Mac Key 1970).

To understand the evolution of tetra- and hexaploid wheats one must know that genome A brought about a high ecological adaptability. This follows from the fact that diploid wheat in ancient times was just as wide-spread in Asia Minor as was barley. That in contrast to *Ae. umbellulata* or *Ae. squarrosa* it became a cultivated plant was due to its more favourable ear structure (Mac Key 1968/69).

The combination of A + B genomes is still more favourable from numerous aspects, but it was particularly useful that a transgression could occur in heat tolerance (Jain and Rana 1963). The development of the vegetative parts and productivity substantially improved. That was the reason why in ancient times the spread of tetraploid wheat was so rapid (Kranz 1967).

The evolutionary importance of genome D is also extremely great, it is to this genome that the hexaploid species owe for their gluten quality which much contributed to the wide distribution of wheat as an indispensable human food. The D genome has at the same time the disadvantage of having introduced a susceptibility to diseases in wheat (Pisarev and Zhilkina 1963).

The Q factor which supresses the brittle rachis and the thick glumae, though present in the tetraploid *T. carthlicum*, is from the point of view of easy thrashing the most effective one in the hexaploids. The D genome has thus an important part in this respect, too (Mac Key 1954, 1963). It was due to this genome that wheats with brittle ears disappeared in the course of cultivation, and the polyploid *Aegilops* species remained weeds (Zohary 1965). Increased winterhardiness was also linked with the D genome which decided the superiority of hexaploid wheats to both the tetra- and diploid wheats and the *Aegilops* species for good.

According to Mac Key (1968) the difference in the trend of evolution between the genera *Aegilops* and *Triticum* means at the same time that the two genera cannot be included in the same taxonomic unit as suggested by Bowden (1959), and Morris and Sears (1967).

In the genus *Triticum* there is another genome found by Zhukovsky in 1923: *T. timopheevi*. This genome is present in *T. zhukovskyi* too, discovered in 1957 by Jakubziner (1958) in Western Georgia. The genome formula is AA GG for *T. timopheevi* Zhuk. and AA AA GG for *T. zhukovskyi* Men. et Er. Genome G is not identical with genome B. Comparing *T. timopheevi* with *T. turgidum* Bozzini and Giorgi (1969) found that the number of submedian and median chromosomes is different. The same difference was revealed by the comparison of *T. araraticum* – a subspecies of *T. timopheevi* – and *T. turgidum*. Difference was noticed between the two genomes by immune biological examinations, too (Bozzini et al. 1970). Wagenaar (1963) holds the view that genome G is identical with genome B, only

there is a mechanism in it which induces desynapsis in the hybrids of the two genomes. The change that produced this mechanism is supposed to have taken place on an isolated mountainous region in the *T. araraticum* var. *nachitschevanicum*. The present author believes that the further evolution of *T. timopheevi* has stopped owing to this genetic isolation. Wagenaar (1970) found the meiotic irregularities observed in the F_1 generation of *T. turgidum* × *T. timopheevi* to segregate in the subsequent generations. According to his opinion this also proves that incompatibility is genetically determined, thus, the incompatibility observed between the B and G genomes of the tetraploids came about under the influence of mutant genes produced during evolution. The difference between the two genomes is thus not essential. This theory is supported by Beridze and Georgidze (1969, 1970) who state that certain *T. monococcum* progenies found in a Zanduri population originating from Georgia changed into forms similar to *T. timopheevi* under the influence of irradiation and polyploidization. In spite of this Mac Key (1963, 1968) considered the difference between the G genomes of *T. timopheevi* and *T. zhukovskyi* so substantial that categorized the carriers as two separate species. On the basis of serological tests Aniol (1973) again concluded that genome G is only a modified form of genome B in *T. turgidum*.

The location and true origin of genome G have not been clarified so far. The difference between genomes B and G may possibly depend on a few genes only, but evidence offered by chromosome morphology and immune biology indicate a deeper cause of incompatibility. The special position of *T. timopheevi* is further complicated by certain plasm differences, as proved by the experience that hexaploid nuclei substituted in *T. timopheevi* plasm produce male sterility (Wilson and Ross 1962).

According to the investigations of Upadhya and Swaminathan (1963) the chromosome morphology of the G genome of *T. zhukovskyi* is similar to that in *T. timopheevi*. It has two pairs of satellite chromosome which morphologically are close to *T. timopheevi*, and one pair to *T. monococcum*. With *T. spelta* viable hybrids were obtained; with *T. macha* and *T. vavilovi* the case was different. *T. zhukovskyi* is still less known. Its first detailed description was published by Menabde and Eritzian in 1960 (in Mac Key 1963). Its plasm can be used as a source of male sterility in the same way as the plasm of *T. timopheevi*. The importance of the G genome has increased since it was found in the hexaploid group, too. Investigations have therefore been carried out recently to clear up its origin.

According to recent data published by Shands and Kimber (1973) and Kimber (1973) in *T. timopheevi* × *Ae. speltoides* crossings an essentially higher homology was found in the meiosis than in the hybrids of *T. durum* × *Ae. speltoides*. Thus they concluded that the G genome of *T. timopheevi* and *T. zhukovskyi* may originate from the *Ae. speltoides* therefore the symbol G should be replaced by S. Kimber (1973) supports this view.

It follows from the above data that the difference between the B and G genomes requires clarification and the origin of the G genome needs further evidence. According to Hadlaczky and Belea (1974 personal communication) the common origin of the genomes G and S is not confirmed by the chromosome comparison performed with Giemsa staining.

It can be supposed that the plasms of *T. timopheevi* and *T. zhukovskyi* are not of *Triticum* origin but may be traced back to the genus *Aegilops*, to the donor of the B and possibly G genomes.

To establish the relationship between wheat genomes their homology, chromosome pairing as well as the frequency of synapsis and desynapsis are studied in the first metaphase of meiosis. These methods are, however, complemented by other control procedures too.

The reliability of the comparative karyotype analysis is questionable. The size, arm ratios and other morphological characteristics of the chromosomes may vary from cell to cell in the same plant during microscopic examination (Lelley 1973*a*). According to Matter and Simak (1968) at least 11 per cent difference in length must exist between two chromosomes if they are to be reliably distinguished. The total length of the individual genomes does not reveal too much either. No doubt, genome D is the shortest and B the longest. Total chromatin content in the wheat genomes and in those of the supposed genome donor species were measured (Pai et al. 1961). The only fact the results seemed to prove was that a part of the chromatin content in genomes B and D was eliminated during evolution.

Still, in order to clear up the relation between genomes many researchers used the method of karyotype analysis, and obtained certain results. For example, Scapova (1970) noticed that the karyotype of *T. dicoccum* and *T. durum* was different only in two chromosomes. *T. timopheevi*, on the other hand, differs in seven chromosomes. Investigations carried out by Giorgi and Bozzini (1969*a*, *b*) proved that the varieties of *T. turgidum* did not differ in karyotype. They found two chromosomes with satellites, seven chromosomes with submedial, two with subterminal and three with medial centromeron in all of them. It was by karyotype analysis again, that Upadhya and Swaninathan (1963) pointed out the similarity of chromosomes in *T. timopheevi* and *T. zhukovskyi*.

Another method was the spectral analysis of proteins. It was by this method that, on the basis of the number of similar and different protein fractions in *T. monococcum* and *T. dicoccum*, Hall et al. (1963) pointed out that the common origin of genome A could be proved. They obtained identical results when examining the proteins of *T. dicoccum* and *T. durum*. With the spectral analysis of nuclear proteins in various *Gramineae* Ewart (1969) proved the structural similarity of proteins synthetized by the A, B and D genomes which suggests a relationship between certain species of the genera *Triticum* and *Aegilops*. Thus, a protein fractionated in the proper gel medium forms a spectrum characteristic of the species. The protein spectrum of synthetized amphidiploids is the total of the spectra of components. This is the best proof that protein analysis is suitable to establish the degree of relationship. The electrophoretic protein analysis of the wheat polyploid series confirmed the findings of cytogenetic examinations (Johnson and Hall 1966*b*, *c*). Johnson (1967) compared the extracts of nuclear proteins in groups with AB and AG genomes, too. The obtained stripes readily separated into slowly and quickly moving groups. Differences were only found between the quickly moving ones. In the AB group eight, in the AG group six fractions of this type were found of which 4–5 were different. He traced back this phenomenon

to the difference between the B and G genomes. Konarev et al. (1970*a*, *b*) pointed out differences between the genomes through the analysis of the gliadine proteins. Johnson and Hall (1966*a*) when carrying out experiments with nuclear proteins obtained results that made the *Ae. speltoides* origin of the B genome questionable. The sensibility of gel electrophoresis is even suitable to distinguish varieties and it was found that the gliadine samples change only in the genotype without any response to the influence of the environment (Barlow et al. 1973).

To determine the degree of relationship between species and genome immune biological methods were also used. It was by this test that Bozzini et al. (1970) confirmed the correctness of the taxonomic grouping suggested by Mac Key (1963). The same method was successfully applied by Konarev et al. (1970*a*, *b*).

As a complementary examination DNA testing is also used. Rees (1963) pointed out that the DNA content in the diploid nuclei of the species was very constant. Therefore on the basis of the DNA content conclusions may be drawn on the origin of the genomes of tetra- or hexaploid wheats. Rees and Walters (1965) found a difference between *T. durum* and *T. timopheevi* in the DNA content readily explaining the incompatibility of the two species, too. Between the S genome of *Ae. speltoides* and the B genome of the genus *Triticum*, on the other hand, the above authors did not find such a great difference that would have excluded common origin.

Nishikawa and Furuta (1969) found the highest DNA concentration in the D, and lowest in the A genome. Between the A, B and D genomes there is no significant difference. When a hexaploid was synthetized, the DNA concentration of the synthetized species was equal to the total DNA concentration of the components. No significant difference in the DNA concentration was found between *T. spelta* and *T. macha*. This is taxonomically justified and shows the sensitiveness of the method.

Attempts are made to disclose the differences between the genomes of the genus *Triticum* through investigations into the base sequence of DNA. Bendich and Mc Carthy (1970*b*) pointed out that genome A is more similar to B than to genome D in the base sequence of their DNA. Still this difference between the A and D genomes is much smaller than the difference between the DNA of wheat and rye. This indicates that the relationship between *Ae. squarrosa* and the genus *Triticum* is closer than between the genera *Triticum* and *Secale*. The similarity of DNA sequences in rye and wheat, in rye and barley, and oat, respectively, may suggest that rye was perhaps the most ancient genus of *Gramineae* from which the genera of oat, wheat and barley differentiated. On the basis of such investigations Dvorák and Schletgen (1973) go as far as supposing that *Agropyron elongatum* is closer to rye than to wheat.

These examinations help to detect more distant relationships, far beyond the identification of the genomes of the *Triticum* genus.

Yet, the evolutionary phases of the genus *Triticum* have not been fully disclosed by the above listed methods, nor are the results quite satisfactory from a taxonomic point of view. However, as regards genetic research and practical breeding work they offer help in planning and carrying out crossing operations, and in understanding the homoeology.

As regards the site of origin of species belonging to the genus *Triticum* the opinions agree. The native land of wheat was in Asia Minor, more closely, the area stretching along both sides of the Rivers Tigris and Euphrates, then turning westwards through Anatolia and in the zone of the Jordan southwards along the eastern coast of the Mediterranean Sea. It was in this region that both the *T. monococcum* and those species of the genus *Aegilops* which might have contributed to the development of tetra- and hexaploid wheats had their native land. According to Harlan and Zohary (1966) the most likely place of origin and beginning of

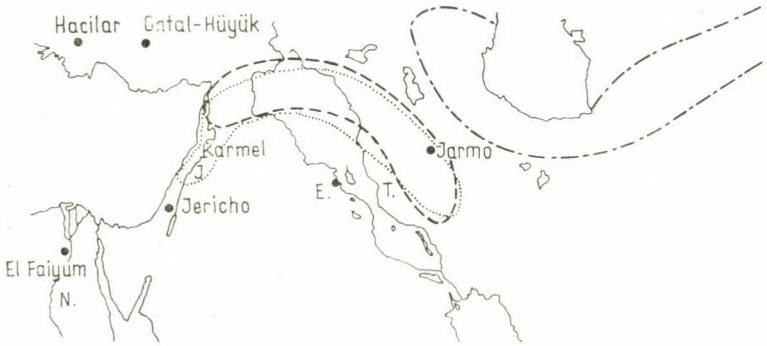


Fig. 1. Map of Asia-Minor
---------- *supposed area of origin of diploid wheat*
. . . . . *gene centre of* Aegilops speltoides
- - - - - - - *gene centre of* Aegilops squarrosa

cultivation of the diploid wheat was in Southern Turkey (Fig. 1). And the domestication of *T. dicoccoides* may have begun in the valley of River Jordan. Human relicts discovered in the caves of Karmel from the Natufian period, the findspots of Hacilar, Catal-Hüyük, Jericho, Jarmo and Alikos are clear evidence to support this theory. Rudorf (1968), Van Zeist and Casparie (1968) give account of a 7500–8400 years old find excavated in the region of Tell Mureybit in North Syria which is identified as *T. boeoticum*. The native country of the genus *Triticum* includes the Transcaucasian region, North, North-Eastern Turkey and North-West Iran. Wheat is extremely rich in forms in that region there are numerous spontaneous hybrids and mutations of which many forms have become stable, but the process of species formation is likely to have started later and is going on even today. In this region many new, mainly pathologically resistant forms are identified (Dorofeev 1968*a*, 1969). Similar experiences are reported from Georgia in Transcaucasia by Dekaprelevich (1969). It was probably this area where *T. timopheevi* and *T. zhukovskyi* came into existence (Upadhya and Swaminathan 1963).

As to the origin of the hexaploid group, it is still under discussion which was the first hexaploid wheat. The supposition that *Tr. vulgare antiquorum* was the earliest one has become questionable; Kuckuck and Peters (1964) say that this fossil wheat was not even hexaploid, but a mere compact variation of *T. carthlicum*. The hypothesis that *T. spelta*, the most primitive hexaploid wheat known today, was not the first one in Asia Minor, but sprang up much later in the area of Switzer-

land and South-West GFR (Andrews 1964) is not – in Kuckuck's opinion – defensible, because in Iran almost all transitional forms from einkorn to *spelta* can be found. These wheats are widely cultivated there in the mountains even today. *T. spelta* forms found in Iran are much like the European ones. Some have tough rachis, but the ear spindles of others are more or less brittle. Kuckuck explains this phenomenon by the mutative change of the Q factor. Monosome analysis revealed that the Q factor is in the 5A chromsome in the Iranian, European and synthetized *spelta* alike. Common origin is thus beyond question. Accordingly, *T. spelta* evolved in Asia Minor and not in Europe, nor is it a mutant form of *T. vulgare*. Jakubziner (1958) also gives account of *T. spelta* as found by André Michaux in Iran (near Hamada), as early as in 1783. Zhukovsky likewise came across *T. spelta* in Iran in 1923. East of the River Euphrates *T. spelta* was still widely grown not so long ago. Its area is very extensive and includes the native countries of *T. dicoccoides* and *Ae. squarrosa*. By mutation treatments Kuckuck and Peters (1964) obtained compact type ears from *T. spelta*. This also proves that *T. spelta* is the most primitive form of the hexaploid series of wheats.

Tanaka and Ish (1973) when processing the material of the expedition carrying out investigations in Turkey, North-East and South-East Iran found that nearly three-quarters of the samples were of *T. timopheevi* type while emmer type only a quarter of them. This suggests that *T. timopheevi* may have played a greater role in the evolution of tetraploid wheat than *T. dicoccoides*.

The origin and relationships of the genus *Triticum* were initially analyzed exclusively on the basis of genome compatibility, although Kihara thought already in 1966 of the plasm in the tetraploid and hexaploid species groups to be alien and to originate from the genus *Aegilops*. Mann's findings (1973) also justify a more thorough study into the origin of the plasm. When the nucleus of *T. aestivum* or *T. durum* is introduced into the plasm of *Ae. bicornis*, *Ae. umbellulata*, *Ae. sharonensis*, *Ae. longissima*, *Ae. haeldreichii* or *Ae. variabilis* male fertility and the growth vigour of the plants decreases. When the nucleus of *T. aestivum* is introduced into the plasm of *Ae. squarrosa* or *Ae. cylindrica* both male fertility and growth vigour remain unchanged. This experience is also worth considering as far as the evolution of the genus *Triticum* is concerned and suggests that the plasm of the genus *Aegilops* is not uniform either. It is thus by a joint analysis of genome and plasm that the history of evolution in wheat may be elucidated.

Chapter 3 The role of wheat breeding in world economy

In Asia Minor it was wheat and barley that made it possible for the wandering groups of primitive man living by hunting and gathering to settle down. At the end of the last glacial period these genera of plants reached a stage of evolution when they were able to supply huge masses of easily stored food. Wheat and barley were the first wider grown cultivated plants whereby man acquired a knowledge of tillage (Helabeak 1964, Mellaart 1958–61, 1966, Rudorf 1968). It follows from this that civilization, culture, urbanization and the sudden growth of population in Asia Minor were made possible by the evolutionary level of these two genera of plants through which man could learn to grow plants and became a ploughman (Lelley 1972*a*); and that it really happened in this way is proved by a large number of archaeological finds (Rudorf 1968). We can thus safely assert that the roots of European culture were set in a soil where the evolution of the genera *Hordeum* and *Triticum* took place. The first agrarian settlements, towns, city-states later empires were formed in Asia Minor. In human civilization and culture a decisive role was played by the cereals of which wheat was the most important one. True that rice later closely competed with wheat in sowing area, but from a European point of view of cultural development wheat maintained its leading role, and it was the Europen culture that exercised the greatest influence on all the cultures of the five continents.

From prehistoric age through ancient and modern times up to the present the economic importance of wheat has not changed in Europe and Asia Minor. In the food supply of world population it occupies the first place even today, moreover, its importance is still growing in spite of the fact that in certain industrially developed countries the per capita wheat consumption is decreasing. Compared to its first rival, the rice, its world cropping area is larger because its adatability is better and has a lower water and temperature demand. Its yield per unit area does not attain that of rice, or even falls substantially behind it, especially where rice is harvested twice a year. According to statistical data the wheat area of the world is growing and yield average is also increasing (Table 1).

The improvement of the methods and implements of soil cultivation as well as chemization have rendered the production of wheat wholly mechanizable. Production costs and manual labour requirement per unit area have decreased. These circumstances also contribute to the increased importance of wheat in world economy.

Owing to breeding the wide ranging pathological resistance, the improved winterhardiness, the extremely high potential productivity as well as irrigation and utilization of high rate fertilizers made possible by the production of semidwarf varieties enable not only the rapid growth of the sowing area but a more

Table 1. Wheat yield averages on the basis of FAO statistics

Country	1961–65 q/ha	1971 q/ha
Bulgaria	18.1	30.0
Yugoslavia	17.9	20.7
Roumania	14.6	17.9
Italy	20.1	23.3
Czechoslovakia	24.2	28.2
Hungary	18.6	31.5
Poland	19.7	23.0
France	29.3	34.4
GDR	31.5	35.9
GFR	33.1	37.9
Sweden	34.4	36.7
European average	20.8	24.6
Soviet Union	9.5	14.4
Canada	13.8	17.9
USA	17.0	20.9
Mexico	20.2	28.4
North American average	15.9	20.5
Argentina	15.3	12.5
Bolivia	7.1	10.1
South American average	13.7	12.0
Japan	23.3	20.7
India	8.4	12.1
China	8.8	—
Asian average	9.0	11.0
African average	8.2	8.8
World average	12.1	14.8

Total wheat area of the world in 1971: 210 291 000 ha

reliable production and larger yields too. If hybrid wheat production fulfils the expectations the importance of wheat breeding in world economy will be further increased. Due to the cultivars indifferent to daylength, the uniform mechanized cultivation methods as well as to chemization the production area of the improved varieties will extend far beyond the borders of the producing countries, even to other continents. This possibility have been realized in the last ten years by the Italian, French, Soviet, and above all by the Mexican improved cultivars. All this promotes the further spread of wheat production.

Wheat is a concentrated food but the biological value of its protein does not even reach 70 per cent. Breeding for quality and agrotechnical research have done a lot to improve protein content, gluten and baking quality. These results have also contributed to the spread of wheat production and to a general liking of foodstuffs prepared from wheat. Recent improvements in the biological value of protein bid fair prospects too. This is a great chance, because the more the world population increases the more the uneconomical energy uptake mediated by animals must be reduced. It is obvious even today that in overpopulated countries like India and China the consumption of food of animal origin decreases and must be

replaced by foodstuffs of plant origin. Therefore the essential amino acid composition of plant proteins must be brought nearer to animal proteins. The importance of wheat in the world supply of food would grow a great deal by increasing the biological value of its protein. A mere agrotechnical device does not help much here, breeding has the possibility only of exercising a favourable influence on the genetically determined essential amino acid composition of wheat protein.

In industrially developed countries wheat consumption has been showing a slowly decreasing tendency in the past fifty years. At the same time, in countries with a higher population density a temporary grain shortage occurs from time to time even today. Some countries produce considerable wheat surpluses every year the selling of which often meets difficulties. On the other hand, others do not grow enough wheat, and the population is hardly sufficed of concentrated vegetal food. Owing to this disproportion in the big wheat producer countries like the United States and Canada even a temporary restriction of sowing area was promoted. In China, India, in the Middle East and even in the Soviet Union, on the other hand, great efforts are made to increase the production of wheat, under warm climatic conditions by irrigation, while in the cold zones by developing more frost-resistant winter wheats or spring wheats with very short vegetation periods.

As a result of the plant breeding and agrotechnical progress of the last two decades a number of countries, former importers of wheat, have become self-supporters, or nearly self-supporters in spite of their growing population. In this regard Sweden, GDR, GFR, Austria, Italy, Mexico, Turkey, Greece and even India have attained considerable results.

The yield averages have grown everywhere; in Sweden, GDR, GFR and Austria this change was brought about by high yielding new home-bred varieties. In Central and Eastern Europe, in Czechoslovakia, Hungary, Yugoslavia, Roumania and Bulgaria likewise a considerable increase of yield average was reached in the last ten years, that was mostly due to the imported new high yielding varieties.

According to data for 1959–60 (Vlach 1962) in Czechoslovakia the varieties Hadmerslebener VIII, Peko and Heine VII gave the largest yields. By 1968 the variety assortment was completely changed and the Soviet origin Miranovskaya 808 and Bezostaya 1 came to the first place (Kábrt 1967). According to Andraščik (1970) the change of variety resulted in an increase of the yield average from 19.5 to 31.7 q/ha by 1968 in Slovakia, and a further 10–13 per cent increase was expected by 1975.

The wheat production of Hungary has always been particularly important in Europe. In the region east of the Danube, and mainly in its southern part grew the best quality wheat in Europe. Wheats selected from the local varieties of the region always played a significant role in European wheat breeding for quality. Until 1958 home-bred varieties were exclusively grown in Hungary. From 1958 attempts were made to increase the 16 q/ha yield average first by sowing Italian and French varieties. San Pastore was the most widely sown variety here. The Soviet Bezostaya 1 was put to trial then grown from 1960 following the advice of Rajki (1954). Yield average increased; between 1961 and 1965 it attained 17.4 q/ha and between 1970 and 1973 it exceeded 30 q/ha, which can be attributed to the high potential productivity of Bezostaya 1 (Lelley 1967*a*).

In Roumania, Giosan (1966) reported a yield average of 12 q/ha for a 3 million ha area between 1957 and 1961, which rose to 15 q/ha between 1962 and 1966. The first results of trials with Bezostaya 1 were published in 1963 (Boldea et al. 1963). From this time on Bezostaya 1 rapidly spread and in 1965 it occupied a considerable part of the sowing area (Crivat 1965); then came the first home-bred high yielding varieties: Dacia, Moldova, Excelsior and Favorit. In 1971 further intensive Roumanian varieties were released: Turda 195, Olt, Lovrin 10, Lovrin 231 (Muresan et al. 1971). The rapid increase of yield average, in Roumania too, was, however, mainly due to Bezostaya 1, the role of which was later taken over by home-bred varieties. Accordingly, the yield average rose to 17.9 q/ha in 1971.

Besides the higher level of cultural practices, the rapid increase of the yield average in Yugoslavia was mainly due to the introduction of high yielding Italian wheat varieties in 1955. According to Blazevski (1962) of the total sowing area of 2.1 million ha, 1.15 million ha was sown to high yielding new varieties in 1963, of which 60 per cent was occupied by the variety San Pastore. Drezgič and Jevtič (1962) gave account of the French varieties Etoil de Choisy occupying 21 per cent of the sowing area. The first experiments with the cultivar Bezostaya 1 began in 1963 (Handzič 1963). Though its sowing area increased still the Italian varieties were invariably grown over a large area. It was first of all Libellula and Leonardo that equalled San Pastore. From 1966–67 important role was already played by the home-bred intensive varieties like Bačka, NS-32, Kragujevacka 75, Crvená Zvezda and Kupa (Borojevič 1967). The latest Yugoslavian high yielding variety is Sava. The yield average of the country reached 20.7 q/ha in 1972.

Between 1956 and 1960 Okerman 17 was the standard wheat variety in Bulgaria (Popov and Boyadzhieva 1962). Experiments were carried on at that time with the extensive Soviet varieties Krasnozernaya 421, 431, 451, Novoukrainka 83 and Odesskaya 12 and 3, too. At the same time Ivanov (1962) gave account of trials with Italian wheat varieties of which Autonomia and San Pastore gave particularly good results. With these a rapid increase of wheat yield averages began in Bulgaria too; in 1964 Popov and Kolev reported already on the first successes of the Soviet varieties Bezostaya 1, Skorospelka 3b and Belotserkovskaya 198. From then on Bezostaya 1 quickly gained ground and gradually replaced the Italian varieties. In 1967 a further Soviet variety, Rannaya 12 was introduced (Mitkov 1967). The first Bulgarian bred rival of the Soviet varieties was Nadesda 2 which mainly proved well in the southern regions (Boev and Zapryanov 1968), then Sadovska Ranozrejka 3 (Popov 1970) and later Burgas 2 (Boev 1971). The change of varieties was just as rapid in Bulgaria as in Yugoslavia. First with the help of Soviet wheats, later by producing domestic cultivars Bulgaria succeeded in raising the average yield to 30.0 q/ha by 1971.

Of the wheat producing countries lying along the River Danube in Austria the rapid increase of the yield average and the gradual reduction of dependence on wheat import were attained mostly by home-bred varieties. This was partly due to the introduction of the system of buying up on the basis of quality. A premium awarded for the quality increased the utilization of nitrogen fertilizers which, in turn, stimulated the import and breeding of high yielding varieties (Leopold 1964).

According to Schober (1968) in 1967 Austria no longer needed to import wheat and this was mainly due to the quick change of the variety assortment. In ten years the earlier grown varieties were entirely replaced by new ones, and in 1967 the high yielding home-bred variety Rekord was grown on almost 60 per cent of the sowing area. Besides it Herla-Kolben, a German and Svenno, a Swedish high yielding cultivar were also sown. In 1968 the newly bred Propsdorfer Extrem and Propsdorfer Geber gave the highest yields (Meinx and Hron 1968). Bezostaya 1 which proved so excellent in the Lower Danube valley could no longer compete in Austria with the domestic varieties. According to data for 1971 (Korič and Korič 1971) even the semi-dwarf Mexican varieties could not come close to the results of the domestic varieties.

In Middle Eastern Europe the first impetus to the production and breeding of new type wheat varieties was given by the Italian breeders where according to the data published by Martilli (1967) the sowing area of wheat decreased by neary 500 000 ha, but the extremely high yielding soft wheat varieties developed by breeders raised the yield averages to the highest level decreasing thereby the import dependence of the country.

Among the North European countries Norway decreased the sowing area of wheat in favour of oats (Haland 1969).

A similar course was followed by Sweden, where the sowing area of spring wheat has decreased in favour of winter wheat (Bengtsson 1966). Yet, with excellent new varieties Sweden has considerably increased the yield average. In this process a particularly important role was played by the varieties Starke, Pope, Svenno and Ring. The latter three are spring wheats (Och and Hummel-Gumaelius 1971). According to Bengtsson (1971) besides Starke, two new varieties, Starke II and Vigo, also contributed to the success of wheat growing in Sweden. Fajersson (1970) gives information that about 90 per cent of the winter wheat area was sown with the varieties Starke and Starke II in 1969. Thus Sweden became self-supporting and it was reached exclusively by home-bred varieties.

Among the larger European wheat producing countries Poland mostly grows home-bred and Soviet varieties.

In France the average yield has rapidly increased since 1958. Of the yield harvested in 1968–69, 60 million q were left over for export. According to Deffontaines (1970) the wheat area is far from being fully exploited. It could be extended by some 40 per cent without any difficulty which would mean a further significant increase in export. In France too home-bred varieties are grown.

In Belgium the rapid increase of the yield average was made possible also by the introduction of new, more intensive varieties. The situation was the same in Holland and in Denmark too. In Holland and Belgium mostly French and German varieties are grown, while in Denmark improved Swedish varieties are given priority.

According to the data published by Udashin (1968), in the German Federal Republic only 16.6 per cent of the total arable area is occupied by wheat, but there the average yield exceeds 30 q/ha. The range of variety is wide; besides home-bred varieties, French and Swedish ones are also grown.

A quick change in variety characterizes the wheat production of the German Democratic Republic. Besides home cultivars important role has been played

since 1969 by the Soviet Miranovskaya 808 (Gruchow 1969). In 1970 this variety proved to be the best (Prickler 1970, Henkel and Moritz 1970).

In England the yield averages are very high, and the change of varieties also has considerably accelerated, since under the rainy climate of the country lodging resistance has become of special importance. In 1965 eleven winter and summer wheat varieties included in commercial production (Fiddian 1965). In 1969 the winter variety Cama and the spring wheat Koga were considered to be the best cultivars. It was in 1969 that semi-dwarf spring wheats were first put to trial (Thorne et al. 1969); in 1970 the newly bred cultivars: Maris-Nimrod and Tommy winter, Kleiber, Maris-Dove and Rask spring wheats, were found to be superior to those grown earlier (Fiddian 1970).

In the whole of Eurasia, the Soviet Union is the largest wheat producing country. The slower rate of increase in yield averages is due to the vast areas newly drawn into cultivation where varieties of intensive type cannot be grown as yet. On the European part of the Soviet Union, the new high yielding varieties show remarkable results. In the western and south-western regions the production of Bezostaya 1, Mironovskaya 808, later Aurora, Kavkaz, Mironovskaya-Yubileynaya 50 and Odesskaya resulted in a sudden rise of the yield average over the last ten years (Smulsky and Moldaver 1970, Lukyanenko 1970, Remeslo 1970).

There was an increase in the yield averages over the past decade in the largest overseas wheat producing countries too, though the rate was not as fast as in some European countries. This may be explained by their difficulties in selling the huge wheat surpluses which discouraged the rapid growth of production.

The very wide range of wheat varieties in the United States of America reflects the varying climatic and soil conditions. In 1963 98 cultivated varieties were registered of which many were earlier improved wheats. Since 1963 signs of an accelerating change of cultivar has been observed. It was stimulated by the appearance of the first semi-dwarf wheat variety. In 1963, two years after its official qualification, Gaines was already in the focus of a general interest in semi-dwarf varieties (Vogel et al. 1963). In 1969 a number of Mexican bred dwarf cultivars were tested: Siete Cerros 66 and Inia 66 gave good results especially in California (Prato and Allan 1969). With this the semi-dwarf wheat cultivars began to gain ground over the total wheat area. The latest varieties such as Logan (Lafever 1969) as well as Trader, Trapper, Scout 66, Scotland and Guide are already representatives of this shorter straw type.

Canada is also characterized by the rapid change in the range of cultivars. In counties Alberta, Manitoba and Saskatchewan, where the wheat area is the largest (17.6 million acres), 8 *T. aestivum* and 4 *T. durum* varieties have been grown. Manitou, Necpawa and Thatchen, and of the *durum* varieties Hercules and Stewart were the widest spread wheats. The sowing area of winter wheats is, however, increasing, due to improving tendency in lodging resistence (Austenson and Anderson 1969). Recently semi-dwarf varieties have been introduced into Canada too, especially since the Mexican cultivar Pitic 62 yielded surprisingly good results in 1967–68 (Morrison and Campbell 1969).

On the North-American continent the greatest change in wheat production has taken place in Mexico (Borlaug 1968). The former importer in wheat owes its

considerable volumes of export in 1967 to wheat breeding; 42 000 tons of seed grain alone. Of the semi-dwarf spring wheats produced in Mexico Pitic 62, Lerma Rojo 64, Inia 66 and Sonora 64 have become particularly well known and, in addition to the American continent, promoted the development of wheat growing in India, Turkey, Afghanistan, Iran and in other countries, too.

The yield averages of Brasil and Argentine, the two biggest wheat producers of the South-American continent, have not made much progress. In Brasil the wheat crop has even been reduced, because under the humid climate great damages are caused by *Septoria nodosum* and *Gibberella Zeae*. Better results are now expected from the resistant varieties and from the Mexican semi-dwarf wheats (Osorio et al. 1973). Breeding for resistance is therefore the first precondition of yield increase in South America (Beckman 1963).

Australia is a continent with growing wheat area. The variety assortment varies according to the 14 wheat districts (Heard 1962). In Australia, too, the sowing area of winter wheats is increasing at the expense of spring wheats (O'Reilly 1964). The yield averages rise slowly because of the very extreme soil and climatic conditions. The range of varieties is, accordingly, very wide. Brown and Fitzsimmons (1968) recommended eight varieties for the northern area, ten for the central and twelve for the southern regions to be grown in 1969. Breeding, here too, gradually changes over to shorter straw cultivars. The new Darka variety (Fisher et al. 1969) as well as Glatcher, a wheat developed in Sidney (Brown and Fitzsimmons 1971), and, on the western areas, Gamenya (Boyd and Leigh 1973) are already of this type.

Among countries with high population density special attention should be paid to India where all forms of cultivation from irrigation to the most extreme dry farming, can be found. Its yield averages were always low; wheat production has never met the country's requirements. It was first in 1964 when the Mexican Lerma Rojo 64 and Sonora 64 wheat varieties were put to trial (Swaminathan et al. 1966). From then on the semi-dwarf varieties rapidly spread and the breeding of new domestic semi-dwarf cultivars began. Sharbati Sonora and Sonalika were produced in 1968. The former is particularly important for India where the majority of the population consumes vegetal food, since it provides more proteins with a higher biological value (Bains et al. 1968). Dargan et al. (1971) were the first to give account of P. V. 18 and Kalayan 227, two new semi-dwarf spring wheats with a vegetation period of 110–115 days. Under irrigated conditions the sowing area in Bengal can be turned to production three times a year with these varieties. The semi-dwarf varieties S 308 and Kalayan-Sona are new results of breeding. With the new semi-dwarf varieties the Indian wheat production has considerably decreased the imports and approaches self-sufficiency. The dwarf and semi-dwarf varieties achieve success in the wheat areas of the neighbouring Pakistan, Afghanistan and Iran, too (Mudra 1972).

In Japan, the leading country in wheat research, wheat is grown on a relatively limited area because rice is more economically produced. Breeding has produced in this country too varieties with very high yields. Breeding for shorter straw began as early as in 1917; the Norin progenies which later gave the semi-dwarf character of the American and Mexican semi-dwarf cultivars as well as the Agakomughi

wheats from which the earliness and short straw of the Italian cultivars originated were produced in 1924 (Forlani 1954, Reitz and Salmon 1968, Lelley 1971*a*). The most recent Japanese varieties, such as Aobakomugi, Nanbokomugi, Hitsumikomugi, Okukomugi, Sakyukomugi, Furutsumasari, are without exception extremely high yielding dwarf and semi-dwarf wheats (Laboratory of Wheat and Barley Breeding 1970, 1971).

In the past ten years an important change occurred in the position and breeding tendency of durum wheats used as basic material in Italian macaroni production. The new breeding tendency is to introduce durum wheats adapted to the Mediterranean climate into areas where they have not been grown before.

This tendency was followed in Italy too, where durum wheats have a large sowing area (Rusmini 1967). Between 1959 and 1968 a number of new varieties were developed with this intention (Gambioli and Pecci 1968). As a consequence, the sowing area of durum grew from 1.38 to 1.46 million ha, and the yield increased from 15.4 to almost 21 million q. Still the domestic consumption has not been fully met even by these quantities, considerable additional volumes have to be imported. According to Danielli (1969) the reason why the yield averages of the durum wheats do not increase as fast as those of the hexaploid wheats is that they have to occupy new areas. Earlier 95 per cent of the durum yield originated from Southern Italy, now with the new varieties, Maliani-11/C, 8/D and 12/D, the sowing area has been extended towards the north (Brevedan 1969). In 1970 34.8 q/ha yield was attained with durum wheats in the northern areas which is hardly lower than what the bread wheats produce (Zanini 1970).

The other large durum producer of Europe is France. Here too the aim in the last ten years was to extend the sowing area of the durum wheats towards the north (Barbut 1960). With the varieties La Cora, Leeds and Wells this aim was duly fulfilled (Grignac 1969). According to Thizeau (1965) in spite of this headway the durum yield still does not cover the demand of France.

The sowing area of durum wheat is increasing in Greece, and in Bulgaria, too (Dimitrov 1962). Similar tendency is shown in the Soviet Union, especially in West Siberia and in the Ural region (Bogomyakov 1964); moreover, durum breeding has been attempted over some areas along the Carpathians (Maksyuk and Maksyuk 1969).

In 1970 the sowing area of durum was 550 000 ha with a yield of 7.7 million q in Canada, and 1.4 million ha with a 26 million q yield in the United States. These results were reached with recently improved varieties: Steward 63, Mindum, Pelisier and Golden Ball in Canada, and Leeds, Welles and Lakota in the United States (Anonymous 1970).

The world-wide increase in the sowing area of wheat in the past decade proves in the first place the success of breeding. The higher yield average is, on the other hand, the result of the joint effect of breeding and an improved agrotechnical level. The best results were obtained by winterhardiness, pathological resistance, dwarf growth and increased potential productivity. The hybrid wheat is the only one that has not fulfilled the expectations so far. On certain areas, mainly in West Europe, baking quality shows an improving tendency, in other places the very efforts made to produce large yields have resulted in some deterioration.

The phenomenon that certain excellent varieties spread beyond the frontiers of the country and enter into competition with domestic wheats have become conspicuous for the last ten years. Large areas have been occupied by Bezostaya 1 in Hungary, Roumania, Bulgaria and Yugoslavia, and by Mironovskaya 808 in Czechoslovakia, German Democratic Republic and Poland. Of the Italian varieties San Pastore and Libellula spread over the south-eastern regions of Europe. Besides them some French, Swedish and German varieties too have extended beyond the frontiers.

Some of the daylength indifferent spring wheats developed in Mexico have covered a still greater distance since they have been introduced into the United States of America, Canada, India, Persia, Afghanistan and Turkey. This is why the improvement of adaptation has recently become an important task of breeding. With this in mind, in the framework of experiments organized by the International Wheat Performance Nursery certain valuable varieties are tested in all wheat growing regions of the world in order to find out their adaptation to the changing conditions. This tendency has resulted in a world-wide international co-operation in wheat breeding, which – at the same time – makes the competition sharper thereby increasing the efforts of each of the participants.

Chapter 4 **Taxonomy**

The first taxonomical classification of the genus *Triticum* was done by Linné in 1764. Linné's categories were modified by Villars in 1787. The name *Triticum vulgare* originates from him. New systems were elaborated by Vilmorin in 1850, Schultz in 1911, Flaksberger in 1935 and Mansfeld in 1951, but neither of them caused such a profound change in taxonomy that occurred in the last 15 years. Since, as the genetic relations between the species and genera became gradually clearer the system changed simultaneously and much approximated categories based on real evolution-genetic relations.

When the alloplasmic, alloploid nature of the tetraploid and hexaploid species of the genus *Triticum* was pointed out, and excepting genome A all genomes were traced back to the genus *Aegilops*, it seemed almost imperative to include the genera *Triticum* and *Aegilops* in the same taxonomic category. In 1959 Bowden suggested a taxonomic modification according to which both *Triticum* and *Aegilops* would have been merged in a common *Triticum* genus. Mac Key (1963), on the other hand, referring to easier orientation disapproved of this merger and suggested a more simple taxonomic arrangement for the genus *Triticum.*

In the emergence of tetraploid and hexaploid *Triticum* species, some species of the genus *Aegilops* played a decisive role, because genomes B, D and G originate from these genera. Kihara (1966) and Suemoto (1968) pointed out that the plasms of the tetraploid and hexaploid wheats are also alien, or more correctly are of *Aegilops* origin. During evolutionary hybridisation the *Aegilops* partner was thus the mother. Accordingly 50 per cent of the genotype and 100 per cent of the plasmotype of tetraploid wheat species are of *Aegilops* origin. In the hexaploid section, except *T. zhukovskyi*, 66 per cent of the genotype and similarly 100 per cent of the plasmotype derive from the genus *Aegilops*. Owing to these facts Bowden (1959) cannot be blamed for merging *Aegilops* and *Triticum* on an evolution-genetic basis. From a taxonomic point of view even the suggestion of including *Triticum* in the genus *Aegilops* should not be reproved, since only the idiotype of the two diploid species is of *Triticum* origin.

Mac Key's (1963) argument that the genus *Aegilops* cannot reasonably be brought together with *Triticum* because then the genera *Secale*, *Agropyron* and *Haynaldia* might just as well be jointed, since they also have constant hybrids with *Triticum*, is somewhat forced. The constant *Aegilops* and *Triticum* hybrids emerged, survived and developed into large species groups in a natural way during evolution. With the genera *Secale*, *Agropyron* and *Haynaldia* no fertile hybrids have been produced in a natural way. The known intergeneric hybrids have only survived as a result of drastic human intervention (Szalai and Belea 1962). No natural evolution of species took place in this way, so the evolution-genetic rela-

tion is more distant. Mac Key (1963) is, however, right in saying that in splitting the genus *Triticum* into species and groups of species the limits should not be determined by morphological differences; and the erected categories should show real specific differences, thus incompatibility may be due either to the different number of chromosomes or to other profound genetic differences. Species cannot be determined by characters found to be of genic heredity. The same applies to the case when incompatibility is genically based. Therefore Mac Key in 1963 divided the genus *Triticum* into five species of which one is diploid, two are tetraploid and two hexaploid. The diploid species has two subspecies, the two tetraploid species are subdivided into seven subspecies and four convarieties, while the hexaploids were suggested to have six subspecies.

If in both propositions we concentrate on what makes them really justified we have to admit that from a taxonomic point of view the merging of *Aegilops* and *Triticum* is in principle reasonable; however, as far as simplicity and comprehension are concerned Mac Key's reasoning is relevant. Nevertheless, before the final integration the members of the *Aegilops* genus should also be subjected to the same intensive genetic analysis that was carried out in the genus *Triticum*. Namely, through integration the number of possible genomes in *Triticum* will be increased by the S, C and M genomes. In addition, the S genome has S^b, S^l and S^v variations, and there exist M^{cr}, M^i, M^v, M^b of the M genome, and C^u of the C genome. This makes the genetic structure of the genus more complicated compared to the earlier four *Triticum* genomes.

Morris and Sears (in Quisenberry 1967) accepted with some alterations Bowden's suggestion and contracted *Aegilops* and *Triticum*. The symbols of the above listed genomes were also simplified since only the S^b and S^l symbols of genome S and M^u and M^t of genome M were taken over. This has provided a clearer view but the *Triticum* genus obtained in this way is substantially larger and more complex (Table 2). Even this simplified integration was not acceptable to Mac Key (1968) and he regarded it as a taxonomic deadlock. Owing to the practice that since the publication of Morris and Sears' new taxonomic arrangement the authors have invariably used *Aegilops* as a valid generic name one may conclude that Morris and Sears' sugestion has not been generally accepted. Mac Key (1968) drew attention to the different evolutionary trends of *Triticum* and *Aegilops* which he regarded as further evidence that the two genera should not be amalgamated. His suggested taxonomic arrangement includes three genera: *Aegilops* L., *Crithodium* Link and *Triticum* L.

The first genus includes all *Aegilops* species, while the genus *Crithodium* has only one species: *aegilopoides* Link, the donor of genome A. The diploid wheat was thus raised to the rank of a separate genus. And as for *Triticum* Mac Key thinks that it is a young hybrid genus where there is room for all constant species that have developed and develop in a natural or artificial manner (Table 3).

By separating the genus *Aegilops* this taxonomic proposition makes the categories of the genus *Triticum* easier to survey. Its raising of *Crithodium*, the donor of genome A, to the rank of a separate genus is taxonomically right. To include artificially produced species in the system is a new idea which can be regarded as an attempt to simplification; yet it is objectionable because if the R genome is

Table 2. Taxonomic arrangement of the genus Triticum *as suggested by Morris and Sears (1967)*

Species	Genome
I. Diploids	
T. monococcum L.	A
T. speltoides (Tausch.) Gren. ex Richter (*Ae. speltoides* Tausch.)	S (= B?)
T. bicorne Forsk. (*Ae. bicornis* (Forsk.) Jaub. & Spach)	S^b (= B^b?)
T. longissimum (Bowden) (*Ae. longissima* S. & M. in M. + *Ae. sharonensis* Eig)	S^l (= B^l?)
T. tripsacoides (Bowden) (*Ae. mutica* Boiss.)	M^t(= B??)
T. tauschii (Coss.) Schmal. (*Ae. squarrosa* L.)	D
T. comosum (Richter) (*Ae. comosa* S. & S.)	M
T. uniaristatum (Richter) (*Ae. uniaristata* Vis.)	M^u
T. dichasians (Bowden) (*Ae. caudata* L.)	C
T. umbellulatum (Bowden) (*Ae. umbellulata* Zhuk.)	C^u
II. Allopolyploids	
T. turgidum L. var. *dicoccoides* (Bowden) (*T. dicoccoides* Körn.)	AB
T. dicoccon Schrank	AB
T. durum Desf.	AB
T. turgidum L.	AB
T. polonicum L.	AB
T. carthlicum Nevski	AB
T. timopheevi (Zhuk.var. *timopheevi)*	AB or AG
T. timopheevi Zhuk.	AG
T. zhukovskyi Men. & Er.	AAB or AAG
T. aestivum L. em. Thell.	ABD
T. spelta L.	ABD
T. macha Dek. & Men.	ABD
T. vavilovi (Jakubz.)	ABD
T. aestivum L.	ABD
T. compactum Host.	ABD
T. sphaerococcum Perc.	ABD
III. Other allopolyploids	
T. ventricosum Ces. (*Ae. ventricosa* Tausch.)	$D\underline{M}^{u+}$
T. crassum (Boiss.) (*Ae. crassa* Boiss.)	$D\underline{M}^t$

Table 2. continued

Species	Genome
T. syriacum (Bowden) (*Ae. crassa* Boiss.)	DMS^{t}
T. juvenale Thell. (*Ae. juvenalis* (Thell.) Eig.)	DMC^{u}
T. kotschyi (Boiss.) Bowden (*Ae. kotschyi* Boiss.)	$C^{u}S^{t}$
T. ovatum (L.) Raspail (*Ae. ovata* L.)	$C^{u}M$
T. triaristatum (Willd.) Gord. & Gren. (*Ae. triaristata* Willd.)	$C^{u}M$ $C^{u}MM^{u}$
T. macrochaeatum Richter (*Ae. biuncialis* Vis.)	$C^{u}M$
T. columnare Zhuk. (Morris & Sears) (*Ae. columnaris* Zhuk.)	$C^{u}M$
T. triunciale (L.) Raspail (*Ae. triuncialis* L.)	$C^{u}C$
T. cylindricum Ces. (*Ae. cylindrica* Host.)	CD

Earlier names in parenthesis.

introduced in the *Triticum* genus in the form of a *Triticale* species group, then *Secale* must also be grouped under this taxonomic unit.

Still the taxonomic problem of wheat has not been solved. Even the taxonomic terminology of wheat genetics was not uniform in the lectures delivered at the 1973 international symposium in Missouri. The situation as yet is not confusing because the genus in question is a subject of intensive research, and even new species may come to light soon, as e.g. *T. petropavlovski* Udash. et Migus., a wheat with 42 chromosomes, whose genome structure according to Udashin and Migusova (1970) is AAVVDD; on the other hand, the substitution and addition methods may give rise to further amphidiploids. In the regions of Transcaucasia, North Turkey and North Iran species formation is still in the making. Due to climatic changes taking place in Asia Minor the gene centre of the genus *Triticum* might shift towards the north, north-east which may involve the emergence of new species.

In the categories suggested by Mac Key (1968) the artificially produced new species also find their places. Recent experience proves the necessity of such an arrangement. Beridze and Georgidze (1970) give account of an octoploid *T. timopheevi* found in a Western Georgian Zanduri population. Jakubziner (1971) describes a new hexaploid wheat: *T. aestivum* L. var. *vavilovianum* Jakubz. Dorofeev et al. (1969) discuss *T. turgidum* spp. *transcaucasicum* and spp. *orientale* found in Azerbaidzhan. In 1969 Jakubziner came across a spontaneous mutant in *T. timopheevi* which he described under the name of *T. militinae*. A great variety of form in the wheat populations of the Transcaucasian region is testified

Table 3. Taxonomy of the genus Aegilops—Triticum *as suggested by Mac Key (1968)*

	2n	Genome type and cluster
Aegilops L.		
Polyeides (Zhuk.) Kihara		
Ae. umbelluata Zhuk.	14	C^u
Ae. ovata L.	28	C^uM^o
Ae. triaristata Willd.	28	C^uM^t
Ae. recta (Zhuk.) Chenn	42	$C^uM^tM^{t2}$
Ae. columnaris Zhuk.	28	C^uM^c
Ae. biuncialis (Vill.) Vis.	28	C^uM^b
Ae. variabilis Eig.	28	C^uS^v
Ae. triuncialis L.	28	C^uC
Cylindropyrum (Jaub. et Spach) Kihara		
Ae. caudata L.	14	C
Ae. cylindrica Host	28	CD
Vertebrata (Zhuk.) Kihara		
Ae. squarrosa L.	14	D
Ae. crassa Boiss. 4×	28	DM^{cr}
Ae. crassa Boiss. 6×	42	DD^2M^{cr}
Ae. vavilovii (Zhuk.) Chenn	42	$DM^{cr}S^l$
Ae. ventricosa Tausch.	28	DM^v
Ae. juvenalis (Thell.) Eig.	42	DC^uM^j
Ambylopyrum (Zhuk.) Kihara		
Ae. mutica Boiss.	14	M^t
Comopyrum (Jaub. et Spach) Sen.-Korch		
Ae. comosa Sibth. et Sm.	14	M
Ae. uniaristata Vis.	14	M^u
Sitopsis Jaub. et Spach		
Ae. speltoides Tausch.	14	S (= B)
Ae. bicornis Forsk. (Jaub. et Spach)	14	S^b
Ae. longissima Schweinf. et Muschl.	14	S^c
Crithodium Link		
Cr. aegilopoides Link	14	A
Triticum L., emend. Mac Key (emend. nov.)		
Dicoccoidea Flaksb.		
Tr. timopheevi Zhuk	28	AB (= AG)
Tr. turgidum (L.) Thell	28	AB
Speltoides Flaksb.		
Tr. zhukovsky Men. et Er.	42	AAB
Tr. aestivum (L.) Thell.	42	ABD
Triticale (Tscherm.) Mac Key, comb. nov.		
Tr. turgidosecale Mac Key, spec. nov.	42	ABR
Tr. aestivosecale Mac Key, spec. nov.	56	ABDR
Trititrigia Mac Key, sect. con.		
Tr. turgidomedium Mac Key, spec. nov.	42	ABX
Tr. aestivomedium Mac Key, spec. nov.	56	ABDX

by the publications of Dorofeev (1968*a*, 1970): 48 diploids, 134 tetraploids, 192 hexaploids are enumerated in them. He identified 251 variations in Azerbaidzhan, 150 in Armenia and 140 in Georgia. With such a degree of variability it is easy to understand why the taxonomy of wheat is yet incomplete.

Essential changes and proposed modifications in the last ten years have rather confused the taxonomic situation. The concrete disadvantage it has given rise to is that the nomenclature of the literature is not uniform.

It is the great variability of form in the genus *Triticum* as well as human intervention that cause the gravest difficulties of systematization, the ephemeral nature of taxonomic grouping and the lack of a perfect harmony in taxonomy. From the tetraploid, and above all the hexaploid species of wheat innumerable cultivars have been produced; it would be desirable to elaborate a key which would ensure the uniform identification and grouping of cultivars. There is also a need for a system of cultivars. No general taxonomic key suitable to identify cultivars has been constructed so far though many experts have attempted to make one. Mándy dealt with this question in 1962, Steinberger elaborated a key of the Austrian varieties in 1970. Gandilyan (1970) tried to solve the problem on the basis of morphological characters, with a code system combining Roman and Arabic numerals with small and capital letters. It would be desirable to co-ordinate the different methods in order to develop a uniform cultivar code system.

Chapter 5 The chromosomes of wheat

The A, B, D and G genomes contain seven chromosomes each. Within the genome each chromosome has its homologous pair which means that in them the same loci are found in the same sequence. Homology between chromosomes of different genomes are far from being perfect, they are therefore called homoeologues, that is, if the "Ph" factor which inhibits the pairing of homoeologous chromosomes does not act, then the latter pair probably owing to their closeness in space. In the absence of Ph, however, pairing is incidental so that inhomologous chromosomes may also pair. In the case of homoeologous paring the synapsis is not so perfect as that taking place between homologous chromosomes, that is probably due partly to the not wholly identical sequence of loci.

From the point of view of genetic research it would be desirable if the morphological identification of chromosomes by microscope were reliable. This has not, however, been completely solved so far, because wheat has several chromosomes showing only slight morphological differences and the proportions of the individual chromosomes may vary from cell to cell in the same microscopic preparation which again makes visual differentiation difficult (Lelley 1973*a*).

Chromosomes cannot be identified by length because whether it is metaphase I or in anaphase II of meiosis. When measuring takes place, the lengths may vary within such wide limits that the differences become indistinct. Gill et al. (1963) found the length of chromosomes in the wheat Wichita to range between 4.66 and 7.87 micron in metaphase I, and from 7.86 to 13.06 micron in anaphase II (Fig. 2). Sears (1954) obtained 5.02–6.87 micron in M I and 5.55–12.32 micron in A II of chromosome length of Chinese Spring.

The arm ratios are no more reliably determined either. According to the investigations of Sears (1954) in Chinese Spring the arm ratios varied from 1.05 : 1 to 2.65 : 1, but the differences mostly were so slight that were unsuitable for identification purposes (Table 4). The chromosome measurements obtained by Larsen and Kimber (1973) in scanning densitometer were partly different (Table 4). A joint examination of arm ratio and chromosome length gives somewhat more reliable results, but even this is insufficient to identify individual chromosomes. Sasaki et al. (1963) have drawn attention to significant differences between the average lengths of chromosomes in samples taken from different flowers of the same ear, which may depend on the technique of preparation, furthermore differences may occur between the ears of the same plant, too. Measurements taken in telophase II of meiosis are suitable to determine the arm ratio, but here too overlapping may occur according to which different chromosomes may show nearly identical arm ratios.

There are chromosomes which can be recognized by their characteristic shape. Such are the two satellite chromosomes of genome B: 1B and 6B. In good preparations the 5D chromosome can reliably be identified, because at one end it has a nearly rectangular curve resembling a satellite. The 5A and 5B chromosomes are more difficult to recognize. In T II they are seen to have crooks at the end of one of the arms which, however, is not always distinct, or it may happen that other chromosomes assume the same position. 6D is the shortest and thickest chromosome of all (Sasaki et al. 1963; Gill et al. 1963; cf. also Fig. 2).

Table 4. Chromosome measurements in wheat according to the data of Sears (1954)

Chromosome	Total length in micron		Arm ratio
	M I	T II	at T II
III 3B	6.87	12.32	1.29 : 1
V 5B	6.71	11.34	2.65 : 1
XIII 2B	6.87	10.92	1.25 : 1
I 1B	6.47	10.42	1.38 : 1
IX 5A	6.43	9.81	1.79 : 1
X 6B	6.61	9.10	1.05 : 1
XI 7A	6.27	9.10	1.21 : 1
XXI 7D	6.16	9.06	1.17 : 1
IV 4A	5.24	9.04	1.13 : 1
VII 7B	5.93	8.76	1.24 : 1
XII 3A	6.21	8.50	1.15 : 1
XX 2D	5.28	8.18	1.23 : 1
II 2A	5.52	8.11	1.26 : 1
VIII 4B	5.85	7.91	1.55 : 1
XVI 3D	5.86	7.45	1.37 : 1
XIV 1A	4.67	7.34	1.91 : 1
XV 4D	4.90	6.85	1.80 : 1
VI 6A	4.71	6.26	1.12 : 1
XIX 6D	4.22	5.90	1.11 : 1
XVIII 5D	4.83	5.77	1.82 : 1
XVII 1D	5.02	5.55	1.82 : 1

Since Sears et al. (1954) produced the monosome lines of Chinese Spring a new possibility has arisen to identify the chromosomes. In the corresponding monosome the univalent chromosome agrees with the chromosome to which it is monosomic. With the help of monosomes all 21 chromosomes of the wheat genus can be identified in the meiosis. In this way the silhouettes of all of the 21 chromosomes have become known at the M-I or T-II stage (Sasaki et al. 1963, Gill et al. 1963). And since the full series of monosomes was produced in a number of cultivars varietal differences between the shapes of chromosomes have also been pointed out. These results question the reliability of morphological identification. In monosomic identification the "univalent shift" may cause consternation owing to homoeologous pairing (cf. also Fig. 5 on p. 53). In this case, instead of the monosomic chromosome one of its homoeologues remains univalent.

A new possibility of identifying chromosomes with light microscope was offered by the special technique of Giemsa staining (Pardue and Gall 1970). At the begin-

Fig. 2. Idiogram of Wichita hexaploid wheat after Gill et al. (1963). The drawing was made in anaphase II. It is conspicuous that chromosomes are shortest in genome D

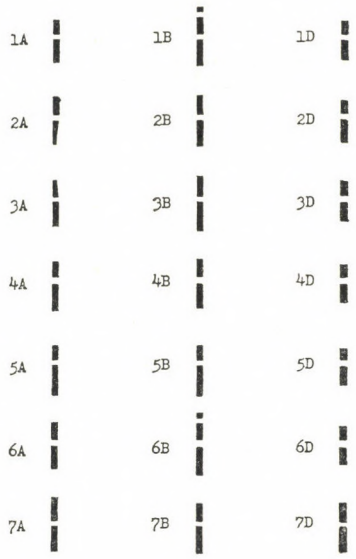
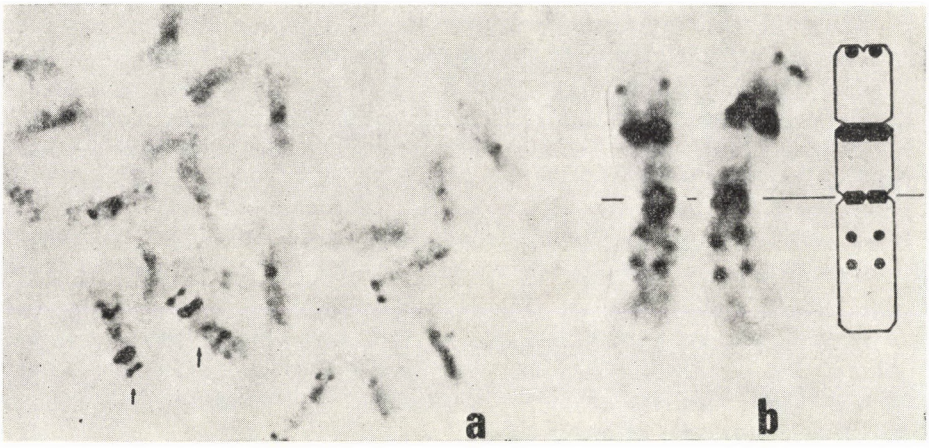


Fig. 3. Chromosomes in the tetraploid wheat genome identifiable by Giemsa staining (after Hadlaczky—Belea, 1974)



ning the method was highly successful in identifying animal and human chromosomes. Recently it has also been found very promising in the case of plant chromosomes (Vosa and Marchi 1922). Using the Giemsa technique Gill and Kimber (1974) stained all seven chromosomes of rye in somatic interphase in such a way that on the basis of the constitutive heterochromatin G-bands all chromosomes could be distinguished from one another. Distinction is made on the basis of the width, darkness (intensity) and distribution of bands. By this method the chromosomes of rye can be reliably separated from those of wheat in the *Triticale* nucleus. For the identification of wheat chromosomes the method is not yet suitable. Only one chromosome of genome B has been identified with certainty so far (Fig. 3; Hadlaczky and Belea 1974). Improving the technique will probably make it suitable to identify wheat chromsomes, though the procedure is rather lengthy.

Recent attempts have succeeded in carrying out Giemsa staining of chromosomes in meiosis as well (Lelley 1975, personal communication). This makes it possible to find out whether it is between homologous or homoeologous chromosomes that chromosome pairing takes place.

In the practice of breeding, the identification of chromosome is of indirect importance. It may be of use only in the case of chromosome substitution, addition, translocation or perhaps aberration.

By producing monosomes the aneuploid research has solved the indirect identification of chromosomes, and through a systematic production of substitution lines (Sears 1954) has made it possible to localize the genes of numerous qualitative and quantitative characters in the chromosomes. And with the production of telocentrics an even more precise localization of genes has been realized. In this way the arm of the chromosome, on which the locus is found, can be determined. As a further possibility, the distance between the locus and the centromeron can be fixed in Morgan units on the basis of the frequency of crossing-over (Sears 1969*a*). In 1973 41 of the 42 possible telocentrics were already established, only the one telocentric to arm 7DL was missing (Sears et al. 1973). With the aid of tri- and tetrasomes as well as isosomes the study of the dosis effect of genes has also become possible.

Through aneuploid research wheat has become the most precisely analyzed plant from a genetical viewpoint. This applies first of all to hexaploid wheat in which, for the very reason of the hexaploid level, there is hardly any difficulty to producing monosomes and nullisomes. In the case of tetraploids, owing to the lower level of ploidy, where the missing chromosomes cannot be fully compensated for, an aneuploid analysis is more difficult, while on a diploid level it is, for the time being, impossible.

The "univalent shift" may mislead the monosome analysis just the same way as it may disturb the identification of chromosomes. As regards the frequency of the "univalent shift" the data do not give sufficient information as yet, but varietal differences are supposed to exist as well. According to Röbbelen (1968) in the F_1 generation of summer wheat Wachtel univalent shift occurred in 15 per cent of the lines. This circumstance calls attention to the necessity of a thorough checking of the method of investigation.

Chapter 6 The control mechanism of homologous pairing

Sears (1958), and Riley and Bell (1958) called attention to a particular genetic system regulating chromosome pairing by which in the tetraploid and hexaploid wheats, in spite of alloploidy, chromosome pairing takes place with a similar regularity as in the diploids. Despite of the homoeology, of the chromosomes belonging to the same homoeologous group only the homologues pair, the homoeologues do not. The mechanism maintaining this state is controlled by a system comprising a major and several minor genes (Riley 1963). This hinders sterility caused by irregularities in chromosome pairing in tetraploid and hexaploid wheats. Thus, it can be supposed that the specificity of chromosome pairing is determined by particular genes; different genes control the synapsis and others the crossing over.

The diploid-like pairing of the polyploid wheat species was attributed mainly to the inhibitory effect of the Ph gene or gene block on the L arm of chromosome 5B (Riley and Chapman 1963; Kimber 1966). The 5B chromosome has a suppressing effect on the homoeologous pairing of chromosomes not only on wheat but on the chromosomes of other species, too. Riley and Chapman (1963) when crossing *T. aestivum* × *Ae. longissimum* found no chromosome pairing when 5B was present. In the absence of chromosome 5B, in the wheat genome the alien chromosomes paired with the wheat chromosomes, and multivalents were also produced. There are, however, alien genomes that eliminate the suppressive effect of the 5B chromosome. Riley and Chapman (1964, 1966*a*) observed that in hybrids of *T. aestivum* × *Ae. speltoides* crosses the *Ae. speltoides* genome suppressed the effect of the 5B chromosome. Consequently, numerous homoeologous chromosomes were paired in meiosis, and multivalents also occurred. By the help of telocentrics, homoeology between some *Ae. speltoides* and wheat chromosomes could be determined (Riley et al. 1966).

The suppressive effect of the 5B chromosome is not entirely independent of environment. By means of compensation lines Riley (1966) pointed out the influence of temperature and dosis on the effect of the 5B chromosome. In 5D nullisome and 5B tetrasome lines, the frequency of chiasmata decreased even between the homologous chromosomes. At 25°C normal inhibition occurred, and at lower temperatures the chiasmata frequency became even less. In euploid plants this was not observed, chiasmata frequency remained constant with the change of temperature. Apparently temperature does not act directly on the chiasmata formation, but influences the premeiotic association in the prophase. Tetrasome and nulli-tetrasome analyses of the fifth homoeologous group of Chinese Spring revealed that all three chromosomes (5A, 5B, 5D) in this group exerted influence on the synapsis.

There is reasonable ground to believe that the 5D chromosome developed this characteristic only after it had been transmitted from *Ae. squarrosa* to hexaploid wheat. It is also supposed that on the S arm of the 5B chromosome there is a gene whose action is opposite to that of arm 5BL. The Ph factor on the 5BL arm is located in the distal part of the arm, at some distance from the centromeron.

Studying the action mechanism of the 5B chromosome Feldman (1971) found the normal premeiotic association to be a precondition of regular meiotic pairing. In the homoeologues the 5BL gene impedes this process, thereby inhibiting pairing. At the same time, on the long arms of chromosomes 5A and 5D, as well as on the short arms of chromosomes 5A and 5D and probably on the short arm of chromosome 5B too there are promoters helping premeiotic association. According to Bennet and Smith (1973) the 5BS chromosome arm mostly influences the duration of meiosis which, otherwise, is lengthened by a decrease in temperature. The extent of premeiotic association depends upon the balance between the 5BL inhibitor and the promoters. In the course of aneuploid research it has been revealed that the balance between the effects of the 5B, 5D and 5A chromosomes may be upset which has an influence on the regular course of meiotic pairing. By the increased dosis of the promoter on the 5DL arm meiotic pairing can be encouraged in some distant hybrids. One extra dosis was sufficient to increase the chromosome association only in the case of interspecific crossing. To promote pairing between chromosomes of generic hybrids one extra dosis was not sufficient. In the case of intergeneric hybridization the 5DL promoter probably has to be increased by more than two doses. With a simultaneous increase of the dosis of 5BL association will significantly decrease compared to a normal 5BL dose. Two extra doses of 5BL can even counterbalance the effect of the *Ae. speltoides* promoter.

This evidence proves that in the case of interspecific or intergeneric hybridization the meiotic association can be both hindered and promoted. With an increase in the promoter doses of premeiotic association meiotic pairing can be increased. On the other hand, with an increase of the dose of factors inhibiting the premeiotic association homoeologous or even homologous pairing can be impeded.

The effect of promoters may depend on environmental factors. The promoter of *Ae. speltoides* which removes the effect of 5BL is hindered in its function by a temperature of 28–30°C.

A thorough knowledge of the controlling mechanism of homologous pairing is highly recommended since through an influence exercised on it chromosome pairing may occur in distant hybrids by chiasma formation which makes translocation possible. By means of this mechanism, Riley (1967) succeeded in introducing the yellow rust resistance of *Aegilops* into the genome of hexaploid wheat. Law (1969) gives account of Riley having transmitted in 1966 the earliness of *Ae. bicornis* to the Holdfast wheat with the aid of 5B nullisome. Sears (1972*a*, *b*) reported on the introduction of the leaf rust resistance of *Ae. speltoides* into wheat genome. It was in this way that the rust resistance of *Agropyron elongatum* was incorporated in the Eagle wheat (Watson et al. 1973). This possibility is fully exploited when crossing distant species.

The Ph gene is supposed to influence the colchicin affinity of wheat cells too, caused by the change of the properties of microtubular proteins. These have

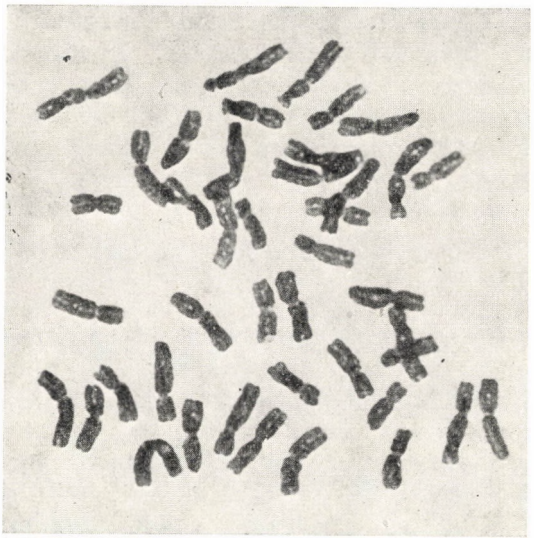


Fig. 4. Somatic chromosomes of hexaploid wheat in a root tip cell (Photo by T. Lelley)

a decisive part in the motion of the dividing chromosomes. The effect depends on the dose. Increasing doses of the Ph gene reduce the sensitivity to colchicin (Avivi et al. 1970*a*, 1970*b*), Avivi and Feldman (1973) while studying the relation between the somatic association and the SAS gene (somatic association suppressor) found that in the tetra 5B nulli 5D compensation lines where the SAS gene present in a fourfold dose the effects of colchicin and vimblastin were essentially lower. This proves that the SAS gene influences the function of the nuclear filament. It is probable that the Ph gene of chromosome 5B controls pairing with a single enzyme while the promoter of the 5D chromosome helps in keeping the balance of the system in extreme temperatures (Fig. 4).

Mello-Sampayo (1971) pointed out that the number of homoeologous pairing increased in the absence of the beta arm of chromosome 3D too, even if 5BL was present. Thus, he draw the conclusion that this chromosome too must have had a suppressor which supported the effect of 5BL. Driscoll (1972*a*) found a similar suppressor on the beta arm of chromosome 3A. These observations prove that the suppressive role of the 5B chromosome is not exclusive either. The evidence was obtained from crossings of *T. aestivum* mono 3D × *Ae. sharonensis* and *T. aestivum* mono 3D × *Secale cereale*. In the absence of the 5B chromosome the chromosomes 3A and 3D were often found to pair which suggests that the suppressors contained in them are alleles of each other. It can thus be supposed that the Ph gene of 5BL plays the leading role in suppression while 3A and 3D assist in it. A full inhibition of homoeologous pairing occurs when all six doses are present. The genes of 3A and 3D are called minor suppressors. If both minor suppressors are present the inhibition of pairing is stronger than when either they act separately or their effects are added. In the presence of 5BL this increasing effect cannot be ascertained. When the 5B chromosome is completely missing, the homoeologous pairing reaches its possible maximum (Mello-Sampayo and Canas 1973).

Chromosome pairing is thus controlled through the influence of suppressors and promoters on the premeiotic association. Then it follows that the location of chromosomes in the interphase is not accidental, but is under a strict control of genes (Feldman and Avivi 1973). This control is exercised by a sensitive and complicated mechanism in which chromosomes 5B, 5A, 5D as well as 3A and 3D play a role. It is not unlikely either that further investigations will reveal some more promoters or suppressors.

The question arises whence the most important gene, Ph on chromosome 5BL originates. Dover and Riley (1972*a*) think it possible that the so-called "Low-pairing" alleles from *Ae. speltoides* or *Ae. mutica* were incorporated in wheat genome immediately when the ancient form of the tetraploid wheat came into being. The results of experiments show, however, that the loci controlling pairing are not identical – homologous – in the hexaploid wheats and the supposed donor diploids. Muchyzuky (1964) thought it possible that "B" chromosomes might participate in the inhibition of homoeologous pairing; in this case the Ph gene would come from the B chromosome. Although Vardi and Dover (1972) produced proof to the contrary, Dover and Riley (1972*b*) still believe that the B chromosome found in *Aegilops* has the same inhibitory effect on homoeologous pairing as the Ph gene. According to Dover (1973), the B chromosomes of *Ae. speltoides* and *Ae. mutica* exert a similar effect on the spindle as the 5BL. Thus, the two systems may be genetically related, still functionally they are not identical with the system that controls chromosome pairing in the *Aegilops* species. The "Low-pairing" allele of *Ae. mutica* assumed by Dover and Riley (1972*a*) cannot be the base of the Ph gene since the former is unable to compensate it. At the same time, the B chromosome found in some *Aegilops* species – though not functioning simultaneously with the control system of the diploid *Aegilops* – due to its similar activity may have been a basis for the development of the 5B system and the evolution of the Ph gene. This hypothesis is supported by the fact that in other grasses where B chromosome is likewise found homoeologous pairing occurs less frequently. It has been revealed also that the B chromosome of *Ae. mutica* deteriorates the effect of the 5D chromosome which eliminates the heat sensitivity of the system. When crossing *T. aestivum* with *Ae. speltoides* the B chromosome causes irregularities in the first and second meiotic division attributed to the functional disturbance of the nuclear filament. It is also possible, of course, that the Ph locus had been formed in a B genome donor which has not been found so far.

The gene sequence and structure are perfectly identical in the homologous chromosomes. Such chromosomes are close to each other in the interphase, at places they join and their ends adhere together to the nuclear membrane. In the leptoten-zygoten state when spiralization takes place the chromosomes come still closer to each other, and at the points of pairing as well as at the ends the synaptinemal complex begins to develop (SC). At the late zygoten and pachiten stage the homologous chromosomes are paired at full length zipper-like by the SC. The SC only disappears in the early diakinese when the spiralization of the chromosomes has been completed. At this stage the synapsis ceases and only the chiasmata keep the chromosomes together (Wetstein 1971). In the diploid wheat meiosis takes place with this perfect regularity, since it has only homologous chromosomes.

It can be supposed that in the tetra- and hexaploid wheats the B and D genomes originate from the same very distant ancestor as the A genome, but as a consequence of mutations through ten thousands of years of evolution their gene sequences and structures have changed and are no longer in perfect agreement with either the A genome or each other. This state is called homoeology. Synapsis between such chromosomes cannot be perfect, therefore in the metaphase of meiosis various irregularities occur, trivalents, quadrivalents appear and even rings containing six chromosomes may develop.

In the nuclei of tetra- and hexaploid wheats homologous and homoeologous chromosomes are thus found close to each other. The complicated mechanism of the 5B system which suppresses the pairing of homoeologues keeps the balance of the homologous chromosomes by forcing the three genomes side by side already at the interphase thereby synapsis only occurs between the homologues. If the 5B system is inactivated, homologous and homoeologous chromosomes are accidentally paired resulting in various irregular chromosome configurations in the metaphase.

Breeding practice utilizes this possibility and produces an exchange of segments between non-homologous chromosomes. In other words, of the related genera of *Triticum*, *Aegilops*, *Agropyron* and *Secale* have some chromosomes which to some extent are homoeologous with wheat chromosomes. Upon intergeneric hybridization being present in the same nucleus if they inactivate the 5B system they may be paired, chiasmata may be formed which might lead to translocations.

Chapter 7 Gene symbols, gene mapping

Chinese Spring, a hexaploid spring wheat cultivar was the first whose full monosomic and nullisomic series were produced by Sears et al. (1954). By using aneuploid series the chromosome or chromosomes on which the loci influencing certain characteristics are found can be detected (Sears 1953, Kuspira and Unrau 1958). Later the full tri- and tetrasomic series were also produced from Chinese Spring, whereby the study of the effect of dose has become possible. An with almost the complete telocentric series produced (Sears et al. 1973) it is possible even to determine whether the examined locus is found on the shorter "S" or longer "L" arm of the chromosome. In chromosomes whose arms are nearly of the same length the one on which the first locus was found is designated by α, the other by β (McIntosh 1973). By crossing over frequency tests even the distance from the centromeron to the locus in the linkage group or chromosome can be determined in Morgan units. By fixing more than one loci their distance from one another can be calculated as well.

For the last twenty years extensive investigations have been carried out in order to find out on which chromosome, and on which arm the different characters of economic importance or valuable in the identification of varieties are found. For twelve years Morris (1962–1973) prepared summarizing reports on the localized genes (Table 5), which testify that almost 140 different characters have been located so far, of which some have been determined by more than one research worker at different times on the same, or on different chromosomes.

The first aneuploid series made it possible to produce aneuploid series of further varieties. This practice soon gained wide recognition. In 1969 monosomic series were produced in Canada from the spring wheat varieties Cadet, Red-Bobs, Rescue, S-615, Thatcher and Lemhi and from the winter wheat cultivar Winalta; the spring wheats Redman and Prelude and the winter wheat Kharkov-MC-22 were also included in the work. In the United States aneuploid series were produced from the varieties Cheyenne, Vichita, Chris 1 and Elgin. In India monosomic and nullisomic series were produced from the spring wheat Pb.C 591. Japanese researchers worked with Norin 10 and Shinchunaga hexaploid wheats. In England the varieties Capelle-Desprez, Bersee and Koga II were included in the production of monosomics in 1970. Production of monosomic series has begun in a number of countries from the following varieties: Caribo, Carsten VIII and Jubilar in the German Federal Republic, Bezostaya 1, Aurora, Kavkaz and Milturum 553 in the Soviet Union, Kiszombori 1, Mironovskaya 808 and Rannaya 12 in Hungary.

The chromosomal localization of genes is made easy by quick though less precise nullisomic and monosomic analyses (Sears 1954); a more accurate identification may be secured by chromosome substitution, when one or two homologous

Table 5. Genes located by aneuploid analysis in wheat chromosomes, on the basis of data published by Morris from 1962 to 1973

Characteristic	Designation of chromosome
Ear	
1. Spike number	3A, 1B
2. Spike length	2, 3, 5A, 1, 2, 3, 4, 5B
3. Awn length	1, 2, 5, 7A, 1, 2, 3, 4, 6B, 1, 5, 7D
4. Awn development manifestation	2B, 2D
5. Awn suppressor	2B
6. Awn development inhibitor (of rye spikelet)	5A, 5B
7. Spikelet number	6, 7A, 1, 4B, 2, 3D
8. Flower development	5A
9. Glumae size	5B
10. Glumae pubescens (Hg-hg)	1A
11. Glumae colour black	1A
12. Pseudo-black chaff	3A, 2, 3B, 1, 3, 5, 6, 7D
13. Glumae colour brown *(Ae. squarrosa)*	1D
14. Glumae colour black *(Ae. caudata)*	1D
15. Glumae colour	1B
16. Long rachis segments length	5D
17. Glumae tenacity	2D
18. Vavilovid expression	5A
19. Hair development & rachis of spikelet	5A
20. Incurved beaks	3B
Grain	
1. Kernel weight	1, 2, 3, 5, 7A, 1, 3, 4, 5, 6, 7B, 1, 2, 5, 7D
2. Kernel/spike	5A, 1, 6, 7B, 6D
3. Protein content	1, 2, 3, 4, 5, 6, 7A, 1, 2, 3, 4, 5, 6, 7B, 1, 3, 5, 6, 7D
4. Gliadin content	1B
5. Gluten content	1, 5D
6. Kernel seed coat colour (R)	3A, 3B, 2D
7. Milling characters	3, 6B, 3, 4, 5, 7D
8. Flour characters	1D
9. Dough characters	2, 3, 4, 5A, 2, 3, 4, 5, 6B, 1, 2, 3, 4D
10. Dough mixing time	7B, 5D
11. Baking properties	1, 4, 7B, 5, 7D
12. Kernel tyrosinase	2A, 2D
13. Tryptophane content	3, 5, 7A, 3B, 1, 7D
14. Alpha amylaseisosyme	6, 7A, 6, 7B, 6, 7D
15. Aminopectidase	6A, 6B, 6D
16. Malate dehydrogenase	1B
17. Alcohol dehydrogenase	4D
Leaf	
1. First leaf development	1, 3, 5, 6A, 1, 2, 3, 7B, 3, 5, 6, 7D
2. 2nd leaf width	7A, 4B

Table 5. continued

Characteristic	Designation of chromosome
3. 2nd leaf width & length	6A
4. Flag leaf length	5, 6A, 5B, 5D
5. Flag leaf width	2, 3, 6A, 4, 6B
6. Flag leaf sheath length	1, 3, 4, 5A, 1, 3, 4, 5, 6, 7B, 2, 3, 5, 7D
7. Flag and 2nd leaf length	1, 5A, 1B
8. Flag and 2nd leaf width	2, 4, 5A, 5, 7B
9. Waxy leaves	2A, 4B, 5D
10. Waxy prod. inhibition	2A
11. Leaf pubescence	3, 7A, 2, 7B, 3D
12. Ligula development	2B, 2D
13. Auricula hairiness	2B
14. Leaf peroxidase	6B
Stem	
1. First internode length	5A, 7B, 5D
2. 1–2 internode length	1A
3. 2–3 internode length	6A, 4B, 2, 3D
4. Culm length	1, 2, 3, 4, 5, 6, 7A, 1, 2, 3, 4, 5, 7B, 2, 3, 4, 5D
5. Dwarfness (semidominant Tom Thumb)	2, 4A, 2, 4B, 2, 3, 4D
6. Dwarfness modification	1, 7D
7. Culm hybrid dwarfness	2B, 2D
8. Grass-clump hybrid dwarfness	2, 4B
9. Solid top internode	5A
10. Solid lower internode	5A
11. Culm colour purple	7B
12. Culm colour inhibitor	3A
13. Hairly peduncle from rye	5B, 6D
14. Tillering	1, 7B, 6D
Root	
1. Root development	3B, 3D
2. Root peroxidase	6B
3. Root peroxidase suppressor	6B
4. Root peptidase	6B
5. Risophaera microflora	5B
Coleoptile	
1. Coleoptile length	1, 2, 3, 5, 6A, 2, 4B, 2, 5, 6D
2. Coleoptile colour purple	7D
3. Coleoptile colour inhibitor	2, 6A, 2, 3B, 2D
Cold resistance	
1. Growth habit	4, 5A, 3, 5, 6, 7B, 1, 2, 5, 7D
2. Cold resistance	7A, 1, 5D
3. Cold resistance, coleoptile stage	5A, 1, 2B, 1, 2D

Table 5. continued

Characteristic	Designation of chromosome
Sterility—fertility	
1. Mf. restoration	1, 5A, 1, 6B, 5, 6, 7D
2. Mf. restoration modificator	2, 3, 4, 6, 7A, 1, 2, 4, 6B, 2, 5, 7D
3. Mf. suppressor	7D
4. Fertility at spike tip	5D
Necrosis—chlorosis	
1. Hybrid necrosis	2, 5, 6B
2. Necrosis modifier	3B
3. Necrosis suppressor	6D
4. Chlorosis	2A, 3D
5. Hybrid chlorosis (Chl)	2A
6. EMS chlorina mutant	7A, 7B, 7D
7. Virescence	3A, 3B
8. EMS virescence mutant	3A
9. Corroded mutant	6D
10. Nullisomic albino	2D
11. Chlorophyll production	7B
12. Anthocianin production	7A, 7B
Chromosome pairing	
1. Suppression of homoeologous pairing	3, 5A, 5B, 3D
2. Somatic association	5B, 5, 6D
3. Premeiotic association of chromosomes	5B
4. Promotion of homoeologous pairing	5B, 3, 5D
5. Homoeologous pairing restriction	3D
6. Chiasma formation	1A, 4D
7. Chromosome condensation	7A, 5B
8. Bipolar segregation of homologous chromosomes	7A, 1, 4, 6B, 2D
9. Centromer integrity	4B, 2, 4D
10. Meiotic behaviour	5, 6, 7A, 4, 5, 6B, 6D
Disease resistance	
1. Stem rust resistance	1, 3, 5, 6A, 1, 2, 3, 4, 6, 7B, 1, 2, 6D
2. Stem rust resistance, seedling and adult	2, 3, 4, 5A, 2, 3B, 1, 4D
3. Stem rust resistance, seedling stage	2A, 2, 5, 6, 7B, 6D
4. Stem rust resistance, adult	5A, 2, 3, 4B
5. Stem rust resistance inhibtor	3B, 7D
6. Leaf rust resistance modifier	7A, 7B, 7D
7. Leaf rust resistance	7A, 7D
8. Leaf rust resistance seedlings	1, 4, 5A, 1, 2, 4, 6B, 2, 4, 5D
9. Leaf rust resistance, adult	5A, 6B
10. Leaf rust resistance, seedling and adult	4A, 7B, 5, 7D
11. Stripe rust resistance	2A, 1, 5, 6B, 2, 5D

Table 5. continued

Characteristic	Designation of chromosome
12. Powdery mildew resistance	1, 2, 4, 7A, 7B, 5D
13. Soilborne mosaic virus resistance	7A
14. Root rot susceptibility	2, 5B, 2D
15. Hessian fly resistance	1, 5A
Other properties	
1. Yielding ability	1, 6A, 1, 4B, 7D
2. Time of maturity	1, 2, 3, 4, 5, 6, 7A, 1, 2, 3, 4, 5, 6, 7B, 1, 2, 3, 4, 5, 6, 7D
3. Photoperiodic responses	1A, 3, 4, 6B, 7D
4. Crossability with rye	5A, 5, 6B, 1D
5. Non-glaucosness	2B
6. Esterase	3, 7A, 3, 7B, 3, 7D
7. Alcohol dehydrogenase	4A, 4B
8. Alkalian phosphatase isosyme	4B, 4D

chromosomes of the tested variety are substituted into the monosomic or nullisomic series of some known variety. Genes contained in the transferred chromosomes have been mostly studied on the basis of genetic changes caused by the chromosomes substituted into the monosomic series of Chinese Spring.

Monosomic and substitution analyses have revealed that the genes determining the realization of most major characters are not always located in the same chromosomes. The conclusion drawn for the practical breeding is that due to the alloploid genetic structure of the hexaploid and tetraploid wheat the major properties are very often influenced by major and minor genes varying in number and chromosomal location from variety to variety. The aneuploid analysis has thrown light on the multigenic character of many properties too. This means – among others – that in cross-breeding both negative and positive transgressions may occur. The results of practical breeding have proved this fact in many cases. The aneuploid analysis completes thus the genetic findings known from the mathematical analysis of the segregation conditions of cross populations. It gives information on the number of genes of certain important properties, and on their dominant or recessive character.

To symbolize the genes determined so far in the course of genetic investigations a uniform system was elaborated by McIntosh (1973). Its main directives are:

Recommended Rules for Gene Symbolization in Wheat

1. In naming hereditary factors the use of languages of higher internationality should be given preference.

2. Symbols of hereditary factors derived from their original names should be written in italics, or in Roman letters of distinctive type.

3. Whenever unambiguous, the name and symbol of a dominant should begin with a capital letter and those of a recessive with a small letter (see also special rules for symbolizing host: pathogen systems).

4. All letters and numbers used in symbolization should be written on one line; as far as possible no superscripts or subscripts should be used.

5. The plus ("+") sign will not be used in symbolization of hereditary factors in wheat.

6. Two or more genes having phenotypically similar effects should be designated by a common basic symbol. No-allelic loci (mimics, polymeric genes, etc.) will be designated in accordance with two procedures:

(i) in sequential polymeric series where an Arabic numeral immediately follows the gene symbol; e.g. Sr9;

(ii) in homoeologous sets where the basic symbol is followed by a hyphen ("—") followed by the locus designation taking the form of the accepted genome symbol and a homoeologous set number represented by an Arabic numeral; e.g. Adh-Al designates the A-genome member of the first Adh set.

Because the letter "l" and number "1" may be confused, the fomer should be avoided as the last letter in a basic symbol. Different alleles of alleles of independent mutational origin are designated by a lower-case Roman letter following the locus number designation; e.g. Sr92, Adh-Ala.

6*a*. Temporary symbol designations. Where linkage data are not available, provision has been made for temporary symbols. These shall consist of the basic symbol followed by an abbreviation for the line or stock and an Arabic number referring to the gene; e.g. SrFr1, SrFr2, etc. refer to two genes for reaction to *Puccinia graminis* in cultivar Federation. It is recommended that official records of temporary designations be kept, but it is not essential that subsequent number from other laboratories (e.g. SrFr3) be checked against earlier numbers either phenotypically or genetically.

7. Inhibitors, suppressors and enhancers are designated by the symbols I, Su and En, or by i, su and en if they are recessive, followed by a space and the symbol of the allele affected.

8. Whenever convenient, lethals should be designated by the letter l or L and sterility and incompatibility genes by s or S.

9. In wheat and related species linkage groups and corresponding chromosomes are designated by an Arabic numeral (1–7) followed by genome designated by a capital Roman letter; e.g. for hexaploid wheat of group aestivum 1A–7D. This system supersedes the original designations using Roman numerals; i.e. I–XXI. Chinese Spring is accepted as having the standard chromosome arrangement. Chromosome arms (or telocentric chromosome derivatives) are designated L (long) and S (short). Where distinction cannot be made on length, arms are designated α and β, α representing the arm corresponding to the telocentric member first isolated.

10. The letters X and Y are recommended to designate sex chromosomes.

11. Genic formulae are written as fractions, with the maternal alleles given first or above. Each fraction corresponds to a single linkage group.

12. Chromosomal aberrations should be indicated by the abbreviations Df for deficiency, Dp for duplication. In for inversion, T for translocation and Tp for transposition. In wheat there are a number of genes derived from related species by introgression. Such genes in different instances reside at different locations. One location will be taken as standard. Other locations will be considered as transpositions relative to the designated standard. When a gene does not reside in its standard chromosome position, the new chromosome designation may be given in brackets following the gene designation: e.g. Hp (Tp 6D) refers to a line carrying the introgressed "hairy neck" gene on chromosome 6D instead of 4A which is taken as standard.

13. The zygotic number of chromosomes is indicated by 2n, the gametic number by n and the basic number by x.

14. Symbols for extra-chromosomal factors should be enclosed within brackets and precede the genic formula.

With a general observation of these rules genetic symbolization in wheat may become perfectly uniform. In McIntosh's scheme the following gene symbols are uniformized:

Anthocyanin Pigmentation:

Red/purple coleoptiles. Colour red is dominant = Rc1 (7A), rc2 (7BS), rc3 (7DS).
Purple/red culm (straw) stem. Purple or red colour dominant = Pc (7BS).
Awnedness:
Dominant Inhibitors.
Hooded = Hd. (4BS).
Tipped 1 = B1. (5AL).
Tipped 2 = B2. (6BL).

Chlorophyll abnormalities:

1. Virescent = v1a, v1b (3B), v2a, v2b (3A).
2. Chlorina = cn-A1a (7A), cn-A1b (7A), cn-A1c (7A), Cn-B1 (7BL), cn-D1 (7D), Cn-D1 (7DL).

Corroded = co1, = 6BS,
co2, = 6D.
Crossability with Rye = Kr1 (5B), Kr2 (5A), kr1, kr2.
Glume Colour:
Red = Rg1 (1BS), Rg2 (1BL).
Black = Bg (1A).
Pseudo-black chaff = Pbc (3B).
Grass-Clump Dwarfness: D1 (2Dα), D2 (2BL), D3 (4BL), D4 (2D).
Hairy Glume = Hg (1AS).
Hairy Neck: (pubescent peduncle) = Hp (4Aβ), 5B (6D).
Hairy Node: (pubescent node = Hn) (5AL).
Height/Semidwarfness = Sd1, Sd2.
Hybrid Weakness:
Hybrid necrosis = Ne1m, Ne1s, Ne2w, Ne2m, Ne2ms, Ne2s.
Hybrid chlorosis = Ch1 (2A), Ch2 (3Dα), Complementary dominant genes.
Pairing homoeologues: = Ph (5BL).
Pollen Killer = Ki, ki (6BL).
Red Grain Colour = dominant R1 (3D), R2 (3A), R3 (3B).
Response to photoperiod = Ppd1, Ppd2.
Response to Vernalization = Vrn1, Vrn2, Vrn3, Vrn4.
Restores for Cytoplasmic Male Sterility = Rf1 (1A), Rf2 (7D), Rf3 (1B), Rf4 (6B), Rf5 (6D).
Tenacious Glumes = Tg (2Dα).
Waxiness (Glaucousness) Glossiness: = W1 (2S), W1I (2BS), W2a, W2b, W2I (2D).
Reaction to Erysiphe graminis: = Pm1 (7AL), Pm2 (5DS), Pm3a (1A), Pm3b, Pm3b (1A), Pm4 (2A), Pm5 (7BL), Pm 6 (2B).
Reaction to Puccinia graminis: = Sr1, Sr2, Sr3, Sr4, Sr5 (6D), Sr6 (2Dα), Sr7a (4B), Sr7b (4BL), Sr8 (6Aα), Sr9a (4BL), Sr9b (2B), Sr9c, Sr9d (2B), Sr10, Sr11 (6BL), Sr12 (3B), Sr13 (6Aβ), Sr14 (1BL), Sr15 (7AL), Sr16 (2BL), Sr17 (2L), Sr18 (1D), Sr19 (2B), Sr20 (2B), Sr21 (2A), Sr22 (7AL).
Reaction to Puccinia recondita: = Lr1 (1B), Lr2a (1B), Lr2b, Lr2c, Lr3 (6BL), Lr4, Lr5, Lr6, Lr7, Lr8, Lr9 (6BL), Lr10 (1AS), Lr11 (2A), Lr12 (4A), Lr13,

Lr14a (7BL), Lr14b, Lr14ab,
Lr15 (2Dα), Lr16 (4A), Lr17, Lr18, Lr19 (7D),
Lr20 (7AL), Lr21 (1D), Lr22 (2Dα).

Reaction to Puccinia striiformis: = Yr1 (2A), Yr2, Yr3a, Yr3b, Yrc, Yr4a, Yr4b, Yr5, Yr6, Yr7 (2B), Yr8 (2D).

Reaction to Tilletia caries, T. foetida, T. contraversa = B1 (2B), B2, B3, B4 (1B), B5 (1B), B6 (1B), B7 (2D), B8, B9, B10.

Reaction to Mayetiola destructor: = H1, H2, H3, H4, H5, H6.

Reaction to Toxotera graminum: = Gb.

Chapter 8 Substitution, addition and translocation of chromosomes

The substitution of chromosomes is a procedure by which in an aneuploid (recipient) variety one, two or more chromosomes of a donor variety, species or genus are substituted. The precondition of the operation is that the recipient should be nullisomic or monosomic.

From the very beginning Sears (1954) regarded chromosome substitution to be an operation suitable both for genetic investigations and in practical breeding too. The substitution of chromosomes makes it possible to transfer desirable genetic information from the genotype of the donor to that of the recipient without changing the genetic information of other chromosomes in the latter. Generally, chromosome pairs are substituted, but single chromosomes can be substituted, too, if they are homologous with the corresponding chromosomes of the recipient, for otherwise irregularities occur in the meiosis.

Substitution of chromosomes or chromosome pairs between varieties is mostly carried out in order to identify the genes localized in the substituted chromosomes and to determine their effect. This method is suitable to establish what properties are determined or modified by the loci transferred with the chromosome to the recipient. Furthermore, this procedure, indicates the mode by which the new genetic background influences the action of the transferred genes. When the substitution line is crossed with the euploid form of the recipient and the donor parent, then the two F_1 generations are compared with the donor and recipient as well as with the substitution line, accordingly a conclusion may be drawn concerning the interactions of the examined loci in the new genetic environment (Law 1966*a*, *b*, Aksel 1967).

To analyze the extent of interactions another method was worked out by Mather and Jinks (1971) by which the mean and extreme values of changes caused by the interactions can be assessed. It was by this method that e.g. in the substitution lines of Chinese Spring × Hope the interaction of thousand-kernel-weight and height, in the substitution lines of Cheyenne and Cappelle-Desprez the interaction of cold resistance and heading time were studied (Law and Worland 1973).

The localization of genes determining quantitative characters, whose effect is either inconspicuous, or the same properties are influenced by other genes too on the identical chromosome, is only possible by a more complex method. Such a procedure has been developed by Unrau (1958) and Law (1966*a*).

Chromosome substitution can be used to study the hybrid vigour, too. To this end all reciprocal substitutions of two varieties displaying high vigour should be carried out. By this method all chromosomes can be tested as to how they influence the hybrid vigour when applied in one or two doses, or when it is in a genome together with the homologous chromosome of the other variety. According to

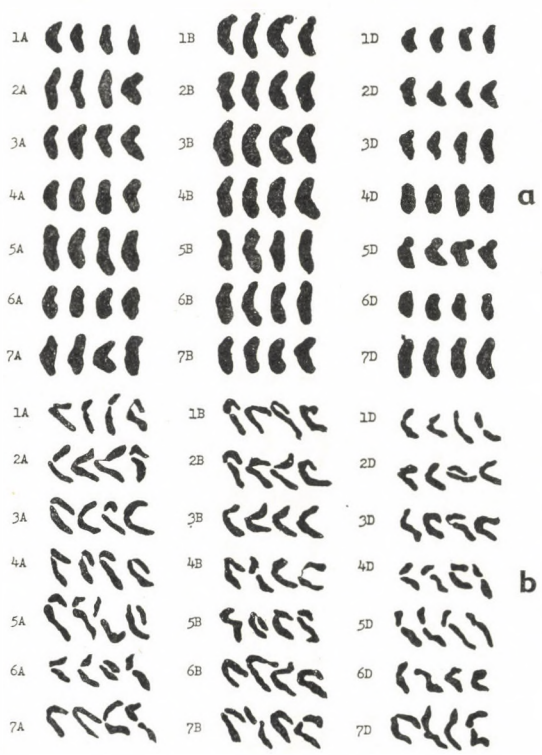


Fig. 5. a) Chromosomes of Cheyenne wheat in metaphasis I (after Sasaki et al. 1963). b) Chromosomes of Wichita wheat in anaphasis II (after Gill et al. 1963). The drawings were made of univalent chromosomes of monosomes. The diversity of forms explains the difficulty of visual identification

Law and Worland (1973) data obtained by substitution analyses may be used to forecast the effect of genes.

If an adequate telocentric line is available even the arm of the chromosome on which the locus in question is found, and its distance from the centromeron can be determined (Driscoll 1966, Sears 1966). However, to determine the exact places of genes localized in the vicinity of the centromeron is still difficult (Endrizzi and Kohel 1966), owing to the modified cross-over frequency of the telocentrics. In the case of telocentric chromosomes cross-over frequency is lower in the vicinity of the centromeron than in the normal two-arm chromosomes.

With substitution tests several hundred loci influencing numerous qualitative and quantitative characters have been identified so far.

Through the accumulation of data obtained in genetic investigations carried out with substitution lines a great progress has been made in understanding the heredity of quantitative characters in wheat.

Chromosome substitution between cultivars may be of direct practical use resulting in a concrete increase of yield as observed by Law (1968) in the substitution line 1B of Chinese Spring × Thatcher. The 1D, 6D and 7D substitution lines of Chinese Spring × Cappelle-Desprez also produced larger yields (Law and Worland 1973).

From other species – and especially genera – chromosome pairs are generally substituted in the wheat genome, otherwise the alien chromosome is eliminated.

The first substitutions of this kind occurred incidentally, since then, however, several substitution lines with *Secale*, *Aegilops* or *Agropyron* chromosomes transferred to the wheat genome have been produced (Zeller and Fischbeck 1971).

Substitution between species is both of practical and theoretical importance. The intergeneric substitution of chromosome pairs is more significant from a practical than from a theoretical viewpoint in spite of the fact that investigations into the effects of genes acting in the substituted chromosomes in the changed genetic background may lead to interesting results. Yet, in most cases, these substitutions are carried out with the purpose of introducing valuable alien chromosomes – primarily those determining a manifold resistance – into the wheat genotype.

A single chromosome of a donor belonging to another species or genus can only be substituted in wheat if it is at least homoeologous with one of the wheat chromosomes. If such a chromosome is transferred to a wheat line monosomic for the homoeologous pair, the alien chromosome will function in the meiosis as the pair of the homoeologous monosomic wheat chromosome. This may be aimed at inducing synapsis and chiasma formation between the monosome wheat and homoeologous alien chromosome so that by a reciprocal translocation a chromosome segment carrying a desirable property be transferred to the monosomic chromosome of the recipient wheat. Subsequently, the alien chromosome can be eliminated by back-crossing, and the new property is thus incorporated in the genome of the wheat. For this kind of substitution aimed at producing translocation compensation lines monosome or nullisome for the 5B-, and tri- or tetrasome for the 5D chromosome should be used. In this way the suppression of homoeologous pairing is eliminated and the synapsis and chiasma formation, respectively, becomes possible (Driscoll 1965). According to Mettin et al. (1973) the wheat cultivars Aurora and Kavkaz carry such a 1B-1R wheat-rye segment translocation. According to Zeller (1973) 1B-1R translocation is in the Salmon and Zorba cultivars as well. In his opinion the cultivars Orlando, Neuzucht, Riebsel 47/51, Wenzel and Weihenstephan 1007/53 also contain 1B-1R chromosome segment.

Chromosome substitution is easier with a hexaploid wheat, since here the chromosomes of the homoeologous groups are able to compensate each other. If in a homoeologous group one or even two chromosomes are missing, the plant is still viable because the other homoeologous chromosomes can make up for the missing store of information. The same phenomenon explains that when a chromosome or a pair of chromosome of the hexaploid wheat is missing but one of the chromosomes in the homoeologous group is trisome or tetrasome, then there is hardly any irregularity in the meiosis, fertility is perfect and the development of the plant is almost normal. This advantageous genetic situation is due to the monosomic and nullisomic lines of the hexaploid wheat produced by Sears et al. (1954), whereby the foundation of a research of substitution and translocation was laid down.

The simplest way of carrying out substitution in practice is the intervarietal substitution using a nullisomic recipient (Table 6). In this operation a nullisomic recipient and an euploid pollen donor are used for the first crossing. Subsequently,

Table 6. Substitution line produced with a nullisome

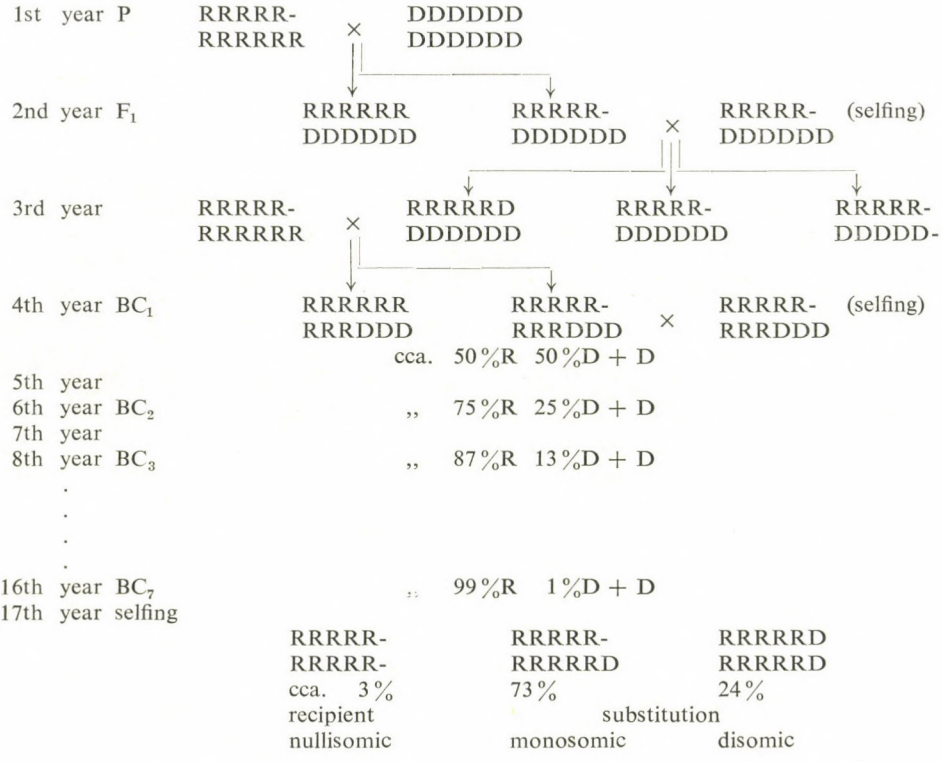
1st year	P			RRRRR- RRRRR-	×	DDDDDD DDDDDD
2nd year	F_1		RRRRR- RRRRR-	×	RRRRR- DDDDDD	
3rd year	BC_1	RRRRR- RRRRR-	×	RRRRR- DDDRRR		RRRRR- RRRDD-
		cca.	50 %R	50 %D + D		
4th year	BC_2	,,	75 %R	25 %D + D		
5th year	BC_3	,,	87 %R	13 %D + D		
6th year	BC_4	,,	94 %R	6 %D + D		
7th year	BC_5	,,	97 %R	3 %D + D		
8th year	BC_6	,,	98 %R	2 %D + D		
9th year	BC_7	,,	99 %R	1 %D + D		
10th year	self-pollination	RRRRR- RRRRR-		RRRRR- RRRRRD		RRRRRD RRRRRD
		cca. 3 % recipient nullisomic		73 % monosomic	substitution	24 % disomic

R = *recipient chromosome*
D = *donor chromosome*
— = *missing chromosome*

the monosomic lines of the F_1 and BC generations, respectively, are used as pollen donors. The recipient is invariably the original nullisomic. The monosomics are selected by cytological examination. After seven back-crosses, in nearly 100 per cent, the recipient genome is restored, with the substituted alien chromosome added. After the final selfing 3 per cent recipient nullisomics, 73 per cent substitution monosomics and 24 per cent substitution disomics are obtained. The disomes can be found with a cytological analysis (Mettin 1970).

In another method of chromosome substitution of varieties the recipient is monosomic. This procedure – though more time consuming – is often used because the development of nullisomic lines is often disturbed and there is a high incidence of male sterility. The procedure is the following (Table 7): in the first crossing the recipient, here too, is monosomic, and the pollen donor is euploid; from the F_1 generation the monosomic plants are selected by cytological examination, and self-pollinated. By further microscopic analyses the euploids are selected from the progeny; in these the substituted chromosome is disomic and the other chromosomes are derived from the two parents in fifty per cent each. In the next crossing the original monosomic line is again the recipient, and the disome selected by cytological examination will be the pollen donor. In the first back-cross generation (BC_1) the monosome plants detected by microscope should be self-pollinated again. This two-way operation should be repeated seven times, and self-pollination follows only then, when apart from the substituted pair of chromosomes the full chromosome complement of the recipient has been restored. As a result of self-

Table 7. Substitution line produced with a monosome

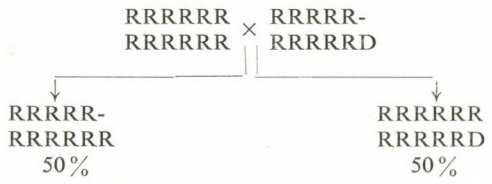


R = *recipient chromosome*
D = *donor chromosome*
— = *missing chromosome*

ing 3 per cent recipient nullisomic, 73 per cent substitution monosomic and 24 per cent substitution disomic plants are obtained again. The latter have to be selected by cytological examination (Mettin 1970). If the substitution monosomic is crossed with the euploid recipient, the progeny will consist in 50 per cent of euploid plants with one substituted chromosome (Table 8). In the third substitution method the recipient is monotelosomic. In this case the procedure is the same as when the recipient is monosomic except that the inserted steps of self-pollination can be omitted (Table 9) because plants monosomic for the chromosome to be substituted can be cytologically separated from the monotelosomic plants. Therefore in this procedure, back-crossing must likewise be performed only seven times to obtain the desired 24 per cent of disomic substitution line.

Still another method is the so-called double substitution (Unrau et al. 1956). The procedure requires a nulli- or monosomic recipient and two substitution lines. The method is quick and requires only a small number of plants, but a high-level microtechnical performance. If nullisomic plants are used as recipients the substi-

Table 8. Substitution of one chromosome

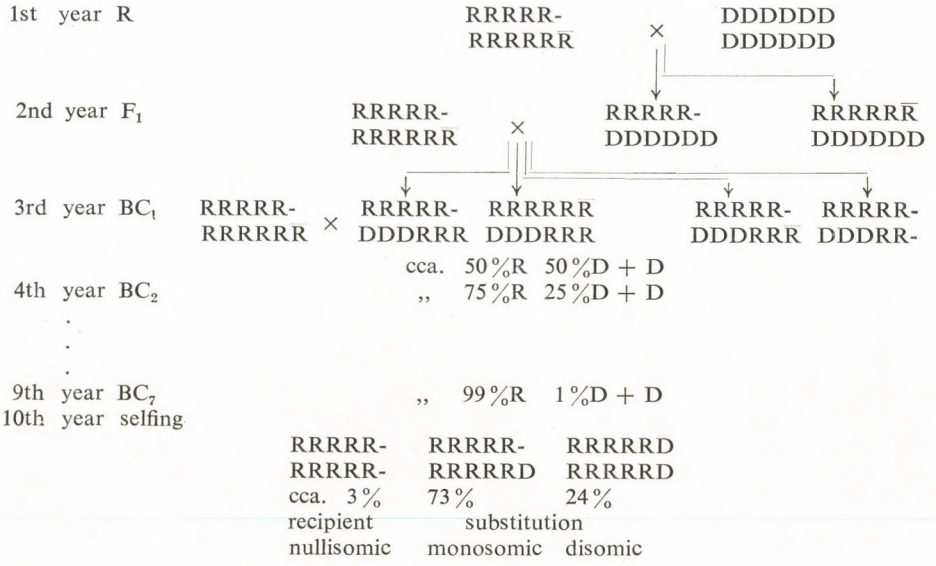


R = *recipient chromosome*
D = *donor chromosome*
– = *missing chromosome*

tution is completed in two or three years, if the recipient is monosomic the process requires more time. As a final result an euploid line is obtained in which a chromosome pair of each of two different donors is transferred (Mettin 1970).

Chromosome substitution is also possible between hexaploid wheat and the diploid species of distant related genera. In this case addition is the first step when the corresponding chromosome pair of the alien species is added to the wheat genome. As a second step, the added chromosomes are substituted for a pair of

Table 9. Substitution line produced with a monotelosome



R = *recipient chromosome*
R = *recipient telocentric chromosome*
D = *donor chromosome*
– = *missing chromosome*

wheat chromosomes. If the hexaploid wheat is crossed with an alien diploid species the F_1 generation will consist of sterile plants in which the alien and the three wheat genomes are in a haploid state (Table 10). The chromosome number should thus be doubled by artificial genome mutation. The germinating grains are treated with colchicin. If the treatment is successful fertile octoploid plants with nuclei containing three genomes of the hexaploid wheat and one genome of the alien species in diploid state are produced. The octoploid is then crossed with the original hexaploid wheat. The progeny will contain the full three genomes of the hexaploid wheat and a haploid chromosome complement from the genome of the alien genera. These plants are self-pollinated and by cytological examination addition monosomic selected. The addition disomic can be selected after the self-pollination of the addition monosomic. In the next step the addition line is crossed with a nullisomic line in which the addition chromosome is to be substituted. In this type of crossing, the addition line is the pollen donor. With the progeny selfed three types of chromosome configuration are produced. The chromosome number is normal (42) in each plant of the progeny. In one of the groups all three genomes of the recipient variety can be found with full number of chromosomes. In the other group, a missing chromosome of the recipient is replaced by the additional chromosome. The third configuration is the desirable one: where the chromosome pair of the alien genera replaces those chromosomes for which the recipient was nullisomic (Mettin 1970). The three groups can be separated by a simultaneous examination of meiosis and phenotype. By this method primarily

Table 10. Chromosome substitution in intergeneric crossing, according to Mettin (1970)

A B D × *S*		
A B D × *S*		
A B D S		(colchicin treatment)
A B D S × *A B D*		
A B D S		(self-pollination)
A B D		
Addition	*A B D* Ṣ	(self-pollination)
monosome	*A B D*	
Addition	*A B D* Ṣ	
disome	*A B D* Ṣ	
Substitution:		
A B—1 *D* × *A B D* Ṣ		
A B—1 *D* × *A B D* Ṣ		
A B—1 *D*		(irradiation + selfing)
A B Ṣ *D*		
Possible combinations:		
A B—1 *D*	*A B D*	*A B*—1 *D* Ṣ
A B Ṣ *D*	*A B D*	*A B*—1 *D* Ṣ

A-B-D = *wheat genomes*
S = *rye genome*
—1 = *missing chromosome*
Ṣ = *one rye chromosome*

valuable chromosomes transmitting resistance can be introduced into the hexaploid wheat.

The results obtained by the research of substitution and addition are of moderate practical breeding use for the time because the first complete aneuploid series was produced with Chinese Spring, a primitive variety. A wide practical application of this method requires therefore aneuploids produced from many valuable cultivars.

Results on substitution between the genera *Triticum* and *Secale* have been given among others by Acosta (1961), Riley (1965*a*), Jenkins (1966), Gupta (1969), Sears (1969*a*), Müntzing et al. (1969), Zeller and Fischbeck (1971). Substitution of *Aegilops* chromosomes is described by Kihara (1963), Riley et al. (1966); of *Agropyron* chromosome by Bakshi and Schlehuber (1959), Knott (1964*a*), Wienhues (1966), Sharkawy (1966), Johnson (1966*a*, *b*), Quinn and Driscoll (1967), Anderson et al. (1966), Knitt (1968), Larson and Atkinson (1970, 1972), Sears (1972), Ruby et al. (1973).

When substituting alien chromosomes it must be borne in mind whether or not the chromosome originating from another genus transmits undesirable properties and that it removes a chromosome pair from the genome of the wheat. Therefore, chromosomes from another genus can be introduced into the wheat genome without greater difficulties only if the alien chromosome pair is homoeologous with the missing one, i.e., able to compensate, at least partly, for its function.

The enumerated disadvantages can be eliminated by the so-called chromosome segment translocation. In this procedure substituton is only a means to help an advantageous gene block translocation between the chromosomes of the alien species or genus and the wheat. This can be realized by substituting one of the chromosomes carrying the desirable genes into the wheat genome where the corresponding homoeologous chromosome is monosomic (see Table 10). Translocation between the wheat and the alien chromosome can be best promoted by the 5B-5D compensation line which, however, has been produced so far only from the wheat variety Chinese Spring (Dvorák and Knott 1972). To eliminate the system inhibiting homoeologous pairing increases the possibility of synapsis and chiasma formation, and promotes thereby translocation. The probability of translocation can be multiplied by physical mutagenes causing chromosome breaking too (Driscoll 1965).

Radiation treatment is applied in the double monosomic state (see Table 10). If the Ph factor is eliminated and the number of chromosome breaking is increased by radiation treatment, the frequency of translocation becomes much higher. Riley et al. (1968*a*) used this method to develop a yellow-rust resistant wheat by inducing translocation between the 2D wheat chromosome and 2M *Aegilops comosum* chromosome. Chromosome segment translocation may occur without mutagene invention, too (Law 1966*a*), but X-ray and gamma irradiation substantially increase the frequency of translocation. Wienhues (1967) attained translocation with a very high (5 per cent) frequency as a response to X-ray and Co^{60} irradiation. The frequency of translocation can be increased by thermal and quick neutron as well as P^{32} treatments, too (Sears 1967*b*, Kimber 1967). After translocation sometimes meiotic irregularity occurs, multivalents or ring formation take

place which, however, gradually disappear in the subsequent generations (M3, M4) (Bozzini and Martini 1966*a*, *b*, *c*).

Alien chromosomes sometimes cannot be substituted into the wheat genome because they are not homoeologous with either of the wheat chromosomes. There are cases when such a chromosome pair cannot even be transferred by addition as it causes severe irregularities in the meiosis. Such is e.g. the highly heterobrachic chromosome of *Ae. umbellulata* which carries leaf-rust resistance (Kimber 1970). In this case, only segment translocation brings success by eliminating the Ph factor. Other alien chromosomes while compensating for the wheat chromosome behave still irregularly in meiosis. Whether they are disomic or monosomic in the wheat genome such chromosomes always cause meiotic irregularities (Riley 1960, 1966; Sears 1967*a*).

The *addition line* is a crossing progeny where an alien chromosome pair is added to the full wheat genome (see Table 10). This procedure is a phase of the alien chromosome substitution but it can be used also separately. It was in this way that Riley and Chapman (1958) produced by chromosome addition the "Hairy-neck" addition line. Sadanaga (1957) transferred rye chomosome to *T. durum* by addition, Lindström (1965) added two adventitious "B" chromosomes of rye to wheat. Lee et al. (1970) obtained rye addition lines from the Kharkow wheat. By adding *Agropyron* chromosome Sharkawy (1966) introduced in to wheat the blue aleuron colour. Dvorák and Knott (1974) produced a full addition series between a hexaploid wheat (Chinese Spring) and *A. elongatum*. Further, they

Table 11. Nucleus substitution

	♀	♂
1st year	RRRRRR	DDDDDD
	×	
	RRRRRR	DDDDDD
	RRRRRR	DDDDDD
	×	
	DDDDDD	DDDDDD
	50%D	50%R
	DDDRRR	DDDDDD
	×	
	DDDDDD	DDDDDD
	75%D	25%R
	87%D	13%R
	94%D	6%R
	97%D	3%R
	98%D	2%R
	99%D	1%R
	♀	
self-pollination	DDDDDD	
	DDDDDD	

R = *maternal chromosome*
D = *paternal chromosome*

developed also an almost complete ditelocentric addition series. This kind of addition research plays an important role in the investigations of interactions between genes, and in evolution genetics.

In another type of addition a total alien genome is added to the wheat genome. In the *Triticale* breeding the rye genome is added to the tetraploid wheat giving the hexaploid *Triticale* (Kis 1966). With a full rye genome added to the hexaploid wheat an octoploid *Triticale* is produced (Tsunewaki 1964).

In addition lines irregularities may occur as a result of incompatibility between the alien chromosome pair or genome and the wheat plasm too (Knott 1964*a*).

Finally, the possibility of nucleus substitution should be mentioned here. By this method full chromosome complements of species or genera can be replaced. After the substitution the full chromosome complement of the donor is transferred into the plasm of the recipient partner. Such a nucleus substitution made it possible to attain plasmic male sterility used in hybrid wheat breeding. Kihara (1951) was the first to produce this type of substitution creating thereby the possibility of plasmic male sterility. Apart from the genetic work related with the production of hybrid wheat nucleus substitution is suitable to study the genetic influence of the plasm. The nucleus substitution is a simple back-cross series without selection (Table 11; Kihara 1963, 1968).

Monosomic or nullisomic lines of tetraploid wheat are more difficult to produce because the missing chromosomes cause sterility and significantly decrease plant viability (Noronha-Wagner and Mello-Sampayo 1963). This phenomenon may be explained by the tetraploid wheat having only two pairs of chromosomes belonging to a homoeologous group, and if one or a pair of them is removed, no adequate compensation exists, which results in great meiotic irregularities. Longwell and Sears (1963) tried to counterbalance this by producing mono-trisomic and nullitetrasomic lines. In the monosomics another chromosome of the homoeologous group was substituted for the missing chromosome. In the case of nullisomics two homoeologous chromosomes were substituted. This solved the problem of compensation and furthered the production of such lines from tetraploid wheat. Since for this operation hexaploid wheat was also used, according to Mello-Sampayo (1970) these aneuploid lines of the tetraploid wheat probably contained chromosomes originating from the D genome, too. By means of hexaploid wheat Mochizuki (1970) transferred the monosomic state to all fourteen chromosomes of the tetraploid wheat. This work was facilitated by the shrivelled grains of the monosomic lines whereby the monosomic state could be readily recognized, and there was no need of a cytological examination. All monosomic plants showed poor fertility, and there was a high incidence of male sterility.

Okamoto and Nishikawa (1967) substituted telocentric chromosomes for the chromosomes of the tetraploid wheat. These lines can be maintained. Eight telocentric chromosomes were successfully transferred in this way from he hexaploid to the tetraploid wheat, while in three cases this attempt failed. By means of telocentric chromosomes genes can be localized on both arms in the same way as in the case of monosomic, and at the same time the arm on which the locus is found can also be determined. By this, all obstacles to the aneuploid analysis of tetraploid wheats have been removed.

Joppa (1973) substituted all chromosomes of the D genome for the homoeologous chromosomes of the A and B genomes in the tetraploid wheat, but the substitution of the chromosomes 4B and 2B failed. Thus, he obtained, in fact, monosomes where the missing chromosome was replaced by the homoeologous chromosome of the D genome. These lines can be used likewise for chromosome mapping.

With the chromosome substitution, translocation, chromosome addition, genome addition and nucleus substitution aneuploid research has developed highly reliable methods for the genetic research of wheat. These methods render service in practical breeding, too, first of all by transmitting the extensive pathological resistance of more primitive species, then by producing plasmic male sterility in wheat, and finally by developing economically useful *Triticale* lines from the genera *Triticum* and *Secale*.

Chapter 9 Major quantitative characteristics and the genetic influence

Yield potential

Yield potential is the most important property of a cultivar, accordingly it is usually recognized as a primary factor among the objectives of breeding.

The flora of an area sown with the seed of an improved cultivar is an artificially homogenized phytocenosis, a population of isogeneous plants. The total yield of a stand like that is the biomass obtained as the end product of the ontogeny of the individuals in the population. The useful phase of the biomass is the grain yield.

If under identical ecological conditions different cultivars are grown, the one idiotype capable of producing the highest amount of useful biomass fractions under the given abiotic and biotic ecological influences will give the largest grain yield. If the same cultivar is sown in successive years the grain yield depends only on changes in the abiotic and biotic factors, since the idiotype is practically constant.

Ontogeny is affected by all abiotic and biotic factors of the growth period. They generally can be divided into two groups. One of the groups depending on the genotype influences the yield once favourably, at an other time unfavourably; the edaphic, climatic and agronomic factors belong to this group. The effect of the second group is always negative; the pathological and entomological factors come under this heading.

According to the evidence of numerous experiments the crop of wheat cultivars show a definite varietal specificity. In the course of a world-wide comparison of the economic values of varieties performed by the organization of the International Wheat Performance Nursery it has become quite clear that some varieties mostly belong to the group of those producing large yields, while others are found in the medium or last category. This suggests indisputable the heritability of yield potential, though none of the varieties occupies the first place every year or in all growing sites. Yields vary according to the sites of experiment, which proves that the idiotype of now one, now another cultivar comes under more favourable ecological conditions.

Since it has been proved that the yield potential of the varieties is an inherited property depending on given ecological conditions, it can be supposed that each cultivar has a hereditary maximum yielding potential, which is fully realized, i.e. the variety gives the largest possible yield, when the factors of the first group meet all the requirements of the genotype and the effect of the second group is nil. For the time being there is no way of knowing exactly the "optimum" ecological demands of any variety, neither can we, in fact, know the "maximum" hereditary yielding potential. And were we in the position of knowing it, we would not get far with it, since the "maximum" yield would require optimum conditions which can hardly be met under field conditions, for in the majority of the cases they are

factors that cannot be influenced at will. Thus, the hereditary yied potential of a cultivar does not in itself ensure high productivity; the latter should be contributed to by two further factors: "adaptability" and "yielding security". Adaptability is that part of the inherited ecological amplitude – ecological tolerance – of a cultivar by which it is able to utilize the changing edaphic, climatic and agronomic effects. Yielding security, on the other hand, is based on the hereditary resistance to pathogens and insect pests.

Due to its complex genetic, ecological and pathological dependence, net yield potential is a property very difficult to determine and classify. In spite of this, breeding work has attained the most outstanding results for the last twenty years in the increase of productivity. This was made possible by disintegrating yielding ability, as a genetically established potential, to its components (Sedlmayr 1953), whereby the role of the individual components as well as their interrelations can be better understood (Wagner 1971).

Grain yield depends on:

1. the number of productive plants per unit area (m^2),
2. the number of productive ears per plant,
3. the number of kernels per ear,
4. the average weight of kernels, the thousand-kernel-weight.

The first yield component is decisively influenced by the germinating ability, the germinating power, in winter wheat by winterhardiness, as well as by those pathological resistances which provide protection against pathogens causing the destruction or backward development of plants after a winter stress.

These factors decide during the 1–3 Kuperman (1950) stages that in a unit area how many plants will reach the generative phase when the productive shoots are formed (Wilson and Swamson 1962).

The second yield component is mostly brought into connection with the "productive tillering" capacity of plants, that is, with the number of productive secondary shoots developed beside the main shoot, depending on spacing. This property is more important in winter wheats, since it helps to make up for the losses caused by the stress of winter. In spring wheats it is of minor importance, especially under irrigated conditions, because after spring sowing the optimum ear density depends on the quantity of seed grain used rather than on the productive tillering capacity of the cultivar. That is why Donald (1968) constructed the "ideotype" of the spring wheat so that the plants do not tiller but have a single, well developed main shoot. Experiences show that populations consisting of plants with high individual capacity for productive tillering do not always form a closed stand of heads when sown dense. There are cultivars which, when widely spaced, develop many productive shoots with nearly equal ears, still, when sown dense, do not grow such a closed stand of ears as could be expected after their productive tillering capacity. Other cultivars of a lower capacity for tillering, when sown with a larger quantity of seed grain, develop a thicker and more uniform stand of heads. Thus a new concept, the "stand forming ability" should be introduced here, which is neither preconditioned by the tillering capacity nor affected by its absence.

The high density resulting from the tillering capacity is only advantageous when the ears of the tillers are nearly equal to those of the main shoot. From the point of view of the second yield component it is thus desirable that the cultivar should be able to make up for occasional losses by developing tillers with ears whose grain number and thousand-kernel-weight are not much inferior to those of the main ears. This requirement is not readily fulfilled though there are steppe type varieties in which productive tillering is the most important component of the yield. For the varieties San Pastore and Mara, Sarič (1966) established that the grain yield of the main shoots was not only larger than that of the tillers, but the plants grown the grains of the main ears were more viable and more productive, too. This speaks for the non-tillering varieties. Today it is accepted that tillering and non-tillering types may equally give high yielding varieties. The tillering type is better suited to a drier climate, while the non-tillering type is most efficiently grown under intensive, mainly irrigated conditions.

The second yield component develops from stage 3 to 7 of Kuperman (1950). The undisturbed realization of this second yield component requires a resistance to all pathological, entomological and climatic factors adversely influencing these stages of the generative phase.

The value of the third yield component is decided from the 5th to 9th stage of development (Kuperman 1950). It is in this period that the number of flowers per spike is determined. Pollination takes place at stage 9. The number of kernel per spike as well as the extent to which a variety is able to compensate for the unfavourable effects exerted on the normal course of stages 5 to 9 are genetically determined. The final result here too depends on climatic, pathological and entomological resistances. The grain number per spike may be made up either by more fertile flowers in a relatively small number of spikelets, or by a lower number of fertile flowers in a higher number of spikelets in the spike. The former case is mainly characteristic of the "Club-Wheat" type spikes; its disadvantage is that within the spike the grain size is uneven, consequently, the thousand-kernel-weight is lower. There are data on third- and fourth-rate grains in the spikelet with smaller embryos, which may be unfavourable from the viewpoint of the first yield component. According to Rowson (1970), long spike is in every respect more advantageous being in positive correlation with the number of grains per spike.

Thousand-kernel-weight, the fourth yield component is realized between the 10th and 12th stages of Kuperman. It is a genetically determined property which, however, may be unfavourably influenced by pathological, entomological and climatic factors in a very short time. Therefore a proper resistance is very important in its realization.

It must thus be emphasized that the realization of each of the four genetically determined yield components depends on a resistance to certain climatic, pathological and entomological effects (Wagner 1971). They play an important role to the extent to which the realization of the yield potential determined in the genotype is inhibited by the negative factors. Against these effects a genetically established protection should thus be provided for. This protective mechanism does not belong to the yielding potential, but gives protection only against the factors inhibiting its realization.

As for the extent to which the yield components are genetically determined information is given by the genetic variability and heritability. The estimated heritability (h^2) = the estimated additive genetic variance divided by the estimated values of full genetic variance + error variance. The calculated heritability is, on the other hand, the ratio of selection progress (R) and the differential of selection (S):

$$h^2 = \frac{R}{S}; \quad R = \bar{X}_F - \bar{X}; \quad h^2 = \frac{\bar{X}_F - \bar{X}}{S}.$$

In the formula the progress of selection is the difference between the mean value of the progeny of the selected part population ($\bar{X}_F$) and the mean value of the unselected original population ($\bar{X}$), divided by the difference between the mean values of the original parent populations (S) (Sváb 1973).

The h^2 value expresses in fraction or percentage the extent to which the difference in the selected part population is due to the hereditary effect or modification, respectively. It gives thus answer to the questions of what percentage the property concerned depends in a given case on genetic factors, what progress can be reckoned with in the case of selection and how early the selection shoud be started. The yielding potential realized in a dense stand can be reliably determined only if

1. there is enough seed-grain for a replicated plot trial (F_4–F_5),
2. the population is for the most part genetically homogenized (F_6–F_8),
3. the special effects of climatic, pathological and entomological factors can be separated.

Practical breeding has thus no objective means to forecast the actual yield potential making use of individual plants or early crossing derivates. Therefore, at first it is compelled to employ such informative methods which make comparative evaluation possible on the basis of the yield components of the partners used for crossing and of the individual plants of the crossing populations, being aware meanwhile of the fact that the ultimate answer can only be expected from the earliest possible comparative field trial.

From the yields of individual plants conclusions on the yield potential of strains or cultivars derived from them can hardly be drawn, in spite of the positive results occasionally reported by some authors (e.g. Alessandroni and Scalatti 1973). In such cases even the most exact individual examination made in the course of artificially balanced edaphon, culture-pot or water culture trials is seldom reliable, though data exist on successful selection performed under such conditions, too (Villanueva-Vovoa 1973). From such data conclusion can be drawn on the individual yield potential of plants, but there is no reliable answer as to collective yield potential.

A plant or pure line realizes its individual yield potential when spacing excludes any considerable competition between both the aboveground and underground parts of the plants. In wheat this begins with a spacing of 20×20 or 10×30 cm. With a spacing like this the plant is not under a stress, but in a thick stand it

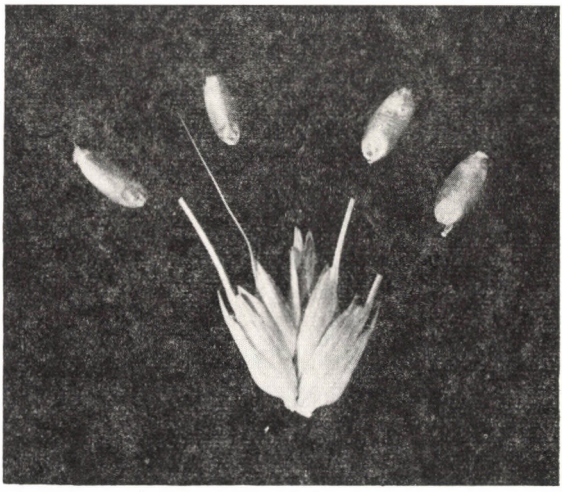


Fig. 7. Wheat spikelet of fourfold fertilization. It is remarkable that the fourth kernel is much smaller than the previous three. The extent of fertilization increases at the expense of uniform grain size (Photo by P. Lelley)

Fig. 6. Club-type wheat spike. Owing to the closeness of spikelets in the upper third much smaller kernels develop at the expense of uniform grain size (Photo by P. Lelley)

would exhibit defensive responses. The genetic factors determining the yield are not identical with the genes that control the reactions to the stress of the close environment. That is why no reliable answer is gained from individual yielding potential to the collective one, that is, from the yield of widely spaced individual plants to that expected in a dense stand. This possibility of individual selection is thus limited and, at most, informative in character. There are, however, some observations (Paroda and Joshi 1970) suggesting a close correlation between thousand-kernel weight, or number of kernel/spike and productivity, but a connection like that is not sufficient for reliable selection. It is therefore useful to consider the four yield components both when assessing the crossing partners and when selecting the derivates, with the reservation that only a final comparative field trial will provide reliable data. Unless the productivity of strains or varieties is elucidated in a replicated, almost large-scale comparative trial, any individual selection, carried out on the basis of yield components, is likewise of informative nature, and only fit to point out the apparently undesirable genotypes.

When evaluating the yield components the correlations existing between them must be reckoned with, too. Concerning these, few concrete experimental data are available only, and the existence of negative correlations between the 2nd, 3rd and 4th yield components after attaining a certain level is only logically assumed.

The more productive shoots develop on a plant the smaller the spikes on the tillers and the lower the number of kernels per spike will be (Nasipaiko et al. 1971).

The negative correlation of these two yield components becomes particularly striking in the case of wide spaced single plants (Knott and Talukdar 1971). The number of kernel/spike is in negative correlation with the thousand-kernel-weight. This is especially conspicuous in the compact wheats, where the high number of grains is due to the fact that in the spikelets many fertile flowers are pollinated. In the top spikelets of the club-wheat the thick set of grains contributes to the reduction of the thousand-kernel-weight (Fig. 6). In large spikelets the biggest grains developed in the first two flowers, while the third and successive flowers will develop smaller grains (Fig. 7). This inverse ratio is less manifest in long spikes composed of many spikelets where maximum three grains develop in a spikelet.

Since beyond certain limits the three mentioned yield components are at an inverse ratio to each other, productivity cannot be increased by a genetic influence alone; the yield components have to be developed in co-ordination.

Yield potential is thus the result of the joint action of the four hereditary components. Unfortunately, its actual value – as we have mentioned – may only be appreciated after the population has become genentically consolidated and large enough to carry out a reliable comparative trial. According to Bhatt and Derera (1973) lines earlier selected from crossing populations usually show a higher productivity. This does not contradict the former statement, since the experience is presumably connected with the heterosis effect. It is a question whether prior to this stage to what extent individuals or strains can still be reliably evaluated on the basis of yield components.

Investigations aimed at revealing the genetic nature of components determining the yield potential are not extensive, for the very reason that the real effects of hereditary factors influencing the productivity can only be delimited in later generations. Therefore, the breeder should first satisfy himself by studying the yield components and carrying out an individual or stock selection on this basis. Concerning the reliability of selection heritability surrenders information. On the heritability of the first yield component no data are available.

Heritability of the number of productive spikes per plant was found to be 7 per cent by Weibel (1958), 5.3 per cent by Pollmer (1957) and 4.6 per cent by Karam (1958). This means that the number of ear per plant, or "productive tillering", is of low heritability. Ecological effects play a dominant role here, so an early selection on this basis, and the overestimation of the results of individual selection may later lead to frustration.

Weibel (1958) fixed the heritability of the number of kernel/spike at 35.4 per cent. Pollmer (1957) obtained 24, Karam (1958) 30.3 per cent. Accordingly heritability of the number of kernel per spike is more reliable, and selection for this component may thus be more efficient.

For thousand-kernel-weight the same authors ascertained a heritability of 52 and 81.7 per cent, respectively. These values suggest the better efficiency of early selection.

Weibel (1958) calculated a mere 15 per cent heritability for productivity as a whole. From the above data it can be concluded that different roles played by the three yield components in the genetic stabilization of "yield potential".

As far as cultivation is concerned Sikka and Maini (1962), Mijo (1962) and Přikryl (1962) considered the role of the second yield component to be more important than that of the third and fourth components. Damisch (1970) found the stand density, kernel/spike number and thousand-kernel-weight to be responsible for the actual yield in 47.5, 29.2 and 23.2 per cent, respectively. It follows that in the growing practice greater importance is attached in the trend of yield to components of lower than to those of higher heritability.

Thus, when comparing the results of heritability calculations and the percentual efficacy of the individual components, a 26.2 per cent total heritability of productivity is obtained against Weibel's (1958) 15 per cent h^2 value.

	h^2	practical importance		
2nd component	7.0%	of which 47.5%	=	3.8%
3rd component	35.4%	of which 29.2%	=	10.3%
4th component	52.0%	of which 23.2%	=	12.1%
				26.2%

On this basis, the difference between the heritability of yield potential and the totalled h^2 values of the yield components shows that the connection between the components is yet inadequately understood.

Recent heritability investigations unequivocally reveal a high h^2 value of heritability for thousand-kernel-weight. Shamra and Knott (1964) obtained 45 per cent, Reddi et al. (1969) 48 per cent, Khadr (1971) 70 per cent, Rachinski (1971) 62.2–76.3 per cent, Sun et al. (1972) 51–85 per cent for heritability of thousand-kernel-weight. These data prove that thousand-kernel-weight is genetically the most reliable yield component in breeding work. That is why practical breeding endeavours to increase the thousand-kernel-weight as long as it does not affect quality (Bingham 1967). Thousand-kernel-weight can be determined by a simple and quick procedure, so selection is easy. High thousand-kernel-weight has the further advantage that large grains have larger embryos, and the larger embryo is in positive correlation with the first yield component: the number of productive plants per unit area (Rosenkova 1964; Sukurov 1966; Jakubziner and Sukurov 1969; Beleckii and Kovalev 1969; Gubanov and Vertii 1970; Austenson and Walton 1970).

There is a possibility of increasing the number of kernel/spike by genetic intervention, i.e. the size of spike is not a limited factor. It has been mentioned too that the inverse relation of kernel/spike concerning thousand-kernel-weight only appears beyond a certain limit (Bohač and Černin 1966, 1968). Yet, this circumstance is of a limiting nature, because – as Knott and Talukdar (1971) have pointed out – the negative correlation may become inhibitory. The influence on thousand-kernel-weight of a higher number of kernel/spike is not so great when instead of the number of grains in spikelets the number of spikelets is increased (Boekholt 1962; Fadrhons 1965; Foltyn 1971).

Productive tillering per plant and spike number per unit area in dense stand are not determined by the same genetic factors though the latter are supposed to be in correlation (Mijo 1962; Přikryl 1962). Bremner (1969) als refers to the temporary advantage of high tillering capacity mainly in winter wheats and at places, like the United States and the German Federal Republic, where the wheat is sown with a wider row distance. Under such circumstances heads of tillers equal to the main head have an important role. Where the row distance is 10 cm or less, tillering is of importance only when the stand becomes thin. In the case of spring wheats, especially under irrigated conditions, the importance of tillering is quite inferior, because spike density can be adjusted by the quantity of seed-grain at will. After the individual tillering capacity has been observed a separate study is required to establish how dense a stand the cultivar or series of derivates is able to form without the decrease of the head size (Boháč and Černin 1968). In the case of a dense stand self-shading must also be reckoned with, as it is not uniformly tolerated by the different genotypes irrespective of their yield components (Willey and Hollidy 1971). It is supposed that a harmony between tillering and tolerance to shading forms the property of "dense stand tolerance" whose genetic and biological aspects in wheat are hardly known as yet, though its existence has been confirmed by observations (Langer 1965). It has been pointed out that as a result of increasing density of stand, respiratory loss will finally exceed the assimilation surplus of the stand (Bálint, written report). The inverse correlation of the two functions may be a genetically determined limiting factor giving some explanation for the tolerance of dense stand.

The other important limiting factor of the stand is lodging. Head number can be increased only as long as lodging does not threaten, otherwise the dense stand itself will be an obstacle to the full development of the yield components. Lodging resistance is dealt with under a separate heading.

It follows from the above that genetic influence can only be exercised on the yield potential through co-ordinated and proportionate improvement of yield components (Saulescu et al. 1963; Grafius 1964; Pinthus 1964; Johnson et al. 1966; Langer 1967; Jha and Ram 1968).

Yield components should therefore be considered when choosing the crossing partners. They are relatively easy to asses and compare. New genotypes appearing in the crossing derivates can likewise be examined for yield components with relative case, and depending on heritability, selection may be started as early as possible. Aspects of evaluation are:

Component 1:

Size of germ (can be assessed visually, or by excision and weight comparison).
Germinating ability.
Germinating power.
Number and speed of development of seminal roots.

Component 2:

Number of productive spikes per plant in single seed sowing.
Uniform maturing of secondary spikes.

Component 3:

Average number of grains in main and secondary spikes.
Average number of grains per spikelet.

Component 4:

Average thousand-kernel-weight.
Difference in thousand-kernel-weight between main and secondary spikes.

These are the possibilities of individual evaluation based on the four yield components. If instead of an individual selection head selection is made, only the third and fourth components can be examined, and even then only the main head may be considered. "Early testing" is in each case the final aim which gives answer to the question of how much selection made by yield components has been efficient.

By investigating the chromosomal place of loci directly determining the yield components the following data have been obtained:

Table 12. Loci directly influencing productivity (Morris 1962–73)

Property	Chromosome
Kernel weight	1, 2, 3, 5, 6A, 1, 3, 4, 5, 6, 7B, 1, 2, 5, 7D
Kernel number per spike	5A, 1, 6, 7B, 7D
Spikelet number per spike	4, 6, 7A, 1, 4B, 2, 3D
Spike number	3A, 2B
Tillering	1, 7B, 6D
Yielding ability	1, 6A, 1, 4B, 7D

Data giving an overall view of the action mechanism of genes influencing "yielding potential" have not been obtained so far. Neither are there symbols that could be brought into connection with the four yield components or productivity as a whole in the table compiled by McIntosh (1973) (p. 50). On the other hand, the number of loci localized on the different chromosomes is so large in each genome that there is hardly any of the 21 chromosomes of the hexaploid wheat that would not in some way influence productivity (Table 12). Comparison of the genetic analyses throws no more light upon the question. Lupton (1966*a*) found productivity to be of dominant heredity in the variety Cappelle-Desprez, but gave account of the high variability of the yield components. Bingham (1966) when crossing Holdfast × Cappelle-Desprez observed an intermediary segregation in the transmission of thousand-kernel-weight. In the case of crossing the varieties Thatcher, Wis 255, Henry and CI.12633 the thousand-kernel-weight was of dominant, and even of additive heredity. The conclusion drawn from these data and the results of gene mapping is that in most cases a polygenic heredity should be reckoned with in the case of the yield components. The possibility of recombination is thus exceedingly high, and transgressive heredity also exists. Transgression may appear in the case of individual components, and also regarding yield potential as a whole. It must be borne in mind, however, that yield potential

cannot always be improved by the change of a single yield component. The positive change of a certain component only manifests itself in the yielding ability if the other components are maintained at their former levels. The practice of breeding knows many examples of both cases.

Hereditary yielding potential can be improved by a co-ordinated genetic influence on the yield components. For this the possibility of early selection is, with reservations, also given, but since it is not efficient enough the practice of breeding is increasingly interested in recent results of biological research with a view to increase the efficiency of early selection. It is a question whether there is any possibility of finding new characters of selection which, together with the yield components or apart from them, may give further information on the perspectives of yield potential. Those characters of the root, ear and foliage are primarily looked for which can be brought into connection with yielding ability and which possibly give information on its extent, too. Simple and quick methods by which mass examinations can be performed without destroying the plants would be particularly useful.

Extensive studies made by Troughton (1962), Dobrinin (1969), Whittington (1970) and others on the *root system* of wheat proved its decisive role in yielding ability. In spite of the fact that due to difficulties in washing out the morphological and biological properties of the root system are not easily studied, attempts have recently been made to find out whether any conclusion can be drawn on yielding ability by comparing the root systems of young plants, and the parameters of young roots can be utilized in selecting for yield potential.

From the point of view of breeding the following relation may be of indirect importance for selection: connection between the length, shape, active surface of root on the one hand, and yielding ability, on the other.

Kruzhela (1965) determined the number of seminal roots at 2.7–4.2 and pointed out a kind of varietal specificity. No connection was, however, found by him between the number of seminal roots and yielding potential. Hurd (1968) detected a difference between the initial development of roots and their ability to penetrate the soil, but these data could not be brought into connection with yielding ability either, except – perhaps – the first yield component. In spite of an initial failure in the early phase of development many have studied the root in culture medium or soil (Subbich et al. 1968; Muhin et al. 1970*b*; Daniltsuk 1970; Velsovskaya 1970*a*, *b*; Cerný and Belzová 1971; Daniltsuk et al. 1971; Bondarenko and Tklaich 1971). These investigations suggest that there is hope of finding some connection between certain parameters of the root and yield potential. If it is proved to be true, then a comparison of the parameters of seminal roots and adventitious roots, as a method of selection, may contribute to the reliability of selection for yielding ability.

The methods of examination are different; Racz et al. (1964) used ^{32}P isotope, Mc Dougall (1970); Mc Dougall and Rovira (1970) ^{14}C isotope, but simpler volume and surface measuring methods were also tried out. Björn et al. (1963) call attention to the fact that different wave-lengths of light have different effects on the development of roots. This circumstance warns us to be careful when evaluating the examination results of roots grown in water culture. Connection

between roots and yielding ability was searched for in later phases of development, too. Pinthus (1969) found a connection between the formation of adventitious roots and productive tillering. This connection has proved to be specific of varieties again, but the effect of environment may conceal the difference. The most intensive root formation was observed during the differentiation of the spike at the fourth and fifth Kuperman stages. The length of these two development phases may thus be correlated with the yield potential, but the correlation is not yet clear. According to Kazakov and Gutsal (1968) the number of adventitious roots is in positive correlation with the hereditary yielding ability, but the connection could not be clarified. Suskevič and Stranák (1970) observed a positive relation between the size of aboveground and underground organs, which may be a pointer for breeding of dwarf wheat, but no connection was found with the yield potential. Velsovskaya (1970*a*) could not show a connection between the volume of the root system and the variety, but found the rate of root development to be characteristic.

In a later phase of development reliable studies on the root system are made difficult by the fact that the amount of precipitation decisively influences its growth and shape. Technical difficulties hindering examination at an advanced stage of development can hardly be overcome. In a later phase the plants are even destroyed by the examination, which is the greatest disadvantage from the viewpoint of selection. Since the characteristics of roots are decisively influenced by the nutrient supply of, and distribution of nutrients in the soil, field selection on the basis of roots is considered to be unreliable (Salim et al. 1965, Balyk 1970).

No doubt, at stages 3 to 9 the root system fundamentally determined the trend of yield. But no direct relation of the grain number per spike and thousand-kernel-weight to the root system could be ascertained so far. It can be supposed that differences in the genotype cause a morphological variability of the root system connected with the yield potential. But for lack of a possibility of exact analyses, at these stages of development of roots in the soil cannot be used for selection, at least for the time being. In water culture, on the other hand, the changing conditions and the effect of extraordinary circumstances render the outcome of selection rather uncertain. Genes determining the properties of roots have been inadequately studied (Table 10). According to Mac Key's most recent investigations (1973) monosome analysis showed that the absence of almost any of the chromosomes has an effect on the length of roots and ratio of underground and aboveground volume of organs.

That winterhardiness, drought tolerance and lodging resistance have connections with the root system are established facts, but since it is only the reliabilty of production that these properties exercise a direct influence, this connection will be discussed later.

About the selective value of yield potential and the morphological and biological properties of the aboveground parts: *stem*, *leaf sheath*, *leaf blades*, *spike* recent investigations provide information.

The role of leaves developing in the first phase of ontogenesis was pointed out in defoliation trials (Jevtič 1964). There are, however, no reliable data concerning the effect the number of leaves and their morphological characteristics exert on

yielding ability in this phase of development. As long as these connections are not clear, the selective value of leaves at stage 1 of Kuperman is uncertain.

According to Lupton and Pinthus (1969) the role of *sterile shoots* must not be underestimated either, as their assimilates are transferred through remobilization to the productive shoots contributing thereby to their nutrient supply. The sterile shoots have thus a part in the trend of yield, but the connection is not sufficiently known to make it possible to trace more productive lines by.

The static and nutrient transporting role of the *stem of spike producing shoots* is clear. The role of internodes, nodes and leaf sheaths in assimilation and nutrient remobilization has been thoroughly studied, but nobody has succeeded so far in finding out to what extent the stem takes part by its assimilates and remobilized nutrients in determining the yield. Therefore it is not considered beyond its static role when selecting for productivity. In the chromosomes 14 loci determining various characteristics of the stem have been found so far (Table 10).

The role of *leaf* varies according to whether it is a lower or upper leaf. Foliage, as an important site of assimilation influences the yield from the differentiation of the ear primordia to waxen ripeness through development stages 4–11.

The number, size, shape, position of leaf blades as well as the intensity of assimilation may be of importance in view of selection. Recent physiological investigations have tried to show connections which would throw light upon the role the leaves play in determining the yield. The investigations were mostly focused on the role of leaves supposed to have an active part in the formation of the yield. Haber (1962) pointed out the anatomical and morphological features of leaves, such as the size of the leaf blade cells and rate of cell division, to be determined by different genes. According to Hodanová (1967) the environmental conditions, mainly the nutrient supply and stand density, are also important. It is thus not only on the size of spike but also on the leaf area that stand density has an influence. Rawson and Hofstra (1969) proved by radiocarbon test the flow of assimilates from the leaves toward the growing organs. A sensitive mechanism controls what is transported to the underground and what to the aboveground parts. After pollination all assimilates move to the inflorescence. At the time of ripening the remobilized substances of stem and spikes are also transferred to the grains. Lyapsina (1967) found a positive correlation between leaf surface area and drymatter accumulation in wheat. This finding suggests a physiological connection between leaf surface area and yield potential. Kranz (1964) constructed a new type electric planimeter to take exact measurements of the leaf surface area. Lazarov (1965) elaborated a quick method to calculate the leaf area. It is thus probable that the total leaf blade surface of the wheat plant is connected with the drymatter production capacity, still its determination is inadequate to be a good method of selection because it is complicated, and the role of the individual leaves varies in the different phases of development. Misselwitz (1973) also found it impossible to conclude from the total leaf surface to yield potential and to differences between varieties. On the other hand, it cannot be decided which is the most suitable time to measure the leaf surface area. Furthermore, the reliability of the total leaf surface in selection is questionable by differences in the intensity of assimilation between the different leaves of a plant and between

varieties. According to Kranz (1967), Leach and Watson (1968) the intensity of assimilation can be measured by phytometer, and there is a connection between the chlorophyll content of cells and the intensity of assimilation, though this connection varies both in the different phases of ontogeny and in different parts of the plant. Dorokhov et al. (1966) determined the maximum of assimilation intensity for the time of heading (stages 9–11). Bondarenko and Saratova (1967) found differences between varieties in the rate at which the assimilates are transported to the head in the successive phases of grain formation. A direct connection between yielding ability and assimilation intensity was already pointed out in 1963–1964 by Birečka and Dakič-Wlodkowska when comparing the varieties Chlopicka and Fortunato. Assimilation intensity measured in the periods of flowering and grain filling was mostly characteristic of yield potential. Thus, from comparative data on the assimilation intensity of total leaf surface conclusions could be drawn as to whether the new crossing derivates show any improvement compared to the parents. This requires, however, a lengthy procedure whether it is performed with the $NaH^{14}CO_3$ method or the Warburg technique (Lawes and Treharne 1971). Reliable comparison can only be made with the averages of many tests, therefore, the assimilation intensity of the total leaf surface is yet not used in selection work. According to Kraljavič-Balalič (1973) total leaf surface shows an intermediary heredity, with 6–47 per cent for the value of h^2.

Recent investigations have been mainly concerned with the role of the *flag-leaf*. This leaf is easier to observe, and according to the evidence of the results of investigations has an important role in determining the yield. The ^{14}C tests performed by Stoy made it clear already in 1963 that the assimilates of the flag-leaf moved mainly to the spike, but the extent of translocation was not of a varietal specificity. From the point of view of yield potential he considered it important that the flag-leaf should maintain assimilation as long as possible. Boodson et al. (1964) thought the role of the spike to be more important in the process of assimilation than that of the flag-leaf, but did not deny the unique importance of the latter in the period of heading. Warldlaw (1965) too called attention to the role of the flag-leaf in supplying the ears with nutrients. According to Lupton (1966*b*, *c*) the share of the spike in determining the grain weight is some 25 per cent, while that of the upper part of the stem, flag-leaf and its sheath about 75 per cent. Turner (1969) also emphasized the importance of the flag-leaf, noting, however, that it transports mostly carbohydrates to the grains. In his opinion the function of the lower leaves hardly reaches 15 per cent. Smoček (1969*b*) found a positive correlation between the length of the flag-leaf and the size of the leaf blade as well as between kernel number per spike and thousand-kernel-weight. Focke (1973) drew attention to a positive relation between the size of the flag-leaf and that of the spike.

The role of the flag-leaf in determining the yield can be regarded as an established fact, but it is not clear to what extent it is influenced by the size, shape and position of the leaf blade and the duration and intensity of assimilation. Accordingly, when selecting for yielding ability the parameters and lifetime of the flag-leaf should be taken into consideration (Simpson 1968; Apel and Lehmann 1970; Hsu and Walton 1971). Its intensity of assimilation too is certainly an important

property, but this is difficult to study. The flag-leaf may be erect, horizontal or bent. It is not clear as yet how much the function of the leaf is influenced by the position of the leaf blade. In a thick stand an erect leaf is supposed to be more favourable than a horizontal or bent one. Since the influence of this character on yield potential has not been fully investigated, this relation requires further study before it can be utilized in selection.

Transmission of leaf properties has been studied by many scientists. According to Table 10 genes have been localized for 13 characters so far.

The *spike*, as an organ controlling the processes of assimilation and respiration has recently been dealt with by a number of researchers. Lupton (1966*a*) estimated the share of the ear in determining the grain yield to be about 25 per cent. Sybanbekov (1965) called attention to a higher intensity of photosynthesis and transpiration shown by the awned spikes. Buttrose (1962) likewise emphasizes the role of spike especially in the period when the vegetative organs are about to cease assimilation. Skoskievicz (1965) elaborated a method for measuring the assimilating surface of spike. Lupton and Ali (1966) studied the photosynthesis of wheat spike with different methods and obtained varying results. Meinx (1965), Nátr (1967) and Lucas and Asana (1968) attempted to clarify the role of spike by defoliation. Evans and Rawson (1970) analyzed the function of awn in relation to grain formation. Sybanbekov (1965, 1966) went as far as placing the role of awn in the process of transpiration before that of the leaves, supposing that in certain periods the awns display a higher transpirative activity than the total foliage. Carr and Wardlaw (1965) estimated the role of glumes particularly high; according to their opinion some 80 per cent of the drymatter content of grain comes from the glumes. Lupton (1966*a*) believes the nutrient translocation to the grains to be entire from the glumes, and only being partial from the other leaves. The role of spike in the processes of assimilation and respiration is thus decisive in determining the yield, but it is not clear what are the morphological characters on which an efficient selection is to be based. It is not even decided whether the awned or the awnless spike is the more favourable one in spite of that Derera and Stoy (1973) found 30–45 per cent of the carbon moving to the head after pollination to originate from the awns. The longer the awns the higher the extent of their carbon assimilation. Comparison of isogenic awnless and awned lines revealed a higher intensity of photosynthesis in the awned ears (Teare et al. 1972). From this point of view the semi-dwarf and dwarf wheats have created a new situation.

From the ear properties 18 have been localized in the chromosomes so far (Table 10).

The grain yield of wheat plants is the photosynthetic result of roots, stem, leaf blades, leaf sheaths and heads. The higher the number of spike per unit area and the number and weight of grain per spike, the larger the grain yield. All morphological and physiological properties that influence the yield are controlled by a complex genetic mechanism which by nature can only be a complex multigenic group of characters. That is why the genetic background and way of transmission of the above listed properties and their relations are so difficult to explore and, as they are, not properly cleared so far. And that is the reason why breeding

practice has not yet found any reliable indication from which conclusions could be drawn on the prospective result. On the other hand, it is a promising perspective that the possibility of transgression still exists (Hänsel 1971). The most outstanding results of breeding, the highest yielding varieties like Bezostaya 1, Sava, Dacia, Propsdorfer Extra, etc. are mostly due to transgression.

To summarize what has been said so far, the main objective is to endeavour to lay out comparative trials, irrespective of the applied method of breeding, which may give information about the yielding ability realized by the strain in thick stand. This can be earliest realized with the second generation of the selected "mother" plant. There are some modest possibilities of an early selection, too, either of plant or of spikes preceding even the comparative plot trials.

Head number per plant, kernel number per spike and thousand-kernel-weight are the most important characteristics. Some help may be expected from a comparison of initial root development and morphological evaluation of total leaf surface, area flag-leaf and spike. The reliability of selecting for these latter characters is not, though, proved as yet, but it is obvious that they cannot be left out of consideration.

Heads or "mother" plants of higher productivity are given priority in selection, though with the reservation that individual yielding ability is not identical with the collective one, and the relation of the two is yet not fully understood. Any character of individual selection is thus only informative in nature. It is for the comparative trial to decide whether or not the early selection was successful. For an earliest possible field trial the following conditions should be ensured:

1. By repeated individual selection a genetic homogenization should be attained as soon as possible.
2. By single seed sowing a high propagation ratio should be ensured.

Early selection for yielding ability requires a certain level of technical equipment. Without adequate mechanization and automatization data indispensable for an early selection cannot be obtained in the short period between harvesting and sowing of winter wheat.

Precise and quick scales produced in a great variety are of primary importance. Precision of 1/100 g and quickness are the first requirements. Scales of this precision are needed to kernel weight per spike, grain weight per mother plant and thousand-kernel-weight. To weigh grain yield per strain scales of 1 g precision are satisfactory enough.

Grain counting is very important, and in fact is indispensable in determining the kernel number per spike, kernel number per plant and thousand-kernel-weight (Fig. 8). For this purpose electronic counters should be used of which three types are described by Hofmann and Kühl (1972) and one by Eimer (1972). The basic requirements of a kernel counter are:

1. Quickness; to count at least 300–400 kernels/min.
2. Preciseness; within a marginal error of 1–2 per cent.
3. When put in operation it should begin counting as soon as possible; this decisively influences the quickness of the operation.

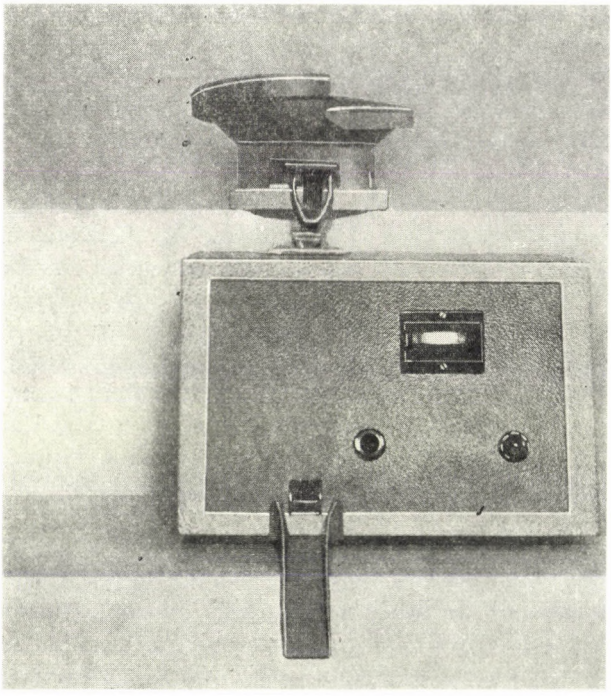


Fig. 8. Electronic wheat grain counter (Photo by P. Lelley)

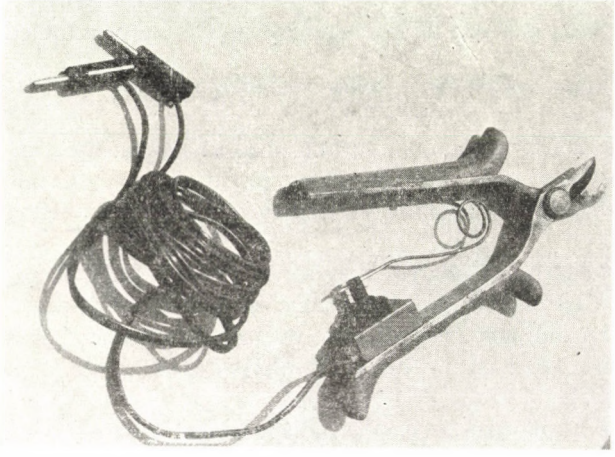


Fig. 9. Scissors constructed for counting cut wheat spikes; it is connected with an electronic counter (Photo by P. Lelley)

4. It should quickly discharge the last grain; this is again important as far as quickness is concerned.
5. Machines automatically stopping after a predetermined number of kernel are preferable.

Technical aid has been devised for head counting, too (Lelley 1971*a*). It is a pair of scissors connected with an electronic counter (Fig. 9). It can be operated with

main current when counting ears in laboratory, but may also be used outdoors with an electric battery. The electronic counter registers the number of ears cut off, eliminating thereby the possibility of error.

Necessary arithmetical operations to be performed in the course of various processes of measuring and counting are facilitated by the use of hand or electric table counters.

Winterhardiness

Among the climatic factors determining the realization of hereditary yield potential a certain range of temperature is indispensable in the different phases of ontogeny. Extreme temperatures exert a hereditarily determined unfavourable effect on the development of yield components.

Winter stress may have an adverse influence on the first yield component by decreasing the number of plants per unit area and reducing the vigour of the surviving ones. Cultivars with a high capacity for productive tillering may partly or wholly make up for winter losses. Yet, the aim is to keep alive possibly all plants that come up in autumn. In this way a higher number of main ears are formed which is favourable as regards the third and fourth yield components. Stop-gap tillering in spring may prolong the growth season which is undesirable.

Winter stress is extremely complex wherefore even its physiological effects cannot be fully explained. The main factors are a decrease in temperature, the fluctuation of temperature, the special microclimate caused by a permanent cover of snow, mechanical effects resulting from frost-bite, water deficiency due to frozen soils, or its opposite: oversaturation caused by a sudden thaw. These effects may occur individually or combined varying in order of succession and duration. Differences between regions and seasons may be extremely great, therefore winter stress as a complex can hardly be examined, and the protective mechanism acting against it is also difficult to study.

The most important factor that may adversely influence the survival of winter wheats is: *frost*. The biological consequence of cooling down and negative temperatures has been a priority subject of research, because a knowledge of unfavourable changes caused by frost and the issuing cytological and histological consequences may help to better understand the protective mechanism acting against cold, and to clarify the genetic implications of the defensive reaction. To know the connections is a precondition of elaborating reliable laboratory methods for studying the extent of hereditary cold resistance ,frost- and winterhardiness, which promote a quick and unfailing selection possible.

Of the frost induced cytological changes Salcheva and Samygin (1963) confirmed the swelling and discoloration of chloroplasts, detachment of plasm from the cell-wall and as originally supposed by Iljin (1933) the presence of ice crystals in the extra-cellular space. The rapid growth of the latter destroys the organelles. A connection between ice crystals and protoplasmic lesions was experimentally proved by Johansson and Krull (1965). Schnelle (1963*a*) observed that a sudden fall in temperature caused the destruction of wheat plants even at a higher temperature

than in other cases when they tolerated much lower temperatures. The destruction of chloroplasts generally begins at −4°C. When cooling down is slow this process begins later. According to Samygin and Varlamov (1964) the extent of damage caused by ice crystals depends on how quickly they are formed. When the process of icing is slow the damage will be much less, since rapid changes of structure are not readily followed by the plasm. According to Protsenko (1969) harmful ice formation is most intensive at −21–22°C; temperatures below that can cause a state of overcooling which inhibits the formation of ice crystals.

Biglov and Stsepteva (1964) studied the effect of freezing on the ribonucleic acid content of the nucleus and found that the ribonucleic acid content decreased at a faster rate than the desoxy-ribonucleic acid content. They observed the deformation of the nuclei, too. Chien and Wu (1966) experienced a decreasing trend in cell division, lower physiological activity of nuclei followed by a gradual plasmolysis as a response to cooling down. The vacuoles become smaller, and a dense reticular structure appears in the cytoplasm, supposedly connected with frosthardiness. Kwiatowska (1970) observed morphological changes in the mitochondria of coleoptyle cells. Barashkova and Alekseeva (1970*b*) found the fractional composition of the protein content to change as a result of cooling down. Hohlova et al. (1969) pointed out a positive correlation between frost induced dehydration, the enzyme activity and sulphhydryl content. All these findings, except the changes of chloroplasts, apply also to the roots; moreover, these processes begin sooner in the roots, since the roots are more sensitive to frost.

Experiences on histological, biochemical and physiological changes caused by frost have not contributed much to the better understanding of damages or destruction and of the mechanism protecting against them.

Heber and Ernst (1967) started from a new hypothesis: the destructive effect of intercellular ice on plasm, originally suggested by Iljin in 1933, has no decisive role in damages done by frost. It is not the ice crystals that destroy the plasm, the damage is caused by the too high concentration of the dehydrated plasm which upsets the metabolic system and the concentrated solutions become toxic for the chloroplasts and mitochondrial membranes. Consequently, assimilation and dissimilation stop irreversibly. According to the authors this is the lethal stage of frost damage. The consequences depend on the concentration and nature of toxic substances which vary with the extent of cooling and the solution concentration in the cell-sap before frost sets in. The lethal effect puts an end to the permeability of membranes (Santarius and Heber 1972).

Certain ecological conditions have an influence on the harmful consequences of freezing apart from a possible cold resistance. A hereditary attitude toward these effects is also included in the complex of resistance. Salcheva et al. (1964) found a permanent intensive illumination to increase cold resistance. Long-wave light stimulates sugar synthesis and sugar accumulation in leaves and tillering nodes, respectively. It can be supposed that the ability of plants to make use of these conditions is also a hereditary feature.

The wheat plant is able to give an intensive protective reaction to winter stress, first of all to cold, which develops in the course of hardening. Gradual cooling and medium low temperatures harden the plants and prepare them to self-defence

against low temperatures. Temperatures optimum for hardening vary with genotype and external circumstances. According to Ullrich (1962) the optimum temperature of hardening ranges from +8 to 0°C. Valeev (1967) obtained the best results by hardening plants for four days at −4°C. He found a considerable sugar accumulation in the tissues during hardening. Trunova (1970) found that the sugar content increased by two and a half times, and that a large proportion is stored in the cell-sap and chloroplasts. Zlobina (1970) observed a remarkable mono-, di- and oligosaccharide accumulation in the tillering nodes. In her opinion it is mainly saccharose that ensures protection under the snow-cover. In winters poor in snow the monosaccharides, mainly glucose, enhance the effect of saccharose, the trisaccharide raffinose supposedly serves in complementing the effect of monosaccharides. The long since known importance of sugar accumulation is thus invariably an established fact. In addition to saccharose and glucose, Trunova (1963) called attention to the role of ramnose, xylose, arabinose, mannose, galactose and cellobiose. These compounds which increase the concentration of the cell-sap have a varying influence on cold tolerance in plants. From the substantial difference between winter and spring wheats in the sugar concentration of the cell-sap Kruzhilin (1963) concluded on the important role of sugar in the process of hardening and a gradual development of cold resistance. In hardening long-wave light is important for it promotes the assimilation and accumulation of these sugars (Salcheva et al. 1964). The longer the period of temperatures favourable for hardening, the more effective the hardening will be (Tumanov and Trunova 1963). This explains why a sudden fall in temperature causes greater losses (Schnelle 1963*b*). If hardening begins in a short-day period, the rate of growth decreases, which is favourable for carbohydrate accumulation. Short-day conditions therefore contribute to the development of winterhardiness (Panchenko 1963). Moderate water supply is advantageous in the hardening period, because if the water content of the plasm is lower, the concentration of the solution reaches a favourable higher level in a shorter period of time (Schnelle 1963*a*).

However, hardening is not exclusively a change of carbohydrate concentration. According to Toman and Pauli (1964) the reduced activity of nitratereductase is one of the biochemical concomitants of hardening. Besides a change in the carbohydrate concentration Vasileva et al. (1964) thinks the modification of the ratio of protein fractions to be also a part of the hardening process. According to Babenko and Gevorkyan (1967) the amount of free amino acids also grows. It is mainly glutamine, glutamic acid, asparagin and prolin that accumulate. After the process of hardening they form some 70 per cent of the amino acids. It can thus be supposed that the amino acid accumulation contributes to the increase of frost resistance too.

According to Trunova (1965), Salcheva and Gramatikova (1965) hardening takes place in two phases. In the first phase mainly the oligosaccharides and the glucose accumulate, in the second phase the saccharose and fructose are mobilized, and it is then that the quantity of amino acids grows. Sugar accumulation is of a much lower rate in the roots than in the aboveground parts. If the hardening period is followed by an increase in temperature, then the sugar concentration decreases again, while a repeated fall in temperature results in an increased con-

centration (Babenko and Gevorkyan 1966). After frequent fluctuations of temperature hardening will always be of a lower extent.

Hisamutdinova and Vasileva (1970) found the activity of iron-containing oxydases to decrease during hardening, from which they drew the conclusion that the biological effect of respiration was reduced too. Trunova and Zvereva (1972) pointed out that chloroplasts isolated from hardened plants maintained their photosynthetizing capacity even at low temperatures. Hardening ensures thus the structural stability of chlorophyll grains.

In principle the same happens in the roots as in the aboveground parts. In the course of hardening the drymatter content and the amounts of reduced sugar, saccharose and free amino acids increase (Paulsen 1968). The activity of nitrate reductase decreases, consequently, the nitrogen content rises, while the formation of acid soluble organic phosphates is inhibited (Korovin and Glyanko 1968).

A smooth process of hardening depends on the mobilizable carbohydrate and amino acid reserves of the plant. Therefore, the activity of enzymes controlling the nitrogen and carbohydrate metabolism has a decisive role in the process of hardening (Kolosa 1965).

According to Santarius and Heber (1972) if the cells contain sufficient amounts of substances that exert no toxic effect on the membrane, then they will be protected against frost damages. They found the sugar, sugar derivates, some special proteins, non-toxic amino acids and organic acids to have this kind of protective effect on the membrane. When toxic substances accumulate in the cell these compounds protect the membranes.

During the process of hardening and vernalization, Vincent (1972) observed a change in the phytochrom which reduced the effect of dehydration.

According to Tsenov (1972) under identical conditions the extent of hardening is specific according to the variety. After very long, 45–60–75 days, hardening frost resistance decreases because the amount of dissolved sugars is reduced, but the rate of decrease also varies with the varieties. Hänsel (1972) studied the process of hardening with seedlings parted with their endosperm. Plants raised without endosperm could not attain the same extent of hardening as normal plants.

Levitt and Sullivan called attention to the relationship between the process of hardening and sulphhydryl formation as early as in 1961 (Schmutz 1962, Levitt et al. 1962). According to Waisel et al. (1962) hardening takes place in three steps and in this sequence important role is played by the formation of sulphhydryl groups. In the opinion of Kohn et al. (1963) the sulphhydryl content increases upon the beginning of vernalization. There is a close positive correlation between frost resistance and sulphhydryl content (Schmutz et al. 1961). Belikov and Semenova (1965) found the sulphhydryl groups to influence the effect of sugars on the frost resistance of protoplasm proteins.

Winter wheats have thus to undergo hardening to be able to overcome the winter stress. There are hereditary differences in winterhardiness between the cultivars. Genotypic differences are supposedly shown in the rate, extent, content and possible repeatability of the hardening process. Its true nature cannot be defined for the time being, because while changes occurring as a result of cold are fairly well

known, there are insufficient number of data on the extent of these changes from which conclusions could be drawn to the degree of resistance.

Concerning the heridity of winterhardiness, the majority of experiences suggest it to be a complex characteristic of multigenic determination. This is also confirmed by the fact that after crossing various intertypes occur (Schmalz 1962*a*), which supports at the same time the possibility of transgression, as indicated by the observations of Dansin (1968) and Pugsley (1973). Popovič arrived at the general conclusion that by crossing winterhardy × winterhardy partners 100 per cent of the progeny would be winterhardy. In the case of crossing winterhardy × non-winterhardy plants the proportion of winterhardy progeny ranged between 5 and 93 per cent in his trials. With non-winterhardy × non-winterhardy partners crossed no winterhardy plants were obtained in the progeny. On the contrary, Stoskopf (1972) obtained sufficiently winterhardy plants by crossing winter wheats with spring wheats. Gorlach (1962*b*, 1968) when crossing low productivity and highly winterhardy plants with high yielding non-winterhardy wheats found intertypes for both characteristics in the progeny, which suggests intermediary heredity. In the case of crossing winterhardy *aestivum* and non-winterhardy *durum* species Tsvetkov (1968) produced a *durum* wheat of higher winterhardiness. Didus and Jureva (1968) attained increased winterhardiness by repeated crossing, and thought this method suitable for a gradual improvement of winterhardiness without impairing other properties. Kirichenko and Urazalyev (1970) found the winterhardy maternal partner to be more favourable in intervarietal crossing.

Petr et al. (1969) called attention to dangers threatening types rapidly developing in autumn. In their opinion good winterhardiness can hardly be expected from such crossing partners. Gorlach (1968) pointed out the advantages of crossing partners with slow autumn development. Zojnič and Djokič (1962) underline the ability for regeneration as an important concomitant of winterhardiness.

Since various degrees of winterhardiness are known, the practice of breeding mostly *uses* the method of *crossing*. There is, though, a possibility of transgression, yet one of the partners, perhaps the recipient, had better be known as a variety of good frost resistance. Crossing partners with reliable winterhardiness are mostly found in the Soviet Union, but the winter climate of the region where breeding is performed should always be taken into consideration. From the point of view of breeding for winterhardiness Jakubziner (1962) considers the wheats belonging to the Volga steppe ecotype to be the best ones. Wheats of the eastern steppe and northern ecotype are sufficiently hardy, too. As regards winterhardiness trials carried out at the All Union Institute of Plant Industry, Leningrad, where the varieties are grouped according to winterhardiness are highly valuable: the Soviet, Norwegian, Swedish and Polish varieties are the best ones. Among the Soviet varieties Sepelev and Tarasova (1970) found Ulyanovka to be the most resistant one to frost. Besides Ulyanovka, Fedorov (1970*a*) mentions the variety Lutescens, 329, Petrov (1970) the Leucorum 456/3, and Ivannikov (1972) the Albidum 114 at highly winterhardy varieties. Without thinning Albidum 114 tolerated a snow-cover lasting for 145–150 days. Suvorinov (1969) found Ferugineum 1239, Ulyanovka and Mironovskaya 808 to be the most frost resistant varieties.

According to the evidence given by the All Union Institute of Plant Industry, Leningrad, some Hungarian wheat varieties, e.g. Székács 1055, Fleischmann 481 and Fertődi 293, also show sufficient resistance to frost (Jakubziner 1962). According to Yugoslavian investigations (Popovič 1964) the American origin Minhardi, the Soviet Odesskaya 3, the Hungarian Bánkúti 1201 and Bánkúti 1205 are also good, hardy varieties. In a particularly dry winter in Bulgaria Tsenov (1965) found the winterhardiness of Bezostaya 1 very good. In Roumania Giosan et al. (1971) qualified the Soviet origin Lutescens 1060/10, Kavkaz and Mironovskaya-Jubileynaya 50 as varieties highly resistant to frost. As regards winterhardiness Fedorov (1970*b*) thinks Zernokromovaya 1336, a *Triticum* × *Agropyron* hybrid of 56 chromosomes to be the best, as well as Mnogoletnaya 470 and 115 perennial *Triticum* × *Agropyron* hybrids produced by Tsitsin which are superior to rye in frost tolerance. In his opinion these intergeneric hybrids may form a valuable initial material in breeding for winterhardiness.

In the course of chromosome mapping many researchers have studied the cold resistance of young plants and found loci influencing cold resistance in the following chromosomes (Morris 1962–1973):

5, 7A, 1, 2B, 1, 2, 4, 5D.

These investigations prove the multigenic transmission of the characteristic concerned. In spite of this, after crossing winter × spring and spring × winter wheats, respectively, decreased winterhardiness in the F_1 generation has been generally observed. This phenomenon must be taken into consideration when choosing the conditions of propagation, to avoid frost damages in the F_1 generation, because plants with high resistance to frost may segregate later in the progeny of plants showing a low winterhardiness in the F_1 generation.

Winter and spring wheats are known to show essential differences in temperature required for *vernalization* and duration of the effect of low temperature. Winter wheats require 0–+3°C for vernalization over 40–60 days (Lisenko 1954). According to McIntosh (1973) the vernalization demands are determined by four genes marked with the symbols Vrn 1, Vrn 2, Vrn 3, Vrn 4,. In Morris's (1963–1973) the vernalization demand is determined by genes in the table following chromosomes: 4, 5A, 3, 5, 6, 7B, 1, 2, 5, 7D.

There is a relationship between the required duration of vernalization and winterhardiness. Genotypes requiring a longer period of vernalization generally show more reliable winterhardiness than those with a shorter vernalization period. The two properties are still not identical and their relation is not always of the same direction, either. Some of the alternative wheats are highly resistant to frost as e.g. the Hungarian Székács 1055, still their vernalization demands do not even come near to those of the true winter wheats.

The required duration of vernalization is assessed by a lengthy procedure and is not therefore suitable to be used in selection for winterhardiness. The relation and multigenic determination of the two properties make the transmission of winterhardiness still more complicated.

Plants with higher resistance to frost may also be found among the artificial mutants (Truchinova 1963). Lines of better winterhardiness can thus be expected from mutation breeding, too.

The adequate hereditary change of vernalization requirement is considered to be suitable too for producing frost resistant winter wheats.

The possibility of adequate genetic changes caused by environmental factors is even now a subject of discussion. Yet, experiences of producing frost resistant winter wheats by repeated autumn sowing of non-winterhardy spring wheats deserve attention. Rajki (1962*a*, *b*, *c*, 1963) produced a winterhardy winter wheat from the spring variety Lutescens 62. By repeated autumn sowing Kishigin (1962) obtained from Garnet spring wheat first an alternative wheat, then when continuing autumn sowing a frost resistant winter wheat. Truchinova (1962, 1963*a*) developed by this method a frost resistant winter wheat from the spring wheat variety Moscow. Mironovskaya 808, a winter wheat known to be highly resistant to frost was produced by Remeslo (1963) from spring wheat by repeated autumn sowing. It was by this very method that Remeslo (1972) developed the winter wheat variety Mironovskaya 264. Koltsova (1963) produced by repeated autumn sowing a frost resistant winter wheat from the spring variety Milturum 321. According to Varfolomeeva (1963) the varieties Bezensukskaya 98 and Ferrugineum 810-1/1 were produced by adequate genetic alteration. The latter two varieties were found to be equal in winterhardiness to Lutescens 1060/10, a variety known to be highly resistant to frost. Hitrinsii (1963) reported on the production of sufficiently hardy lines from non-winterhardy *durum* wheat by repeated autumn sowing. In the relevant Soviet literature numerous similar references are found.

By this method spring wheat is sown on two or three occasions in early autumn, and according to the experiences of the above listed authors a satisfactory winterhardiness develops already after the second sowing. By this method Rajki and Rajki (1972) produced a frost resistant winter wheat from the Mexican semidwarf spring wheat Penjamo 62.

According to the data of some authors varieties more resistant to frost could be produced by this method from winter wheats of poorer frost hardiness. It was in this way that Glavinich (1963) developed more frost resistant plants from Italian wheats of poor winterhardiness. Fedorov (1962) and Karapetyan (1963, 1964) transformed alternative wheats into winter wheats with the same method. Rajki (1962*b*, *c*), Truchinova (1962) and others observed morphological changes too as a result of repeated autumn sowing.

The above listed authors regard autumnization as a quick and efficient method. Maksimchuk (1963) considers autumnization to be a method equal to crossing.

Some explain the phenomenon by mutation or genetic canalization while others see an adequate genetic change in it.

Whether it is by crossing or artificial mutation or even by an adequate genetic change that winterhardy types are produced, as far as the results are concerned the main points are:

1. In which generation should the selection be started?
2. How much the method of selection is reliable?
3. How can varieties or lines be compared for winterhardiness?

Since winter stress consists of manifold effects which vary according to region and season and in intensity as well, it is difficult to conjure up a selection method reliable by itself in every respect.

It would be very simple if we knew a morphological character related with winterhardiness. Once a close correlation was supposed to exist between prostrate growth habit and winterhardiness. Ruskowski and Jaworska (1964) carried out comparative trials with 500 varieties and concluded that selection for winterhardiness could not be made on this basis in spite of some advantages of prostrate growth habit during winter. Nor could Fischbeck's (1962) trials produce phenological characters suggesting winterhardiness.

Selection may be supported by laboratory methods meeting the following requirements:

1. The different degrees of cold tolerance should be measurable.
2. Small differences should be perceptible too.
3. The method should be suitable to study plants without destroying them.
4. It should be simple and suitable for mass analyses.
5. It should be applicable in every year irrespective of the actual weather.

Sulphhydryl content and its change have been found to be related with winterhardiness. Levitt and Sullivan (1961) studied the sulphhydryl content by argentometric-amperometric measuring and found a real connection with cold resistance. Schmutz (1962) examined the sulphhydryl content in European and American cultivars with a simple calorimetric method and likewise found it to be connected with winterhardiness. Investigations made so far have not, however, unambiguously proved the efficiency of the method (Levitt et al. 1962; Waisel et al. 1962; Kohn et al. 1963; Belikov and Semenova 1965).

According to Oglezneva (1971) the relative quantities of water-soluble nitrogen compounds and the higher proportion of albumins can be brought into connection with winterhardiness, and this test is suitable for early selection. Limar (1971) advises the use of phosphorus isotope in measuring frost resistance. Pisarev and Batrshina (1968*a*, *b*) consider the oligosaccharide content of the endosperm to be a fairly reliable indicator in selecting for winterhardiness. Experimenting with wheat seedlings Rammelt (1967) pointed out a close connection between the soluble adenosine derivate contents of the coleoptyle and root, on the one hand, and winterhardiness on the other. Of these laboratory methods sulphhydryl analysis has now the biggest number of followers. Recently Milaev et al. (1973) found a positive correlation between the electric resistance of tissues in the tillering nodes and winterhardiness. This examination can also be regarded as a laboratory or greenhouse method. None of these laboratory methods have found so far wide application in practical breeding.

Comparative trials performed under field conditions are even today the most reliable and the least expensive methods ensuring at the same time the possibility of mass selection. However, it only can be applied in areas where an intensive winter stress is bound to occur every year. Where this cannot be expected for sure,

Fig. 10. Selection for winterhardiness. Micro-plots are protected by a thin, close-meshed wire screen from snow. The plants overwinter without snow protection (Photo by P. Lelley)

or where in certain years a thick snow-cover may give protection, artificial exposure is required for a reliable selection. For this purpose regions increasingly affected by winter stress are chosen: the crossing derivates to be tested are sown in mountain areas or definitely frosty spots (Lelley 1964*a*). To prevent protection by snow various means are used as e.g. close-meshed wire netting easy to remove but keeps off snow (Fig. 10). When studying winterhardiness in the field Kostecki (1972) used plastic covers to keep off snow. When there is no possibility of making selection for winterhardiness in particularly exposed sites, under field conditions, various culture box systems are used (Schmutz 1964) which are obviously completely snowless and the more intensive freezing of the soil in the culture box increase the adverse influence exercised on the roots, increasing thereby the efficiency of selection. To further increase the intensity of selection the artificial breaking of plants was performed which, however had no considerable influence on winterhardiness as reaction (Schmalz 1962*b*). Schmalz, nevertheless, obtained results by repeated cutting back. It is, in fact, suitable to reduce the protective reactions to cold, and differences between cultivars or lines can thus be better demonstrated. Schwarzbach (1966) found cutting back highly efficient and underlined its simpleness and mass applicability. Rammelt (1972) thinks the continuous check-up and comparison of the growth rate of plants to be a reliable method when temperature is falling.

Where the possibility of testing under field conditions cannot be provided for, artificial freezing may be the means of selection. Full winter stress can be reproduced with an approximate reality only in properly automatized phytotrons. This possibility is offered but seldom, since a phytotron is an expensive equipment. Simple cold-storage rooms or houses are more frequently used in carrying out selection for winterhardiness. In artificial freezing Voblikova (1965) calls attention to the importance of gradualness and previous hardening. The same applies to warming up, where gradualness is even more important. Keppler (1962) completed the cold-storage treatment by subsequent studies on the growth rate of leaves. After freezing he cut back the leaves and roots of plants to a length or 1–2 cm and measured the growth intensity three days later. On the third day there were already differences indicating the varying extent of frost resistance. Similar method was recommended by Vogel and George (1966). By their method young 2–4-leaved plants are exposed to frost for about seven days, then cut back and their capacities for regeneration assessed. Regeneration following the artificial freezing of young seedlings was also studied by Tsenov (1967). Grains with 3–5 mm long germs were kept at -10 to -18°C, then the degree of frost tolerance was expressed in percentage. Similar method is proposed by Valeev (1967), Baraskova and Alekseeva (1970*a*).

Successful comparative trials have recently been carried out by the so-called "crawn-freezing" method, described in detail by Marshall (1965): grains are sown one by one in the field, after three weeks of natural hardening the plants are removed; the aboveground parts are cut back to 2–2.5, the roots to 1–2 cm of length. Then the plants are gradually cooled down to -14 to -17°C after the roots have been placed in plastic cups or among plastic foam. Subsequently, the effect of frost is gradually decreased and the plants are planted in sand; then the course of regeneration exhibited by the roots and foliage is recorded at a temperature of 10–12°C (Johnson et al. 1970; Warnes and Johnson 1972; Everson and Gullord 1973).

Of all testing methods it is winter stress acting under natural conditions and increased artificially that gives the most reliable result. If there is no such possibility, then artificial freezing techniques may also promote the work of selection. The reliability of laboratory analyses requires further proofs.

Drought tolerance

The site of origin of the genus *Triticum* had a gradually drying climate, consequently, evolution took place under arid conditions. Accordingly, the primitive forms of the genus are mostly drought tolerant types. The first cultivated species had no higher water demand either. The new high yielding cultivars require, however, a considerable water supply to produce a large amount of drymatter.

In the case of a 50 q/ha grain yield the proportion of stalk, leaf and ear produced is some 1.0–1.2 while that of the root 0.15–0.35 (Nosatovsky 1959). In a mature state with a 15 per cent water content calculating with the same grain yield the amount of drymatter per hectare is:

Drymatter of grain	42.5 q
Drymatter of other aboveground parts	49.0 q
Drymatter of root	22.6 q
Total drymatter	*114.1* q

With a "field transpiration coefficient"* of 500 g taken as basis (Nosatovsky 1959), the total water quantity of 565 mm precipitation should be used up by the wheat plant in order to produce that amount of drymatter. The value of the field transpiration coefficient may be lower than 500 if the distribution of precipitation and the nutrient supply are highly favourable. A balanced nutrient supply and the required amount of moisture are thus preconditions of large yields. If the amount of precipitation is not sufficient it should be supplemented by irrigation. In unirrigated regions of continental climate temporary disturbances in water supply may occur in any year even if a balanced nutrient supply is guaranteed.

In consequence of drought, the water regime of the plant is gradually upset. The water content of the cytoplasm decreases bringing about a situation similar to that caused by frost. The concentration of the cell-sap increases until it reaches a level where a toxic effect occurs followed by an irreversible change in chloroplasts and mitochondria. This process ends up with the death of the cells (Santarius and Heber 1972). However, it is only the final stage of a very long period of drought which under normal conditions is relatively rare, though in certain years and regions it may occur. Drought generally is not as severe as to destroy the plants, only the metabolism may be adversely influenced by disorders in water supply whereby ear number, kernel number per ear and thousand-kernel-weight may be reduced.

Chinoy (1962*a*) determined the *drought tolerance coefficient* of wheat as the difference in yield between plants with an optimum supply of water and those exposed to drought. The drought tolerance coefficient makes it clear what yield decrease the examined type of drought causes and demonstrates the difference in drought tolerance between cultivars. By this method the consequences of drought at various stages of development can also be examined. In subsequent trials Chinoy (1962*b*) studied the connection between dry periods artificially produced at various development stages and changes in the yield components. These trials greatly contributed to the better understanding of the effect of drought but indicated no difference between varieties. The genetic relations of drought tolerance have not been proved yet. Lelley (1964*a*) studied the interrelations of drought, development stage, changes of yield components and varieties in large culture pot experiments and described how dry periods occurring at different development stages influence the individual yield components. He pointed out that the varieties gave different responses to the same type of drought, which proves that there is a genetic basis for drought tolerance. In transpiration coefficient tests performed by Grebner (1964), some varieties showed increased water consumption suggesting a reduced hereditary resistance to drought. Varietal differences have been

* According to Nosatovsky (1959) the "field transpiration coefficient" is the amount of moisture taken up by the wheat plant for the production of 1 g drymatter plus the amount of water lost from the soil during the vegetative period.

pointed out by a number of authors (Milica and Juncu 1968; Kozhusko and Volkova 1971). Kaul (1969) made comparisons on the basis of osmotic pressure. It was again by culture pot experiments that varietal differences have been established by Vlasyuk et al. (1970). Jakubziner (1970) gave evidence of varietal differences by comparing the spring wheats of the world collection of cultivars, and found the highest tolerance to drought in the hexaploid group. The above listed results make it probable that drought tolerance is a genetically established hereditary property but give no information about the physiological or morphological characteristics it could be assessed by.

Vlasyuk et al. (1971) assume the existence of a self-controlled protective mechanism in the drought tolerant varieties which in the case of a temporary water shortage reduces the adverse effects. Investigations made by Lelley (1964*a*) revealed that the wheat plant did not give the same response or display the same sensitivity to water deficiencies in all the phases of development. Farsky (1961) thinks the appearance of the third leaf to be a critical period for the adverse influence of drought. Joffe and Small (1964) observed a considerable yield decrease after dry weather in the time of tillering and heading. Through a dry stress Todd and Webster (1965) induced yield decrease in all development phases except the period after waxen ripening. Similar observations were made by Pavlov (1967), though he too is convinced of the existence of critical phases. Drought while possibly decreasing the yield in any of the phases of development has the most drastic effect at the beginning of heading. Milica and Juncu (1968) found the beginning of shooting to be the most sensitive stage of the wheat plant. El Nadi (1969) considers flowering and seed setting to be the most critical phases as far as water demand is concerned.

Thus, according to the results of research the effect of drought does not disappear entirely in any of the development phases of the wheat plant, but there are critical periods when the effect is more pronounced. At the time of tillering dry weather influences the number of spike per plant by inhibiting the differentiation of new spike primordia. It is at this stage when the number of spikelets per spike are set, so a dry weather may even reduce the head size. Upon the occurrence of a drought during spike differentiation in some varieties the apical or basal spikelets may become sterile. At the time of flowering a dry weather may affect fertilization whereby the number of kernel per spike will be lower. After fertilization, on the other hand, thousand-kernel-weight may depend on the duration of the dry period. Drought setting in after the late dough stage of ripening no longer has an influence on yield but may have an effect on quality.

It is not clear whether reactions to drought in the different phases of development depend on the genotype. There are not sufficient number of data concerning this question. It is, however, probable that the protective mechanism against drought develops gradually. Thus the plants undergo *hardening* against drough too, and the possibility of hardening is not the same in the different phases of ontogeny.

In wheat hardening for drought Shu-Wen and Tsing-Tsi (1964) observed the acceleration of root growth. In hardened plants the amount of chlorophyll was larger, and they had a higher capacity of drymatter accumulation. According to

Belyakov (1968) varieties with a more rapid growth of seminal roots possess a higher tolerance of drought. If in an early phase of development water supply is poor, the wheat plant hardens and later displays a higher resistance to drought. After the artificial hardening of young wheat plants for dry weather Novoselova et al. (1966) observed a higher resistance in them in later phases of development, too. Under the influence of drought the prolin content was found to increase (Tyamkova 1966). By the same author prolin accumulation, a consequence of protein decomposition, was considered to be an important momentum in hardening against drought. Protsenko et al. (1968) think the accumulation of free amino acid, asparagin, glutamin, glutamic acid, prolin and alanin contents in the leaf, stem and ear to be a characteristic of drought tolerance. They are thought to have a protective role. These findings should, however, be supported by further experiments.

Resistance to drought, like winterhardiness, is a gradually developing reaction probably a consequence of physiological and morphological changes. Its biochemical explanation is yet incomplete, no distinction can therefore be made between varieties concerning drought tolerance. There are neither physical properties nor morphological characters from which reliable conclusions could be drawn concerning drought tolerance. Ilyin (1929) observed increasing osmotic pressure in drought tolerant plants. Strebeyko and Domanska (1962) performed similar tests but could not support the connection found by Ilyin. Levitt (1956) pointed out a close inverse correlation between the cell size of leaves and drought tolerance. However, selection cannot be made on the basis of cell size.

The resistance of cells to desiccation, their water retention capacity gradually increases upon the effect of drought and supposedly is connected with changes in the permeability of the protoplasm (Uglov and Volkova 1970), as a consequence of the contraction of openings on the plasm membrane (Schmidt et al. 1940; Uglov and Volkova 1970). Unfortunately, this property again is difficult to check. Resistance to desiccation shown by the whole shoot, and its assumed connection with drought tolerance have been studied by many experts. Attempts mostly concerned conclusions on the water retention of the tissues owing to weight losses by shoots cut off (Protsenko and Smatko 1963; Salim et al. 1969; Oleinikova et al. 1970). Pospelova (1971) weighed the water loss of removed leaves and thought to have found a connection between the yellowing of leaves, the rapidity of their weight loss and drought tolerance. Popov and Makedonska (1960) kept the leaves in dark and from the degree of etiolation tried to draw conclusions on drought tolerance. However, none of these methods have been introduced into the breeding practice.

The narrower leaves, thinner culms, smaller cells, light green colour are general characteristics of more drought tolerant steppe wheats. In breeding cultivars of high productivity these morphological characteristics of the steppe types cannot, however, be taken into account, since plants possessing these qualities are of insufficient productivity and are inclined to lodging.

Earliness or rapid spring development may be a point to consider. It may mean a more economical use of the available water reserves and within certain limits can be combined with high productivity, too.

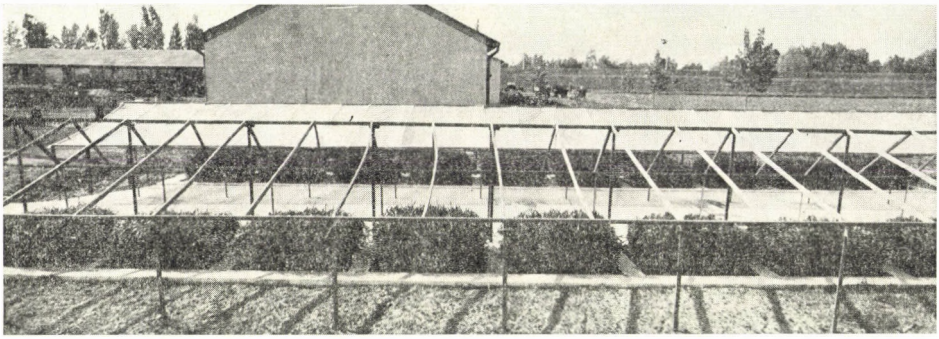


Fig. 11. 150×150 cm concrete culture pots made for the examination of drought tolerance. Culture pots kept dry are protected from rain with plastic cover (back row). The control is watered (front row) (Photo by P. Lelley)

Due to its complexity resistance to drought is assumed to be a property of polygenic heredity. Consequently, and owing to difficulties in checking, segregation is impossible to follow. There is, however, a possibility of transgression. A method to compare the degree of this property has not been worked out so far, consequently, relevant genetic studies are lacking. Polygenic transmission is only hypothetic, and no research has been made to find out the number of possible genes. This is why chromosome mapping has not been extended to drought resistance so far.

Since its hereditary nature and varietal differences have been proved, crossing is the most promising method of breeding (Jakubziner 1970). There are possibilities of mutation too, though no such experiences have been obtained so far.

A great disadvantage is that in selecting the crossing derivates and choosing the partners there are no reliable laboratory methods of analysis by which individual distinctions could be made. Individual selection can be made only visually on the basis of the mentioned few uncertain morphological characters.

The only acceptable way to indicate differences between strains or varieties is to carry out experiments with large culture pots.

The reliability of culture pot experiments depends mostly on the size of the culture pots, and on the number of replications (Lelley 1964*a*) (Fig. 11).

Its advantages are:

1. Time, length and intensity of the drought periods can be adjusted at will.
2. The effect of drought on the yield components can be directly studied.
3. In culture pot experiments the effect of drought can be assessed at various nutrient levels.

For the investigation different culture pot systems have been used (Schendel 1963; Lelley 1964*a*). It is very important in each case to provide conditions similar to those prevailing in the field, this explains the advantage of large culture pots (1.5×1.5×1 m).

The osmosis values of seeds or radicles, the water retention of removed leaves or shoots only give superficial and uncertain information. Selection made on this basis is unreliable and cannot substitute the culture pot experiment.

Lodging resistance, dwarfness

Lodging is mostly the consequence of climatic effects: great excess of precipitation and strong wind. In exceptional cases it may be caused by parasites, too (Carles 1962). Its adverse effect begins with a deficient seed-setting resulting in a reduced number of kernel/spike. As a further damage, the thousand-kernel-weight falls back owing to an insufficient filling of the endosperm. Lodging makes the mechanical harvesting of wheat more difficult, resulting in a further loss of grain and straw. It may also influence quality. According to Gotsova and Gotsov (1965) early lodging caused a yield decrease of 29.8–30.9 per cent, while the same occurring in early dough stage reduced the yield to 9.9–17.6 per cent only. Thousand-kernel-weight and hl-weight decreased, but the protein and wet gluten content somewhat increased. Under the influence of artificially induced lodging Weibel and Pendleton (1964) observed a decrease in the thousand-kernel-weight also. Decrease of yield was 31.0 per cent when lodging was induced at heading time, and 25.0, 20.0 and 12.0 per cent when in early dough, late dough and full mature stage, respectively. Jankovič (1966) found the variety Bezostaya 1 to react to artificial lodging by a yield loss of 20.1 to 86. 4 per cent depending on the duration of lodging. Thousand-kernel-weights and hl-weights decreased while protein content increased by 2 to 4 per cent. After lodging Peev and Dekov (1967) found a deterioration in milling and baking qualities and a reduction in flour output. It was mainly the glassiness of grains that worsened when lodging occurred at about flowering time. Qualitative deterioration in spite of an increase in the protein content is observed when the spikes repeatedly become wet after lodging, and they dry slowly. Quality deterioration caused by lodging was again pointed out by Dekov and Peev (1967) in *Triticum durum.*

There are two types of lodging: irreversible bending at the node of the stalk (Fig. 12), or turn over due to loosened adventitious roots (Fig. 13). Both are caused by the increased weight of ear, leaf and stalk due to rain, as well as by the pressure of wind. The first type occurs in flexible, long-stalked wheats, the second is the lodging type of wheats with medium long, stiff culm. Lelley (1964*a*) reported that the weight of wheat shoots increased in rain by 18.7–33.0 per cent due to moisture adhering to them. The examinations were carried out with green plants when the water did not penetrate through the epidermis but only adhered to the surface. Measurement, further revealed that at the same time when the spike weight of the awnless wheats increased by 24.99 per cent, that of the awned ones grew by 29.55 per cent. Lelley (1964*a*) constructed a special instrument to measure the pressure exercised by the wind on spike carrying shoots and found the bending force to be proportional to the length of the culm. Furthermore, it was proved that the awn increased wind stress, though the difference was not significant. The awned character cannot thus be regarded as a disadvantage from the point of

Fig. 12. Lodging type of long, thin straw wheats. At the lower internodes the stalk irreversibly bends (Photo by P. Lelley)

Fig. 13. Lodging type of wheats with short, firm straw. The stalk does not bend but the roots get loose and the plant falls down (Photo by P. Lelley)

view of starding ability. Bauer (1964) found a close correlation between the intensity of tillering, culm length at flowering time, relative length of the lower internode, number of adventitious roots and lodging resistance. Pinthus (1967) pointed out a positive relation between the spread of roots and standing ability. Kyzlasov (1969) found the property to be connected with the index determined by the length and width of the flag-leaf.

According to the evidence of a series of observation there may be substantial differences in lodging resistance between varieties of the same height and phenotype. The hereditary nature of the property is thus an established fact. In the case of varieties of the same height and phenotype the anatomical cause of the difference is still difficult to explain, though it is obvious that the stiffness and flexibility of the culm, and the size and toughness of the roots play an important role in the development of this property.

According to the anatomical explanation given by Ilinskaya-Centilovich and Teteryachenko (1963) for stability in the culms of stable varieties a number of

thick-walled cells of mechanical tissue are found between the phloem and metaxylem. Vaidya and Malkani (1963) made similar observations in *Triticum durum*. Nátr (1964) found an increased number of vascular bundles in the stable varieties. Miller and Anderson (1963) consider the proportionate development of culm length and mechanical tissues to be of primary importance, it is, however, influenced by the level of nitrogen and phosphorus supply, too. Gradchaninova and Dorofeev (1966) measured the volume of supporting tissues in the nodes. According to Milică et al. (1966) the stiffness of culm develops gradually. The process begins in the period of heading, and the culm is gradually gaining strength until full maturity. Göbö et al. (1971*a*) think the wall thickness of mechanical tissues to be of decisive importance, which, though a hereditary property, is influenced by environmental factors, first of all by stand density.

Data of the anatomical study of culm as well as differences in its length give explanation of the varietal differences of culm toughness. It is, however, a question whether on the basis of these properties varieties or strains can be compared for lodging resistance, and whether distinction can be made between them. Halász (1962) used a histological method in his investigations which was insufficient for simply considering anatomical factors. It is thus not enough to determine the number of vascular bundles when assessing the lodging resistance; on this basis neither distinction nor selection can be made (Göbö et al. 1971*b*). Lignin content which stiffens the supporting tissues cannot be brought into direct connection with lodging resistance either. The thickness of the culm is again unreliable in value (McNeal et al. 1965*a*, *b*). On the basis of visual selection, anatomical studies and comparison of mechanical test data Proskurnin (1967) arrived at the conclusion that only a joint application of various methods could give an approximately reliable result. For the mechanical examination of culm toughness a great diversity of methods have been tested (Biskupski et al. 1963; Strutsovskaya 1966; Proskurnin 1967; Schulzke et al. 1974, etc.), they have not, however, solved the problem of reliable selection nor give information about protection against lodging. The diameter of internodes is not a reliable character either (Milică et al. 1964). Teteriachenko et al. (1968) devised an instrument to study the pricking resistance of tissues above the nodes and found it to be in relation with culm strength; this method has not, however, been widely introduced.

The above-listed methods were aimed at revealing the possibilities of individual selection by analyzing the characteristics of the stem alone.

Resistance to lodging was studied by Udagawa and Oda (1967*a*, *b*, *c*), who measured the required force to pull out plants from the soil. The results were not, however, reassuring. Holienka and Hruška (1962) grew a thick plant stand in culture pots, then laid down the culture pots on their sides and measured the time required by the stems to assume a vertical position. This special method also gives certain information, though not directly, about lodging resistance. For the time being visual assessment or morphological comparison are the only widely used methods of individual selection. The most reliable answer to the question of resistance to lodging is given by comparative field trials of large populations carried out with dense plant stands. For this type of investigation various methods have been elaborated, too. Udagawa and Oda (1967*a*) suggested an artificially

produced too dense stand and intensive sprinkling irrigation by which not only the extent of lodging but also the resulting yield decrease could be demonstrated. Pyatigin and Smihov (1967) also consider sprinkling irrigation as the best method of testing. Good result was obtained with Lekes and Zenisceva's (1962) storm machine, a portable device, by which wind of any force, and rain can be produced over the test plots. The wind tunnel of Ugadawa and Oda (1967) was based on the same principle and gave reliable results. If wind is strong and sudden rainfalls are frequent on the experimental area, or abundant sprinkling irrigation is ensured, larger populations or varieties can be compared for lodging resistance under natural conditions.

As to the hereditary nature of stability, unambiguous answer is given by Gulkayan et al. (1971). Lodging resistance depending on complex morphological, anatomical and physiological properties is obviously a complicated polygenic character whose gradual development is influenced by environmental factors, too. There is, consequently, a possibility of transgressive segregation. In interspecific crossing Haun (1966) observed transgressive segregation in the appearance of solid internodes, too. In the progeny of crossing partners of hollow stem he found plants whose lower internodes were solid.

The chances of breeding by crossing are thus promising, and if the morphological or anatomical causes of culm strength can be established, the crossing partners can be chosen so that their characteristics complement each other.

Gene mapping concerning lodging resistance has not yielded much result so far. According to the table compiled by Morris (1962–1972) the stiffness of the lower and upper internodes is determined by a gene in chromosome 5A. In the durum varity Golden Ball, Larson and Mac Donald (1963) identified the gene of stem strength in chromosome 3B. However, in the presence of genome D this gene produced hybrids with weak stems. Namely, in chromosome 3D a suppressor impairing culm stiffness was found. That is why the stem strength of *T. aestivum* lines could not be improved by crossing with Golden Ball. By crossing the strong-stalked line of S-615 with the gentle-stalked variety Apex, Larson and Mac Donald (1966) have shown that in this combination the chromosomes 2A, 3B an 2D shared in the genes influence the stability of culm.

In breeding practice several firm-stalked wheat varieties reaching or even exceeding 100 cm in height are known. They are: Bezostaya 1, Kavkaz, Aurora, M. Yubileynaya 50, Felix, Odin, Blue Boy, Heine VII, Capelle-Desprez, San Pastore, Ben Hur, Parker, etc.

Breeding through mutation has also a chance to improve the lodging resistance of long-stalked wheats, therefore populations of mutation are worth being studied for lodging resistance as well. Bozzini and Avanzi (1962) produced firm-stalked types from the *durum* variety Cappelli by X-ray treatments. Among 297 induced durum mutants Scarascia-Mugnozza (1965) found 41 types of better lodging resistance. Some of them did not become shorter stalked, still showed a higher lodging resistance than the initial variety.

Irrigated wheat production requires such degree of lodging resistance which is very difficult to attain by wheat varieties exceeding a height of 1 m. In dense stands of irrigated long-stalked wheats the microclimate and particularly light conditions

brought about the weakening of tissues in the lower internodes. Lelley (1964*a*) said that with the shortening of the stem the bending stress of the lower internode decreases, very high lodging resistance can therefore be attained only with shorter wheats. Culm length can be reduced by the application of growth inhibitor hormones too, but the best way to utilize is the genetically determined character of dwarfness or semi-dwarfness.

The first really short-stalked wheats were produced in East China and Japan. The Japanese Akagomughi was used in Italy and Norin 10 in the United States as crossing partner in breeding semi-dwarf wheat. Strampelli (in Antoniani 1960) produced two well-known short-straw Italian wheats: Mentana and Ardito by crossing Hybrido × Akagomughi. Ardito crossed with Klein Vencedor was the basis of the Argentine semi-dwarf wheats, including Klein 33 (Lelley 1971*b*). Vogel used for crossing the Norin 10 dwarf to produce the first American semi-dwarf wheat: Gaines [Norin 10 × Brevor (1949) × Orfed × Burt (1952)]. Later it was again by using Norin 10 that Borlaug improved the Mexican semi-dwarf wheats. The origin of the first and best known ones is:

Pitic 62 = (Yaqui 48 × Kentana 48 × Frontana) Norin 10 × Brevor 26-1c.
Sonora 64 = (Yaqui 48 × Kentana 48 × Frontana) Norin 10 × Brevor × Yaqui 54.

Reduced length of culm means protection against lodging, which makes sprinkling irrigation possible, whereby an unheard stand density and yield may be attained. Low stands are better ventilated and illuminated, and are under more favourable conditions of assimilation and transpiration even if the density of stand substantially exceeds that of the long-straw wheats. In a thick but low stand not only the possibility of lodging decreases but the danger of the spread and multiplication of pathogens is also reduced. This made it possible to break through the limit of record yields attained by long-straw wheats (Jain et al. 1973), and to utilize still larger doses of fertilizer.

As a result of semi-dwarf and dwarf growth the ratio of straw to grain yield shifts in favour of the latter. This would mean a more economic utilization of drymatter production if semi-dwarf wheats converted a larger proportion of the nutrients taken up for kernel production per unit area than long-straw wheats (Jain et al. 1973). This hypothesis is not, however, adequately supported, so much so that some authors even think to find a negative correlation between culm length and yielding potential (Schlehuber et al. 1967; Balla 1969, etc.). Under irrigated conditions the full realization of hereditary productivity in normal wheat varieties is limited by lodging at an earlier stage, as it was unambiguously proved by the trials of the Winter Wheat Performance Nurseries in 1970 and 1971 (Stroike et al. 1972). In very dense stands the semi-dwarf wheats do not lodge under irrigated conditions, therefore their potential productivity remains effective at a time when lodging puts an end to any further yield increase in the long-straw varieties. Anyway, if the observed negative correlation really exists, there may be a genetic possibility of breaking it.

That in spite of the more favourable kernel/straw ratio of dwarf wheats why a possible negative correlation between yield potential and dwarfness exists, has

not been genetically or physiologically explained as yet. The mechanism inhibiting longitudinal growth in the culm is supposed to limit it in any other organs, too. The embryo in dwarf wheats is proved to be smaller, therefore, such wheats require shallower sowing because they only are able to break through a thinner layer of soil (Chowdhry and Allan 1963, 1966*a*). There is also a correlation between straw length and leaf size. The growth inhibition of culm may involve a decrease in the longitudinal growth of leaf blade (Chowdhry et al. 1966*b*). With the shortening of the culm the number of nodes does not always change, only the length of the internodes becomes shorter. As a result of a decrease in length of leaf blades, leaf sheaths and internodes the assimilating surface may be reduced which cannot be indifferent from the point of view of yield potential. The length of shoots and roots is supposed again to be regulated by the same mechanism (Mac Key 1973). If the length of the culm is reduced the roots will shorten too. This may explain why dwarf wheats react to drought earlier than long-straw wheats do (Lelley 1973*b*). However, Karmacharya (1973) observed just the exact opposite in the variety "Mex-26", consequently, the supposed correlation does not always hold true. The smaller size of embryo and endosperm in dwarf wheats may involve the reduction of thousand-kernel-weight as well. This may also be a cause of the inverse relationship between dwarfness and productivity. Zitelli and Mariani (1973) have shown by correlation calculations that in the relationship between culm length on the one hand, and spike length, number of kernel per spike and thousand-kernel-weight on the other, it was the latter that reacted most actively to the shortening of the stem. The shortening of the culm reduces the length of the spike and the number of spikelets, and thereby the number of kernel per spike, too, but the correlation is less pronounced here. In semi-dwarf wheats originating from crossing with Norin 10, Heyne and Campbell (1972) pointed out that thousand-kernel-weight was higher in semi-dwarf wheats with one recessive gene than in dwarfs with two genes. Thus, it follows that the extent of dwarfness and the rate of decrease in thousand-kernel-weight are directly proportional. Owing to this undesirable connection the production of true dwarf varieties encounters considerable difficulties. However, there is no correlation that could not be dissolved. This possibility is offered to the breeders of dwarf wheats, too. Almost all currently cultivated semi-dwarf and dwarf wheat varieties have been produced by crossing.

Among the known semi-dwarf crossing sources the heredity of culm length reduction in Akagomughi have not been cleared up, although in Europe and South America this variety played an important role in breeding wheat for short culm.

The origin of Norin lines is known, they come from the following crossing:

Fultz × Paruma (1917),
Fultz-Paruma × Turkey Red (1924) = *Norin*

The dwarfness of Norin derivates can be found in many modern semi-dwarf varieties. According to Tarakanov and Udachin (1970) Norin 10 has virtually opened a new chapter in the history of wheat breeding. Norin 10 is one of the

ancestors of the internationally recognized new semi-dwarf varieties like Gaines, Pitic 62, Lerma Rojo 64, Sonora 64, Inia 66, etc. (Reitz 1970). The dwarfness of Norin is caused by two partially recessive genes (Allan 1970) marked with the symbols Sd1 and Sd2.

After the advantages inherent in dwarf growth had been realized further dwarf sources were looked for, and this is how they came upon the winter type variety Tom Thumb (C.I. 13563) whose semi-dominant or dominant dwarfness is localized in chromosome 4A proved by monosomic analysis. The dominant dwarfness of Tom Thumb was introduced in a number of varieties including the winter variety Kharkov and the spring wheats Topo and Tordo (Morris et al. 1972).

Hermsen (1963*c*) pointed out genes in chromosomes 2B and 2D causing dwarfness in the variety Timstein. By the monosomic analysis of the crossing Norin 10 × Brevor 14, Allan and Vogel (1963) arrived at the conclusion that shorter culms were caused by the absence of eight, while longer straws by that of three chromosomes. According to them genome B has the least effect on culm length. Gale and Law (1973) when adding gibberellin to monosomic plants in the second homoeologous group obtained a higher increase of culm length than in other monosomic plants. Accordingly they said that dwarfness was due either to a slackening in gibberellic acid synthesis or to an inhibition of its effect. In the Norin derivates the released gibberellic acid is supposed to exert its effect in other biochemical processes. This may partly be an explanation to the success of these semi-dwarf wheats.

In investigating the mode of transmission of dwarfness increasing attention has been paid to the genetics of stem length (Alvey 1963). According to Morris's table (1962–1973) the aneuploid analysis has shown that with the exception of chromosome 6B all chromosomes carry genes determining the culm length. The length of the first internode is modified by special genes in chromosomes 5A, 7B and 5D. The lengths of the second and third internodes are simultaneously changed by loci in chromosomes 6A, 4B, 2D and 3D. There are genes in chromosomes 1A, 2A, 4A, 2B, 4B, 2D, 3D, 4D and 6D causing expressed dwarfness. Genes modifying dwarfness have been localized in chromosomes 1D and 7D. According to Gale and Law (1973) in controlling the synthesis and accumulation of endogenous gibberellin the main role is played by the homoeologous group II. In crossing derivates of the Olesen's dwarf Hoff et al. (1973) found the heritability of dwarfness to be 69.70 per cent. That is why in different combinations the number of loci influencing height is so variable. In crossing the varieties Seu Seun 27 and Blue Jacket, Johnson et al. (1966) have shown three semi-dominant major genes. Le Grand (1966) too, has found in crossing trials three partially dominant genes. Piech and Evans (1967) pointed out the action of a dominant and an inhibitory factor. In crossing Norin 10 × Brevor 14 Powell and Schlehuber (1967) observed the additive inheritance of dwarfness. In various crossings Allan et al. (1968) at one time found the height to be dominant, at other times superdominant. Dwarfness was determined by one or two separate genes whose activity was, however, influenced by a number of modifiers. Zeven (1970) attempted to group the genes causing dwarfness in hexaploid wheats in geographical units. In his opinion there are three dominant genes determining dwarfness, one occurring in Southern

Europe, Africa and Asia, the other exists only in Europe, while the third is found in any wheat area. He believes that the first (D_1) gene originates from *Aegilops squarrosa;* the source of the other two (D_2, D_3) is yet unknown.

Dwarfness has also been transferred from the hexaploid to the durum wheat. Jain et al. (1973) report results from India, Gale and Law (1973) from New-Zealand, Heyne and Campbell (1972) from America. Kis (1973) introduced the dominant dwarfness of Tom Pouce into hexaploid *Triticale*, in Hungary.

For the last ten years experiments on breeding wheats for short culm have been carried on all over the world. The results are promising. According to height dwarf wheats are divided into three groups: 1. true dwarfs are 65–70 cm high, 2. semi-dwarf wheats 75–95 cm, 3. the so-called "single gene dwarfs" 90–105 cm. To produce new short-culm varieties dwarf sources already described are mostly used. Recently Olesen's dwarf S948A1 is used in crossing for dwarfness, a variety selected from Mkwasine/Olesen's S948 (Sasaki et al. 1973*b*). In this variety dwarfness is transmitted by a single dominant gene. Dominant dwarfs are advantageous first of all in the "back-cross" method, because the selection is simpler.

Artificial mutation is a particularly efficient method for producing dwarf wheats. Most mutagenes induce dwarf growth in the mutation populations. Eiges (1966*b*) obtained dwarf mutants after ethylenimine treatments; Scarascia-Mugnozza (1967) produced them in *T. durum* by a quick neutron irradiation. Zoz and Makarova (1965*a*) found dwarf mutants after treatments with 1.4-bis-diazo-acetyl-butane, ethylenimine and diethylsulphate. Scalfati and Alessandroni (1965) obtained mutants mostly with short straws by X-ray irradiation at 15 000 r. Zarubailo et al. (1966) used gamma irradiation to produce dwarfs. Qualset et al. (1970) observed a 15–30 per cent shortening of straw induced by gamma irradiation of 3.2 kr. The results show that both culm shortening and definite dwarfness are frequent phenomena after mutagene treatments. If this type of dwarfness does not involve other defective characteristics, then it can be successfully used in the practice of breeding.

With semi-dwarf, and mainly with dwarf varieties outstanding results have only been obtained so far under irrigated conditions or moist climate. The advantages of dwarfness are most apparent under such conditions (Lelley 1973*a*). Recent economic survey have revealed that certain semi-dwarf wheats are inferior in nutrient utilization to varieties of standard height, which is not indifferent from an economic point of view. As a contradiction Smoček (1973) found short-straw wheats to utilize nitrogen better than those long with stalk. These observations require, however, further proofs.

We have to mention here an aberrant form of dwarfness recorded as "Grass-Klump-Dwarfness" or "Grass-Dwarfness" (McIntosh 1973). The property was first described by McMillan (1937). It is determined by four complementary genes marked with the symbols D1, D2, D3 and D4. According to monosomic analysis, gene D1 is found in the α-arm of chromosome 2D, gene D2 in the L-arm of chromosome 2B, gene 3D in the L-arm of chromosome 4B, and gene 4D in chromosome 2D (McIntosh 1973). However, it has no practical importance, but may even occur after mutative treatments, too. With various radiation treatments Singh (1966) obtained such mutants at a frequency depending on the variety.

Time of maturity

In the temperate zone the vegetative period ranges between 260 and 280 days for winter, and from 96 to 115 days for spring wheats. The length of the vegetative period is connected with many important economic properties of varieties.

Correlation between yield potential and the time of maturity has not been proved. An extremely short vegetative period cannot be coupled with a very high yield potential, but according to the evidence of the most recent results Mexican spring wheats giving record yields have not a long vegetative period, in some case it is even shorter than that of the earliest varieties with poor yield. Late maturing cultivars are thus not necessarily high yielding. Thus increased yield potential is not preconditioned by a long vegetative period, though it is possible that a further substantial increase can only be attained in the future by prolonging the vegetative period.

Therefore as far as winterhardiness is concerned varieties with protracted autumn and early spring development are desirable. This can be explained by a general demand for a longer period of vernalization, and these varieties are mostly of late maturity.

Early wheat cultivars with a short vegetative period are better protected against rust damage. In regions where rust is not of common occurrence, and the urediospores are transported by the wind from other regions, earliness means a particularly reliable protection against stem and leaf rust.

As regards drought resistance, varieties completing the generative phase of ontogenesis earlier are in a more advantageous position. They utilize the winter reserves of soil moisture more economically, and the generative phase is exposed to drought for only a shorter time. The wheat plant requires a long-day period. illumination over more than 12 h a day, to start the generative or sphorophytic phase of ontogenesis. Nosatovsky (1959) divided the wheats into three groups according to their demands for day length:

1. wheats highly sensitive,
2. less sensitive,
3. indifferent to day length.

The time when the generative phase begins, i.e. the demand for day length decisively influences the time of maturity. It is therefore important that genes determining this demand have been localized by Halloran and Boidell (1967) in chromosomes 1A, 3B, 4B, 6B and 7D. Puglsey (1965, 1966, 1971) found the long-day requirement to be sometimes of monogenic, at other combinations of digenic heredity. The latter finding was confirmed by Piech (1969). According to McIntosh (1973) photoperiod insensitivity is generally a dominant character. The two loci determining the photoperiod response are marked by the symbols Ppd1 and Ppd2.

Regarding the response to photoperiod McKinney and Sando showed already in 1935 that illumination of long duration activated the wheat plant only if the

air temperature was at least +5°C. At lower temperatures the vegetative period is not shortened at all by a longer period of illumination. Genes determining the photoperiod response are thus sensitive to temperature changes.

The vernalization and light phases jointly determine the length of the vegetative period; and since the two properties are of poly- and digenic in origin, respectively, the time of maturity is of multigenic heredity.

On the basis of monosomic and substitution analyses loci determining the length of the time of maturity have been localized in each chromosome of the wheat plant (Morris 1967). It follows that besides the genes determining the vernalization and photoperiod responses many other factors exert their effects on this property.

According to a number of publications, by crossing varieties possessing different time of maturity in the F_1 generation earliness is generally dominant, and even transgression has been observed (Kiss 1963; Keim et al. 1973). Mutants of a different time of maturity have been found in mutation populations, too. Crossing and mutagenic treatment are thus equally suitable to influence the time of maturity.

Differences in earliness between varieties or crossing derivates are easily shown by the visual determination of heading time, but the time of heading is not always reliable.

The lengths of stages 8 to 11 in the embryonal phase (Kuperman 1950) are not uniform in the varieties. In some varieties the period from flowering to mature stage is longer by days than in others. The development of the embryo is completed in 10–14 days from fertilization. Even this period is not of the same length. The length of the starch accumulation period depends partly on environmental conditions (temperature, precipitation, nutrient supply), but hereditary differences should also be considered. Its genetic variability, owing to lack of relevant examinations, is a not sufficiently known though it is an important characteristic since it affects the thousand-kernel-weight and probably the quality, too. It is not insignificant how much time is available for filling the endosperm. It is a general observation that the length of the embryogenic phase is in positive correlation with the thousand-kernel-weight. On the other hand, connection with quality is rather of a negative sign. For this reason the length of stages 10–11 (Kuperman 1950), i.e. the period of filling the endosperm, must by all means be taken into consideration when selecting for earliness.

The uniform appearance and ripening of the main spike and tiller spikes are connected with the length of the vegetative period (Pinthus 1966). In the case of wider spaced plants sown by single seed the uniform ripening of secondary spikes can be seen by the naked eye. From the point of view of yield potential and time of maturity only secondary spikes ripening nearly at the same time with the main spike can be taken into account.

The time of maturity had better be decreased only as long as it does not cause a reduction in hereditary yield potential.

For the last ten years the geographical adaptation of spring wheats has been greatly promoted by the day-length insensitivity (Borlaug 1968). So much so that this property being advantageous in spring wheat, may become dangerous in

winter wheat. If due to favourable autumn and early winter weather a day-length insensitive winter wheat completes its vernalization period, the next increase in temperature starts its generative phase irrespective of the photoperiod, and the plant may assume a state in which it becomes highly susceptible to recurrent frost. In which case the day-length insensitive winter wheat may suffer serious frost damages.

Chapter 10 Pathological resistance

Stem rust

Puccinia graminis tritici Erikss. et Henn.

Among the fungal diseases of wheat it is stem rust that has caused and causes even today the heaviest losses of yield. According to Reeves (1964*b*) in 1963–1964 the epidemic deteriorated the quality of some 25 per cent of the crop causing thereby a loss of ten million pounds in Australia. Hamilton and Stman (1967) gave account of 11 more or less severe epidemics between 1921 and 1962 in the Mississippi basin. In various regions of the United States 65–76 per cent of the durum wheat crop was destroyed by stem rust in 1953–54. It was estimated here that some 40 million bushels, about 4 per cent of the total amount of crop was lost each year between 1951 and 1960 owing to stem rust infection (Quisenberry 1967). In India it is the most wide-spread wheat disease periodically causing serious damages (Rao et al. 1962). In 1958 stem rust caused a severe epidemic throughout Europe, and in some regions even later considerable losses occurred. Wheat crops were seriously infected by stem rust in the following years and countries: 1961 Yugoslavia (Numič 1963), 1960 Czechoslovakia (Brückner 1969), 1972 Hungary. In spite of an organized world-wide control stem rust means a constant danger.

Investigations into stem rust resistance began in the years following the severe North-American epidemic in 1916. Then the appearance of the extremely agressive race of 15B in 1950 started a world-wide research (Johnson,T. et al. 1967). Since then the following results have been achieved:

1. The physiology of the pathogen has practically been cleared up.
2. In every major wheat producing country there is an organized control to detect any change in the range of physiologic races.
3. The relation between pathogen and host plant as well as the physiological and genetical causes of resistance have been elucidated in some respects.
4. Numerous resistant varieties have been produced by combination breeding, moreover, by means of interspecific and intergeneric crossing new resistance genes have recently been introduced into the genotype of wheat.
5. Some results have been attained by chemical control too, though compared to the genetic resistance it is expensive and not easy to put into effect, nor is it quite free of problems from the viewpoint of environmental protection.

Unfortunately, there are some negative aspects of the question, too:

1. Increased stand density and longer vegetative period due to the higher rate of nitrogen fertilization provide more favourable conditions for the pathogen (Zwatz 1969).
2. In many places wheat is grown under irrigated and moist conditions which again promotes the spread of the pathogen.

These negative factors must be reckoned with in the future when breeding for resistance. Obviously, the rate of nitrogen fertilization should not be affected, because by using nitrogen not only the maximum utilization of yield potential but an increased protein content of kernels too are attained. The prolongation of the vegetative period is not a general tendency yet, since the yield potential of early varieties has not even been fully exploited. But this situation cannot be maintained for long. For time will come when yield potential cannot be further increased without prolonging the vegetative period. Even a few days shift in the vegetative period may be decisive concerning rust damage, for it is known that the pathogen spreads suddenly and in a few days it may ruin the entire crop. Owing to the introduction of semi-dwarf varieties irrigated wheat production has been widely accepted even in regions where the long-straw wheats had not been irrigated before. In Mexico, India, Middle-East Africa and the southern parts of the Soviet Union considerable yield surpluses have been attained by irrigating semi-dwarf wheats, whereby the irrigation of wheat becomes profitable. Unfortunately, besides prolonging the vegetative period, irrigation creates a microclimate favourable for the epidemic of stem rust.

Thus, by breeding for stem rust resistance we not only attempt to control the disease but create the precondition of a further increase in yield. Regarding reliability, chemical disease control does not match resistance, and the high costs involved challange the economic efficiency of its application.

Taxonomic and ontogenetic aspects of stem rust are dealt with in detail by a number of manuals (Lelley et al. 1963; Quisenberry 1967). Investigations carried out in recent years have made the related questions even more clear.

The development phase harmful to wheat begins with the primary infection of aecidiospores, or else the overwintering mycelium originating from uredial infection in autumn starts the pathogenic process in spring (Milatovič 1967; Smirnova et al. 1968). Uredial infection in spring is thus a secondary attack which has an incubation period of 7–10 days. According to a recent statement of Smith (1969) an urediospore not able to germinate on the wheat leaf maintains a 75 per cent virulence for five days, but fifteen days later its virulence is scarcely 1 per cent. The higher the temperature, the sooner the spore loses its pathogeneity. The quick sporulation and the great mass of spores produced are responsible for the sudden spread of the epidemic. The agressive phase is started by the monokaryotic spores and continued by the haploid mycelium. In culture medium the urediospore forms dikaryotic mycelium (Kuhl et al. 1971). The dikaryotic mycelium does not infect the wheat (William and Hartley 1971). With the formation of dikaryotic teleutospores the ontogenesis is completed. Although the pathogen has no sexual phase in wheat, the possibility of new physiologic races, genotypes and biotypes coming into existence through spontaneous mutation, somatic hybridization or as a consequence of a parasexual process following heterokaryosis is not excluded at all (Nelson et al. 1955; Watson and Luig 1958; Christensen 1961; Hartley and Williams 1971*c*; Prasad and Sharma 1973). The sexual phase is accomplished on the leaves of *Berberis vulgaris* or *Mahonia*, where new genetic recombinations of physiologic races may be effected through insect mediation. This too may contribute to changes in the virulence of the pathogen (Watson and Luig 1968).

Crossing of races by human intervention was also successful (Gough and Williams 1969). For the spread of the physiologic races the specific selectivity of the host is important, as it may cause the rapid multiplication of virulent and sudden disappearance of avirulent races. So it may happen that a race totally disappears within some years (Šebesta and Bartoš 1969*a*; Oglae and Brown 1970). Again, specific selectivity accounts for the fact that sooner or later every varieties looses its resistance.

With the aid of Stakman's test sortiment nearly 200 biotypes have been identified so far, but races can even be further differentiated. To point out differences between the physiologic races morphological characteristics have recently been searched for, and not without success (Hartley and Williams 1971*a*, *b*). The fact that the pathogen is highly variable increases the danger. The period of incubation is short, primary infection is quickly followed by the secondary one, the epidemic spreads therefore at a very fast rate. According to Line and Bugbee (1964) the far spreading of the epidemic is promoted by the fact that in low humidity cold air (10 per cent, and +4°C, respectively) the urediospores remain virulent for months, so in great heights they might even be air borne to a distance of 1000 km. This explains why in places where neither infection by aecidiospores nor overwintering in the form of mycelium occurred, stem rust can still be found. According to Hassebrauk (1967) infections in Europe are caused by urediospores carried by the wind mostly from the south, possibly from North Africa. Luig and Watson (1970) pointed out that even the wheat areas of New-Zealand and Australia were affected by urediospores transported by wind from overseas regions.

In spite of its high variability, fast rate of development and rapid spreading, an actual epidemic requires two preconditions:

1. The pathogen should be virulent enough on the host plant, or the resistance of the variety should not countereffect the attacking physiologic race.
2. Weather conditions should be favourable for the rapid ontogenesis of the pathogen.

The genetic conditions of infection are given if the resistance genes in the genotype of the wheat variety do not inactivate the virulence genes in the genotype of the pathogen (Gough and Williams 1969). Thus, the host population should possess susceptibility genes, and the pathogen population virulence genes. Any genetic obstacle to a rapid and abundant urediospore formation may check the development of an actual epidemic, no matter how much the weather conditions are otherwise favourable for the ontogenesis of the pathogen. This particularly holds to regions with weather conditions favourable for rust infection, where high temperature and air humidity only occur at an advanced stage of the ontogenesis of the wheat plant, at the end of shooting or beginning of heading (Lelley 1969). Under such climatic conditions a kind of resistance manifesting only in the protraction of the incubation period, and a smaller number of urediospores or slower rate of sporulation is enough to give protection.

Among the meteorological factors, air humidity and daily mean temperature

are of decisive importance, but Burrage (1969) observed that the infectious embryo sac growing out of the urediospore avoided the dewdrops on the leaves. The urediospores require a high percentage of air humidity for 6–10 h to be able to germinate on the leaves, otherwise the appressorium formation does not start. According to recent observations the waxy layer of the leaf surface is probably rearranged by the tigmotrop reaction of the embryo sac, thus giving no more protection against the attack of the pathogen (Lewis and Day 1972). The urediospores need a mean temperature of 16–20°C to germinate, and were found to germinate at a faster rate in dark than in light. The optimum temperature of penetration is 24–26°C when light is also advantageous. Humid nights followed by sunny, rapidly warming mornings are most favourable for the infection to take place. In artificial infections performed in growth chambers these observations may be of use. The incubation time is the shortest when the temperature is between 20 and 28°C, and when there is an abundant quantity of water in the soil. Cool, dry, or cool rainy or cloudy weather of soma duration slows down the process of penetration.

Stem rust attacks through the stomata only. The aecidio- or urediospore develops an embryo sac which reaches the next stomata where an appressorium is formed. From here the infectious peg sets out, and in the presence of light penetrates the leaf through the stomatal openings (Yirgou and Caldwell 1963), where a substomatal vesicle is formed from which the hyphae grow through the intercellular space. Carbon dioxide even in a very low concentration (1 per cent) is able to prevent almost entirely the process of penetration (Yirgou and Caldwell 1968). According to the investigations of Brown and Shipton (1964), and Shipton et al. (1967) penetration shows a kind of specificity of variety. Where the hypha reaches contact with the cell-wall, the latter is dissolved, and a protuberance penetrates the cell and branches off around the nucleus (Chakravarti 1966). Apparently the protuberance does not penetrate into the plasm, it does not even get in contact with it. Upon its action the vacuoles contract, the plasm swells and the plastids degenerate. Soon after this Manocha and Shaw (1966) found a substantial increase in the ribonucleic acid content. According to Bhattacharya and Shaw (1967) the protein synthesis becomes more intensive. After the epidermal cells the haustoria penetrate the cells of the mesophyllum as well (Chakravarti 1968). Einaghy and Shaw (1966) pointed out a continued hexakinase activity in the affected cells. Lunderstadt and Fuchs (1968) observed a general enzyme activation around the site of infection. According to Andreev (1968) following infection, the hydrolytic processes become dominant over the synthetizing processes. In the centre of the developing uredio pustules respiration increases fifteen-fold, while at the edges three-fold. Where hyphae are not present, respiration does not become more intensive which means that the hypha acts only in the immediate surroundings (Bushnell 1964). Pfeiffer et al. (1969) used ^{14}C labelled molecules to demonstrate that the hypha extracted glucose from the host cell and built it into its own organism.

Recent studies have thrown light upon many details of the mechanism of infection and the behaviour of the infecting hypha, but the cytological aspects of the host-parasite relation are not quite clear yet, although a full exposure of the

physiology of host–parasite relation would contribute to a better understanding of the causes of damages.

The extent of the actual damage depends mostly that in which phase of the ontogenesis the pathogen attacks the host plant. It depends on this circumstance whether the number of spikes, the number of kernel/spike or the thousand-kernel-weight will be reduced, or the quality impaired. The inhibition of nutrient supply to the developing kernels is the direct cause of yield decrease, because a part of the assimilates is consumed by the parasite, respiration increases, transpiration of leaves slows down, large amounts of carbohydrates accumulate around the spores which incorporate them (Semenko 1968).

The existence of a hereditary resistance has been proved many times, but its causes are not quite clear even today.

According to Király and Farkas (1962) the quick accumulation and oxidation of phenolic compounds, and the rapid decrease of reducing compounds are connected with resistance. The oxidation products of phenols are toxic. It is these products that supposedly cause the necrosis of tissues which inhibits the spreading of the pathogen. It is not excluded either that they have a toxic effect on the pathogen too. Einaghy and Linko (1962) have drawn attention to the fact that in resistant wheat varieties oxazines were found in substantially larger quantities than in susceptible ones. The aglucon fraction of these compounds inhibits the development of rust and the germination of urediospores even in very low concentrations, and has a toxic effect on the plant tissues, too. Daly and Mrupka (1962) observed a rapid increase in the amount of organic acids after infection. On the chlorotic spots the amount of malic and succinic acids, and at the time of sporulation citric acid increases. Heitefuss and Fuchs (1962) observed the reduction of the ADP content. Due to a sudden increase of RNA as well as of the concentration of purin and adenin Heitefuss (1964) attributed the change of RNA concentration to a relation with resistance. Peruansky and Peruanskaya (1965) thought the change of the glucoside content to be one of the causes of resistance. Tsigrin and Alesin (1965) brought the intensity of floroglucin oxidation into connection with resistance. According to Alesin and Tsigrin (1966) in the resistant varieties the amount of the polimer forms of carbohydrates increases after the infection contrary to the sensitive varieties where the protein content, mainly that of the albumin grows. Cheung and Willetts (1973) also observed an increase in the protein content of infected leaves. Einaghy and Shaw (1966) found again a connection between glucoside content and resistance. He found more glucosides in the less susceptible varieties Kubanka and Mindum than in those showing a higher susceptibility. Tsirgin and Rozum (1969) noted the absence of beta-glucosidase activity in the infected leaves of susceptible varieties. Seevers and Daly (1970) found no relation between the change of peroxidase activity and resistance. Fric and Fuchs (1970) observed a sensitivity to temperature of the Sr6 resistance gene in Marquis wheat. This agrees with the statement made by Heitefuss (1965) that Marquis wheat shows sensitivity at 25°C and resistance at 20°C to the race 21 of stem rust. This suggests a possible heat instability of resistance.

None of the above listed observations can be brought into direct connection with hereditary resistance, only the relation of the phenol oxidation theory to the

hypersensitive reaction is regarded to be a proved fact. However, Brown et al. (1966) think the hypersensitive necrosis to be a result rather than a cause of resistance.

The existence of a hereditary resistance has been proved by experience beyond no doubt, but its unambiguous biological explanation is still lacking. That is why no biochemical laboratory method is available by which the extent of hereditary resistance in plants could be established, or an explanation to Chakravarti's (1968) observation given to the changes occurring in the host cells which check the further development of the pathogen.

There are differences between the types of the biologically inadequately understood but experimentally repeatedly proved hereditary resistance. There is a so-called seedling resistance and an adult plant resistance. The two types of resistance are not identical, nor always conditional of each other. Further, there are specific and general resistances, field and "slow rusting" resistances and finally, there is tolerance (Knott 1974*a*, Knott and Hughes 1974).

The resistance categories elaborated by Stakman and Levina (1922) do not perfectly correspond to practical breeding (Lelley 1969), namely, the degree of resistance sufficient to protect the variety depends on climatic and epidemiological conditions.

Full protection against stem rust could only be attained by a "general" resistance of the variety to all possibly existing races of the pathogen. General resistance has the further advantage that the pathogen does not get under the stress of selection. In this way new physiologic races do not come into existence in contrast to "specific" resistance which is favourable for the development of new races and protects the cultivar against several races only (Knott 1974*a*). The former degree of resistance cannot be found in the genus *Triticum*. It can only be transferred by translocation or substitution from another genus perfectly immune of stem rust. To this end intergeneric crossing has been carried out in many instances and the perspectives are promising (Knott 1963, 1968; Wienhues 1966, 1967, 1971; Cauderon et al. 1973).

Considering the dangerous nature of stem rust the constant control, the registration of physiologic races, and reporting of changes in their range are important tasks performed by research institutes in most cereal producing countries. From these observations conclusions can be drawn as to what the races are most frequently occurring in the major cereal regions and how quickly their range changes.

According to Stewart et al. (1965) in 1963, race 56 had been dominant for six, and race 15B for four years in the United States. Green and Campbell (1965) called attention in 1965 to the prospective spreading of a new race: 32B, which, however, later did not ensue. Stewart and Roberts (1968) reported a 65 per cent spread of race 15B-2 in 1966, Stewart and Romig (1968) described a remarkable propagation of races 11 and 151 in 1967. Stewart and Rothman (1971) reported races 32, 113 and 38 to have been spreading. Hazen (1971) gave account of the fact that in spite of the success attained by breeding, stem rust is even today a disease of wheat causing the heaviest losses in the United States.

In Central Europe mainly the North African and Southern European range of rust is important. The urediospores causing primary infection are borne by the wind from the south. Abdel-Hak and Kamel (1966*a*) have shown in Egypt a 70 per cent share of the races 14, 17, 19, 21 and 24. Concerning the race reserves of this

region data published for 1963 by Abdel-Hak and Kamel (1966*b*) show their magnitude. On the cereal area of the UAR 20 races of stem rust were then identified. The number of stem rust races identified so far are 16 in Syria, 6 in Iraq and 2 in each of Lybia, Iran and Ethiopia (Abdel-Hak et al. 1966). Between 1961 and 1965 Dodoff and Domchev (1967) identified 15 rust races in Bulgaria of which No. 21 was the most wide-spread one. In Yugoslavia Licic (1961) established the presence of races 14 and 21. In Italy Basile et al. (1964) found 23 races of which Nos 14, 17 and 21 were the most virulent ones. Massenot (1971) identified in France races 14, 21, 133, 160 and 169. Hassenbrauk (1963*b*, 1964) identified 12 races in the Federal Republic of Germany. Here too No. 21 was among the most wide-spread ones. In Hungary Bócsa (1969, 1970) reported on the constant presence though varying proportions of races 17, 21, 40 and 128. Šebesta and Bartoš (1969*a*, *b*) demonstrated the presence of races 14 and 21 as the most active members of the population in Czechoslovakia. Rassadina (1963) described races 21, 116, 100, 126, 13 and 40 to be spreading in the Soviet Union.

From these publications it is seen that in Europe Nos 14, 17, 21 and 40 have been the most agressive races of stem rust in the last ten years.

According to the table compiled by Morris (1962–1973) "seedlings" resistance to stem rust have been indicated in the following chromosomes: 1A, 2B, 5B, 6B, 7B, 6D.

Only adult-plant resistance was identified in chromosomes 5A, 2B, 3B, 4B.

Seedlings and adult-plant resistance were simultaneously present in the following chromosomes: 2A, 3A, 4A, 5A, 2B, 3B, 1D, 4D.

Not closely identified, supposedly field resistance was found in the following chromosomes: 1A, 3A, 5A, 6A, 1B, 2B, 3B, 4B, 6B, 7B, 1D, 2D, 6D.

Taking McIntosh's (1973) simplified system of gene symbolization into consideration, 27 resistance genes have been identified so far of which 23 have even been localized in chromosomes. The symbols of genes are: Sr1, 2, 3, 4, 5, 6, 7A, 7B, 8, 9a, 9b, 9c, 9d, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23.
The chromosomal location of genes:

2A	Sr21	
4A	Sr23	
6Aα	Sr8	? Sr9c
6Aβ	Sr13	? Sr10
7AL	Sr22, Sr15	? Sr3
1BL	Sr14	? Sr4
2B	Sr1, Sr9b, Sr9d, Sr19, Sr20	
2BL	Sr16, Sr9a	
3B	Sr2, Sr12	
4B	Sr7a	
4BL	Sr7b	
6BL	Sr11	
7BL	Sr17	
1D	Sr18	
2D	Sr6	
6D	Sr5	

Table 13. Chromosomes containing resistant genes (on the basis of Morris's table, 1962—1973)

Races examined	Designation of chromosome
11	3B 1D 2D 6D
15	5A 2B 2D 6D
17	3B 6B 1D
21	1A 4A 5A 6A 4B 6B 2D
24	6A 3B 4B 6B 2D
34	1A 6A 2B 4B
40	4A 6A 3B 6B
42	6A 1D
15B	6A
42B	6D
111	2A
121	2A 6D
198	6D

When identifying genes in the different varieties, resistance to the individual races turned out to be not always in the same chromosomes.

Table 13 shows the chromosomal localization so far for the genes of resistance to the major races.

Resistance to 15B, the most agressive race, originates from the United States from the Khapli wheat (Sr7). To race 56 the genes Sr13 and Sr14 are resistant, while the same genes are slightly susceptible to race 15B (Knott 1961, 1962). The aforementioned genes can be found in the variety Khapstein too, as supplements of gene Sr7. Gene Sr7 is present in the variety Kenya, too, indicating the common origin of resistance in the two varieties. Resistance in Khapli is dominant though not to the same degree in the various races. According to Atuallah (1963) in races 21-2, and 222-4 the resistance of Khapli is determined by two dominant genes, while in race 126-1 by a single gene. In combination populations of Kenya 184 × × Timstein, Bansal and Rao (1962) found the resistance to be mostly dominant, and identified generally a single gene for each race. In the wheat variety Kenya-farmer, Knott (1964*b*) found the genes Sr7, Sr9, Sr10 and Sr11 and observed an additive effect. In a crossing population of Milan, Merkle and Atkins (1964) observed a varying extent of dominance for resisting different races. Atuallah (1967) showed that the course of heredity was either dominant or recessive depending on the crossing partners and genes. The same gene which in a variety was dominant proved to be recessive in another one. Kao and Knott (1969) found the relationship between resistance and the virulence of the pathogen to be at one time dominant, then recessive, or of a complementary nature. Weeraratne and Williams (1971) give account of a similar variability of dominance in *T. durum*. Sanghi and Baker (1971) pointed out three genes of additive effect in the varieties Pusa and Mona. According to Luig and Rajaram (1972) the resistance of Marquis, based on genes Sr5, Sr8 and Sr9b, becomes inactive at temperatures 27–30°C.

It is possible that high temperatures reduce the effectiveness of other resistance genes, too.

The above-listed data show that no general rule concerning the heredity and dominance of resistance to stem rust could be established so far. In some cases more than one genes ensure resistance to the same physiologic race, while in other cases a single gene gives protection against more than one races. Genes are sometimes dominant, at other time recessive, but there are ones of additive effect and transgression may also occur (Knott 1974*a*). It has been pointed out that in a different genetic background the behaviour of a gene may change. Mono- or multigenic determination may equally occur.

According to Luig and Rajaram (1972), considering that a full control of the pathogen could not be attained in fifty years by breeding for resistance, a complex genetic resistance should be aimed at in the future, which is, in fact, resistance determined by accumulating many resistance genes.

The physiological mechanism of host-parasite relation is inadequately known as is the biological explanation of resistance. Király (1968) stated that the connection between the degrees of resistance and the phenol content is not quite clear yet. The protective measure of the waxy layer is open to debate. The slow rate of stoma opening, though a characteristic feature of the variety Hope, has not been observed in other resistant varieties. There is a supposed but not quite clear connection between the increase of dehydrogenase activity, rise of phosphate level and the symptoms of histogen demarcation observed in wheat. The supposed connection of protein antigens and hypersensitive reaction is also a phenomenon that cannot be used in laboratory tests by which to show differences in resistance between the crossing derivates. Resistant genotypes can only be identified by natural or artificial infection.

Investigations into the genetic aspects of host-parasite relation have reached at a stage where it is supposed that the virulence of the pathogen is determined by genes counteracted by resistance genes in the host plant. If the virulence gene of the pathogen is opposed by the corresponding resistance gene of the host, infection will not take place (Williams et al. 1966). If there is no resistance gene opposing the virulence gene of the pathogen, or its action is not sufficient, then the infection will take place. According to recent views virulence and pathogeneity are not identical concepts. Pathogeneity means the capacity of causing damage; it is not determined by genes in the pathogen. Virulence means a competition within the population of the pathogen, determined by genes (Watson 1970, Frankel et al. 1970).

Genetically the pathogen always is a population or varying composition (Bugbee et al. 1968; Fric and Heitefuss 1970); the host plant, in turn, makes selection, and that against itself (Kak and Yoshi 1963). That is why resistance to a small number of races, based on a single gene is unreliable, instead "group" resistance determined by a number of genes is desirable. This can be attained in two ways: either by incorporating more than one resistance genes in a single genotype, or by mechanically mixing nearly isogeneous lines resistant to various races (Borlaug 1968; Knott 1971). The latter, so-called "multilineal" variety can be produced by carefully planned back-cross series. As a precondition, the race composition

of the pathogen population must be continuously checked. In the multilineal variety the pathogen develops at a slower rate, and the possibility or the development of new races is limited. The method elaborated by Roefis et al. (1970) consists of appropriate screens fitted to the meteorological pluviometer; from the samples thus collected the race composition can be established. Besides knowing the composition of the race, genes resistant to the individual physiologic races as well as to the varieties in which they are found should also be known if a successfull breeding programme is to be started. Planning of such a programme is complicated by the fact that the dominance and effect of resistance genes may vary in the different varieties, and – in addition – one cannot always know in advance what the behaviour of the individual genes will be like in the new genetic background (Weeraratne and Williams 1971; Luig and Rajaram 1972). Some resistance genes may, in fact, modify their dominance conditions and even their race specificity in the changed genetic background. There are data suggesting that the degree of resistance or virulence depends on temperature, nutrient uptake and even on light conditions (Daly 1964; Prabhu and Wallin 1971). The age of the plant, and other, even less known factors also influence the disposition, which should all be considered when planning the breeding programme (Király 1968).

In breeding practice combination is the most frequently used method.

Selection is very effective, it must therefore be started as soon as possible, because the heritability of resistance is high. If resistance is transmitted by the back-cross method, selection must be carried out after the individual crosses. There are various methods developed for early selection.

By the laboratory procedure pieces of the leaf blades of plants to be examined are floated on the surface of a solution containing kinetin. This treatment maintains the green state of the leaf for a long enough time to see the effect of artificial infection performed with urediospores (Tkalenko 1966).

To study seedlings resistance young plants are artificially infected in greenhouse with spore suspension or dry spore dust.

In studying adult plant resistance, plants are infected by spraying or inoculation in the field (Lelley 1964*a*). Artificial infection is not, though, identical with the natural epidemic, but the results generally show a good agreement (Ossicini-Leonori 1973).

For artificial infection certain races or race mixtures are used. The races are identified with the method suggested by Stakman. To identify certain frequently occurring races, like races 56 or 15B, even quick methods have been elaborated (Browder 1966). In airtight ampoules, at zero degree the urediospores can be stored for months; in liquid air, when deep-frozen they remain virulent for years.

It is a debated question whether to take into account the capacity of self-adaptation of the pathogens and develop a resistance to several races of a single major pathogen, or to ensure partial resistance only to more than one pathogen. Resistance to all races of a single pathogen can be interpreted as vertical resistance. Horizontal resistance, on the other hand, means a resistance to more pathogens (Caldwell 1968). According to experiences gained so far this kind of resistance can only be attained by the so-called distant hybridization. Knott (1963) produced wheat lines transferring a vertical stem rust resistance by chromosome

translocation from *Agropyron*. Resistance transferred from *Agropyron elongatum* to the hexaploid wheat ensures protection against both stem and leaf rust (Knott 1968). Cauderon et al. (1973) succeeded in transferring by addition resistance to stem, leaf and yellow rust from *Agropyron intermedium* to wheat. Addition and substitution were used by Wienhues (1966, 1967, 1971) to transfer resistance from *Agropyron intermedium* to hexaploid wheat. Gerechter-Amitai et al. (1971) transferred rust resistance from *T. boeoticum* to the wheats Spelmar and Mindum.

By breeding for stem rust resistance numerous resistant cultivars have been developed so far. Some of them occupy a distinguished place, as valuable crossing partners. The cultivars Khapli (durum), Khapstein (hexaploid), Kenya 184 and Kenya Farmer are classical examples of breeding for stem rust resistance (Maia and Écochard 1965). Recent results include Lerma Rojo, a variety resistant to more than one race (Jha 1968). According to Massenot (1969) to races 14, 17, 21, 34 and 116 high resistance is shown by the varieties Moisson, Topaze, Rudepi Prieur and Joel. The varieties Norka and Thaev are valuable partners for resistance, too (Watson and Luig 1966). Sanghi and Baker (1971) give account of the resistance of Pusa and Mona of which the former carries three, the latter four resistance genes. Important sources of resistance are *T. timopheevi* (Lelley 1953*a*) and *T. araraticum* (McIntosh and Gyárfás 1971). The best known varieties resistant to stem rust are listed in Table 14.

Besides crossing, artificial mutations also stand for a chance in the work of breeding. There is evidence of resistant plants found in the population after mutagene treatment. Jech (1966) having irradiated the variety Diana found rust resistant mutants in the X2 generation. In the mutant population of Little Club produced by EMS treatment mutants resistant to 15B and other stem rust races were found in the M2 generation (Edwards et al. 1969). These experiences prove the perspective nature of breeding by mutation.

Possibilities of controlling stem rust by chemicals have also been tested. Among the attempts made by using antibiotics the result obtained by Hagborg and Chelck (1962), i.e. that the antibiotic P-9 produced by an unidentified *Streptomyces* species inhibited the development of rust, is worth mentioning. This antibiotic, though particularly effective in glass-house tests, is unsuitable for practical use (Hagborg and Rohringer 1966). Stewart and Hill (1965) observed that the filtrate of *Helmithosporium sorokinianum* culture also inhibited the spread of rust. Hobbs and Eutrell (1966) tested the inhibitory effect of nickel + di-thiocarbonate (Dithane-31) on rust. Rowell (1967) experimented with Maneb (zink + nickel sulphate) and a chemical marked F-461 (2-3-dihydro-5-carboxanilide-6-methyl-1,4-oxathin-4,4-dioxide), and found both, particularly the latter, to be efficient in checking infection by rust. Pathak and Joshi (1970) treated seed-grains with the fungicide DCMOD; this ensured protection against rust for 50 days, while leaf spraying gave full protection. Zwatz (1970) tested the chemical Sabithane-M which, when applied 4–6 weeks before ripening secured good results. Reliable protection is offered in glass-house by the 1–5 per cent solution of Daconil. In field trials good results were obtained by the fungicide Rhorianebe (Mohamed et al. 1971). Pommer et al. (1973) found the application of 2-iodo-benzoic acid anilide to be effective.

In spite of the genetic and other methods of control, yield losses caused by stem

Table 14. List of major varieties carrying "Sr" stem rust resistance gene (after McIntosh 1973)

Africa	Sr6	Lee	Sr11
Admonter Früh	Sr5	Mengavi	Sr9c
Bowie	Sr6, 8	Marquillo	Sr3, 4
Bonus	Sr15	Mentana	Sr8
Chris	Sr5, 6, 7a	Marquis	Sr5, 7b
Charter	Sr11	Manitou	Sr5, 6, 7a
$CS_7 \times$ Marquis	Sr12	McMuratshy	Sr6
$CS_5 \times$ Tatcher	Sr12	Magnif	Sr8, 9b
Erithrospermum	Sr5, 8	Mendos	Sr11, 17
Eureka	Sr6	Tr. monococcum	Sr21, 22
Aeurga	Sr6, 11	NP-790	Sr5, 11
Egyptian Na 95	Sr7a, 9b, 10	NO-466	Sr6, 9b, 10
Étoile de Choissy	Sr23	PI · 60599	Sr7a, 8, 9b, 10
Exchange	Sr23	Pitic	Sr8, 9b
Fortuna	Sr6, 7a	Reliance	Sr5, 16, 17, 20
Frontana	Sr8, 9b	Red Egypt	Sr6, 8, 9a
Einkorn	Sr21	Red Bobs	Sr7b, 10
Egyptian Na 101	Sr7a	Redman	Sr7b, 9d, 17
Festival	Sr9b, 15	Renown	Sr7b, 9d, 17
Flevina	Sr11	Rio Negro	Sr8, 9b
Gamut	Sr6, 9b, 11	Robin	Sr9b, 11
Gamenya	Sr9b	Scout	Sr2, 9d, 17
Gabó	Sr11	Stabil	Sr5
Hope	Sr1, 2, 7b, 9d, 17, 18	Siete Cerros	Sr6, 11
H · 44	Sr1, 2, 7b, 9d, 17	Selkikr	Sr6, 7b, 9d
Khapli	Sr7a, 13, 14	Spica	Sr7b, 17
Hochzucht	Sr5	Sonora 64	Sr11
Hybrid 80-3	Sr5	Thatcher	Sr5, 16
Kanred	Sr5	Timgalen	Sr5, 6, 8
Kenya Stocks	Sr6	Timvera	Sr9c
Kentana	Sr6, 7a	Timstein	Sr11
Khapstein	Sr7a, 13, 14	Tobari 66	Sr11
Kenora	Sr9b, 15	Tr. boeticum	Sr22
Kenya Farmer	Sr11	Veadeira	Sr9b, 10
Lnacer	Sr2, 9d, 17	Warden	Sr23
Lawrence	Sr7b, 9d, 17	Yalta	Sr11

rust infection reach millions of bushel a year (Manners 1969). Neither breeding nor chemical intervention have been able to give full protection so far (Skaman 1964).

Leaf rust

Puccinia rubigo-vera [DC] Wint. f. sp. *tritici* [Eriks.] Carl. (*P. recondita* Rob. ex Desm.)

Leaf rust occurs in all areas where wheat is grown. It depends on the weather conditions whether it appears as an epidemic each year or at greater intervals. In regions with a cooler climate its occurrence is sporadical. The damage done by leaf rust may be considerable but seldom reaches a similar magnitude as that

of the stem rust. The cause is the smaller size of the spore pustules and the fact that it never attacks the spindle and even on the glumes its small pustules are found at most on the inner surface. Very seldom tiny pustules are formed on the inner surface of the leaf sheats too. The upper surface of the leaf blade is almost exclusively the actual place of attack, large pustules are only formed there. Yet, in some years the damage is considerable. Over certain regions of the United States it has occasionally afflicted 20–25 per cent yield losses, meaning not only quantitative but qualitative losses, too (Caldwell et al. 1934; Quisenberry 1967). Chumakov (1963) estimates the loss caused by leaf rust to be about 4–5 per cent in the Soviet Union. It is especially on irrigated areas where from time to time it causes sharp drops in yield (Hitrova and Grigoreva 1964). Since the fungus is less sensitive to fluctuations in temperature, it is wider spread in the wheat areas of the Soviet Union than the stem rust.

In Europe it has been known as a pathogen for a long time; in Central Europe the urediospores causing the primary infection are transported by air currents from regions mostly from the south or south-west where infection by aecidiospores begins very early, or the mycelium overwinters (Boskovič 1964; Lelley 1969). It has been reported as a dangerous pathogen in Australia, too.

The life cycle of the pathogen is in many respects similar to that of the stem rust. Penetration takes place though the stomata, whether they are open or closed. That infection through the spike, glume, awn and leaf-sheath is very rare is not due to the absence or closed state of stomata, nor to the thickness of stomatal cell-walls, in fact, it is due to the fact that the appressorium or haustorium in these organs degenerates after penetration and does not continue growing. The cause of this phenomenon has not been cleared so far, though it is supposed that the inhibitory effect is connected with the intensity of nutrient supply. Later, if for some unknown reason, or owing to the advanced stage of ontogenesis this inhibition decreases, a delayed infection may appear on these organs, too (Romig and Caldwell 1964). According to Caldwell and Stone (1936) the apressorium rarely penetrates through the epidermis, too, but this is only possible on the leaf blade.

Rowel and Romig (1966) found that relative air humidity has scarcely any influence, while rainfalls exert a highly stimulatory effect on the course of infection. At temperatures of 5–8°C the urediospores maintain their germinative ability for as long as 45 days on the leaves, while at 18–19°C they do not survive more than nine days (Eversmeyer and Burgleigh 1968).

Of the biochemical processes ensuing from the attack of the fungus changes in the RNA, DNA and protein contents are very conspicuous (Quick and Shaw 1964; Bhattacharya et al. 1965). In the attacked tissues the "A" coenzyme, the first link of the chain of synthesis of citric, tartaric and malic acid increases in quantity (Krstev 1964). Photosynthesis becomes more intensive, not only in the infected leaves but also in the unaffected parts of the diseased plant (Livne 1964 *a*, *b*). This higher intensity of photosynthesis compensates somewhat for the loss caused by the disease in the dry matter content. At the site or infection the nutrient accumulation increases (Johnson, B. L. et al. 1966). In the dark period the infected plants fix more carbon dioxide (Daly and Livne 1966). Bhattacharya et al. (1965) observed a change in the quantities of amino acids. Quick and Shaw (1966),

Johnson, B. L. et al. (1967) found the activity of decarboxylase to increase with the beginning of sporulation. The amount of soluble nucleotides increased, too The kinate and sikinate metabolism became more intensive in the leaves, mainly in susceptible plants, and the amount of soluble esterase grew (Rohringer et al. 1967). Johnson, B. L. et al. (1968) observed the accumulation of glucose-6-phosphate dehydrogenase. Yield decrease is caused in the first place by transpiration loss and nutrient deficiency, but reduced root development also has an important role in it (Johnston 1929).

As for the biological causes of resistance the investigations have not found an ample explanation so far. Király (1968) pointed out some connection between phenol accumulation and oxidation on the one hand, and resistance on the other in the case of leaf rust, but beyond this no further biological connection which would throw light upon the essence of host-parasite relation and cause of resistance is known as yet. That is why no biochemical index suitable to measure the degree of resistance is available. Thus the cause of resistance still remains to be explained, in spite of the fact that its existence has been reliably proved. Investigations have pointed out that much that the hereditary resistance is influenced by the nutrient level and general physiological condition of the plant. Winterhardiness and drought resistance are therefore important supplements to leaf rust resistance in winter wheats (Gorlach 1962*a*). Raju et al. (1969) noticed that in the case of virus infection leaf rust epidemic had a more severe course. Thus, resistance also depends on the "health" condition of the plant. Sandu-Ville and Hatmanu (1962) proved the influence of weather on resistance. Johnson and Schafer (1965) pointed out a connection between temperature and resistance. At temperatures below 20°C light inhibited the formation of urediospores, while above 20°C this effect was not observed (Givan and Bromfield 1964). Hermansen (1962), and Donchev (1967) gave evidence of a connection between resistance and ontogenesis, and the age of the plant, respectively. Seedling-resistance and adult-plant resistance should be regarded as separate characteristics in the case of leaf rust, too. Distinction is made, here too, between specific resistance, to one or two races, and general resistance. Further, "slow rusting", or field resistances and tolerance are also reckoned with (Knott and Hughes 1974). Ripening time may also exert an influence on resistance. According to Rustagi and Mohan-Ram (1968) early and medium early varieties are resistant in a higher proportion than late varieties.

The variability of the pathogen is very high. There is a possibility of recombination both in the sexual and vegetative phase (Barr et al. 1964; Sharma and Prasada 1970). The number of races identified so far is approximately 200. Prescott and Young (1968) give account of computers used in the quick identification of races. Identification was originally carried out with the aid of a test sortiment of nine members (Mains and Jackson 1926). Later it was complemented by further varieties, so that identification became more circumstantial. Basile (1957) describes a diagnostical key which simplifies the procedure by grouping the physiologic races.

In the change of the range of physiologic races important role is played by the resistance of the cultivated variety. Pathogens virulent with a cultivar are selected

by the resistant cultivar itself, that is, races affected by the resistance are suppressed. It is in this way that selection pressure which accelerates the formation of new races comes into existence (Knott 1974*a*). The range of physiologic races is influenced by weather, too, therefore, the race composition, may be modified without the change of the varieties. In the formation of physiologic races mutation has also a part besides recombination. The race composition sometimes changes very quickly. The strict control of races is institutionally organized in every country where leaf rust occurs (Nover et al. 1964).

In the development of leaf rust epidemics important role is played by air currents which carry the infectious urediospores from great distances. Central Europe is from time to time infested by infectious material from North Africa and the Mediterranean area, it is therefore important to know the range of races in these regions.

Hermansen (1962) pointed out 6 races in Sweden and 5 in Denmark. In Western Europe Hassenbrauk (1963*a*) found 9 races of which No. 77 was highly virulent and quick in spreading. In Portugal Freitas (1972) identified 19 races in 1966. Donchev (1964) found 11 races in Bulgaria; in Syria, Iran, Lybia and in the UAR 16, 6, 6 and 12 leaf rust races were identified, respectively (Abdel-Hak et al. 1963). Race No. 77 proved to be the most agressive one in Egypt, too (Abdel-Hak et al. 1973).

In Europe Italy is a storehouse of races, Basile et al. (1966) pointed out in fact 38 races. In Hungary 20 leaf rust races have been identified in 1969 of which No. 77 was again the most virulent one (Bócsa 1969).

In the United States 100 races were pointed out in 35 years (1926–1960) (Johnson, B. L. et al. 1968). In India 7 race groups are registered of which Nos 77 and 164 are the most dangerous ones (Sheodhan and Singh-Ahmad 1969). In North Caucasus 53 races have been identified in a period of six years (Kraeva and Alekseeva 1972).

Owing to the variability of the pathogen breeding for resistance is obviously not an easy task.

According to the new system of symbols (McInstosh 1973) 26 Lr genes have been identified so far whose symbols are: Lr1, 2a, 2b, 2c, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14a, 14b, 14ab, 15, 16, 17, 18, 19, 20, 21, 22.

The individual genes give protection against the different races of the pathogen, but as it has been mentioned in the case of stem rust, in changed genetic background the same gene may ensure resistance to another race or several other races.

Table 15.

Type of resistance	Chromosome
Leaf rust resistance	7A, 7D
Leaf rust seedlings resistance	1, 4, 5A, 1, 2, 4, 6B, 2, 4, 5D
Leaf rust adult-plant resistance	5A, 6B
Leaf rust adult and seedlings resistance	4A, 7B, 5, 7D
Leaf rust resistance modification	7A, 7B, 7D

By monosomic analysis it has been revealed that in the different varieties, the reristance genes may be found in different chromosomes. Up to 1973 leaf rust resistance genes were pointed out in 21 chromosomes (Table 15).

Chromosomal localization for a part of the genes is known. According to the table compiled by McIntosh (1973) chromosomal placement have been determined for the following genes:

Lr1	1B, 5DL	Lr19	7D
Lr2a	1B, 2Dα	Lr20	7AL
Lr3	6BL	Lr21	1D
Lr9	6BL	Lr22	2Dα
Lr10	1A		
Lr11	2A		
Lr14a	7BL		
Lr15	2D		
Lr16	4A		

Genes causing the resistance have been identified in many valuable varieties (Table 16).

Results obtained concerning the hereditary nature of resistance are varying. Pokhrival and Kohli (1962) pointed out two pairs of dominant complementary genes in the Varieties Rionegro, Yakvui 53, Frondozo and H-167. In crossing NP-824 × Yakvui 53 resistance in the latter was oppressed by a dominant inhibitor of the former. Rao and Prasag (1963) identified two recessive resistance genes in the varieties E-817 and E-957. Schafer and Caldwell (1963) observed additive genic effect on the varieties Exchange, Aniversario, Frontana. Anderson (1963) described transmission when crossing the variety Bage to be now recessive, now partially dominant. Soliman et al. (1963, 1964) found dominance or partial dominance in the varieties Prelude and Thatcher. Statler (1973) identified a dominant and a recessive gene in the variety Waldron (LrW1, LrW2).

According to Boyd (1966) resistance is brought about by two types of gene: the potential resistance "R" and the inhibiting or modifying "P" gene, or genes. By this hypothesis the modifying effect of P genes is influenced by the age of the plant as well as by temperature and other environmental factors. Dyck et al. (1966) when crossing various varieties noticed that while the resistance of the variety was of dominant heredity in one case, became recessive when crossed with another variety. Luthra et al. (1967) give account of the resistance of the variety Bowie affecting three races. After crossing, resistance to one of the races became blocked. Law and Johnson (1967) identified a modifying gene beside the major gene determining the resistance in the variety Hope. Seedlings resistance to the most frequent races, Nos 20 and 77, in Europe was found in certain combinations to be a linked property (Kholousya et al. 1969). Others fixed the resistance to race No. 20 for 5 dominant genes. Abdel-Aziz (1969) pointed out the resistance to race No. 77 to be in four complementary genes. Dyck and Samborski (1970) identified the resistance to races Nos 9 and 161 with two genes of which one was dominant, the other recessive.

Table 16. List of major varieties carrying "Lr" leaf rust resistant gene (after McIntosh 1973)

Centenario	Lr1	Warden	Lr10, 16
Halle 9H 37	Lr1	Selkirk	Lr10, 14a, 16
Malakoff	Lr1	Exchange	Lr10, 12, 16
Mexica 120	Lr1	Hussar	Lr11
Sharbati Sonora	Lr1	Frontana	Lr13
Sonora 64	Lr1	Klein Aniversario	Lr13
Tarsa	Lr1	Manitou	Lr13
Uruguay	Lr1	Aotea	Lr14a
Eritrospermum 142–953	Lr1, 3	Gala	Lr14a
Norka	Lr1	Glenwary	Lr14a
Festiguay	Lr2a	Hofed	Lr14a
Webster	Lr2a	Hope	Lr14a
Carina	Lr2b	H-44	Lr14a
Brevit	Lr2c	Lawrence	Lr14a
Loros	Lr2c	Redman	Lr14a
Belocerkovskaja 149	Lr3	Regent	Lr14a
Besostaja 1	Lr3	Renown	Lr14a
Democrat	Lr3	Spica	Lr14a
Fertődi 293	Lr3	Maria Escobar	Lr14b
Mediterranean	Lr3	Thatcher	Lr14a, b
Mentana	Lr3	Marquis	Lr14a, b
Mironovskaja 264	Lr3	Kenya W 1483	Lr15
Mironovskaja 808	Lr3	Étoil de Choisy	Lr16
Osetinskaja	Lr3	Klein-Lucero	Lr17
Pawnee	Lr3	Africa 43	Lr18
Ranaja 12	Lr3	Red Egyptian	Lr18
Shirakada	Lr3	Agrus	Lr19
Skorospelka 3b	Lr3	Axminster	Lr20
Sladkovicova	Lr3	Birdpoot	Lr20
Bowic	Lr3, 14a, b	Bonus	Lr20
Transfer	Lr9	Converse	Lr20
Timstein	Lr10	Festival	Lr20
Federation	Lr10	Kenora	Lr20
Gabó	Lr10	Kenya W 744	Lr20
Lee	Lr10	Normandie	Lr20
Mayo 52	Lr10	Thew	Lr20
Mayo 54	Lr10	Tetra Canthatch	Lr21
Parker	Lr10	Tetra Canthatch 5404	Lr22

Owing to the variability of the pathogen and irregularity of transmission, other species of the genus *Triticum* as sources of resistance to leaf rust deserve special attention. Highly resistant species are: *T. monococcum* var. *hornemanni*, *T. timopheevi*, *T. carthlicum*, *T. timonovum*, *T. zhukovskii* and *T. fungicidum* (with 56 chromosomes) (Zhukovsky and Migusova 1969). Resistance originating from *T. timodheevi* is carried among others by the so-called FTF wheat line which consists of two hexaploid wheats and a hybrid of *T. timopheevi*. Development of vertical resistance (resistance to all races) might be solved, according to Samborski (1963), by the translocation of genes from a different genus, first of all from *Aegilops*. On the basis of experiences gained by Sharma and Knott (1966) the transfer of resistance from the genus *Agropyron* looks promising. Driscoll (1963) and Wien-

hues (1963) transferred leaf rust resistance by means of addition from *Agropyron elongatum* to *T. aestivum*. From *Aegilops umbellulata* a chromosome part translocating resistance to all leaf rust races (Lr9) was transferred by Soliman et al. (1963) to the variety Chinese Spring. By translocation and irradiation Driscoll and Jensen (1964*a*) produced a highly resistant line. Luig (1969) found the line Transec W 3016 originating from rye translocation to ensure both seedlings and adult-plant resistance to all leaf rust races of Australia. The resistance gene was localized in the 4A chromosome and found to be dominant.

Combination is the most frequently used method of breeding for resistance. According to plan the backcross method and the convergent crossing are extensively used. Borlaug (1958) proposes the production of multiline varieties. Chromosome substitution and segment translocation belong to tne more complicated methods but promote vertical resistance.

Extensive investigations have been made to find resistant varieties. From various variety collections many resistant varieties are used in breeding as crossing partners (Anpilogov 1964; Abdel-Hak et al. 1966*a*; Nover 1967; Manninger 1969; see also Table 16).

Breeding by mutation may be efficient, too. Mutant populations are always worth being selected for leaf rust resistance irrespective of the origin of the mutagene. It is therefore advisable to sow the M_2 generation at a place where the probability of an epidemic is high. Namely, there is no possibility of physiological or biochemical testing in selecting either crossing or mutant populations.

The degree of seedlings resistance can be evaluated by artificial infection carried out in greenhouse either by spraying or with spread spore suspension. Infection can be accomplished by using dry urediospores as well, but then it must be made sure that the leaves be covered uniformly with spores. To attain this aim Eyal et al. (1968) constructed a special sedimenting tower. For the collection of spores required for the infection Lelley (1971*a*) constructed a spore collector (Fig. 14). The collected spores when kept in air-tight ampoules at 0°C remain infectious for months, and in liquid air for years.

Leaves cut off for the purpose of artificial infection should be kept in Petri dishes. For floating kinetin-6-benziladenine solution of 1×10^{-4} M concentration

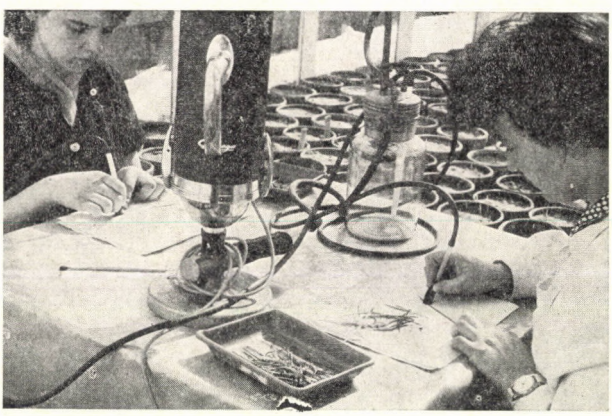


Fig. 14. Spore collector working with air current. Spores are loosened from the leaves with a brush at the end of the sucking pipes (Photo by P. Lelley)

is used, or a drop of a 1×10^{-2} M solution of benzimidazol, $NiSO_4$, $NiCl_2$ or $COCl_2$ is added to the water in the Petri dish. When floated on these solutions the leaves remain green, and so both seedlings and adult-plant resistance can be checked, but the method can also be used for the identification of races (Zadoks 1963; Prasannakumari and Pillai-Wilcoxson 1970). Sodium-2,3-dichloro-isobutyrate increases susceptibility. Under its influence even resistant varieties can be infected. It may be excellently used for propagating infectious material.

Adult-plant resistance is tested in the field by spraying or developing artificial infectious centres (Lelley 1964*a*). Assaul and Shelepov (1972) suggest a genuine method for the natural field infection of larger strains. In a part of the plot plants are cut back 3–5 days before heading; this sets back development so much that natural infection is bound to occur on the new secondary shoots.

In contrast to hereditary resistance, chemical control stands for no chance against leaf rust, due to the high cost of the operation and short duration of its effect. Šebesta and Bartoš (1964) describe the effect of *Darluca filum* (Bav.-Bern). Cast., a hyperparasitic fungus, on the leaf rust of wheat, but the rust cannot be controlled with this parasite. Müller (1969) gives account of the successful use of oxytetracyclin-hydrochloride for spraying and for root treatment. In greenhouse trials the fungicide Sabithane Z proved to be reliable, though in some varieties a toxic effect was observed (Boskovič 1962). The effectiveness of Sabithan Z was confirmed by Benni (1966) too. The fungicides Maneb, Zineb, Thiovit and Miltox have been tested with success by a number of authors (Tandon et al. 1968; Kuznetsova and Nikulina 1969). Rowell (1973) and Williams (1974) applied 4-n-butyl-1,2,4-triazol with satisfactory results. This chemical can be used in greenhouse or comparative field trials since it does not influence the metabolism of the plant. However, owing to the high cost of chemicals field control is not economic.

Yellow rust

Puccinia striiformis West.
(*Puccinia glumarum* [Schm.] Erikss. et Henn.)

The yellow rust is of limited importance, since the temperature optimum for its infection is between 9 and 12°C. When temperature reaches 24°C, both the growth of the infecting mycelium and sporulation are inhibited. Its occurrence on wheat areas under warm climate is insignificant, it only appears in cooler years, and even then only sporadically (Schröder and Hassenbrauk 1964; Sharp 1965). In Europe it occurs mainly in the north-west and along the shores of the North Sea, sometimes as an epidemic. In Asia the pathogen is known in the cooler eastern and north-eastern regions, while on the American continent in North Canada and the north-western states of the Unites States (Sharp and Hehn 1963). Occasionally it appears in regions with a milder climate, this is explained by the fact that in higher mountains it survives in various wild grasses even in warm years (Hendrix 1963).

Views about the dangerousness of the pathogen have for some years been slightly modified. It is more dangerous than was thought before, having recently

caused yield losses more often than several decades ago. The explanation is simple. As a result of breeding wheat production has been extended to areas where the climate is cooler and the conditions required for the development of the pathogen are more favourable. This applies in the first place to the Soviet Union, North America and Canada. In North America the yellow rust epidemic caused in 1960 and 1961 12.5 and 25 million bushel losses, respectively, and in some places destroyed some 30–40 per cent of the crop (Quisenberry 1967). The pathogen is spreading in Europe, too, e.g. in Austria the mycelium was found to overwinter (Zwatz 1968). It caused considerable damages in England, where Doling and Doodson (1968) estimated a yield loss of 8–20 per cent. An epidemic occurred in 1967 in the neighbourhood of Rostock, GDR (Seidel and Becker 1968). In Switzerland an epidemic raged in 1965 (Brönnimann 1965). In Czechoslovakia the pathogen has been observed to spread since 1961 (Benada 1963). In some wheat varieties the yield decrease was about 20 per cent. According to Depkarelevich (1952) and Savosta (1963) on the eastern parts of the Soviet Union the spread of the pathogen assumes such dimensions that yellow rust resistance has become an important precondition of successful wheat production. In India it is spreading on the northern wheat areas, at the foot of the Himalaya (Ahmad and Sheodhan Singh-Msira 1969). It is kept in evidence in the northern part of Japan, too (Kajiwara et al. 1964). In province Kansu (China), at an altitude of 500–800 m it is considered to be the most dangerous pathogen of wheat stands (Chin-Ching et al. 1965).

Recent investigations has not much contributed to the better understanding of its biology. Its uredio and teleuto states continue to remain the only ones known. Concerning the sexual phase nothing new has been come to light. It has been found to survive and overwinter on many wild grass species, that is why it appears so suddenly, like an epidemic (Shaner and Powelson 1973). A temperature as high as 25°C entirely checks its spread.

The infecting hypha is supposed to do no immediate damage to the cells of the host plant but have a symbiosis-like relation with them. In spite of this it has an adverse effect on, and may even upset the water regime of the tissues, increasing thereby water loss and respiration. It upsets the equilibrium of the processes of synthesis and oxidation wherefore the vegetative organs remain smaller and the roots shorter. Infection in autumn has a very unfavourable influence on winterhardiness (Hassenbrauk 1970).

High air humidity is indispensable and rainfalls are favourable for the spread of the pathogen. Under such conditions the urediospores disseminate in clusters, and according to the observations these clusters germinate and infect at a higher intensity. Sporulation is, otherwise, very quick. Five hours following the detachment of the spore a new spore is produced. The spores are heavy, wind does not carry them far. The time of incubation depends on the temperature. If it is cold it may even require 50 days. The pathogen sometimes overwinters in the state of incubation (Rapilly et al. 1970). Its survival is ensured by the overwintering mycelium, resulting in a very early appearance of the infection. The mycelium tolerates severe cold, but the urediospores are frequently destroyed by frost (Radulescu and Negulescu 1965). The mycelium requires a minimum temperature

of −2 to +3°C to grow (Quisenberry 1967). Tollenhaar and Houston (1967) divide the mycelia in two groups in the USA according to the optimum temperature of growth. Georgievskaya (1966) found the illumination required for the development of the pathogen to be optimum at 30–40 000 lux, that is why infection is more threatening at a higher altitude. Just the opposite was experienced by Stubs (1967). In some susceptible varieties infection increased with the decrease of light intensity. In autumn and winter light intensity had an inverse effect. The pathogen shows the highest reactivity to the intensity of light immediately after infection. Tu and Hendrix (1970) believe a lasting dew to be necessary for the infection to develop.

Besides the leaf blade, the leaf sheath and spikes are also infected. This makes the cause of the considerable yield shortage obvious. It must certainly be more than the decrease of assimilation and increase of respiration only. The damage caused by the fungus has been experimentally shown to exceed the effect of artificial defoliation (Hendrix et al. 1965*c*). The physiological consequence of the infection is very complex: the number of spike, kernel number per spike and thousand-kernel-weight decrease; growth vigour becomes inhibited, but leaves and root system will be smaller, tendency to lodging increases (Doodson et al. 1964). Hendrix et al. (1965*b*) even observed a decreased tillering and restricted longitudinal growth of the culms.

It has a lower variability than the other rust fungi, only 57 physiologic races have been identified so far. The probable reason is that pathogen has no generative phase, or if so only very seldom, and races can thus be produced only through somatic association or mutation (Fuchs 1956, 1960). The continuous checking of the races is institutionally organized in all threatened areas.

In Western Europe No. 27 was the most wide-spread physiologic race between 1959 and 1964 (Fuchs 1965). Macer and Doling (1966) found race 8B to be the most wide-spread in England. Slovenciková (1969) in Czechoslovakia identified races 54, 54x and 3/55, and found race 8 to recede. In India races 48 and 38 were identified (Ahmad and Sheodan Singh-Msira 1969). In the United States Beaver and Powelson (1969) identified a new race on the wheat variety Moro and marked it W57. In Japan races 31 and 14 were identified (Kaswara et al. 1964).

Physiologic races have recently been named after the varieties most susceptible to them (Johnson, V. A et al. 1972). Accordingly, in Western Europe race Cleo is the most wide-spread one (Ubels et al. 1965). Further distinct races are: Falco, Opal and Étoile de Choisy. In Switzerland race Probus was shown to occur (Corbaz 1966). This system of designating the races is not, however, generally introduced.

Thus, the variability of the range of physiologic races does not even come close to that of the other two rusts, and the rate of transformation of races is also much slower.

Breeding for resistance was started in 1905 by Biffen (1905*a*) in England. He produced the first resistant variety: Little Jos. In the United States breeding for resistance began in 1915. Today, resistant cultivars are developed in all countries where yellow rust causes damages.

Table 17. Major varieties carrying "Yr" yellow rust resistance genes (after McIntosh 1973)

Chinese 166	Yr1
E-2026, 7700, 8594	Yr1
Kalyanzona	Yr1
Nadadores	Yr1
Heine VII	Yr2
Merlin	Yr2
Soissanais-Desprez	Yr2
Capelle-Desprez	Yr3a, 4a
Hybrid 46	Yr3b, 4b
Minister	Yr3c
E-5555, 8510	Yr5
Tr. spelta album	Yr5
Heines Kolben	Yr6
Peko	Yr6
Thatcher	Yr7
Compair	Yr8

According to McIntosh's table 11 genes: Yr1, 2, 3a, 3b, 3c, 4a, 4b, 5, 6, 7, 8b, have been identified so far, of which only Yr1 and Yr8 have been localized in chromosomes 2A and 2D by monosomic analysis (McIntosh 1973).

In the course of chromosome mapping carried out by monosomic analysis loci influencing resistance to yellow rust have been pointed out, according to the table compiled by Morris (1962–1973), in the following chromosomes: 2A, 1B, 5B, 6B, 2D, 5D. Table 17 contains the major varieties in which these genes are found.

The heredity of resistance is varied, even the forms of its appearance are different. As to the stages of resistance Depkarelevich (1952) distinguished tolerant, resistant and immune varieties in Georgia. Mohamed (1964) set up four groups of resistance resistant in greenhouse and field, susceptible in both places, susceptible only in greenhouse and susceptible only in the field. Seedlings and adult-plant resistance exist in yellow rust as well (Allan et al. 1966). In some cases even the temperature dependence of resistance could be demonstrated (Lewellen 1967). Brown and Sharp (1969) observed the type of infection to be modified by the heat treatment of plants. Straib (1934) and Lupton and Macer (1962) found the conditions of dominance to change with the races. Allan et al. (1963) pointed out a complementary gene effect in crossing Norin 10 × Brevor 14. Macer (1963) identified a locus in each of seven varieties. Lewellen et al. (1967) found a major and several minor genes in the variety Chinese 166. Henriksen and Pope (1971) observed both dominant and recessive inheritance of resistance. Multigenic inheritance was also experienced (Allan and Purdy 1970). According to Slovencikoká (1969) varieties Zlatka, Oktavia, Hadmerslebener Qualitas and Draga may be used in Europe as very good resistant crossing partners. In spite of the complex nature of resistance transmission good results have been obtained by intervarietal crossing. There is evidence of successful interspecific and intergeneric crossing too *T. dicoccoides* is highly resistant to yellow rust. According to Gerechter-Amitai and Stubbs (1970) its resistance could be relatively easily transferred to the hexaploid wheat. The yellow rust resistance of *Ae. comosa* was translocated

to wheat by genetic interference through *Ae. speltoides*. This latter removes the inhibitory effect of 5B in homoeologous pairing. In this way translocation could be attained between the alien chromosomes. The name of the new resistant hybrid is "Compair", the gene of resistance is marked Yr8 and is located in chromosome 2D (Riley et al. 1966*a*, 1968*a*, *b*).

Yellow rust resistance has been introduced to the wheat genome from genus *Secale*, too, by the translocation of the longer arm of the second chromosome of rye (Riley and Macer 1966).

Breeding by mutation has also perspectives. Hanis et al. (1969) having applied a radiation treatment of 23 000 r obtained 15 resistant mutants in the M2-M8 generations of variety Diana I.

Breeding work can thus utilize intrageneric and intergeneric crossing as well as induced mutation. Considering that resistance has been found in several cases to be of polygenic character, the possibility of transgression can be reckoned with too.

For artificial infection all those methods can be used which have worked well in the case of stem and leaf rust. In greenhouses the intensive illumination and lower temperatures cause the primary difficulties because above 25°C the development of the pathogen ceases entirely.

There is a possibility of chemical control too, but, as in the case of the other rusts, the high costs and difficulties involved in the execution make breeding for resistance preferable. Bohnen (1963) obtained satisfactory results with the fungicides Zineb and Sabitan. Powelson and Shaner (1966) treated seed-grain with the fungicide Oxathiin (F461). The plants were immune to infection up to the two-leaf stage.

Powdery mildew

Erysiphe graminis tritici E. Marshal

Due to growing intensity in wheat production powdery mildew is constantly spreading; this can be traced back to the following causes.

The continually increasing rate of nitrogen fertilizer has provided favourable conditions for the pathogen. Concerning the physiological effect of nitrogen fertilizers the experiences are partly contradictory. According to Konstantinov (1963) one-sided nitrogen fertilization directly supports the attack of the pathogen. Roder (1967) and Janke (1970) observed no such connection but are of the opinion that the indirect effect of nitrogen fertilizer, the one exerted on the density of stand is an established fact. The microclimate of dense stands enhances the sporulation and the spread of powdery mildew. Even the semi-dwarf or dwarf growth habit gives no protection against this fungus, since the stand density of dwarf varieties is particularly high. For example, in the case of Gaines, the first American semi-dwarf variety (Kendrik 1965*a*), the frequent occurrence of powdery mildew has become a factor limiting its wide introduction.

Irrigated wheat production also promotes the spread of the pathogen since the conidia require high air humidity for a rapid germination (Yarwood 1957). In irrigated and abundantly fertilized wheat stands this condition is always present

in the night and morning hours. Dry, warm weather is the optimum condition for the reproduction of conidia, which is ensured by sunshine at noon. That is why in irrigated stands powdery mildew appears very early on the lower leaves and leaf sheats, and spreads rapidly upwards (Manners and Hossian 1963). The danger of powdery mildew is increased by the elimination of the crop rotation system and the introduction of wheat monoculture. Monoculture decidedly helps the pathogen in spreading, because the latter overwinters in the stubble-field in the form of mycelium (Moldovan and Sapa 1966; Smedegart-Petersen 1967).

Increasing powdery mildew damages have recently been reported by some authors. In England the damage was estimated at an average of 70 kg/ha between 1959 and 1962. In 1966 Moldovan and Sapa gave account of a 30 per cent coverage of powdery mildew already. In 1971 Zwatz (1971*a*) reported a 5–20 per cent yield loss from Austria. According to Pyzhkova (1970) damage was estimated to be 3 q/ha in the Federal Republic of Germany. Data on considerable infections by powdery mildew were reported from Czechoslovakia (Mráz 1965), from the Soviet Union (Rigina and Rigin 1972) and from Israel (Eshed and Wahl 1970). In the United States Kendrik (1965*a*) observed in certain years as high as a 70 per cent coverage in the variety Gaines.

The minimum temperature of infection is 6°C, the maximum 27°C, the optimum being 20°C. That is why the disease appears very early, and its harmful effect is felt already at the beginning of ear differentiation, at the 3rd–4th stages of the embryogenic phase (Masri et al. 1966).

The infecting mycelium does not penetrate the plant tissues but spreads on the surface, and thorough an enzymatic reaction removes the waxy layer of the leaf surface (Schwinn and Dahmen 1973). The haustoria live symbiosis like with the host cells. The fungus seems, however, to control the metabolism of the host cell, because near to the site of infection the leaves remain green even if more distant tissues become necrotic (Bushnell and Allen 1962*a*). As a consequence of the symbiosis the metabolism of the affected cells changes. Respiration and transpiration increase, but owing to the coverage the surface of assimilation is reduced. The roots receive less carbohydrates, therefore in the case of an early attack the development of the whole plant will be retarded (Bushell and Allen 1962*a*). The roots reflect this effect more clearly than the aboveground parts, though a shortening of the culm can also be established (Paulech 1969). Boev and Dobrev (1971) found the amino acid content to decrease after infection.

In contrast to an early infection which hinders the development of the whole plant, the disease, when occurring later, at most reduces the number of kernel per spike and the thousand-kernel-weight, and has a harmful effect on quality.

The variability of the pathogen is not as high as that of the rusts. In Europe 38 physiologic races have been identified so far (Wolf 1967). New races may come into being as a result or sexual recombination in the course of peritecium and ascospore formation (Powers et al. 1957). Somatic association occurring through the sexual process and the possibility of mutation must, however, be borne in mind. Leijerstam (1962*a*, *b*, *c*, *d*) identified 28 races in Scandinavia and 14 in Western Europe. Wolf (1965) found 13 races in England and 11 in Northern Europe. In 1965 and 1966 10 and 12 races, respectively, were identified by Mráz

in Czechoslovakia. Kartoshkina (1964) in Leningrad records 15 physiologic races.

The biological explanation of resistance is deficient. According to Bogdan (1968) the degree of resistance depends on the differences between the pH-value and the isoelectric zones of cell proteins. The greater the difference between the pH-value and the isoelectric zone, the more reliable is the resistance. Resistance is – supposedly – based among other things on the fact that the proteins of the host plant become useless for the pathogen. According to Kunovski and Bakrdzyev (1971) in the leaves of resistant varieties the amount of nitrogen originating from protein is higher than that of the non-proteinic one. Briggle and Scharen (1961) found both seedlings and adult-plant resistance to powdery mildew as well. It seems probable that the thickness of the epidermis plays a role in these two types of resistance. In the variety Hope resistance was found to change under the influence of temperature; at 24°C its resistance almost completely ceased to exist (Diercks 1962).

The complementary gene effect in the host-parasite relation supposed by Flor (1956) to exist in the case of leaf rust is thought to be present in powdery mildew resistance, too (Slebinski and Ellingboe 1969). Powers and Sando were able to prove as early as in 1957 the complementary relation of two virulence and two resistance genes.

There is a total of six resistance genes identified so far, which according to the list and system of symbol of McIntosh (1973) are:

Pm1, Pm2, Pm3a, 3b, 3c, Pm4, Pm5, Pm6.

The chromosomal localization of genes has also been almost wholly clarified:

Pm1 = 7AL	Pm3c = 1A
Pm2 = 5DL	Pm4 = 2A
Pm3a = 1A	Pm5 = 7BL
Pm3b = ?	Pm6 = 2B

The identified genes of resistance were found in different varieties. Table 18 shows the major resistant varieties and the resistance genes of their genotypes.

Resistance was found to show varying forms of transmission. Masri and Ellingboe (1966*b*) pointed out resistance as determined by a pleiotropic gene. Similar way of transmission was observed earlier by Nyquist (1963) in the case of powdery mildew resistance transferred from *T. timopheevi*. This resistance gene influenced at the same time stem rust resistance, too. Bozzini (1966) found simple dominant segregation in the tetraploid wheat. Briggle and Sears (1966) observed gene Pm3 and the gene producing hairy glumes to be in close connection in chromosome 1A. Szunics (1969) found both dominant and recessive courses of transmission. In two crosses resistance was of intermediary heredity. Briggle (1969) was able to prove the existence of at least four resistance loci in 12 nearly isogeneous lines. According to Szunics and Szunics (1973) the way of transmission of seedlings resistance was once dominant, then intermediary. The value of heritability was found to be 57–66 per cent.

Table 18. Major varieties carrying "Pm" powdery mildew resistance gene (after McIntosh 1973)

Axminster	Pm1
Birdproov	Pm1
Bonus	Pm1
Converse	Pm1
GI · 13836	Pm1
Fedka	Pm1
Festival	Pm1
Fram I	Pm1
Huron	Pm1
Kenora	Pm1
Kenya W 744	Pm1
Norka	Pm1
Pika	Pm1
Sweeden W 1230	Pm1
Thew	Pm1
TU 4	Pm1
Normandie	Pm1, 2
H · 8810/47	Pm2
Jumillo	Pm2
Maris Beacon	Pm2
Maris Dove	Pm2
Maris Hundsman	Pm2
Maris Nimrod	Pm2
Maris Templar	Pm2
PI · 92378	Pm2
PI · 181374	Pm2
Sea Izland	Pm2
S · 2303	Pm2
T · P · 114/2	Pm2
Ulka	Pm2
CI · 12632	Pm2, 6
CI · 12633	Pm2, 6
TP · 114	Pm2, 6
Asonan	Pm3a
Chul	Pm3b
CI · 3008	Pm3c
CI · 4546	Pm3c
Indian	Pm3c
Sonora	Pm3c
Surqueon	Pm3c
Khapli	Pm4
Yuma	Pm4
Aotea	Pm5
Glenwar	Pm5
Hope	Pm5
H · 44	Pm5
TP 114/2	Pm6
Laurence	Pm5
Redman	Pm5
Warigo	Pm5
Spica	Pm5
Renown	Pm5

The way of transmission of resistance can thus be mono- and multigenic, dominant, recessive or intermediary, moreover, there exists a pleiotropic gene effect, too (Pugsley 1965; Briggle 1966*a*, *b*). Its manifestation is supposed to be also influenced by environmental factors. According to Shaner (1973) there are varieties which, while young, are resistant, but later become susceptible. The supposed influence of potassium and phosphorus fertilization on the spread of the epidemic by Konstantinov (1963) may likewise be connected with a change of resistance.

The most frequently used method of breeding is the intervarietal crossing though resistance to powdery mildew can be translocated to the hexaploid wheat from other species, too. Briggle (1966*a*) thinks it desirable to transmit the resistance of diploid and tetraploid species. Zitelli and Vallega (1968) studied the substitution of resistance in *T. durum*. Powdery mildew resistance may also be a consequence of mutation. Selection of mutant population for powdery mildew resistance has given so far promising results.

Laboratory methods cannot be used for selection because there are no biochemical tests by which the degrees of resistance can be determined. Plants grown in a greenhouse in culture pots, or leaves floated in Petri dish are infected. With a view to the even distribution of the infecting material, Sadasivan and Ellingboe (1962) suggest the use of a roller covered with cotton-wool by which the spores can be evenly spread over the leaves. Greenhouse and field conditions of conidium formation are not uniform. Optimum conditions of successful powdery mildew infection in greenhouse are more difficult to realize than in the case of rusts (Benada 1970); artificial powdery mildew infection in greenhouses requires a more precise control of humidity, temperature and illumination.

Since the chemical control of powdery mildew have long since been used for other crops, its possibilities are better known. Owing to the high cost and difficulties in execution it still cannot compete in practice with the inherited resistance (Lein 1962; Leijerstam 1963; Bauers 1971). Castelliani and Matta (1964) give account of the successful use of "Esso Princess 95", a mineral oil derivate. Fischbeck and Bauer (1964) found spraying with calcic nitrogen to be efficient. Donchev (1965) obtained good results by spraying with calcium sulphite. Kradel et al. (1969) proved the efficiency of a dimethymorpholin derivate. Bent (1970) was able to ensure protection with the fungicides Milzurb and Milstein. Nissinen (1973) obtained good results by applying 1 kg/ha of Karathane. Other fungicides have also been found effective, still the possibilities of chemical control are limited.

Some authors, among others Zwatz (1971*a*), Krivchenko and Gruzdev (1972), observed certain changes in the powdery mildew epidemic after applying CCC growth inhibitor. The conclusion is that the microclimatic consequences of height reduction are not favourable for the pathogen. The direct fungicide effect of CCC could not be proved.

Powdery mildew may be a matter of concern as a greenhouse pathogen to wheat as well. Here the mentioned methods of chemical control can be successfully used, though a simple dusting with powdered sulphur or burning sulphur provides sufficient protection.

Other pathogens

Besides rust and powdery mildew various other fungi, bacteria and viruses also attack the wheat plant. However, in breeding they play an inferior role because either the damage can be prevented by efficient chemical control, or due to their restricted distribution the pathogens are of local importance only.

Common bunt (*Tilletia caries* [DC] Tul. and *T. foetida* [Wallr.] Liro) was regarded as one of the most dangerous diseases of wheat half a century ago, because it not only caused heavy yield losses but its penetrating smell made even the healthy crop uneatable. According to Özkan and Bremmer (1963) they are among the earliest of pathogens because their gene centre is in Anatolia, the native country of wheat. The two pathogens cause identical symptoms. It depends on climatic conditions which of the two will multiply (Zwatz 1971). *T. caries* prefers a climate with more precipitation. The ontogenies of these pathogens are fairly well known (Lelley and Rajháthy 1958; Witkowski and Witkowska 1962). The biology of the pathogen has been studied still more thoroughly since a dicariotic mycelium culture was prepared from the stalks of infected plants (Singh and Gupta 1969).

The chlamydospores either adhere to the grain or each the soil; the infecting mycelium attacks the coleoptyle. This type of infection makes chemical control easy. Seed-grains have been treated with highly efficient chemicals for decades. The best active agents according to Todorova (1962) are formalin, mercury, copper preparations and acetic acid. Mercury and copper stimulate germination too, which in itself promotes protection (Jagielski 1966). With proper protective measures damages can be wholly avoided. Nevertheless, Studzinski (1968) gives account of a yield loss of some 36 million Zloty in Poland caused by *Tilletia* in 1968.

Dwarf bunt (*T. contraversa* (Kühn)) has an ontogeny highly similar to that of the former two pathogens. The main difference being that it shortens the culm; in the case of mechanical harvesting most of the infected spikes do not even get into the thrashing mechanism but remain in the stubble field, and chlamydospores get into the soil instead of infecting the grain (Schumann 1966). Thus, *T. contraversa* mostly spreads by infecting the soil, seed-grain treatment, therefore, does not ensure as reliable a protection as it does against the former two pathogens (Meharabani 1969). The spores of *T. contraversa* do not readily germinate, and wheat plants coming up in autumn are sometimes infected in spring only (Hoffmann and Purdy 1967). Not even a wet treatment with mercury gives protection for the grain against this pathogen; perhaps some dust preparations of which a mixture of hexachloro-benzol + mercury is the most promising one (Zwatz 1971) might be formulated to counter act *T. contraversa*.

Owing to the efficient chemical control of *T. caries* and *foetida* breeding for resistance is not so important, while immunity against *T. contraversa* must be ensured by breeding for resistance in the first place.

The variability of the two smuts is not uniform. For *T. caries* and *foetida* 30 races have been identified so far (Quisenberry 1967). The number of identified races of *T. contraversa* is only 10 (Hoffmann et al. 1967).

There is hereditary resistance against both pathogens. Naqvi et al. (1963) described 20 resistant varieties, Johnston and Johnson (1964) found 60 of 163 varieties to be resistant. Kendrick (1965*b*) describes 38 resistant of a total of 102 varieties. Rabinovich and Melnikov (1968) found 27 to be resistant among the examined 808 varieties.

In McIntosh's table 10 genes of resistance to *T. caries* and *T. contraversa*, respectively, are found.

Their symbols and chromosomal localizations are:

Bt1	2B	Bt6	1B
Bt2	?	Bt7	2D
Bt3	?	Bt8	?
Bt4	1B	Bt9	?
Bt5	1B	Bt10	?

These resistance genes were found in different varieties (Table 19).

Transmission of resistance to *T. caries/foetida* and *T. contraversa* is relatively simple since it is determined by 1–2 or maximum 3 genes (McKenzie 1964). Resistance is dominant. Penchukova (1964) pointed out an occasional heat sensitivity of resistance, too. Breeding by crossing is efficient, but resistant mutants may occur, though there are no data testifying it.

Selection is simple. Artificial infection of seed-grains with dry spores or spore suspension is a reliable method, especially when initial growth is delayed by late sowing in order to have enough time for the infection to take place. The practice of breeding is not much concerned with resistance to *T. caries/foetida* for chemical control is reliable. *T. contraversa*, on the other hand, does not do much damage

Flag smut (*Ustilago tritici* [Pers.] Rostr.) is a wheat pathogen of minor importance. It spreads by wind-borne chlamydospores up to a distance of two-three hundred metres (Zwatz (1964). The ontogeny of the fungus is well known (Lelley and Rajháthy 1958; Danko and Michalikov– 1968).

Hot water treatment of seed-grains was for a long time the only method of control; for this purpose a special machine was constructed (Lyzlov and Silyanova 1962). Later thermochemical (Bobes 1962) and anaerob methods (Dobrev et al. 1967) were tried out; but these procedures are complicated and the results are not satisfactory either.

In spite of these difficulties, systematic work of breeding for resistance is hardly worth mentioning. Namely, the infected plants are so easy to recognize that on every wheat test nurseries a systematic selection was carried on which has proved efficient. Thus, today *Ustilago tritici* scarcely does any damage to wheat at all. Susceptible plants affected mostly do not yield, so the pathogen selects itself. This has greatly contributed to the disappearance of susceptible lines.

Since the problem of chemical control was solved breeding for resistance has become even less important. Of the chemical treatments the effect of synthetic fungicides, like Vitavax and Plantvax, belonging to the oxathiin group is nearly hundred per cent (Breth 1967). According to Reinbergs and Edington (1968) 5–6 kg/ha fungicide when mixed with the soil offers reliable protection. Maude

Table 19. Major varieties carrying "Bt" genes determining resistance to T. caries/foetida (after McIntosh 1973)

White Federation	Bt1
Albit	Bt1
Banner Berkley	Bt1
Federation 41	Bt1
Regal	Bt1
Sharman	Bt1
White Odessa	Bt1
Hussar	Bt1, 2
Hyslop	Bt1, 4
Columbia	Bt1, 6
Martin	Bt1, 7
Odessa	Bt1, 7
Canus	Bt2
Florence	Bt3
Ridit	Bt3
Bison	Bt4
Kaw	Bt4
Nebred	Bt4
Omaha	Bt4
Turkey 1558	Bt4
Turkey 2578	Bt4
Turkey 3055	Bt4, 7
Oro	Bt4, 7
Hohenheimer	Bt5
Rio	Bt6
Turkey 10095	Bt6
Turkey 10097	Bt6
Heyenne	Bt7
Baart	Bt7
Galiopoli	Bt7
Onas	Bt7
Ranec	Bt7
Yayla	Bt8
CI 7090	Bt7, 9
PI 116301	Bt10
PI 116306	Bt10

and Shuring (1969) suggest the use of wet seed-grain treatment. The authors treated seed-grain with a 0.2 per cent solution at 30°C over six hours and found the result to be hundred per cent again. Bombach and Beyme (1974) attained good results by using the fungicide Falisan-CX-Universal for dressing seed-grain.

Besides chemical control the possibility of breeding for resistance is also given. Hereditary resistance has been proved by a number of authors. *T. durum* wheats generally are more resistant than the *T. aestivum* species. *T. turgidum*, *T. turanicum*, *T. carthlicum* and *T. dicoccoides* are also resistant (Scelko 1964). Whole examining 800 hexaploid wheat varieties Krivchenko found some resistant ones. Olofsson (1966), on the other hand, found that in Sweden all varieties were susceptible.

Tne pathogen is not too variable (Krivchenko 1967). In the United States 19 races have been identified so far (Quisenberry 1967). Mitov (1968) found only one race that infected *T. durum.*

According to investigations into the heredity of resistance protection is determined by one or two dominant genes (Agrawal et al. 1963; Mathur and Kohli 1963). In Chinese Spring, Heinrich (1967) localized a resistance gene in chromosome 5B. McIntosh et al. (1967) found a gene determining resistance to *Ustilago tritici* in chromosome 7B of the variety Hope.

Since the symptoms are conspicuous, readily recognizable by naked eyes the breeders, instead of a systematic breeding for resistance, have always selected out the lines in which the number of infected plants was high. Selection carried out by the pathogen itself is also effective, since the overwhelming majority of the infected plants does not produce fertile grains. That is why the varieties introduced in commercial production are almost without exception free of flag smut infection.

Breeding either by crossing or through mutation can likewise be effective. In a systematic work of breeding for flag smut resistance artificial inoculation methods are also used. The simplest one being the infection of flowers with spore dust or with a wet spore suspension. To increase the efficiency of the method vacuum inoculators are used (Danko and Michaliková 1968; Bineeta Sen-Munjal 1970). Besides the infection of flower the chlamydospere suspension can be injected into the 0.5–1.0 cm long coleoptyle; this too is a highly effective method (Wandervalle and Sommereyns 1965). Infection can be pointed out already in the coleoptyle by fucsine staining in laboratory (Michaliková 1968).

Fusarium. Damages done by various types of *Fusarium* to wheat are growing in dimension.

Snow mould (*Fusarium nivale* [Fr.] Ces.) is a long since known pathogen of cereals. After a lasting snow cover it invades the weakened plants. Yet, it is of minor importance owing to its sporadic occurrence. According to Cassini (1969) grain dressing with preparations containing thiobenzol gives reliable protection. Otherwise the existence of resistance has not been proved.

Fusarium culmorum (W. G. Wm.) and *F. graminearum* (Schw.), both damaging the spike, have recently been gaining ground in the wheat stands. Snyder (1968) explains this phenomenon by the changed system of crop rotation and the high rate of nitrogen fertilization. Susceptible varieties are most likely to have a part in this too.

According to Leijerstam (1962*a*) infection in Sweden was 81 per cent in 1954. In certain regions of Yugoslavia serious *Fusarium* damages occurred in 1963 (Perišič 1963). In 1967–1968 it appeared in Hungary too, and since then has become a customary pathogen (Kükedi 1972; Mesterházy 1974*a*). Owing to its rapid spread the biology of the pathogen and breeding for resistance have recently been dealt with much more thoroughly (Mesterházy 1973). If the weather is dry and warm infected seed-grains result in a pre-emergent or postemergent destruction of plants (Colhoun and Park 1964; Malalasekera and Colhoun 1968). If infection occurs during vegetation the plant produces kernels but the thousand-kernel-weight will be reduced, the gluten content lowered and the farinographic water uptake restricted (Bockmann 1964). In winter wheat both types of *Fusarium*

may cause root and stem rot (Mesterházy 1974*a*). The extent of damage depends on the degree of contamination of the soil (Cook. 1968). *Fusarium culmorum* also reproduces in a saprophytic way, on bits of straw in the soil (Cook and Bruehl 1968; Cook 1970), and spreads with seed-grain as well. According to Viennot-Bourgin (1970) effective treatment have not been found so far; a suitable fungicide will perhaps be prepared from the oxathiin group.

The fungus can be grown in culture medium which will lead to a better understanding of its ontogeny (Gréc 1972*a*, *b*; Mesterházy 1973). A method has been elaborated for artificial infection, too. From spores washed off the wheat straw a suspension is prepared with water which contains 1 million/ml spores. The spike is isolated before emergence, sprayed with the suspension 3–5 days after flowering, then isolated again. If the plants are abundantly supplied with water the artificial infection will be successful (Leijerstam 1962*a*). Mesterházy (1974*b*) applies the infecting material propagated in bubble culture on Czapex-Dox culture medium with a fog-thrower on the spikes and ensures the required high humidity ever 48 h with plastic bags used as isolators. A reliable method of infection is undoubtedly a necessary precondition of breeding for resistance.

The degree of infection is determined in an original way. The endospermium having been detached from the embryo is placed on culture medium and kept for 5 days under humid conditions at 25°C. The degree of infection is classified according to the diameter of the *Fusarium* colony developing on the culture medium (Malalasekera and Colhoun 1969). Mesterházy (1974*b*) considers the reduction of thousand-kernel-weight to be suitable to measure the degree of infection by in the case of both types of *Fusarium*.

Breeding for *Fusarium* resistance has not produced any considerable result so far. Hereditary resistance is supposed to exist though its genetics remains to be cleared up. Since the pathogen is spreading, a still more intensive research is expected to take place in the coming years.

Wheat streak mosaic. Wheat is attacked by a number of viruses, of which the streak mosaic virus is the most important one as it has recently appeared on wheat areas where it has not been known before.

More serious damages were first observed in the United States where the pathogen has been known for some time (Quisenberry 1967). Breeding for resistance has been carried on in America almost for twenty years. According to Pop and Tusa (1964) Roumania was the first country in Europe where the virus appeared in 1958. In Yugoslavia the pathogen was identified in 1961 (Tošič 1962). In 1964 it appeared in the neighbourhood of Belgrad (Sutič and Tošič 1964). Its occurrence in the Soviet Union was first reported in 1962, from the region of Krasnodar (Razviazhina et al. 1963). Damage caused by streak mosaic virus in Finland was reported in 1966 (Jamaleinen and Mortomaa 1966).

Owing to the sudden spreading of the virus intensive biological and genetic researches have been started in Europe too (Tošič 1971*a*, *b*). Its increase in Europe is explained first of all by the large areas of wheat sown after wheat (Wiese et al. 1970).

Streak mosaic virus is spread by various vectors. According to Serjeant (1967) and Plumb (1970) one of them is a leafhopper: *Javesella pellucida*. Pridantseva

et al. (1966) pointed out that infection was transmitted by another leafhopper: *Psammotettix striatus* as well. In America *Calligypona pellucida* is the most important vector. According to Orlob (1966) the mite *Aceria tulipae* is a further vector of the virus. Its rapid spread is promoted by the great number of vectors too. Direct mechanical infection without a vector as intermediator is ineffective (Lee and Bell 1963). Vectors become infectious 4–24 days after sucking infected plants. Fifteen minutes of sucking is already enough to transmit the pathogen to another wheat plant (Slykhuis 1963). The symptoms appear on the plant 15–25 days after infection (Nowacka and Hope 1969). The pathogen causes longitudinal streaks on the leaves. Streaks are more conspicuous when the leaves were cut back after infection, because they can be better seen on newly developed leaves (Rao and Brakke 1970). According to Ikäheimo (1964) infection by streak mosaic virus affects 34 grass species and 11 dicotyledonous species, thus the possibility of overwintering is extremely high.

The virus is stiff, bacilliform, about 700 mμ long and 15 mμ thick. In the cytoplasm it is located between the nucleus and the cell-wall (Lee 1967). Its presence can be ascertained from the extracts of plant and vector by serological test (Lee 1963*a*, *b*; Sinha 1968). By a detailed examination the virus was found to be present in the whole organism of the vector, excepting a few organs (Sinha and Chiykowski 1969).

According to Panič and Tošič (1969) most wheat varieties are susceptible. Jakubziner and Belyanchikova (1970) observed various degrees of susceptibility after artificial infection. As the final results of selection repeated several times Bohnenblust and Kolp (1965) produced a resistant strain marked CI-13600.

In the genus *Agropyron* there are many resistant species. Sebesta and Bellingham (1963) found resistance in a hybrid of wheat and *Agropyron*. Resistance was translocated by an *Agropyron* chromosome. Raj (1965) obtained amphidiploids with 56 chromosomes from *Agropyron elongatum* × hexaploid wheat hybrids, and found five resistant lines among them. The resistant TA-25 line was produced by Lay et al. (1971) by crossing the wheat variety Carsten with *Agropyron intermedium*.

According to Quisenberry (1967) on the basis of infection by spraying whose reliability is, however, questionable a number of varieties are supposed in the United States to possess a certain extent of resistance to streak mosaic virus. These varieties are: Apache, Bison, Blue Jacket, Comanche, Concho, Kiowa, Radco, Stafferel and Triumph. There are thus possibilities for intervarietal crossing too, however, it is most likely that a really effective resistance can only be attained through intergeneric crossing.

Hessian fly (*Mayetiola destructor* [Say]). Hessian fly is an insect pest of wheat which is to be controlled by breeding for resistance. Resistance is proved to exist though its cause has not been cleared yet. It is probably due to the different structure of certain tissues.

According to McIntosh's (1973) table six resistance genes have been identified. The symbols of genes are: H1, H2, H3, H4, H5, H6. Patterson and Gallun (1973) found further two genes in the variety Seneca with the symbols H7 and H8.

In the table compiled by Morris (1962–1973) gene determining resistance to Hessian fly is found in chromosomes 1A and 5A.

Table 20. Varieties carrying "H" gene determining resistance to Hessian fly (after McIntosh 1973)

Big Club	H1, 2
Dawson	H1, 2
Poso	H1, 2
Ace	H3
Arthur	H3
Dual	H3
Georgia	H3
Ionia	H 3
Logan	H3
Monon	H3
Ottawa	H3
Red Coat	H3
Reed	H3
Riley	H
Russell	H3
Shawnee	H3
Todd	H3
Java	H3
Dixon	H4
Riberio	H5
Benhur	H6
Knox	H6
Lathrop	H6
Kawvale	?
Marquillo	?
Seneca	H7, H8

There are quite a number of resistant varieties known in which the genes have been identified (see Table 20).

Resistance is transmitted by one or maximum two genes. Thus crossing promises some success. Resistant strains are not readily recognized because the fly is difficult to multiply. Selection is mostly possible in the case of a natural invasion only.

Chapter 11 Quality improvement

For human consumption three kinds of product are made from wheat flour:

bread or other bakery products raised with yeast;
pastry, cookie, cakes and other manufactured goods raised chemically, with baking powder instead of yeast;
macaroni, spaghetti and vermicelli.

Wheat and its milling products are also used for feeding animals.

For the production of raised products hexaploid hard wheats are the best for only they contain an adequate quality gluten.

Cakes are again manufactured from hexaploid wheats, though from the soft ones. Though the demands on their gluten quality are lower.

It is for the production of Italian pastes that tetraploid durum wheats are grown.

The poorest quality hexaploid soft wheat or defective crops unsuitable for food processing serve the purpose of animal feeding.

The first step in processing wheat is milling. The first demand on the quality of bread wheat is raised by the milling industry. Since milling is a highly important industry all over the world, it is obvious that its demands must be considered in the work of breeding. From a milling point of view the wheat is good if with a few runs of milling, little screening and low energy it yields the largest possible amount of semolina and the highest total output of flour. Furthermore, a low ash content and a colour of flour meeting market requirements are also important demands. The milling industry raises the same demands on the quality of durum wheats used for manufacturing Italian paste. As to soft wheats forming the basic material of cookie industry the demands of milling industry are not so high.

Milling quality depends on the

1. size and evenness of the kernels,
2. texture of the endosperm,
3. percentage ratio of the seed-coat,
4. colour of endosperm and seed-coat.

The *size of grain* is in close correlation with the weight of grain. The latter is known to be an important component of yield potential transmitted with a relatively high heritability (see page 68). From the point of view of milling quality the importance of larger kernels consists of the lower ratio of the seed-coat. Some authors have found, on the other hand, that if the size of the grain exceeds a cer-

tain limit, glassiness, also being an important factor of quality, decreases. This means the structural deterioration of the endosperm. Thus grain size should not exceed this limit.

Grain size can be reliably determined by the thousand-kernel-weight, but since thousand-kernel-weight depends at the same time on the compactness or structure of the endosperm, the size of grain can be most accurately identified with a series of screens of adequate mesh. The system of screens simultaneously yields information on the evenness of grains if the different fractions are compared.

The transmission of thousand-kernel-weight is mono-, di- or polygenic. The conditions of dominance may also vary with variety (see page 68). Its heritability is about 50–70 per cent. Today the thousand-kernel-weight of high yielding wheats generally reaches or exceeds 40 g. Genes influencing the heredity of grain size have been pointed out in chromosomes 1A, 2A, 3A, 5A, 7A, 1B, 3B, 4B, 5B, 6B, 7B, 1D, 2D, 5D, 7D (Morris 1962–1973).

The *evenness of kernels* is very important if the hulling loss is to be reduced to a minimum, otherwise the lot has to be divided into fractions and processed accordingly. This means a surplus in time and energy. With smaller fractions the flour output is also lower.

Kernels are the largest in the middle of the spike and become smaller towards the ends (Ali et al. 1969). Within the spikelets the largest kernels develop in the lower flowers, while in the upper ones they are smaller. Thus, from the point of view of the evenness of grains wheats with large spikelets and high fertility are not favourable. This finding contradicts to some extent the tendency of increasing the number of kernel/spike as a factor of importance. The antagonism of the two characteristics explains the thesis that beyond a certain level high productivity and good milling quality are in negative correlation. Thus, from the point of view of milling industry it is more favourable if the spikes contain more spikelets but the fertility does not exceed three flowers per spikelet. To the evenness of grains the squarehead type club-shaped spike is particularly disadvantageous, because the upper part of the spindle is shortened, the spikelets are close-set, consequently, the grains developing in them are smaller than in the lower part of the spike. In wheats of good quality the increased number of kernel per spike can be attained by a high number of spikelets, moderate fertility of flowers and elimination of club-type spike.

Genes determining the transmission of the number of kernel/spike have been found so far in chromosomes 5A, 1B, 6B, 7B and 6D (Morris 1962–1973). The characteristic can be determined mono- and multigenically, its conditions of dominance are varying (see page 68). Genes determining the number of spikelet/spike have been localized so far in chromosomes 5A, 6A, 1B, 4B, 6B, 7B and 7D (Morris 1962–1973). Conditions of transmission are less known for this character, because until now attention has been paid primarily to the transmission of millimetre spike length. This character is in correlation with the number of spikelet/spike, but since the compactness of the spike decisively influences the relationship, the correlation is not reliable. Genes determining the length or spike have been found in chromosomes 2A, 3A, 4A, 1B, 2B, 3B, 4B, 5B (Morris 1962–

1973); the course of transmission for this character, and the number of genes indicated in the case of crossing are varied.

Thus the evenness of kernels depends, in fact, on the harmony of three characteristics related with components determining yield potential. The analysis of these characteristics can be linked up with the examination of the yield components. Their joint- and interaction decide the number of kernel-spike, too. The evenness of kernels can be precisely measured with a vibrating seed grader already in young strains (Fig. 15).

Besides the stock of information fixed in the genotype the size and evenness of the grains may also depend on certain climatic and pathological effects. Drought and heat tolerance, resistance to rust, powdery mildew and *Fusarium* may deteriorate indirectly the manifestation of both groups of character.

The *texture of the endosperm* is characterized by glassiness or pearling index and hardness. Both features are hereditary characters as pointed out by Biffen as early as in 1905. They influence the utilization of energy required for milling, as well as the amount of semolina obtained. They are in connection with the gluten content (Svarkina et al. 1965), the total protein content and its distribution within the endosperm (Berké 1964, Wenzel 1971), as well as with the quality of the gluten (Williams 1963). These properties determine, though, other categories of quality, their relation with the texture of the endosperm is proved beyond doubt.

Glassiness or pearling index can be measured with various instruments. One of them is based on the principle of a simple transillumination. The method is not quite reliable but has the advantage that after the examination the kernels remain intact which is important when evaluating young strains. By another method the kernels are cut into two and the extent or percentage of glassiness is determined on the basis of the texture of the cut surface (Fig. 16). Milling industry gives preference to varieties with a glassy texture of endosperm. It is a hereditary feature, though influenced by environmental factors (Babadzanyan 1964). Reduced water supply increases glassiness (Kartavschikov and Udachin 1966). It is favourably influenced by a balanced supply of nitrogen while repeated rainfalls after the late dough stage have an adverse effect on it. A proper supply of phosphorus is also favourable from the point of view of pearling index (Lipsett 1963). According to some authors varieties with loose spikes more often have glassy grains than those with compact spikes (Wunderlich 1963). Some have found glassiness to be in negative correlation with large kernel number per spike and high productivity, that is why it is a rare phenomenon among high yielding varieties. Glassy texture, however, does not always mean large quantity and high quality gluten and high protein content (Berké 1964).

Howard pointed out in 1912 that this property may be of monogenic heredity. Later a polygenic segregation was observed by Clark et al. (1928). In most cases there is a positive relation between glassiness and protein content, because the gaps between the starch grains of the endosperm are filled with protein. In other words, the starch grains do not get into the vacuoles but remain in the plasm. During drying the protein-containing plasm closely adheres to the starch grains which makes the structure of the cells transparent (Babadzanyan 1964). Since

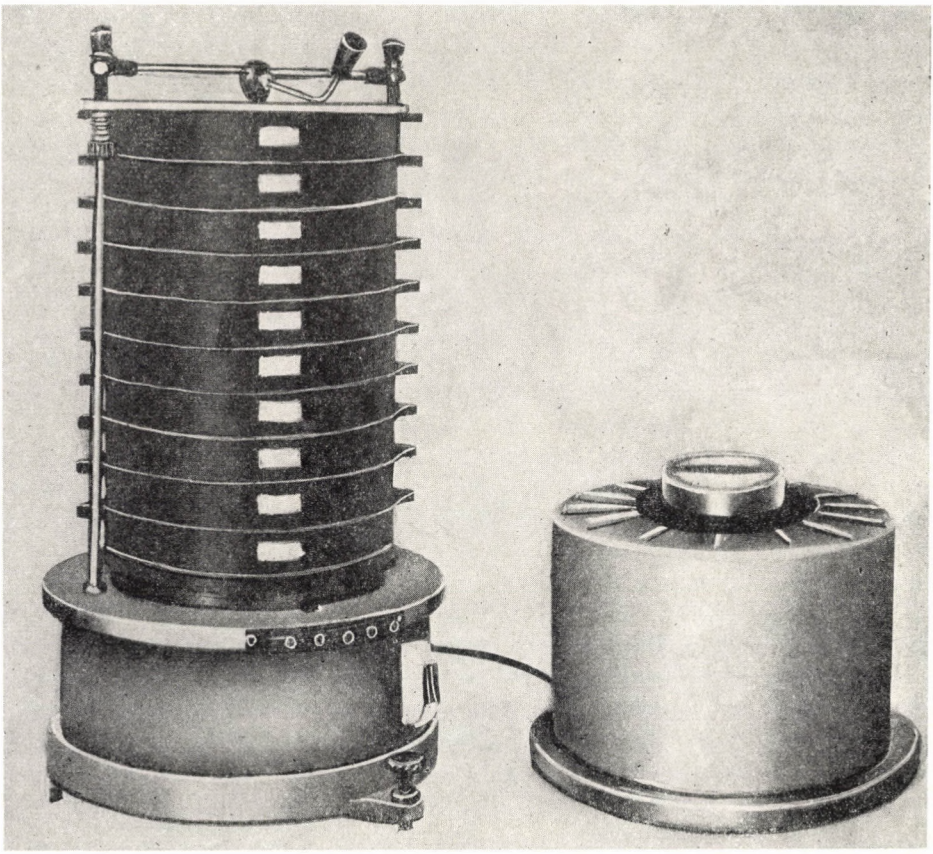


Fig. 15. Vibration grader with different size screens. The examined wheat sample can be broken up to a number of fractions. By this the evenness of grains can be measured (Labor Instrument Works, Budapest, Type QB-109)

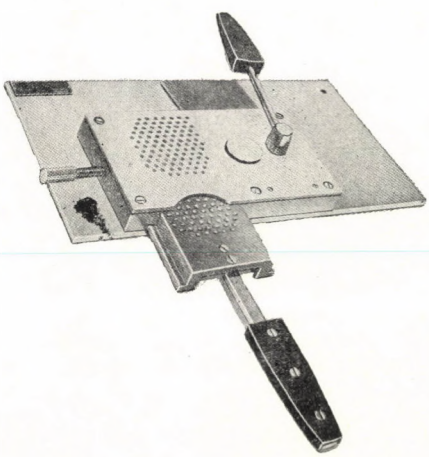


Fig. 16. Grain cutter to determine the glassiness of kernels (Labor Instrument Works, Budapest, Type QB-127)

according to the table of Morris (1962–1973) genes determining the protein content are found in all chromosomes except 2D and 4D, the number of genes determining glassiness is consequently high, therefore, a mostly multigenic transmission must be reckoned with.

From the point of view of milling too hard wheats are not desirable either. Therefore, besides glassiness, the *hardness of the endosperm* should be checked, too (Greenaway 1969). Hardness can be measured with the Brabender's instrument (Anderson et al. 1966). Shelef and Mohnesenin (1967) describe several methods by which the hardness of grains can be determined. The "Jelinek" apparatus is another means of determining the hardness of grains (Hyza 1968). Greenaway (1969) describes how to calculate the so-called "index of hardness": energy required for milling of 100 g wheat divided by the percentage of flour obtained. Samsonov and Ryzhkova (1973) determine the hardness of the wheat grain by the size of fractions obtained with grinding.

The practice of breeding has paid little attention to the hardness of grain so far. All the more interesting it was in the milling industry where the connection of hardness and flour output is thought to be important. Energy consumption is also taken into consideration though it is known that hardness and energy consumption do not parallelly change.

The close connection of *seed-coat percentage* and flour output is obvious (Pelshenke et al. 1966). The larger the kernel the lower the ratio of seed-coat, and if the layers are not thicker, then the percentage of the seed-coat will decrease too. The depth and shape of the furrow are important factors. The seed-coat, consists of epidermis, hypodermis, longitudinal and diagonal cell layers as well as of pellicle and nucellar epidermis. Its percentage value ranges from 9 to 11 per cent (Lelley 1958), considerable deviation may occur, however, in both directions. Two highly reliable micromethods are known to determine it. One of them is the improved Pelschenke technique (Lelley 1958), when from grains cut into pieces the endosperm and the embryo are extracted with lactic acid so that only parts of the seed-coat are left behind. The other method is suggested by Lazányi (1961): the kernels are germinated, then after 4–5 days of germination washed out so that only the seed-coat is left behind.

The heredity of seed-coat percentage has not been studied so far, although it is an important character and may show considerable varietal differences. From the point of view of specificity to variety hereditary differences can be reckoned with especially in the depth and shape of the furrow, for some 15–25 per cent of the total area of seed-coat covers this crease. Its depth is influenced by any environmental effect that causes sudden or forced ripening.

When determining the colour, distinction should be made between the *colour of the pigment strand of the seed-coat and that of the endosperm.* Milling industry generally prefers red-coated wheats because seed-coat remnants of this colour, mainly when present in semolina, moderate the chalk-white colour of flour. Nilsson-Ehle pointed out in 1908 that the reddish colour of the seed-coat and pigment strand, was determined by three dominant genes of additive effect. According to the table of McIntosh (1973) the symbols of the three genes are: R1, R2, R3. Their chromsome localization is:

R1 = 3Dα
R2 = 3A
R3 = 3B

The degree of the red-grain colour is judged visually. Its manifestation is influenced by the weather. Excess rainfalls at the time of ripening change the reddish colour into dull brown.

If there is not a single dominant R gene in the genotype then the colour of the grain will be light yellow, or almost white.

Unlike the usual colours of wheat grains there are wheats with blood-red and also green pericarp. These colours of grain are unacceptable in varieties used for milling purposes, but may be useful for the reliable distinction of feeding wheats.

There are slight differences in the colour of the endosperm, too. When manufacturing macaroni and vermicelly it is important that the endosperm be of dark yellow rather than chalk-white, because Italian paste made of darker flour is more attractive. Colour is connected with the carotinoid content of the endosperm (Lepage and Sims 1968). The lipoxidase content is also very important, as in watery solution it breaks down the carotinoids and whitens the Italian paste. To measure the colour substance in the wheat flour, Sims and Lepage (1968) elaborated a method based on photometry.

Genetic research concerning the transmission of the colour of endosperm is scarce. It is, however, supposed to be a hereditary property. The extent of influence exercised on it by the environment is not yet clear.

The *hl-weight* (bushel weight) of wheat is brought into connection with some milling qualities. With the change of grain size, glassiness, grain shape and endosperm texture the hl-weight is modified, too. Milling research has found a rather close correlation between hl-weight, flour output and ash content. The larger the hl-weight the higher the flour output and lower the ash content (Quisenberry 1967). It is a general experience that the ash content of flour obtained from 80 kg/hl wheat in the case of a 75 per cent milling efficiency is 0.30–0.40 per cent. When buying up wheat either in Europe or in the United States a hl-weight of 80 kg is regarded to be a mean value (Hoeser 1961). According to the investigations of Yamazaki and Briggle (1969) the hl-weight is an artificial value, it is not a property of the variety, since it is decisively influenced by the size of gaps between the wheat grains. This is, on the other hand, mostly determined by environmental factors. A connection between hl-weight and flour quality is also brought into question by Ghader et al. (1971). Its significance can be judged therefore from the point of view of trade only, its connection with the chemical properties of flour is not proved. There are special instruments to determine the hl-weight of wheat, they render a quick and early examination possible.

The above listed components of milling quality are separately studied by the practice of breeding. Complex evaluation can only be made by experimental milling. The main task of experimental milling was once to produce flour samples required for the examination of gluten quality and quantity as well as for baking test. Since high milling was successfully miniaturized, instruments imitating the industrial milling have been constructed whereby obtained flour from smaller

samples and examining the different qualities of flour directly have become possible. Brabender Quadromat Senior (Fig. 17) was constructed specially for this examination. With the help of this experimental mill milling quality can be reliably determined even in a 1 kg wheat sample, because in the Quadromat Senior all technical parameters are constant and it may produce four kinds of flour, thus, there is an excellent possibility for comparison (Schäfer 1960, Zucker and Brabender 1962). Another experimental mill Labor Frangimond QC 103 (Fig. 18) has been constructed for the same examination. It is fully automatized and furnished with a wheat slicer producing four kinds of flour and two kinds of bran.

To check up milling quality by experimental mills samples of at least 1 kg weight are necessary, thus, examination is suitable only for older, genetically homogenized strains.

Baking quality is important in the case of hexaploid hard wheats. Their flours supply the bakery products, first of all bread.

From the point of view of baking industry wheat is good when its flour absorbs the largest possible quantity of water and, besides, the bread made of it is of a large loaf volume spongy and of good taste. It is in this way that from a unit quantity of flour large loaves of bread of good texture, not easily drying and crumbling are made.

It is thus very important that the bread baked from the flour should be as large a volume as possible, and its crumb of uniformly spongy structure. Fajersson (1961) considers the volume of bread to be one of the most important standards of baking quality.

Again from the viewpoint of baking industry it is an advantage if dough handling is made quick. This requirement is influenced by the variety. Flours obtained from different varieties absorb various quantities of water and swell in different times.

The above listed properties are influenced by the mill too, which by the method of milling grading, and mixing the different fractions can promote the manifestation of the hereditary qualitative features of the wheat variety. Meteorological, agrotechnical and fertilization conditions have also some effect on baking quality, but the most important, fundamental determinants are fixed in the genotype (Pollhamer 1973).

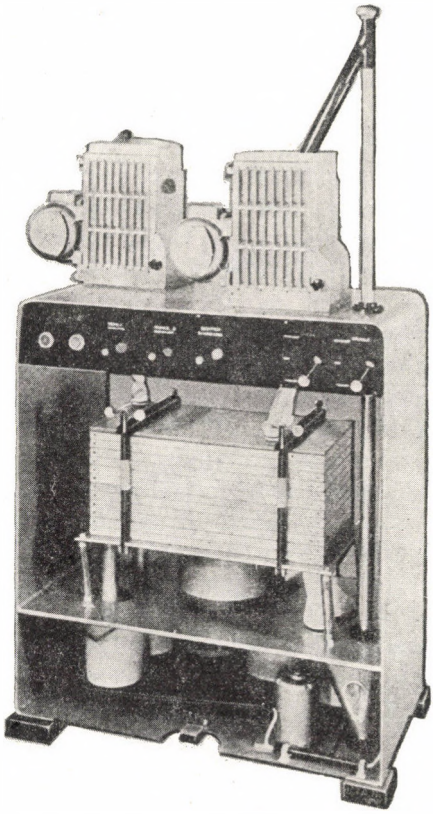
Hereditary factors determining the baking quality of wheat are:

1. quality of gluten,
2. quantity of gluten,
3. chemical properties of starch.

In Canada and in the United States, the largest exporters of quality wheat, in the qualitative evaluation of the wheat variety the quality and quantity of gluten are the main aspects, but starch quality and amylase activity are not neglected either (Spillane and McGovern 1966).

When evaluating a wheat variety first the quality of gluten is considered. Its characteristics are: rate of swelling, stretchiness, elasticity and rate of softening. All properties of gluten are hereditary characters though they are influenced by

Fig. 17. Brabender "Quadromat senior" laboratory mill. It consists of two roll mills and a plate-screen system (Brabender, OHG, Duisburg)



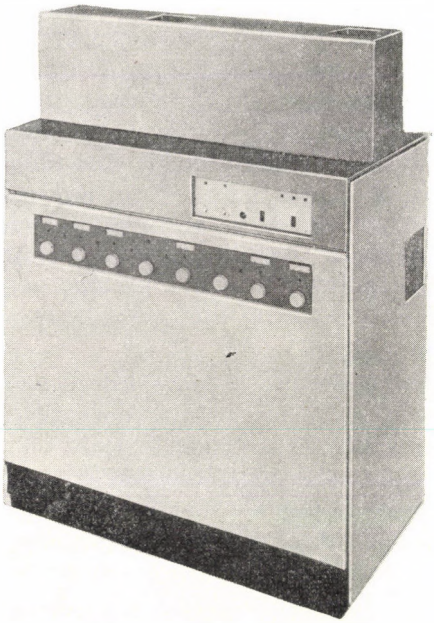


Fig. 18. "Fragimond" laboratory mill (Labor Instrument Works, Budapest, Type QC-103)

the environment. Temperature and precipitation conditions after flowering and fertilization, conditions of ripening, nutrient supply, balanced supplementation of nitrogen, all act on the quality of gluten (Pollhamer 1973). These modifying factors are effective, however, only within the limits determined by heredity (Schäfer 1962–63; Brouwer 1962; Jankowsky and Jankiewicz 1963).

The quality of gluten is decisively determined by the ratio of the two main components: ethanol soluble gliadine and insoluble glutenine. These two components consist of 18 amino acids and numerous fractions separable by electrophoresis (Hall 1966). The elasticity of gluten depends on the amount of gliadine. The ratio of these two components may be modified by environmental effects whereby the quality is influenced to some extent, but any kind of change is kept within limits by the genotype (Babadzanyan 1963). This applies primarily to the gliadine content considered by Lee and Ronalds (1967) to be so stable that they regard it as a genetic index of quality.

In the course of studying the gliadine and glutenine it was supposed that the lipids played an important role in determining the cementing force of the network of gluten developing in the dough (Hird 1963; Shiyomi and Fukunaga 1967). Lipids have been thought by some to contain gluten components suitable to determine the baking quality in a simple way (Stevan and Houston 1966; Seckinger and Wolf 1967). Fischer et al. (1966), on the other hand, pointed out that the lipids changed under the influence of weather and were not so important from the point of view of baking quality. Investigations made by Ponte and de Stefanis (1969) did not shed light upon the role of lipids either. Thus, the most reliable way of deciding the quality of gluten is invariably by the determination of the physical properties of wet gluten. Colour, shine, stretchiness, elasticity reveal much more than either the ratio of gliadine to glutenine or the lipids.

The relationship between the quantity of gluten and the total protein content is not yet clear. Gluten gives some 80 per cent of the total protein content. In spite of this from the total protein content no reliable conclusion can be drawn either on the quantity of on the quality of gluten (Springer 1964). Maes (1966) found connection between total protein content and baking quality but pointed out a negative correlation with the amount of water soluble proteins. According to Olered and Olsson (1969) the ratio of water soluble and insoluble proteins influences the stability of the dough. Fajersson (1971) found a positive correlation between total protein content and loaf volume being an important parameter of baking industry. These results prove that the examination of the quantity and quality of gluten gives a more reliable information about the baking quality than evaluation on the basis of the total protein content.

The baking value of flour depends on the starch quality too (Medcalf and Gilles 1965). The role of starch in influencing baking quality is not yet quite clear. The two components of starch are the spiral molecular structure, water-soluble *amylase*, and the branching molecular structure *amylopectin* which is scarcely soluble in water. Their role in determining baking quality is a subject of intensive research even today. According to Buttrose (1963) there are differences between starch grains in the structure of crust too which again affects baking quality. The theory that the stratification of starch grains is the result of a continuous sedi-

mentation and tension is not acceptable according to Innamorati (1963). Differences have been found between the varieties in the size of starch grains as well which may cause variation in the rate of decomposition of the grains (Lakalina 1968). The size of starch grains changes from year to year depending on weather conditions. No correlation has been found so far between gluten quality and starch content (Ringlund 1965).

The *sugar content of the endosperm* is not indifferent when baking quality is concerned (Dokič and Popovič 1966). The quality of dough is therefore also influenced by the sugar-forming activity of amylase (Greenwood and Milne 1968). Kulp (1968) emphasizes specially the role of pentosanes. According to Hristof (1969) baking quality is influenced by other enzymes functioning in the endosperm too.

Consequently, it is quite obvious that baking quality is the result of the coordinate action of gluten, total protein, starch and of various enzymes. As a complex characteristic it depends on environmental factors according to modifications in its components. Such environmental factors are: precipitation, temperature, nutrient supply, stage of ripening, etc. It is principally a hereditary character of the variety and its variation depending on modifying factors is likewise specific of the variety (Pollhamer 1973).

Genes determining baking properties have been identified in chromosomes 2A, 3A, 4A, 5A; 2B, 3B, 4B, 5B, 6B; 1D, 2D, 3D, 4D (Morris 1962–1973). Loci separately determining the qualities of gluten are found in chromosomes 1B, 4B, 7B; 5D, 7D. The gliadine–glutenine ratio is influenced by a gene in chromosomes 1BS. The quantity of gluten is controlled by loci found in chromosomes 1D and 5D. According to Maistrenko et al. (1973) in the development of quality particularly important role is played by genes in chromosomes 5A, 4B, 5D and 6D, as main inhibitory factors. Inhibitors of minor importance are found in chromosomes 7A, 3B, 5B and 2D. Very poor quality is produced by those in ditelo 2A, 2B, 6B, 1D, 3D and 7D chromosomes. Chromosomes 2B and 1D are also thought to be important to determine quality. According to Kerber and Tipples (1969) retetraploidization proves the decisive effect of D genome on baking quality, because its exclusion results in an intensive qualitative deterioration. According to Morris et al. (1966, 1968) the hardness of dough is modified by genes in chromosomes 4B, 7B, 5D, the volume of bread and quality of crust by those in 1A, 1B, 4B and 7B. The quality of variety Cheyenne was not influenced by the absence of chromsomes 2A, 2B, 2D and 7D. Inthe same variety genes exercising the highest influence on quality have been pointed out in chromosomes 5D and 7B (Mattern et al. 1973).

The heritability of loaf volume is according to Maistrenko and Troshina (1965), 60–90 per cent, the h^2 value of elasticity of gluten 71–74 per cent. The transmission of gluten quantity was found to be intermediary with a h^2 value of 24–44 per cent. The heritability of gluten quality ranged between 66 and 72 per cent.

Gluten quality was pointed out by Gotsova (1969) to be of an intermediate heredity though a positive transgression was also observed. In derivates of crossing Atlas 66, Triumph and Kaw, Lofgren et al. (1968) found 2, 3 and 4 factors respectively which determine quality. The transmission of baking quality is thus

of complex nature, the conditions of dominance are varying but the possibility of transgression can be taken into account (Balla 1973).

Intervention by inducing mutation may also be fruitful. Dunduk and Ermakova (1966) obtained good quality mutants as a response to ionized radiation. Jech et al. (1969) selected progenies of higher swelling value after X-ray and EMS treatments. Cerný (1965) used gamma irradiation to produce mutants of better gluten quality. Scarascia-Mugnozza (1966), Gotsova et al. (1971) too gave account of successful mutation treatments.

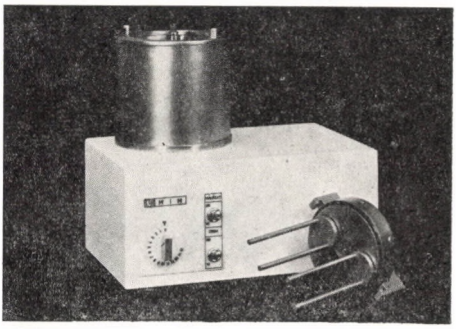
When improving baking quality a reliable method of selection is of special importance. The baking test is undoubtedly the most perfect method. Since the usual laboratory ovens are constructed for 1 kg bread size, this test can only be performed when the quantity of flour to be tested is at least 500 g (Hall and Olered 1969). This requires a wheat sample of minimum 1 kg. It is desirable, however, that selection for baking quality should be carried out much earlier, and on the basis of much smaller samples. This is made reasonable by the relatively high h^2 value. In some authors' opinion even the laboratory baking test is not satisfactory, because it differs from the industrial techniques (Gotsova et al. 1971), although for the usual laboratory procedure producing breads of 500–1000 g weight highly reliable instruments are available.

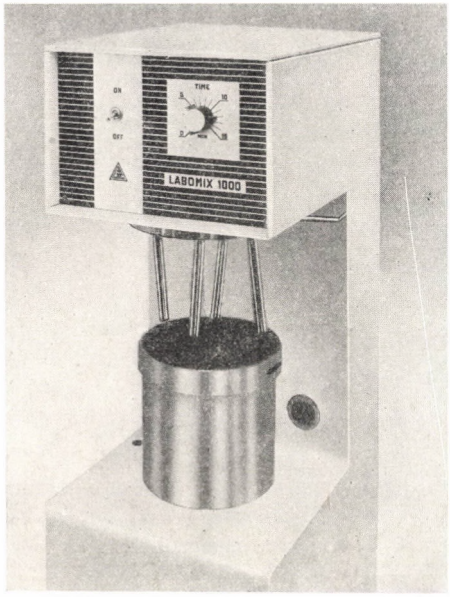
To eliminate subjective errors flour samples are kneaded into dough by laboratory kneading machines like "Labomix 500" (Fig. 19) and "Labomix 1000" (Fig. 20). Dough is raised in thermostat. The bread is baked in laboratory oven with strictly controlled temperature (Figs 21 and 22). Heights and widths of breads are measured by special laboratory instruments (Fig. 23). The precise volume of bread is determined by different size bread volumeters (Fig. 24).

Considering the relative reliability of the baking test some experimenters have tried to bake bread from smaller quantities of flour. Piech (1965) suggested the use of a microbaking test that required only 50 g of flour. Atanasova (1966) attempted to carry out an early quality testing by baking breads of 15 g size each. For this test 10 g flour is required. Melnikov and Kravets (1968) advised microbaking test from 5 g flour. In their opinion this microbaking is more reliable than either the Farinograf or the Alveograf (Melnikov and Rabinovich 1969*a*). For microbaking ovens with strictly controlled temperature are of particular importance (Fig. 21).

The baking test decides the water absorbing capacity of dough, the weight, volume and sponginess of bread, the colour and quality of crust as well as the taste of bread. The baking test is a comparative evaluation, as quality is difficult to standardize. The test, on the other hand, must be carried out accurately, according to strict prescriptions so that the comparison should really disclose the qualitative differences of flours. In the case of larger volumes flour samples used for the baking test can be milled with the Brabender Quadromat (Fig. 25), Laboratory Flour Mill (Fig. 26) or the high-milling Quadromat Senior (see Fig. 17), or the Frangimond mill (see Fig. 18). The flour yield is generally 60 per cent. It is particularly important that the samples should be milled with the same method because the result of the baking test depends to a great extent on milling.

Fig. 19. "Labomix 500" kneading machine to knead 500 g samples (Labor Instrument Work Budapest, Type 212)





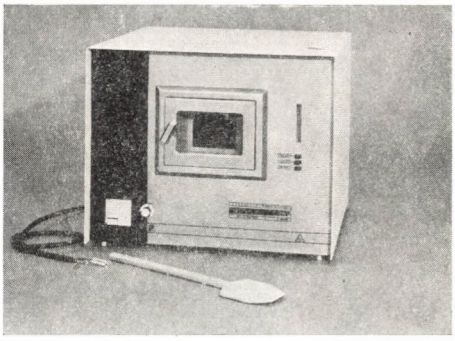


Fig. 21. Controlled temperature laboratory oven (Labor Instrument Works, Budapest, Type QA-226)

Fig. 20. "Labomix 1000" kneading machine for kneading 1000 g samples (Labor Instrument Works, Budapest, Type 212)

In spite of its reliability the baking test is not readily used for early selection even if baking is carried out with 5 g flour only. The reasons are:

1. The baking test is slow, that is, not suitable for mass examination.
2. The 5 g sample is still too large to make the baking test suitable for individual selection.

Therefore in order to establish baking quality some indirect laboratory methods had to be devised by which reliable conclusions could be drawn on baking quality.

To determine the amount of wet gluten the gluten has to be washed out. For mechanical washing various types of apparatus have been constructed. The promilograf serves for this purpose, too, but according to Waltl (1962) this method is not reliable. Samsonov and Zarova (1968) think centrifuging at 5500–6000 r.p.m. with a 2 per cent salt solution on to be a good method. The Aleuron Washing Apparatus (Fig. 27) of the Labor factory has been constructed for the purpose of washing out gluten.

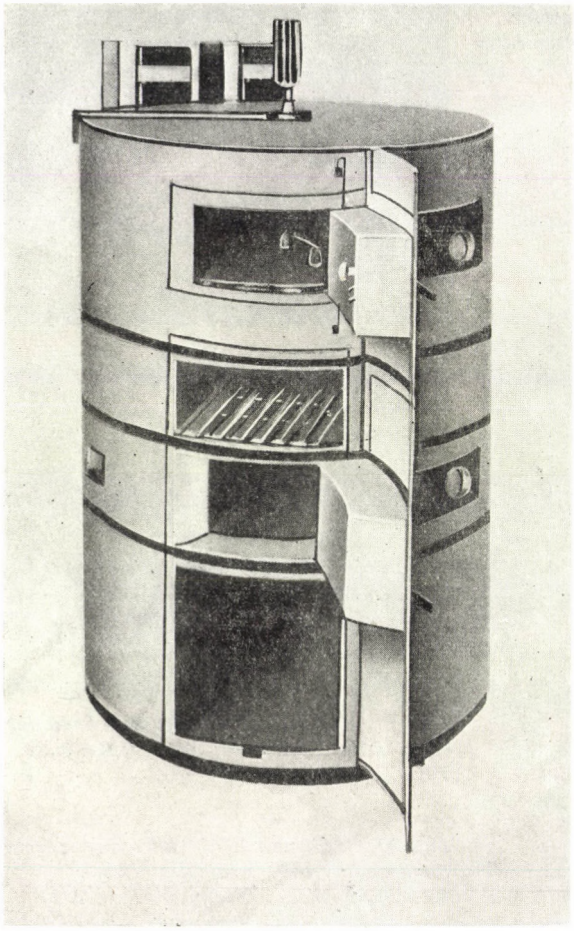


Fig. 22. Larger size laboratory rotary furnace (Labor Instrument Works, Budapest)

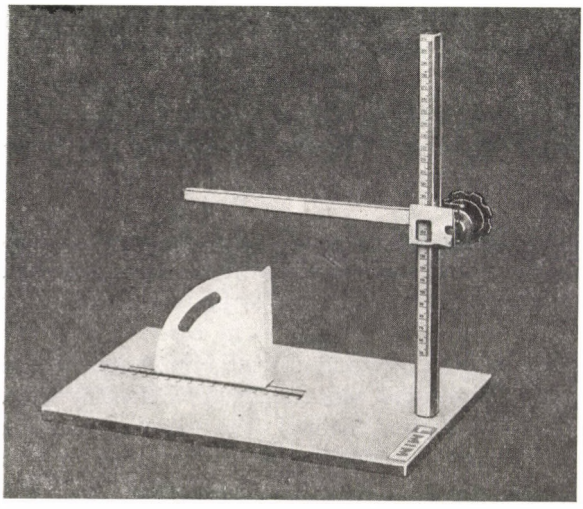


Fig. 23. Instrument for measuring the height and width of loaf (Labor Instrument Works, Budapest, Type QA-217)

Besides the quantity, the quality of gluten has to be evaluated as well. Berliner-Koopmann's lactic acid gluten swelling test gives the so-called "Quelzahl" used especially in Germany. Pollhamer (1964) considers the flattening of gluten to be an easily determined, reliable standard value. Schwarzbach (1965) suggests a micro-method of gluten quality analysis by which conclusion can be drawn on the quality already from 15 grains, and 1000 samples a day (Hodova and Schwarzbach 1966). Melnikov and Kravets (1968) suggest the measuring of expansibility, penetrability, plastometrability and swelling capacity. They expect to obtain a reliable value from the hydrochloric swelling test of gluten (Melnikov and Rabinovich 1969*a*).

The micro-methods of quantitative and qualitative gluten analysis cannot give a wholly reliable picture of baking quality since the latter does not exclusively depend on the gluten but on the whole product of milling. Micro-analytic methods providing information on certain properties of the whole milling product have therefore been elaborated, the earliest being Pelshenke's Schrottgehrmethode (Hoeser 1963). Some authors disputed the value of this method. Welsh and Normann (1972) consider the result reliable only when completed with a Mixograph.

Recently Zeleny's (1947) sedimentation test and its modified forms have been widely introduced. From the relation between the different sizes of sample and the sedimentation value Dewey (1963) arrived at the conclusion that the method gives useful information about samples of any size. Zeleny and Doty (1963) pointed out a close correlation between sedimentation value and flour yield percentage. Dewey (1963) even brought the bread volume and flour mixing index into connection with Zeleny's sedimentation value. Zeleny and Laubis (1964)

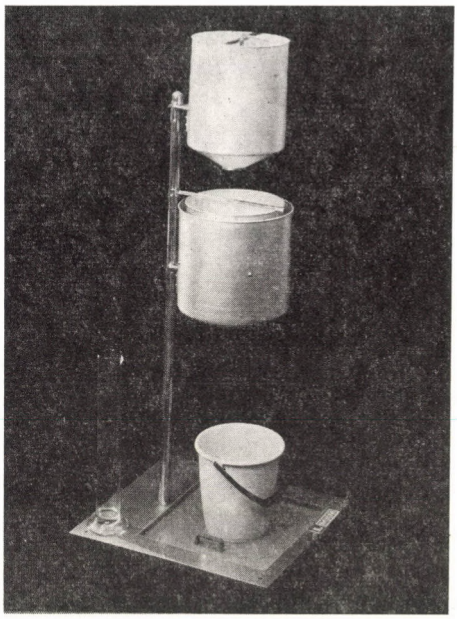


Fig. 24. Loaf volume gauge to 1000 cm³ (Labor Instrument Works, Budapest, Type QA-216)

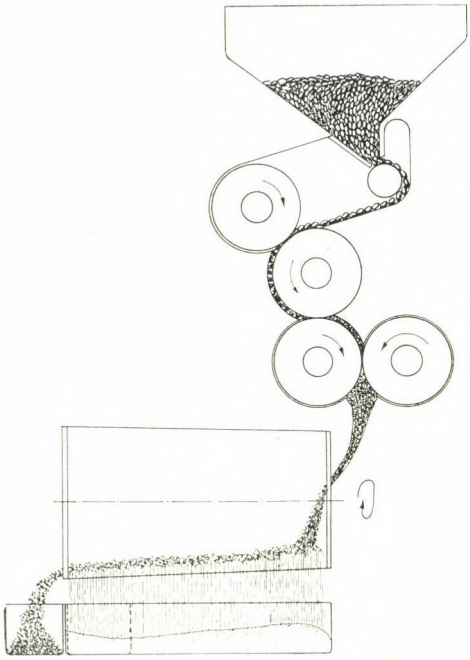


Fig. 25. "Brabender Quadromat" laboratory rolling mill with rotary screen (Brabender, OHG. Duisburg)

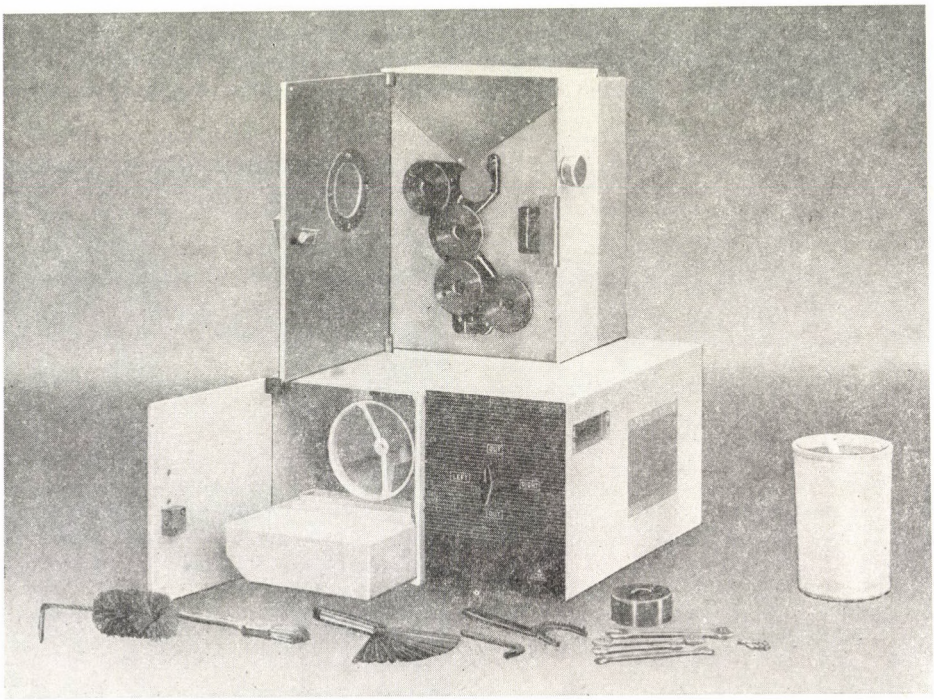


Fig. 26. "Labor small rolling mill" with rotary screen (Labor Instrument Works, Budapest, Type QC-109)

found correlation between mixing time, mixing tolerance and swelling index. A close correlation between the sedimentation value and numerous baking characteristics have been ascertained by Lebsock and Field (1964), and Sundermann et al. (1965), together with many others. The micro-sedimentation test of Zeleny requires only 0.32 g grinding product, thus already 1 g wheat may give a reliable result (Greenaway et al. 1966).

The usefulness of the sedimentation test in the practice of breeding has been confirmed by many authors (Sozinov and Pavlovich 1964; Zabel 1965; Atkins et al. 1965; Fajersson 1972). There are some, like Sellenberger (1963), and Mesdag (1964) who criticize the method. In spite of this, Zeleny's procedure is rapidly spreading in the practice of breeding so much that even the heredity of the "Zeleny value" has been studied already. Kaul and Sosulski (1964) found two partially dominant genes when studying the sedimentation value. The heritability of the property has been fixed at 97.68–92.13 per cent.

A method suggested by Melnikov and Kravets (1964) as well as Pumyanskij's procedure (Scherbina 1964; Gotsova and Berova 1964) are similar to the Zeleny's method. Both agree in principle with the Zeleny's test, with some alteration in the execution. To mechanize Zeleny's method Lelley (1973*a*) constructed a semi-automatic apparatus (Fig. 28).

In the sedimentation test the uniform milling of samples is an important aspect. Special milling apparatuses constructed for this sole purpose are the Brabender's small mill "Sedimat" (Fig. 29) or the Laboratory Universal Chopper (Fig. 30).

The sedimentation test is a quick mass method of qualitative evaluation which is a great help in the work of breeding.

Micro-methods aimed at studying the qualitative differences of grains inside the ear are in the course of development. They serve, however, mainly the purposes of physiological research (Tietze 1970).

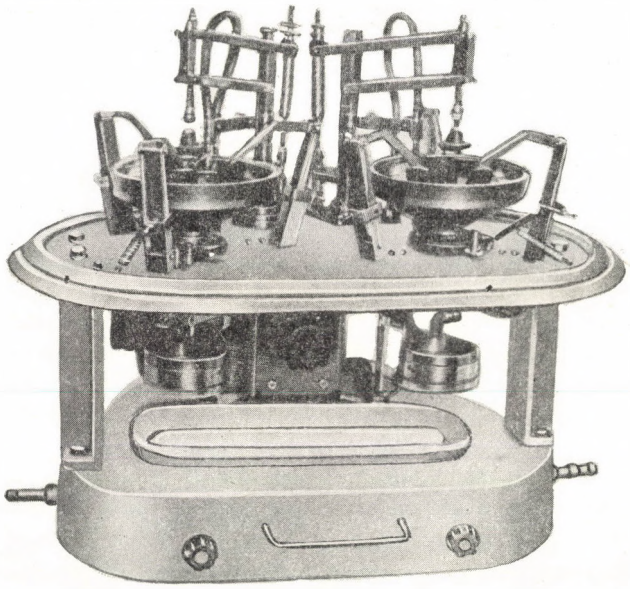


Fig. 27. "Aleuron Washing Apparatus" (Labor Instrument Works, Budapest)

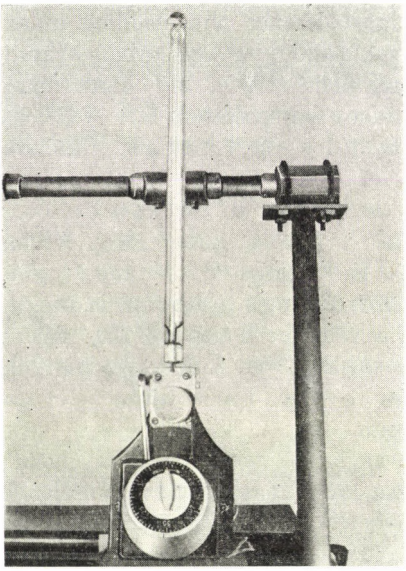


Fig. 28. Lelley's sedimentator for mechanizing Zeleny's sedimentation test (Photo by P. Lelley)

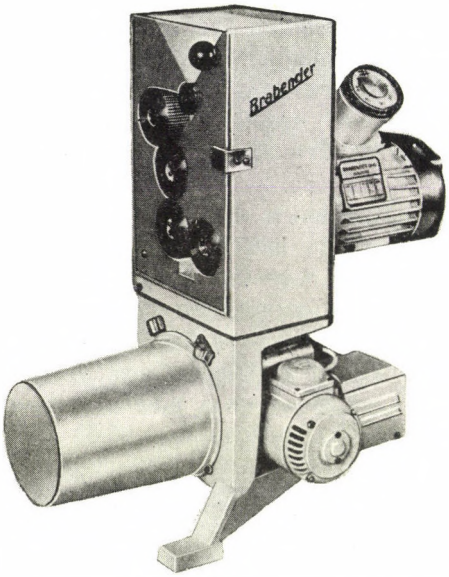


Fig. 29. "Brabender Sedimat" small rolling mill with rotary screen, to mill samples for Zeleny's sedimentation test (Brabender, OHG, Duisburg)

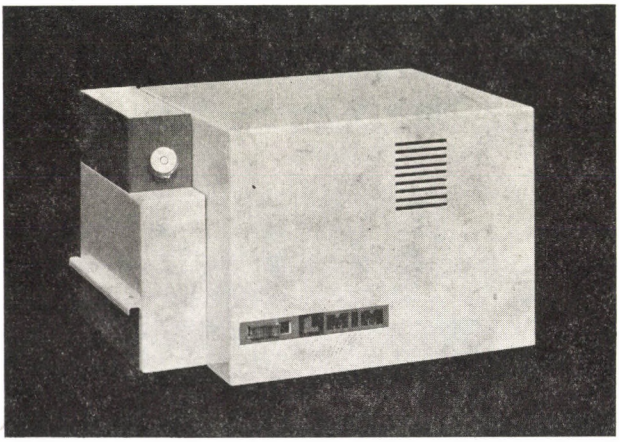


Fig. 30. "Labor universal grinder" for grinding small samples without a bolting work. It is made for milling samples required for Zeleny's sedimentation test, but bolting has to be solved separately (Labor Instrument Works, Budapest, Type QC-107)

Zeleny's procedure combined with the determination of protein content has found application in the commercial practice in the German Federal Republic and also in Austria (Toussaint 1964; Waltl 1963).

Highly reliable instruments of breeding laboratories used for the quick and detailed baking qualification of larger samples are the Alveograf and Mikro-Alveograf. The latter is operated with flour samples as small as 15 g in weight (Semenova 1965; Shogren and Finney 1963). The instrument is used mainly in the Soviet Union, Spain and France. A more widely used testing instrument is the Brabender Farinograph Resistograph (Fig. 31) which serves for examining

flour samples of 50 and 250 g weight. This instrument gives information about the water absorption of flour, swelling time, constancy and elasticity of dough and about the time of softening (Quisenberry 1967). The Valorigraph (Fig. 32) is operated partly on the same principle as the Farinograph and serves for testing samples of 50 g. The Mixograph is an instrument widely used in America; it measures the energy required for kneading based practically on the same principle as the Farinograph. A flour sample of 35 g is needed for the examination (Quisenberry 1967). By this method selection is made mainly for water absorption capacity (Heyne and Finley 1965). Mechanized and automatized evaluation means a great help in breeding for quality (Gilles and Sibbit 1965).

When evaluating the baking quality of flour the properties of starch should also be taken into consideration. Data provided by the above listed instruments include the properties of starch too, though not separately.

In a sense it is mainly the behaviour of starch and of the enzymes functioning in it that are examined by the Brabender's Fermentograph (Fig. 33) and the Labor Fermentometer (Fig. 34). Both instruments are suitable to determine the carbon dioxide-producing and gas retaining capacity of the dough. The first property reflects the rate of formation and quantity of carbon dioxide produced during fermentation, which is a result of certain enzymatic processes. The second, the gas retaining capacity indicates the extent of pressure the dough endures without tearing. This depends mainly on the elasticity of gluten. These examinations reveal certain information about the properties of starch, too. Frogner (1968) assumes a multigenic transmission of starch quality. The activity of amylase reducing the starch can also be measured. The determination of the "falling number" is a suitable method to measure this property (Hagberg 1959; Perten 1964; Tunger et al. 1969). There is strong evidence of the amylase activity as being specific of the variety (Mosonyi et al. 1973).

Selection for baking quality may be started quite early (McNeal et al. 1969). Kaul (1969) suggests to measure the total protein content and carry out the Pelschenke test in the F_2 generation. In the F_3 this is completed by the sedimentation test, and from the F_5 on milling and baking tests are performed.

The reliable evaluation of quality requires optimum conditions at the site of cultivation (Kalimenko and Chorba 1964; Primost and Rittmeyer 1964). From this point of view the soil quality, cultivation, fertilization, particularly the nitrogen supply, are equally important (Schober 1968*a*; Rybak and Arkusha 1971; Edelstein and Smirnova 1971; Pollhamer 1973). On irrigated areas where the effect of fertilization is somewhat different, quality should be judged from a special angle (Semin et al. 1969; Vertii 1972).

Quality of soft wheats: in this case the demands are lower. The physicochemical processes of manufacturing pastries, cakes and fancy biscuits differ from those in bread making. Here the dough is not raised with yeast, the extent of fermentation, if any, is very low, therefore the elastic, tough gluten is superfluous. During the process of manufacturing even the colour of the product is changed by different additives. Thus, the yellowish colour of the flour is no requirement. Flours of the lowest quality required by the baking industry are generally satisfactory for manufacturing biscuits. For the biscuit trade, therefore, varieties are

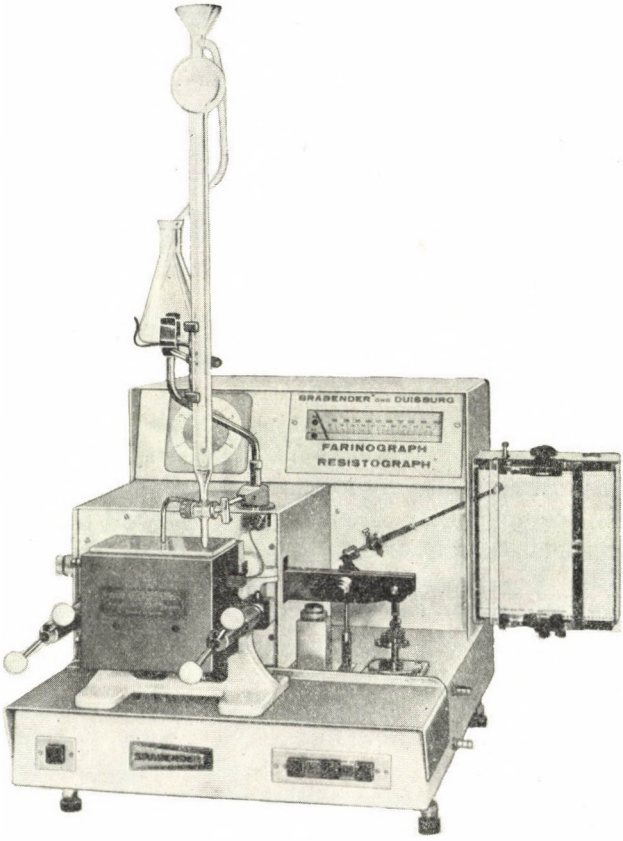


Fig. 31. "Brabender Farinograph-Resistograph (Brabender, OHG, Duisburg)

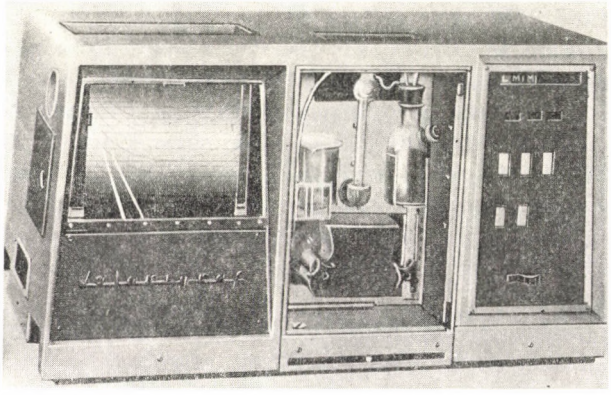


Fig. 32. "Valorigraf", a modified form of Farinograph (Labor Instrument Works, Budapest, Type QA-203)

not specially improved, nor are the combinations examined, although there is possibility of such examinations. The "micro-cookie test" is, in fact, a biscuit baking test. It is used in the first place to determine the mixing ratio of flour and the technology to be followed during the process of manufacture (Finney and Yamazaki 1950). The test requires 40 g of flour and is aimed at revealing how

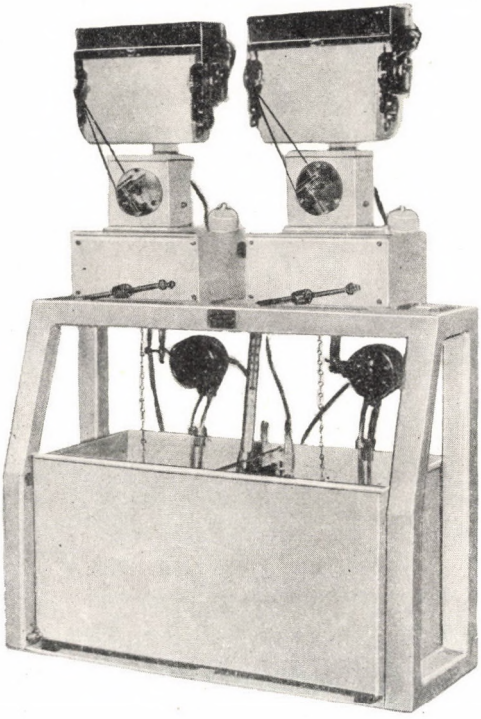


Fig. 33. "Brabender Fermentograph" (Brabender, OHG, Duisburg)

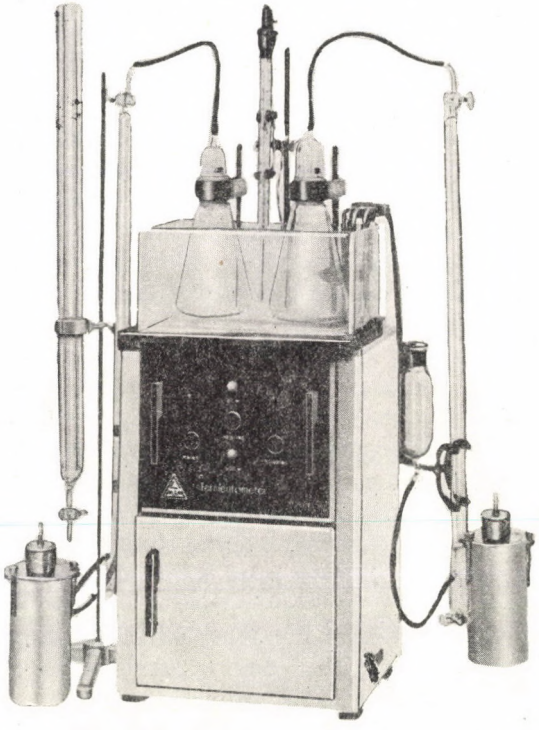


Fig. 34. "Labor fermentometer" (Labor Instrument Works, Budapest, Type QE-101)

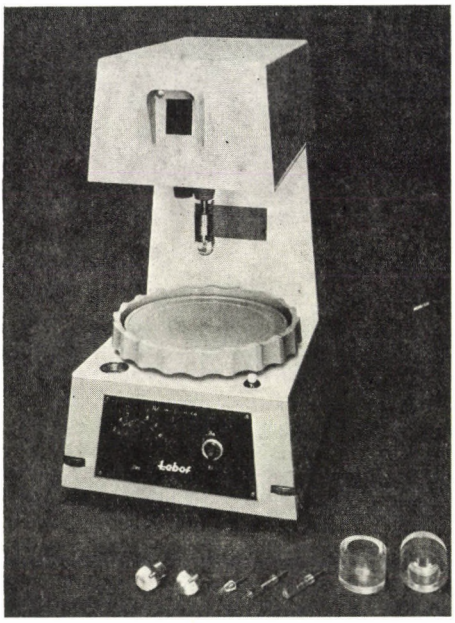


Fig. 35. "Labor penetrometer" (Labor Instrument Works, Budapest, Type QA-204)

high and wide the rolled dough out into uniform discs will be after-baking and what its inner consistency is like. The quality of biscuit manufacture can be checked by Penetrometer (Fig. 35), too, which measures the resistance of dough to the penetration of a definite shape figure. According to Finney and Yamazaki (1953) the hydration value of the flour is in correlation with the growth of biscuit diameter. Yamazaki (1953) thinks the "alkaline water relation capacity test" to be likewise suitable to examine the biscuit quality of dough. In the United States a "mini" variation of this method has been elaborated too.

Thus the production of varieties suitable for biscuit manufacturing is not a separate breeding objective. The biscuit quality test is important when evaluating hybrid derivates which, while of good agronomical characteristics, are not suitable for baking purposes. Genetic research has not studied the transfer of biscuit quality so far.

Paste used in vermicelli production contains only 29–31 per cent water, is not viscous, nor elastic, but tears and crumbles away. Its gluten content becomes but partly hydrated. The manufacturing process is quick, requiring only 20–25 min which is not enough for the gluten to get hydrated. Gluten remains thus crumbly, the dough is a hard material without a network of gluten in it. The degree of decomposition of carbon hydrates during the process of kneading is also lower than in bread baking. During resting only 2–3 per cent of the starch becomes saccharified, then the paste is placed in a press to assume a uniform consistency, following this the paste is pressed and cut. Pressing takes place under an atmospheric pressure of 150–250 by which the starch becomes to some extent hydrated and dextrinized. Macaroni is dried for some 18–24 h at 18–35°C. The finished product contains 11–13 per cent water.

Macaroni and noodles for soup have to meet the following requirements. They should be:

1. dark amber in colour;
2. pearly in lustre;
3. of smooth surface;
4. free of bubbles;
5. hard without breaking;
6. solid while boiled, should not soften;
7. compact, should not swell;
8. original in colour, should not fade.

The production of Italian paste like that requires flours which having absorbed a little water can be kneaded into smooth, hardy, easy to shape, not swelling, not sticky, not stretching dark yellow paste in a short time. It should be readily pressed and keep its shape after pressing.

For Italian production durum wheats are used. Of the properties listed above the physical ones depend on the quantity and quality of gluten, the starch quality as well as on the activity of enzymes decomposing the starch and protein.

The gluten content of the good macaroni wheat ranges between 10 and 30 per cent, is hard and does not soften in water (Quisenberry 1967).

The role of starch in the macaroni wheats is not quite clear as yet, but like in the bread wheats it is important for the consistency of the paste.

It is desirable that the amylase activity should not cause a rapid saccharification. Enzyme activity must not result in a quick softening of gluten, thus an intensive activity of proteolytic enzymes is not advantageous. The lipoxidase should not decompose the carotenoids for the paste becomes colourless (Irvine and Anderson 1953). Tiroxinase is an important enzyme because it increases the melanine content during the drying of the paste which gives it a darker shade (Kozmina and Kretovich 1958).

Of the properties listed it is the quantity and quality of gluten in the first place that can be determined by washing and a subsequent physical or visual examination. These data can be obtained already from quite small samples, an early selection may be carried out. Gluten is examined by the afore-mentioned method (see Fig. 27); the activities of the different enzymes are measured by the change of volume occurring in the paste while resting. After a test kneading the properties of the paste can be adequately measured with the penetrometer (see Fig. 35). Carotenoid content and a discoloration following its possible decomposition, respectively, are checked visually or by spectrophotometry.

Genetic investigations concerning the quantity and quality of gluten (see page 147) suggest a mostly multigenic heredity and varying dominance of the property. Data on the heredity of gluten properties are small in number (see page 147). According to Whiteside (1931) the carotenoid content changes with the amount of precipitation, too; in dry years it is higher. In colder years increased carotenoid formation was observed. Ausemus et al. (1946) and Braaten et al. (1962) found the carotenoid content to be of intermediary heredity and observed the

occurrence of transgression, too. Heritability ranged between 79 and 94 per cent. The hardness of gluten is considered to be of monogenic heredity. Swelling value is a character determined by 2–5 genes. From the point of view of the firmness of gluten it is an important parameter (Stuke 1962). It is of high (60–91 per cent) heritability. The elasticity of gluten is determined by more than one gene; its heritability ranges between 71 and 74 per cent (Braaten et al. 1962). Transgressive quality improvement has also been observed in a number of cases when crossing durum wheats. For the heritability of the complex feature of macaroni quality a 72–96 per cent value was obtained. In the case of durum wheats selection for quality on the basis of the high heritability values can be started quite early.

Biological values (digestibility) of wheat products depend on two factors: the total amount and the amino acid composition of protein. Starch, vitamins and mineral substances – though playing a considerable role – are negligible, since they generally are found in other human foodstuffs, too (Dumanovic and Ehrenberg 1968). Due to a general protein shortage in the world the total amount of protein has a great priority. Wheat is a mass food, therefore even a slight increase in the protein content would be of great importance in world economy. The amino acid composition is decisive from the point of view of digestibility and the rational utilization of protein.

Total protein content of wheat may reach or even exceed 22 per cent, but its average level is around 12–15 per cent. Protein content is a hereditary property, but depends on certain ecological conditions (Johnson, V. A. et al. 1973*b*). Shilbom (1962) in Sweden found the total protein content to be higher in spring wheats than in winter wheats. On an average, the tetraploid wheats contain a larger amount of protein than the hexaploids. Differences in the protein content were found between plants within the same population, and even between grains in a spike (Stuber et al. 1962). Besides the hereditary factors precipitation and temperature conditions prevailing at the time when the kernels are filled, as well as irrigation and nutrient supply equally affect protein content (Williams 1966; Hopkins 1968; Pollhamer 1973; Knott 1974*b*). Rinno et al. (1974) observed again the positive effect of nitrogen: the amount of protein increased, though the lysine content decreased. The favourable effect of nitrogen and phosphorus fertilization, both separately and combined, has been confirmed in numerous trials (Pollhamer 1973).

The ecological factors influencing the total protein content also include pathological effects, nevertheless, the total protein content is a hereditary character with a rather high heritability. Davis et al. (1961) found a 45–69 per cent, Kaul and Sosulski (1965) a 66 per cent and Hsu and Sosulski (1969) a 55 per cent heritability. They observed partial dominance, polygenic transfer and even the occurrence of transgression. In the variety Atlas 66, generally known to be a hexaploid wheat of the highest protein content, Morris et al. (1973) found loci determining the protein content in chromosomes 5A, 5B and 5D. Otherwise, according to the table of Morris (1962–1973) with the exception of chromosomes 2D and 4D, all the other 19 wheat chromosomes contain loci influencing protein content.

The complex nature of heredity can be concluded on from these data too. Yet, the possibilities of improving by hybridization are highly promising.

Since the heritability value is high and today a sample of 1–2 g weight is sufficient for a reliable examination, selection can be started early. The best known method is the Kjeldahl determination. Hecht (1964, 1965) criticized the applicability of the so-called Pro Meter quick method, nor did he consider suitable either the Feinsteins-Hart turbidimetrio-, or the sulpho-salicilic acid method. Schwarze (1966) suggested the use of a photometric method based on the biuret reaction. Recently, the automatized Kjeldahl method combined with computer was suggested by Davidson et al. (1969). Kaul et al. (1969) described a micro-method suitable for the determination of protein content in a single grain. Mosseberg (1969) gave account of the application of a method based on stain fixing and colorimetry. This method too can be automatized. The conditions of an early mass selection are thus provided for.

Mutants of higher protein content have been produced by induced mutation too. Kedrov-Zihman and Borisova (1963) obtained mutants with significantly increased protein contents after applying ^{60}CO treatment. Contradictory results were described by Sosedov and Vakar (1963). Schmalz (1973) found plants containing 1–2 per cent more protein in the variety Poros, especially among the Sphaerococcoid mutants.

Amino acid composition is important because of the lack of two essential amino acids: lysine and methionine. The lack of lysine causes mainly a fall in the digestibility of wheat protein, so that it is only 68.8 per cent of that of the protein of hen egg. In this calculation the error of the Oser method, namely, that it leaves the non-essential amino acids out of consideration and neglects the role of superfluous amino acids in causing imbalance was already kept in mind (Korpaczy et al. 1961). The amino acid composition of the egg-protein is the closest to the human protein, its lysine content being 7 per cent while that of the wheat is 2.9–3.9 per cent. Its methionine content is 4 per cent, while that of the wheat 2.4 per cent.

Thus, considering the role of wheat protein in the world economy the increase of lysine content is of paramount importance (Thielebein 1969). Lysine content is a hereditary character though may change under the influence of ecological factors (Simmonds 1962). According to Ivanko and Javor (1965), Abrol et al. (1971) the amino acid composition of wheat protein is influenced by some conditions of cultivation. High rate NPK fertilization increases the phenilalanine content but reduces the amount of lysine and threonine. Similar results were obtained by Pessi et al. (1971). Hojjati and Maleki (1972) observed the same effect when applying potassium and nitrogen fertilizers. Pokrovskaya and Morozova (1969) found the fertilizers to cause a greater change than the specificity of the variety. It is an other experience that the total protein content can be increased by fertilization, but the total lysine production cannot. According to Dzugaryan (1969) the amino acid composition may be influenced by some herbicides too.

Breeding has paid the greatest attention to lysine, one of the essential amino acids. According to numerous observations there are hereditary differences in the lysine content of different species of the genus *Triticum*. Lysine content is higher in the diploid and tetraploid species, like *T. boeoticum, T. dicoccum, T. timopheevi.*

It is the lowest in *T. macha* and *T. turgidum*. The components of wheat proteins like albumin, gliadin, globulin, glutenin, prolamin, differ in amino acid composition too (Halid and Pleskov 1965). According to Hepburn and Bradley (1965) if the nitrogen content in the kernels of different varieties is the same, then the amino acid composition of their proteins is likewise nearly identical. Conclusion cannot, however, be drawn on the ratio of amino acids from the nitrogen content (Robinson and Sageman 1968). The percentage of the lysine was found to decrease in the course of maturation. The protein of the aleuron layer differs in lysine composition from the other proteins of the grain (Kent and Ever 1969). The bran contains more lysine than the flour (Lawrence and Grant 1964; Pomeranz et al. 1966; Villegas et al. 1968).

The amount of lysine varies with the different lines of the same variety, and is not the same at the different levels of the spike either.

In general, there is no great difference in lysine proportion between varieties thus making the study of hereditary conditions difficult. On the average the proportion of lysine was 3.5–3.6 per cent in winter wheats and 3.2–3.9 per cent in spring wheats (Janicki 1963). Johnson,V. A. et al. (1968) examined three thousand lines in Australia and the United States and observed no considerable fluctuation, though they found lines with 4 per cent lysine content whereas the average is 3 per cent.

There are not but a few data available concerning the hereditary nature of lysine property. Since variability is low, the possibility of intervarietal hybridization is limited.

The methods of examination cause further difficulties. The comparative results of simpler, quick methods are not sufficiently exact. Determination by paper chromatography is rather quick and simple, but quantitatively not precise enough. Column chromatography while giving more exact results is a slower procedure. Thin layer chromatography is a simple method but cannot be used for quantitative determination. The paper electrophoresis though an accurate technique is of low capacity. The microbiological methods are precise enough, but their application is circumstantial and expensive. For this purpose *Pediococcus cereviciae*, *Geotrichum candidum* and the dependent strains of *Streptococcus faecalis* were put to trial (Block et al. 1956). Tkachuk (1966) attained good results with an automatic ionizing chromatograph. Bell and Mason (1970) described a quick chromatographic method which they considered to be good. Mattern et al. (1970) performed experiments with the amino acid analyzer, the Beckman Spinco Model 120 C. The instrument is very precise but its capacity is low. An examination method based on the behaviour of dependent mutant strains of *Escherichia coli* is described by Oguchova and Paskar (1972), which she believes to be useful in breeding for lysine content.

The large number of analyses performed in recent years prove that the importance of the task has been realized and efforts are currently made to develop a suitable method of examination. With a simple, reliable and quick method available breeding by crossing will certainly not fail to achieve results.

From the relatively small difference between varieties Johnson et al. (1971*a*) concluded that heredity is probably polygenic in nature. Since lines with higher

lysine contents have been encountered so far, transgressive segregation is likely to occur, too (Johnson et al. 1973).

Varieties with higher lysine contents are:

Nap Hal PI. 176217,
Pearl CI 3285,
Hybrid English CI 6235,
April Bearded CI 7337,
Fultz CI 11849,
Mintuki CI 12756 (–) (Johnson et al. 1971*a*, *b*).

Lysine content in protein percentage of varieties containing the largest quantities of lysine:

CI 13449 4.2 per cent
CI 9364 3.8 per cent
CI 13447 3.9 per cent

In the line containing the lowest amount of lysine, the percentage of protein lysine was found to be 2.2 per cent.

Up to a protein content of 16 per cent a negative correlation was found between total protein and lysine content. In spite of this negative correlation, if lysine production is expressed as a percentage of dry matter, the total lysine content increases with a higher percentage of protein. Namely, the protein content even attained 20–21 per cent while the lysine content only decreased from 4.2 to 3 per cent at the most (Johnson et al. 1973*a*, *b*). It follows that the comparison of lysine percentages in wheats with different protein contents is not, in fact, right. A so-called "adjusted" lysine reduced to standard protein and a protein unit should be taken as basis. In this way varietal differences would be yet more reduced. In 12 613 variety the lysine content thus determined ranged between 2.3 and 3.7 per cent (Johnson et al. 1969, 1973*a*, *b*). According to Johnson et al. (1972) the higher lysine content causes a decrease in the amount of the other, non-essential amino acids.

Genes similar to opaque and Flory 2 in maize have not been found in wheat so far. The rye, on the other hand, turned out to have a higher lysine content, so it is not unlikely that this property may be translocated to wheat (Janicki and Kowalczyk 1966). Varieties with higher total protein contents produce more lysine per unit area even if the lysine percentage of their proteins is lower. In this way an increase in the total protein content of the varieties may largely contributed to the solution of the lysine problem too (Johnson et al. 1970*b*).

Breeding through induced mutation may be successful too. Sharbati-Sonora was also produced by mutation from the variety Sonora (Swaminathan et al. 1969); the former exceeded the latter both in protein and lysine content. Mutants with a better amino acid composition have been obtained by other breeders, too (Zabenkova et al. 1972; Solonenko et al. 1972). Johnson et al. (1970*b*) hold the view that breeders should strive first for a high protein content followed up with

an increase in total lysine production because, at least for a while, this course seems to be more reasonable to adopt.

Wheat contains a considerable amount (0.3–1.6 microgramme) of *vitamin B.* Determination is carried out by biological methods (Gassmann and Haenel 1963). The B-vitamin content has been found to be specific of variety though it is influenced by weather conditions. B_2-vitamin content varies to a lower, B_1 to a higher degree (Schuphan et al. 1968). Sozinov and Zhukova (1967) pointed out that the grain contained a larger quantity of vitamin B than the flour, because tissues accumulating in the bran contain more B-vitamin. For the time being the B-vitamin contents is not important as far as breeding is concerned, though it should be borne in mind.

Quality improvement is a very important task of breeding, it is therefore followed with unrestrained attention and wheat varieties of excellent quality are always in demand. Šenborn et al. (1962) consider the Hungarian wheat varieties Bánkúti 1201 and Bánkúti 1205 to be of excellent quality. According to Boldea and Oproiu (1962) Ponca, Triumph and Bezostaya 1 are crossing partners with a high capacity to improve quality. Tarasenko and Tkachenko (1970) think the Soviet varieties Kavkaz and Aurora to be of good quality. According to Fajersson (1970) in the quality improvement of Swedish wheats important role was played by the Bánkúti 178 strain which was taken from Hungary to Sweden in 1928. Hänsel (1970) believes that the good quality of the Austrian variety Propsdorfer Extrem originates from a Hungarian local variety too.

The soft wheat Atlas 66 whose existence is due to the up-to-date examination methods is known to have the highest protein content. It was produced in 1953 by crossing (Redhard × No 11 [2] × Frondosa, at the Nebraska Research Station of the USDA. Among its crossing derivates many high protein content lines have been selected (Mattern et al. 1968; Johnson et al. 1971*a*, *b*). The lysine percentage of high protein content lines produced by crossing from Atlas 66 is not outstanding. In the variety Atlas 66 the high protein content is determined by two genes. One of them is combined with resistance to leaf rust (Johnson et al. 1972).

On the basis of investigations made by the All Union Research Institute of Plant Growing, Leningrad (VIR) a number of Australian, Argentine, Indian, Canadian United States and Hungarian varieties have been found to be of high quality. Local varieties having developed on the central chernozem area of the Northern Caucasus are considered to be of particularly good quality (Rabinovic et al. 1968).

The question of quality is closely affected by the statement of Sibbit (1971) that the quality of semi-dwarf wheats generally does not attain that of the standard height wheats. The explanation of the relationship is not yet clear. It can be supposed, however, that there is no incontrovertible negative correlation between quality and plant height.

We should refer here to the long since supposed negative correlation thought to have been proved several times between yield potential and quality (Boldea et al. 1962; Hänsel and Ehrendorfer 1973). The "quality" of wheat is an extremely complex group of characteristics rather than a homogeneous property, apart from the different demands on it. The overall assumption of a negative correlation

cannot thus concern the whole complex of characteristics. Potential productivity is likewise a complex character which also excludes the possibility of a simple negative correlation.

True, that among the up-to-date highly productive varieties outstanding quality seldom occurs, though there are exceptions e.g. Bezostaya 1 and Mironovskaya 808. It should be pointed out, at the same time, that combining high productivity with excellent quality is an increasingly difficult task. Thus, above a certain level the two properties may be truly in negative correlation, but even then perhaps it is not an unsurpassable obstacle.

Chapter 12 **Breeding methods**

Apart from some special procedures the practice of breeding imitates, in fact, processes taking place in the course of natural evolution; hybridization, mutation and selection. Though the difference is great, because while natural hybridization and selection are chance processes, and spontaneous mutations occur but very seldom, the breeder carries out purposeful crossing and multiplies the frequency of mutation. Furthermore, breeding provokes the environment and modifies it in such a way as to promote selection in a planned direction. Breeding has, besides, such tools of selection which are missing from the natural environment, e.g. chemical analyses and various laboratory or green house techniques.

Breeders well-versed in theory try to realize definite objectives in which they are assisted by other branches of science like genetics, cytogenetics, biochemistry, mathematics and so on. To be successful the breeder has to make subjective observations too which becomes efficient only after years of practice.

For precisely formulating breeding objectives we should be aware of all requirements of agronomy, milling, baking and pastry industries as well as the demands of human nutrition biology. To realize such a manyfold task obviously a collective activity is needed so the best qualified experts should deal with their respective lines. Therefore, wheat breeding today is generally a team work although the result – as shown by many examples – depends mainly on the head of the group who organizes the activity and has a good working knowledge of his subject. That is why the best known varieties are named even today after persons like Rosenstiel, Vogel, Borlaug, Lukyanenko, Remesio, Wienhues, Fajersson, Hänsel and others. In the future the practice of breeding will increasingly become a collective activity, because the varieties go beyond the borders of countries and the competition will be all the more sharp. To exceed the properties of current varieties will be more and more difficult, at the same time – in a paradox way – the life of the varieties becomes shorter although the demands of producers and industry are constantly increasing. In a competition like that only a highly qualified team is able to keep abreast.

The first task is to precisely define breeding objectives. Then it has to be decided by what methods they are likely to be realized in the shortest possible time. There is a close connection between the task and the method chosen.

In carrying out the breeding tasks the wheat breeder can choose between the following alternatives:

1. Genetic combination produced by crossing.
2. Utilization of the possibility inherent in the hybrid vigour.
3. Induced mutation.
4. Inducing adequate variation.

The overwhelming majority of the commercial varieties are the results of neocombination produced by hybridization. A special form of crossing is the hybrid wheat production which has focused the attention of a fairly large number of researchers in the last ten years, but still it remains to be seen whether the hybrid wheat production will have any practical result. By induced mutation deficiencies which reduced the values of varieties have been eliminated in several cases. Adequate variation has been induced so far only when producing winter wheat from spring wheat, or vice versa, and that mostly in the Soviet Union.

Hybridization is a method of breeding by which all breeding objectives can be realized. Its possibilities are:

1. intervarietal hybridization,
2. interspecific hybridization,
3. intergeneric hybridization.

The intravarietal hybridization has been proved to be hopeless (Boháč and Kuzmiak 1968), therefore it is no longer in use.

The most frequently applied method is the *intervarietal crossing. Interspecific crossing* is only used for special purposes. It is only in exceptional cases that the method of *intergeneric* crossing is made use of. An outstanding result of the latter is *Triticale. Triticale* breeding is, however, a separate chapter of the history of cereal breeding and will not be discussed here.

Intervarietal hybridization is based on the careful choosing of components. In most cases one of the components, generally the one used as maternal partner, is a domestic variety well adapted to local conditions, but some of its properties must be improved or a new type is to be developed from it. The other component or components are varieties known to have in their genotype the genetic information required for a desirable neocombination. The choice of crossing partners decides in advance the possibility of success or failure, that is why special care must be taken when choosing them.

In choosing the crossing partners great help is offered by the wheat variety collection available almost in every country. In addition, there is a possibility of international co-operation. So crossing partners can be obtained from the largest variety collection of the world, the A.R.I.P.G. (VIR) Leningrad (Soviet Union), or from the USDA international variety collection, Nebraska (United States). Further useful assistance may be obtained from the International Wheat Rust Testing Center, Nyoro (Kenya), or from the Food and Agriculture Organization of the United Nations World Catalogue of Genetic Stocks. On request these organizations send the varieties included in their catalogues and supply detailed information on them.

Before using them the varieties obtained from the above-mentioned institutions or other places, should be strictly controlled at least for a year under the local conditions of breeding to make sure that the changed environmental conditions did not cause certain effects making the utilizability of the crossing partner questionable. In the previous chapters it was clearly shown how far the environmental factors may influence the realization of the hereditary characters. When

analyzing crossing partners it is on individual observation rather than on characteristics shown by the dense stand that emphasis is laid. Dense sowing is in the first place an adaptation study which may lead to the introduction of a new variety. If a new variety is as good in dense stand as competing with the one to be improved, then it is worth grown directly, without hybridization. On the other hand, a variety which in thick stand is inferior to the one to be improved may still be an excellent crossing partner. Thus, when choosing crossing partners an individual evaluation most reliably made of plants sown one by one at a plant distance of 10–20 cm and row distance of 30–50 cm provides better information. For this purpose 3–5 m long single seed drill plots with 1–3 rows are suitable. It is advantageous of the other crossing partners are sown in the same way whereby the possibility of visual comparison is provided for.

Crossing population can be obtained from the so-called gene banks, too. The First World Gene Bank was established at the Cornell University in the United States of America (Jensen 1962). However, in the gene bank the population mixtures of different crossing derivates are stored. The genetic composition of such a material is generally dubious, and can therefore be used for purposeful crossing only after a longer period of observation, disjoining and evaluation. This considerably lengthens the time of a systematic cross-breeding activity.

Having chosen the crossing partners the method of crossing is decided. Wheat breeding can choose between the following possibilities:

Single cross $A \times B$
Three-way or top crossing $(A \times B)\ C$
Four-way or double crossing $(A \times B)\ (C \times D)$
Multiparental or sequential crossing $((A \times B) \times C) \times D \ldots$
Incomplete back-crossing $(((A \times B)A)A)A$
Complete back-crossing

$A \times B$
$F_1 \times A$
$BC_1 \times A$
$BC_2 \times A$
$BC_3 \times A$
$BC_4 \times A$
$BC_5 \times A$
$BC_6 \times A$
$BC_7 \times A$
A (99.8%)

The artificial crossing of autogamous wheat is described in detail in every handbook. In essentials the principle of execution is unchanged though crossing must be performed many times to realize the increasingly difficult tasks; therefore, the acceleration of the crossing operation has recently been attempted by a number of authors who try to increase the percentage of fertilization, too. The application of gametocides has failed so far to replace castration with pincers (Jos and Singh 1967). Mass castration remains thus to be solved. Besides the usual means of

artificial pollination with pincers and brush, some simpler methods promising better seed setting have been tried out, too. One of them is to cut the pollinating spikes of the pollen donor and isolate them together with the spikes of the recipient so that the cut stalks are places in a vessel filled with water. By another method the maternal spikes are castrated with pincers and isolated, then when the flowers have opened the spikes of the pollen donor are cut and the pollen poured from them into the opened isolator, then the isolator is closed again.

The seed setting percentage of artificial pollination is varying but seldom exceeds 60 per cent, moreover, in most cases it is substantially lower in spite of the fact that in varietal crossing there is no genetic incompatibility. Low percentage can be explained by possible injuries caused by the intervention itself, and also by unfavourable microclimate inside the isolators. Seed setting is better when fresh pollen is used. Pollen directly shed from the anthers are the most effective ones. According to Kováčik and Holienka (1962) the wheat pollen loses vitality in about 20 min and after 60 min it is practically inactive. The pistil, on the other hand, is susceptible even after 8–10 days. A temperature of 20–25°C and air humidity of 60–70 per cent are most favourable for fertilization. Temperatures above 25°C and lower than 50 per cent air humidity cause disturbances in fertilization. The pistil is most susceptible 2–4 days after appearing among the glumes. Under favourable conditions the pollen begins to germinate 3–5 min after reaching the stigma. Favourable temperature and air humidity accelerate the growth of the pollen tube, which reaches the egg-cell within 18–20 min (Perunova 1965; Kihara and Hori 1966). According to Palilov and Dylyanok (1964) stimulative fertilization may also occur in wheat causing occasional shifts in the segregation ratios. From the point of view of successful crossing the development stage of anthers is a very important factor (Rajki-Cicer 1962). Kubarev (1963) proves the advantage of additional pollination with the 9 per cent higher rate of seed setting he obtained by this method. These aspects have to be taken into consideration especially when carrying out artificial pollination in greenhouses, as in this case seed setting is mostly inferior to that in the field. This phenomenon is due to the undeveloped state of anthers rather than to the deficient susceptibility of stigmata (Lelley 1972, unpublished data).

Data on the selectivity of fertilization are published by Abramova (1964), Kozera (1966) and others. Friend (1964) attributes selectivity to differences in peroxidase, amylase and catalase activities. Concerning the trend and extent of selectivity no reliable data are available. According to Puhalskii and Ronis (1969) selective fertilization depends on the pollen and not on the seed parent, it is thus the pollen that makes the selection. The problem of selective fertilization requires further investigations not only because of its possible disturbing role in crossing, but from an evolution-genetic point of view, too. In the work of breeding by crossing no attention has been paid to it which does not mean at all that it is in fact of no importance.

Single-cross serves to solve less complicated tasks, or by crossing two valuable varieties to produce an intermediary neocombination in which the largest possible number of desirable properties of the two parents result in transgressive segregation. In this method pollination of many flowers has the advantage that from an

F_1 generation of high individual number a larger F_2 population can be raised which increases the possibility of selection and helps to recognize the transgressive segregants.

The F_1 generation in mostly sown without selection at a wide spacing one by one in order to obtain the largest possible number of progeny, and the parents are sown in the same way side by side with them, in view of a detailed morphological and phenological comparison. This comparison is very important because from the manifestation of certain properties in the F_1 conclusion can be drawn on the prospective neocombinations and the conditions of dominance determined for certain characteristics. Selection in F_1 is only justified if properties suggesting an origin of accidental selfing or undesirable cross-pollination appear in some plants. They must be discarded before flowering, because later they tend to obscure the trends of segregation. If the crossing partners are "homozygous" varieties, the F_1 generation must be phenotypically balanced. The success of crossing is especially easy to forecast when the pollen donor crossing partner possesses a visually perceptible dominant character.

When raising the F_1 generation it is important to exclude any possibility of an outcross, otherwise the trend of segregation will be confused in the F_2 generation (Dorofeev 1968*b*). The extent of cross-pollination depends partly on genetic, partly on ecological effects and may even occur at a frequency of 0 to 3 per cent. If F_1 is raised in a greenhouse at an accelerated rate, outcross is easier to eliminate. In the nursery, on the other hand, it is advisable to sow it under isolated conditions. Comparison with the parents is desirable with a view to a possible hybrid vigour effect, too. That is why it is important that the parents should be sown in the same way as the F_1 generation. According to Borojevič, S. (1963) the extent of hybrid vigour found in F_1 indicates what the prospects of the crossing population are.

Single-crossing is, in fact, the genetic synthesis of two partners for the purpose of finding the best neocombinations or transgressions. Actual selection should only begin from the F_2 generation.

In the case of *three-way crossing* only reliably hybrid F_1 plants can be used for the second crossing. The use of this method is justified when the breeding objective can only be realized with the genotypic synthesis of three varieties.

It can be carried out in two ways:

1. $A \times B$
   $F_1 \times C$
2. $A \times B$
   F_1
   F_2 (selected)
   .
   .
   $F_x \times C$

According to Borojevič (1968), Potocanac and Engelman (1969) in this method of crossing special care should be taken in choosing the C partner because the result mostly depends on this.

When crossing according to scheme 1, the number of F_1 plants required is not high. Thus, in the first crossing it is enough to pollinate a limited number of flowers. In the case of scheme 2, the F_1 generation had better consist of a higher number of individuals in order to obtain a larger population for the subsequent selection. The individual number of the crossing population to be used in the different methods depends on the prospective frequency of the expected neocombination. The higher the number of properties for which a favourable recombination is to be attained, the larger the individual number of population required for crossing. Namely, the number of possible genotypes is very high. With the 3^n rule taken into consideration where n = the number of differing properties, in the F_2 generation the number of possible genotypes is 243 in pentahybrids, 2187 in heptahybrids and 59 049 in a dekahybrid. Of genotypes as many as that the possibility of selection is very high and this possibility should be exploited.

If the realization of the breeding objective set requires the synthesis of properties from four varieties, then the quickest method is the *four-way crossing.*

In the first year crossing is carried out twice, and in the second year the F_1 plants of the two combinations are crossed. The method can be modified in such a way as to make selection of the F generations for one of two years and carry out the second crossing afterwards.

A × B		C × D
F_1		F_1
F_2		F_2
F_3	×	F_3
	F_1	

This method of crossing is a more complex operation and is suitable to solve complicated tasks. During the first selection the emphasis usually is laid only on one or two important features and detailed selection is only started after the second crossing. In this method Hänsel underlines the substantial increase of variability. According to Imrie (1969) the best results have been obtained with this method.

Multiparental sequential crossing is again suitable to solve complex tasks and to develop a manyfold resistance (Roane 1973). This method too is used in cases when the population originating from two- or three-parent crossing does not yield the expected result, or when a property has disappeared during selection and has to be introduced into the genotype by further crossing. For example, if after crossing A × B the quality needs further improvement, it can be attained by top-crossing with variety C, but if after a reselection of the population with the simultaneous improvement of quality winterhardiness turns out to have decreased, then this property has to be introduced into the genotype by further top-crossing with variety D. Breeding by sequential crossing is a lengthy process because after each crossing one or two years of selection is necessary.

The method of sequential top-crossing is applied without intercurrent selection too. The hybrid population is multiplied for some years by the so-called "bulk" method, and selection is only carried out afterwards. This is also a lengthy though somewhat simpler procedure.

There are different variations of the above-listed ways of crossing, but an over-complicated crossing programme does not always serve the final aim.

1. The population of unknown genetic composition increases so that it can only be selected superficially and at random.
2. Possible recombinations in the crossing derivates cannot be surveyed.
3. The procedure is time consuming which means a disadvantage in the increasing competition of breeding.

The *backcross or "BC" method* was put into limelight by Harlam and Pope as early as in 1922 (Briggs 1958). Briggs applied it successfully in 1930 and ever since it has been used in breeding work, hybrid wheat production and also in genetic research. It is, in fact, a form of gene or gene block substitution when from the donor variety genetic information determining a single property is transferred in the recurrent variety whereby the genotype of the latter is nearly completely restored. The full procedure requires eight backcrosses to restore the recurrent genotype in 99.8 per cent. The method is simpler if a dominant property is transferred but takes more time in the case of substituting a recessive property. The main point is to make selection for the characteristic to be substituted before each occasion of backcrossing. Individuals showing this property can be used for crossing only. Dominant characteristics can be identified in the F_1 and all BC generations. Recessive characters can only be found in F_2, and are more difficult to identify in the BC generations. Substitution of a recessive character consumes more time, therefore Briggs (1958) suggested the introduction of the incomplete BC method, so after 2–3 backcrosses when the recipient genotype has been restore to some 93 per cent, the selected lines are selfed. The efficiency of the method was confirmed by Borojevič (1965). If the aim is to produce a multilinear variety (Borlaug 1958) which consists of a mechanical mixing of isogenous lines resistant to different pathogen races, backcross breeding must be completed so that the other properties of the lines should be identical. Simple backcross breeding serves in the first place for the purpose of transferring a single desirable property to some known excellent genotype (Rudorf 1965).

A more complex variation of backcross breeding is the *convergent method*, when from a number of donor varieties different genes should be substituted in a recurrent genotype so that more than one parallel backcrosses are carried out simultaneously. With the BC_7 generations selfed nearly isogenous lines are obtained which contain a property of each donor genotype. They are then crossed, and a recurrent genotype selected in which all substituted genes can be found. Convergent breeding is the most systematic method to produce a new cultivar.

The rate of backcross and convergent breeding can be accelerated. In a properly equipped greenhouse two generations of winter wheat in a year, and occasionally five generations of spring wheat in two years can be raised. In modern growth chambers or phytotrons accelerated change of generation can be attained when the vegetative period is reduced to 60 days for spring wheats and 80 days for winter wheats. This means that the number of generations raised in a year may be 6 in spring wheat and 4.5 in winter wheat. Mukade et al. (1973) keep the

plants at a constant temperature of 25–30°C after pollination. After 15–20 days the spikes are cut, dried for two h at 45°C, thrashed, then the kernels are soaked in a 1 per cent solution of H_2O_2 at 25°C for 16–17 h. Then they are cooled down to 11°C and kept for 30 h on filter paper, then germinated in tap water on germinating paper, spring wheat at 25, winter wheat at 11°C. On the fourth day from the beginning of the treatment in winter wheat the pulmula and in spring wheat even the radicula appear. At the one-leaf stage the plants are vernalized at 8°C under constant illumination. According to Bühring (1973) in the case of prolonged or constant illumination 3000 lux of mercury vapour illumination is enough for the differentiation of the spike. With short-day illumination 20 000 lux of light is necessary.

Intervarietal crossing generally has no genetic difficulties. There is a phenomenon, however, which may jeopardize the result of hybridization, and in extreme cases even cause the inviability of F_1 hybrids. This is the *hybrid necrosis*. The phenomenon was first described by Caldwell and Compton (1943). Two types of hybrid necrosis are known. In the first case the leaves are of dull green colour, though the chloroplasts do not shrink, their content conglomerates. In the second case the leaves turn yellow and the chloroplasts become very small. The first case is more dangerous (Toxopeus and Hermsen 1964). The hybrid necrosis is caused by complementary dominant genes (Hermsen 1963*a*, *b*; Kulsherestha and Rawat 1968), which are latent separately in the two parents, but if they meet in the F_1 generation necrosis symptoms appear and may cause destruction.

Nishikawa (1967) supposes that all three genomes of the genus *Triticum* may contain necrosis genes. Hermsen (1961) marked the genes by the symbols Ne1 and Ne2, and they were localized in chromosomes 2A and 5B (Hermsen 1963*a*). Their effects depend on the genetic background and are influenced by ecological factors, too. When hexaploid or tetraploid partners each containing a necrosis gene are crossed, then in the F_1 generation various degrees of necrosis may occur depending on whether the genes are of weak (w), medium (m) or strong (s) activity. To detect the necrosis genes extensive investigations have been made by Hermsen from 1963 and by Zeven from 1965. In the course of the investigations the genes were classified by geographical distribution, and the areas where necrosis genes were not found pointed out. According to the table compiled by Zeven (1971) in the species and varieties examined so far the two genes are distributed in the following way (Table 21).

Among the known varieties the Ne1 necrosis gene have been found in Diana I, Novi Sad 58, Parker Pilot, Produttore, Pusa 12, Rieti II, Scout 66, Timstein, New-Tatch, Arnautka. While the Ne2 gene has been found in Bezostaya 1, Butler, Ciano 67, Inia 66, Joss-Cambier, Kasticka osinatka, Klein 157, Lerma Rojo, Peragis, WW, Hadmerslebener Qualitas, Rannaja 12. So far 313 *T. aestivum*, 4 *T. compactum*, 1 *T. durum* and 4 *T. spelta* varieties have been proved to include no necrosis genes. The more important of them are: Autonomia, Axminster, Backa, Belocerkovskaya 198, Diamat II, Heines I, Kenya 58, 117a, Kooperatorka, Norin 33, Rio Negro, Sonora, Turkey Red, Székács 1055. Depkarelevich and Naskidasvili (1971) found in Georgia *T. timopheevi* lines in which the Ne 1 gene could be pointed out. Zeven (1971) arrived at the conclusion that of 2531 examined

Table 21.

Ne1		Ne1		Ne2	
Number of variety	Species	Number of variety	Species	Number of variety	Species
117	*T. aestivum*	1	*T. spelta*	215	*T. aestivum*
1	*T. carthlicum*	1	*T. sphaerococcum*	3	*T. spelta*
2	*T. compactum*	1	*T. vavilovi*		
11	*T. durum*				
1	*T. macha*				

varieties 23.8 per cent contained Ne1, 26 per cent Ne2 genes and 50.2 per cent was free from both. According to Morris et al. (1970) in the homoeologous group No. 6 a suppressor can be pointed out which reduces the effect of necrosis genes but is not strong enough to fully eliminate the consequences.

Hybrid-chlorosis though less important is worth mentioning when speaking of breeding by crossing. It is likewise caused by two complementary dominant genes (Tsunewaki and Hamada 1968). When in the same genotype they cause different degrees of chlorotic lesion. The symbols of the two genes are Ch1 and Ch2. The first is found on chromosome 2A (Hermsen and Waninge 1972), the second on the α arm of chromosome 3D (Tsunewaki and Jenkins 1961*a*). According to McIntosh's (1973) table gene Ch1 was pointed out in *T. macha* var. *colchicum*, *T. macha* var. *subletschumicum* and in the Khapli, further in *T. dicoccoides* var. *cottschyanum* and var. *stranssianum*. The Ch2 can be found in Chinese Spring and *T. vavilovii*.

Varietal crossing has thus genetic difficulties of this nature only. The action mechanism and evolutionary importance of the four disturbing gene pairs have not been disclosed so far. The fact that certain geographical factors have a part in the distribution of the necrosis genes suggests that they may have played a role in the phylogenesis of wheat genera too.

Hermsen (1967) pointed out a *hybrid dwarfness* determined by three genes. In some cases he found dwarfness linked with a gene causing necrosis.

Interspecific hybridization has substantially been extended in the combining of the genera *Aegilops* and *Triticum*. Crossing of wheat species of different ploidy level is made difficult by differences in the chromosome number. When crossing *Triticum* species deriving from the genus *Aegilops* with the original *Triticum* species differences in genome are added to those in ploidy level. In the case of crossing *T. timopheevi* with tetraploid and *T. zhukovskij* with hexaploid wheat difference exists only in the genome.

Interspecific hybridization and the choice of the crossing partners, respectively, depend on the objective of breeding. The most frequent purpose of crossing different species is to introduce a gene of a species into another. With hexaploid and tetraploid wheats crossed introduction of winterhardiness in the tetraploid wheat may be such an objective (Kirichenko 1962*a*; Jakubziner 1963). From

tetraploid to hexaploid wheat a better pathological resistance is transferred in the first place. Such a case is reported by Lelley (1953*a*) who transferred leaf and stem rust resistance genes from *T. timopheevi* to *T. aestivum*, and by Aastveit (1968) who introduced the powdery mildew resistance gene of *T. persicum* into *T. aestivum*. Numerous *T. durum*, *T. dicoccum* and *T. aestivum* interspecific hybrids have been produced so far (Stankov 1968). In interspecific crossing hexaploid recipients and tetraploid pollen donors are considered more favourable.

In the case of crossing *T. aestivum* with *T. timopheevi* male sterility in the F_1 generation is almost complete owing to the differences of the B and G genomes (Belea 1964, 1966, 1970). To attain some seed setting the forced selfing of the F_1 generation is advised by tearing the anthers open. Namely, owing to meiotic irregularities the pollen grains are in the anthers mostly empty, therefore, the anthers cannot open and the pollen is not scattered (Lelley 1953*a*). According to Emmerikh (1965) in the case of crossing *T. durum* × *T. timopheevi* seed setting in the F_1 generation can be improved by using the pollen of one of the parents instead of selfing. The fertility of interspecific hybrids is restored after some generations, and translocation may occur in the meantime. The frequency of translocation can be increased with mutagenes.

In the case of hybridization of species with ABD and AB genomes, respectively, fertility is usually restored in the F_6 generation. Derivates with 28 and 42 chromosomes are produced among which translocation lines can be found as well (Arcara 1966). According to Bozzini and Martini (1966*a*) such populations include translocation heterozygotes, too, they are, however, phenotypically and genetically unstable. Jackson (1966) points out that the extremely high variability observed in interspecific hybrids is due to an additive genetic variance.

In crossing species of different ploidy level the backcross method has proved to be good enabling the restoration of the chromosome number of the recurrent parent and the occurrence of segment translocations. The compensation lines of the hexaploid partner – in which the 5B chromosomes are missing while four 5D chromosomes are present (5B nullisome 5D tetrasome) – are suitable to induce translocation in. The absence of chromosome 5B makes homoeologous pairing possible which promotes the chiasma formation and translocation between these chromosomes. Probability of translocation in interspecific hybrids can be increased when a certain chromosome of the hexaploid parent is monosomic. Monosomic chromosomes pair more often with alien chromosomes. On monosomic chromosomes translocation occurs therefore more frequently. The number of translocations can be increased by ionizing irradiation applied at the time of megasporogenesis. Certain chemical mutagenes may also be efficient.

Hybridization between the genus *Aegilops* and *Triticum* species, with the exception of *Ae. squarrosa*, is mostly carried out for the purpose of evolutionary genetic research, or occasionally may serve for resistance breeding (Evans 1964; Goshal and Belea 1974; Belea et al. 1974). Wagenaar (1968*a*, *b*) gives account of crossing *T. crassum* with *T. turgidum*, Siddiqui and Jones (1968) describe *T. durum* × *Ae. squarrosa* hybrids. Upadhia (1968) produced *T. aestivum* × *Ae. umbellulatum* hybrids by transferring leaf rust resistance of an alien segment incorporated in chromosome 6B. Lacadena (1967) describes *Ae. columnaris* and *T. aestivum*

hybrids where the *Triticum* partner was monosomic for chromosome 5B. Recently the production of many new interspecific hybrids have been reported.

Intergeneric hybridization, here the genera *Secale* and *Agropyron* can be taken into account in the first place; the genus *Haynaldia* has a less important role. The chromosomes of these genera are likewise homoeologous with the chromosomes of the wheat genome. In the rye genome more than one chromosomes have been proved to be homoeologous with some homoeologous groups of wheat (Mettin et al. 1973; Zeller 1973). Rye chromosome 1R has turned out to be suitable for substitution into two homoeologous groups of wheat at the same time (Gupta 1971).

Hexaploid and octoploid *Triticale* plants are also the results of intergeneric hybridization between wheat and rye. Hybridization of wheat and rye may be aimed at improving winterhardiness in wheat or increasing the lysine content of protein. A similar purpose may be served by translocation forced between homoeologous chromosomes of wheat and rye.

Of the genus *Agropyron*, *A. glaucum*, *A. elongatum*, *A. repens*, *A. intermedium* have been hybridized so far with wheat (Lyubimova 1963; Quinn and Driscoll 1967). Beyond a genetic research the aim of crossing *Triticum* × *Agropyron* is to transmit the manifold pathological resistance supposed to exist in the *Agropyron* genus by attempting to translocate the chromosome segment that carries the resistance to some wheat chromosome (see page 120).

Furthermore, intergeneric crossing between *Agropyron* and *Triticum* may be aimed at producing a new amphidiploid species. Golubovskaya (1969) gives account of wheat – *Agropyron* hybrids with 56 chromosomes produced. Sulydin and Gorban (1969), and Gorban (1969) describe hybrids with 70 chromosomes. Lyubimova (1970) writes about perennial winter wheat × *Agropyron* hybrids.

In intergeneric hybrids, in spite of a partial homoeology, haploidy and male sterility must always be reckoned with in the F_1 generation owing to differences in the chromosome number (Szalai and Belea 1963). Fertility can only be restored by producing amphidiploids through colchicin treatment to F_1 kernels or plants. Driscoll et al. (1967) suggest 0.25 cm^3 of 1–2.5 per cent colchicin solution to be injected into the tip of the young spike, so the chromosome numbers in the pollen and egg-cell double.

The aim of intergeneric crossing may thus be

1. production of new amphidiploid,
2. chromosome addition,
3. substitution of whole chromosome or chromosome pair,
4. induction of chromosome segment translocation.

The practical use of producing *Triticum* × *Agropyron* amphidiploids is not quite clear. The best results in this field have been achieved by Tsitsin (1957) with perennial wheat, but the practical importance of perennial wheat is not much (Golubovskaya et al. 1966). In the system developed by Mac Key (1968) *T. turgidocereale* is an amphidiploid species in which the complete genome of *Secale cereale* has been additioned to the genome of *T. turgidum*. *T. aestivocereale*, on the other

hand, is an amphidiploid species in which the *Secale* genome has been additioned to the genome of *T. aestivum*. Thus, amphidiploidy is, in fact, a genome addition.

Addition lines are difficult to maintain because the additioned chromosomes are later eliminated. It is only in exceptional cases that addition lines can be maintained. Such a case is reported by Müntzing (1970). The Lindström wheat strain contains a rye chromosome pair, but the chromosome pair transferred to the alien plasm causes disturbance during meiosis. The additioned chromosome pairs show regular pairing.

The substitution of a single chromosome is not a simple case either, because in the alien genome the substituted chromosome may also cause meiotic irregularities. When a whole pair of chromosome is successfully substituted, the meiotic irregularity as a rule no longer occurs.

Segment translocation is very promising especially since 5B monosomic, 5D trisomic or 5B nulli, 5D tetra compensation lines have been used to increase the frequency of translocation. Utilization of pure 5B nullisomics in often prevented by sterility. Compensation lines have been produced so far only from the Chinese Spring variety.

If the inhibition of homoeologous pairing by chromosome 5B has been eliminated the desired translocation can be attained with mutagenes in two ways. Dry seed may be treated with ionizing irradiation. Plants raised from the treated kernels are selfed and the property (e.g. rust resistance) whose transfer was the aim of breeding is to be found in the progeny. The next step is the cytological examination of the resistant plants. Plants in which the additioned chromosome is still present are discarded. Resistant plants in which additioned chromosomes are no longer found have undergone translocation. Detailed cytological examination can even identify the chromosome that has been enriched by a new segment. It is indicated by irregularities of the synapsis.

By another method of radiation treatment (Knott 1961) some young spikes of the addition line are irradiated at a stage when the meiotic division of the sexual cell has not yet begun. The untreated spikes are pollinated with the pollen of the irradiated spikes and the progeny selected as described above.

It is the terminal segment that is most frequently changed, although the intercalaric translocation is preferable because in this case the incorporated segment joints the recipient chromosome at both ends. This does not often occur as it requires a three- or fourfold chromosome breaking. Terminal translocation has sometimes the disadvantage that a part of the recipient chromosome gets lost which never happens with an intercalaric translocation.

According to Larter and Elliott (1956), and Qureshi et al. (1961) dormant kernels can be more efficiently treated with thermal neutrons than with X-rays. Osborne and Elliott (1955) obtained good results with X-ray treatment too when the treated kernels were kept in oxygen. Radioactive isotope solutions are best injected into the spike immediately before micro sporogenesis or right after fertilization. These interventions had better take place in greenhouse with great care in providing optimum conditions and preventing accidental cross pollination.

If the desired translocation has succeeded the normal state of chromosome

5B must be restored otherwise instability will be maintained in the meiosis owing to the pairing of homoeologous chromosomes (Riley and Chapman 1966).

It was through chromosome breaking induced by radiation treatment that the rust resistance of the genera *Agropyron* and *Secale* was introduced into wheat (Elliott 1957; Driscoll and Jensen 1964). Planned translocation can be greatly promoted if the chromosome in which the property in question is located is known. Work can be done still more systematically if the additioned chromosome is isosomic for the desired arm.

Breeding by crossing has thus all these possibilities too, although interspecific and intergeneric hybridization have been not frequently used in the practice of breeding so far, because their application requires special laboratory and greenhouse equipment, and involves cytological and cytogenetic studies.

Hybrid wheat: a special opportunity of crossbreeding is the exploitation of heterosis effect in its production. Wheat breeding and genetic research have done much in this field in the last ten years.

In the first concrete heterosis wheat breeding trials Lelley (1953*b*) attempted to produce the necessary male sterility first by mechanical, then by chemical intervention. These attempts, though failed to achieve concrete results revealed some aspects of the hybrid effect and difficulties of hybrid wheat production. Efforts have ever since been made to induce male sterility by chemical means, so far without any considerable success. Meyer (1967) obtained some results in spring wheat by using Omnidel as gametocide, but the effect of the chemical depended on the weather. Jos and Singh (1967) studied the effect of Na-2,3 dichloro-isobutyrate on pollen sterility. According to Borghi et al. (1973) spraying with a 2000 ppm solution of 2-chloroethyphosphonic acid (etaphon) at the late and early stage of "boot" as well as in the initial phase of heading caused complete male sterility with considerable allogamic seed setting. In their opinion this result is promising. Chemically induced male sterility is invariably an important subject of research, as its successful application would substantially facilitate the utilization of heterosis effect.

Kihara in 1951 reported on plasmatic male sterility by substituting wheat nucleus into the plasm of *Ae. caudata*. Fukasawa (1953) obtained similar result by using the plasm of *Ae. ovata*. Wilson and Ross (1962) substituted *T. aestivum* nucleus into the plasm of *T. timopheevi* and obtained male sterile derivates. As it was found later, male sterility caused by the plasm of *T. timopheevi* was the most suitable for practical use.

With this relatively simple solution of the problem of hereditary male sterility research began with a great swing. However, to realize hybrid wheat production in practice further tasks had to be solved:

1. The actual measure and stability of heterosis effect observed in wheat had to be determined.
2. It was necessary to find adequate methods for establishing and forecasting combining ability.
3. Possibilities as well as genetic and biological reasons of male sterility needed clarification.

4. Utilization of genic male sterility had to be studied.

5. Reliable and full restoration of fertility had to be solved.

6. It was necessary to re-assess the biological conditions of wheat flowering and fertilization from allogamy point of view.

7. Possible obstacles to the practical production of F_1 hybrid seed-grain were to be indicated.

The *hybrid effect* on the morphological characters, yield components and earliness of wheat was observed long ago. Briggle (1963) published a detailed review of early data reaching back to the 1910s. For the last ten years heterosis effect manifesting in the yield has been observed in a great number of varieties on the basis of diallele and cyclic crossing (Briggle 1963; Briggle et al. 1967; Škopik 1968; Rajki and Rajki 1970; Bhatt 1971; Walton 1971; Balla 1971; Varenica et al. 1971; Allan 1973; Szunics and Szunics 1973, etc.). According to Shing and Shing (1971) the greater the genetic difference between the parents the higher the prospective hybrid effect. Besides positive results it has become clear that crossing does not always give a surplus yield; in some cases the heterosis effect turns out to be of negative character (Scherbina 1964; Miržinski and Jankovič 1966; Kozlenko and Anikeeva 1969; Kozlenko and Puhalski 1969; Nettevic et al. 1970; Szunics and Szunics 1973; etc.).

During the investigations of the heterosis effect the question has arisen to what extent the results obtained with only a few plants in a thin stand are reliable compared to dense stands where the number of spike per plant has less effect, while in a thin stand this parameter may be of decisive importance. Zeven (1972) thinks it to play no important role in determining the heterosis effect, although the experience that in most cases the heterosis effect is lower in a thick than in a thin stand contradicts his opinion. There are data available which suggest that of the yield components it is productive tillering that the heterosis effect best manifests itself in (Smoček 1969*b*). The conclusion that hybrid wheats can be sown with a smaller quantity of seed because of their better productive tillering has been drawn from such experiences, too (Kozlenko and Puhalski 1969). This advantage is, however, felt only under irrigated conditions. Thus, as long as surplus yields of hybrids are not checked up in a thick stand in field trials the result should be accepted with reservations.

As for the experiences concerning the heterosis effect, data obtained so far show that the heterosis effect has been observed with the most diversified properties of which the excess height of culm is an undesirable feature because it may reduce plant stability (Briggle 1963; Miržinski and Jankovič 1966; Szunics and Szunics 1973). Quality is mostly intermediar though occasionally some positive hybrid effect has been observed (Mukhin and Koptik 1970). In contrast to a heterosis induced surplus yield the hybrid may even be less productive than the parents. In productive tillering mostly an outstanding heterosis effect is felt, it must therefore be tested in each case how much is the yield surplus in a dense stand compared to the better parent. The extent of the hybrid effect changes mostly from year to year, hybrids must therefore be studied over several years. Yield surplus originating from hybrid effect had better be analyzed according

to the share of the individual yield components because from this conclusion can be drawn on the reliability of the heterosis effect. Reciprocal combination does not always give the same heterosis effect (Kozlenko and Anikeeva 1969; Kozlenko and Puhalski 1969; Kovbasenko 1970). It is worth elucidating in every case whether a heterosis effect is still felt in the F_2 generation. Observations concerning this point are contradictory (McNeal et al. 1965*a*; Fonseca and Patterson 1968; Boháč and Orenčák 1970; Wells and Lay 1970).

The prospective measure of heterosis effect can be assessed by the *analysis of combining ability*. This test establishes the value of varieties or lines as heterosis partners. The combining ability is indicated by cyclic or diallele crossing (Shing and Gupta 1969; Smoček 1969*c*; Szunics and Szunics 1973; see Table 22). Kronstad and Foote (1964), Gyawali et al. (1968) used the diallele method without reciprocal crossing.

McDaniel and Sarkissian (1966) called attention to mitochondrial complementation to yield conclusion on hybrid effect and combining ability, without the use of crossing. Studying the isolated mitochondria of the parent varieties mixed and their intensity of respiration compared to that of the same in each parent separately, conclusion can be drawn on whether any hybrid effect is to be expected by crossing the two partners. This examination has the advantage that it can be performed in the laboratory, though surrendering information only whether or not a higher vigour of development can be expected in the F_1 generation produced by crossing the two partners. The analysis gives an ambiguous answer to the question whether the hybrid effect will be manifested really in surplus yield, since it can be influenced by pathological and climatic resistance, too. The method itself is elaborate (Sage 1973). It can be used to obtain preliminary information, but further investigations are required to ascertain its efficiency (Sarkissin and Srivastava 1969; Hobson 1971; McDaniel 1972, 1973).

In the course of investigating the sources inducing *plasmic male sterility*, in addition to the plasms of *Ae. ovata*, *Ae. caudata* and *T. timopheevi*, a number of other plasmic sources have been found to cause male sterility. The plasm of *Ae. caudata* has the disadvantage that besides male sterility it may also cause pistilloidy. The undesirable effect of *Ae. ovata* plasm is felt in the prolongation of flowering time. Both phenomena result in deficient seed setting (Porter et al. 1965). Further male sterile sources are *T. zhukovskii* and the octoploid *T. timonovum* Heslot (Nettevich and Fedorova 1966). According to Kobylyanskii (1969) and Dimova (1969) *T. timonovum* gives the most viable male sterile progeny with hexaploid wheats, while *T. timopheevi* with *T. durum*. Amler and Zadražil (1969) used *T. monococcum* while Skurygina (1970) *T. arraticum* as sources of male sterility. According to Maan (1973) whether it was from *T. aestivum* or *T. durum* that nuclei were substituted into the plasms of *Ae. bicornis*, *Ae. umbellulata*, *Ae. sharonensis*, *Ae. longissimum*, *Ae. heldereichii* and *Ae. variabilis*, makes no difference, male fertility and vitality are equally reduced. Lacadena and Pérez (1973) having transplanted the nucleus of Chinese Spring into the plasm of *Ae. umbellulata* attained male sterility and normal viability. The decrease of vitality may thus be specific of the variety, too. According to Kihara (1973) hexaploid nucleus in *Ae. squarrosa* plasm does not cause sterility, while tetra-

Table 22. Cyclic and reciprocal cyclic crossing

B
×
A
G×A ♀ A×C
F×A A×D
A
×
E

A
×
B
A×G ♂ C×A
A×F D×A
E
×
A

Diallele crossing

♀ \ ♂	A	B	C	D	E	F	G
A		×	×	×	×	×	×
B	×		×	×	×	×	×
C	×	×		×	×	×	×
D	×	×	×		×	×	×
E	×	×	×	×		×	×
F	×	×	×	×	×		×
G	×	×	×	×	×	×	

The possible number of crossing is 7×7–7, i.e. n.n–n, where n = the number of crossing partners.

ploid nucleus does. Accordingly, genome D obviously contains a gene that restores male sterility in *Ae. squarrosa.*

The plasms of the above-listed *Aegilops* species have no phenotypic effect, but that they differ from one another is proved by the fact that the extent of sterility is not uniform and fertility can be restored in different degrees, too (Maan 1972). The nuclei of *T. aestivum* and *T. durum* even when in the plasms of *T. comosum, T. cotshii* and *T. cilindricum* produce male sterile plants. According to Maan (1972) a lower number of backcross is necessary in the case of *T. durum* than in *T. aestivum.* Decrease of vigour caused by the plasm was noticed in earlier generations of *T. durum* and in later ones of *T. aestivum.* The extent of decrease in vigour is also influenced by the environment. Thus, within the genus *Aegilops* numerous species have been found so far in which plasm the nuclei of *T. aestivum* and *T. durum* cause male sterility. Yet, most attempts made in practice are based on male sterility produced with *T. timopheevi* plasm. One of the reasons is given by the experience that the *T. timopheevi* plasm has no adverse effect on the properties of hexaploid wheats (Varenica 1973).

The biological and genetic explanation of male sterility originating from alien cytoplasm is not quite sufficient as yet. The exploration of numerous new plasmic

sources has not helped much in clarifying either the biological or the genetic mechanism of male sterility.

Male sterility may be of genic origin. Pugsley and Oram (1959) found a male sterile mutant in the F_3 generation of Kenya Farmer × Javelin 48 that he crossed with the variety Chancelor and obtained a recessive male sterile form of monogenic heredity. Genic male sterility is reported by Savchenko and Lastovich (1964) in the varieties Mironovskaya 264, Veselopodolskaya 499 and Bezostaya 1. Genic male sterility is described by Suneson (1964), too. Athwal et al. (1967) give account of polyfactorial male sterility transmitted in a recessive form. Krupnov (1968) found a mutant with hereditary recessive male sterility in the variety Saratovskaya 29. Gill and Anand (1970) describes a recessive male sterile form determined by three genes where the extent of seed setting depended on the number of genes. In the case of three genes present male sterility was 95 per cent while two genes caused 65, and one gene 35 per cent of male sterility. After X-ray treatment Fossati and Ingold (1970) isolated in the variety Prelude a genically determined male steril mutant which showed monogenic recessive heredity. Briggle (1970) described a male sterile combination where the segregation ratio of normal to male sterile was 3 : 1 without intergrades. Trupp (1971) likewise gives account of a male sterile form of simple genic heredity.

From a practical point of view only the recessive monogenic male sterility is of significance which can be completely restored by a dominant fertility gene. Homozygous recessive male sterile lines cannot, however, be maintained by autogamic fertilization, only through allogamy, and even then dominant restorer gene must not be contained in the pollen of the partner. Driscoll (1973) elaborated a method of solving the problem of male sterility and restoration, and the maintenance of male sterile lines on the basis of genic transmission. In his opinion, the gene-pair causing recessive male sterility ("ms") must be located on a definite, known pair of chromosome. The dominant "Ms" restorer gene-pair has to be incorporated in a chromosome pair homoeologous with that carrying the "ms" gene-pair. This should be additioned to the genome of the male sterile variety (Driscoll 1972*b*). The system requires three lines: X, Y, Z. All three are homozygous for gene "ms", that is, each contains a male sterile gene-pair. Further, line X contains two additioned chromosomes with a "Ms" gene-pair, and line Y one additioned chromosome with the same gene. The X plants produce only hyperploid gametes with 22 chromosomes. The Y lines produce gametes with 21 and 22 chromosomes of which the former shows a higher vitality than the hyperploids. The Z plants do not contain alien chromosomes, are male sterile, but only remain so when fertilized by pollen containing "ms" gene. Such pollen is, however, produced only by the Y plants. With the Y plants removed after flowering and the Z plants separately harvested, homozygous "ms ms" sterile seed-grain is obtained. In practice the operation can be carried out by the following scheme:

	male block		female block		seed-grain
first step	X	×	Z	=	Y
second step	Y	×	Z	=	*Z*

After this *Z* seed is the recipient partner of the F_1 seed-grain mass production, the pollen donor and restorer is a normal variety, and so the hybrid F_1 seed-grain is Ms ms heterozygous for the property in question, it is fertile and does not contain alien chromosomes!

According to Driscoll (1973) the chromosome mapping confirmed that chromosomes 4A, 4B, 5A, 5B and 5D carry "Ms" gene or genes which restore male fertility. The chromosomes carry the "Ms" gene on one of the arms only. The deletion of this arm may cause male sterility. Hybrization with monosomic F_1 plants may result such deletions. Recessive male sterile "Z" forms can thus be produced.

The 4E chromosome of *Ae. elongatum* contains an Ms gene and a factor determining the blue colour of aleuron. There is an Ms gene on chromosome 5R of *Secale*, too. The C chromosome of *Ae. umbellulata* likewise carries an Ms gene. Thus, the incorporation of an Ms gene carried by an alien chromosome in the X line can be carried out as well (Bielig and Driscoll 1973, Driscoll 1973). This form of utilization of genic male sterility is much more complicated than plasmic male sterility induced by nucleus substitution. The restoration of genic male sterility means no problem, but it is all the more difficult to restore plasmic male sterility.

Restoration of plasmic male sterility would be easier if we knew the mechanism of male sterility. Unfortunately, this point has not been fully clarified yet. According to Joppa et al. (1966) the pollen of plants with plasmic male sterility contains only a little – if any – starch. The filament shows an irregular growth, its vascular system is abnormal. According to Fukasawa (1968) in sterile anthers the amount of proteins precipitable with alcohol is smaller and the alcohol-soluble amide nitrogen level is higher. Srivastava et al. (1969) pointed out a decreasing tendency for the biological activity of mitochondria in the sterile plants. These and other details do not, however, give details about the true principles of plasmic male sterility.

A total of six Rf genes restoring plasmic male sterility have been identified so far, which are capable to restore the *T. timopheevi* type of male sterility. According to McIntosh (1973) they are:

Gene Rf1 is in chromosome 1A and was found in the crossing *T. timopheevi* × Marquis.

Gene Rf2 was likewise found in the same crossing but this time in chromosome 7D.

Gene Rf3 is in the 1D chromosome. It was identified in *T. spelta* var. *duhamelianum*.

Gene Rf4 is in chromosome 6D in the combination of *T. timopheevi* × *Ae. squarrosa* × Canthatch.

Gene Rf5 was located in the same combination again in chromosome 6D.

Gene Rf6 is in *T. zhukovskii*.

Modifiers influencing the Rf genes have been identified in chromosomes 1B, 2A, 6A and 6B (Robertson and Curtis 1967).

According to Maan (1972) male sterility induced by the plasms of *Ae. ovata* and *T. timopheevi* is restored by the genotypes of *T. dicoccoides* var. *kotschyanum*, *T. spelta* var. *duhamelianum* and Chinese Spring, though by the latter only partially. The male sterility of *Ae. caudata* is partially restored by the line *T. compactum* 44. The genotypes of *T. zhukovskii* and *T. boeoticum* fully restore male sterility when originating from *T. timopheevi*, and partially when derived from *Ae. caudata*. Genes Rf5 and Rf6 fully restore male sterility caused by *T. boeoticum* plasm and also stop the decrease in vigour; partially restore male sterility and decrease in vigour caused by *Ae. umbellulata* and *Secale cereale*. Gene Rf4 restores male sterility when caused by *Secale* plasm but not when originating from *T. boeoticum*. An addition line containing but a single *Secale* chromosome restores male sterility when caused by *Secale* plasm, but not when by *Ae. umbellulata* and *T. boeoticum* plasm. Medvedeva (1967) found among the crossing derivates of *T. timopheevi* × *T. durum* var. *hordeiforme* 432 plants with normal pollen fertility which inherited a good restoring capacity.

It follows from these data that in the genus *Triticum* – according to the new taxonomic system – there are great differences in male sterility caused by plasm. The possibility of genic restoration is thus given concerning almost all the sterile plasms. The incorporation of restorer genes in the pollen donor variety by the backcross method is a relatively easy procedure (Nettevich 1967).

However, the capacity of restorers tested so far is not sufficient in the practice (Lafever 1968). Environment has a too great influence on restoration which to some extent affects the manifestation of male sterility itself (Roberts 1968). Long day-time, cool spring, cool summer with varying precipitation all inhibit restoration. In such cases restoration was found to be restricted to the lower flowers of the spike. The adverse effect of environment can probably be counterbalanced by the incorporation of more than one restorer genes, that is, by the increased action of dose (Done 1973).

From unfavourable experiences male sterility is known to promote the spread of certain diseases infecting through the flower, e.g. *Ustilago tritici* and *Claviceps purpurea* (Schmidt et al. 1971).

According to Sasaki et al. (1973*a*) active restorer mutant genes can be expected to appear after radiation treatments, too.

Attempts made to induce and subsequently inactivate male sterility by means of special viruses have failed (Zeven 1967).

To explore genotypes containing restorer genes a number of methods have been tested. A simple method of recognizing spontaneous restorer mutants possibly arising under natural conditions was suggested by Lelley (1970). The exploration of varieties whose genotypes contain innate restorer genes is a possibility not yet exploited (Popov 1969). According to the experiences the restoring capacity of the variety Primépi proved to be relatively good, better than that of the *T. timopheevi* × Marquis restorer (Nettevich 1970; Auriau 1973). According to Bahl and Maan (1973) in the variety Primépi the restorer gene is found in chromosomes 1B and 5D. Mihalev (1973) found the line VK-64-28 to be a good restorer; its restoring capacity is dominant and of polygenic heredity. In spite of an extensive investigation fully restoring lines have not been found

so far. This explains the opinion that it will take some time until a hybrid wheat suitable for commercial production is produced (Lafever 1968).

Deficient cross-pollination caused by the *autogamic fertilization* of wheat is one of the main obstacles to the introduction of hybrid wheat in commercial production (Briggle 1964). Intensive studies have recently been started to throw light on the fertilization conditions of the hybrid wheat. Cross-pollination has been found to have relatively wide possibilities depending on meteorological conditions and variety (Suneson and Cox 1964; Medvedeva 1968). Cross-pollination is unfavourably influenced by the fact that the wheat pollen is heavy, and quickly drops, it is therefore better if the pollen donor is higher in growth (Lelley 1966). In some wheat varieties 80 per cent of the pollen is carried away, still it is not enough; the anthers of rye produce about nine times as much pollen as those of wheat. The rye pollen covers twice the distance under the same conditions in the air than does that of wheat. The wheat pollen is fertile for only 30 min, the rye pollen for 72 h. Yet, D'Souza (1970) considers it desirable to select lines whose anthers emerge from among the glumes in higher numbers. Rajki (1962*a*), Lyfenko et al. (1969) think it favourable from the point of view of free pollination if the flowering time of the recipient precedes by 3–4 days that of the pollen donor.

According to Krupnov (1970) the number of pollen grains found in an anther ranges between 600 and 2200, so the size of the anther may be a good basis of selection when breeding for more productive pollen partners. Császár and Rajki (1972*a*, *b*) studied the varietal specificity of pollen production. Beri and Anand (1971) found the varieties higher in growth to produce more pollen than the short-stalked ones. According to Ageev and Udalov (1972) there is a close positive correlation between the number of anthers rising above the flower and cross-pollination. Similar experiences are reported by De Vries (1971). Varenica et al. (1968) call attention to the fact that the flowering period of male sterile flowers is always longer than that of the fertile ones. Improvement in the cross-pollination of wheat and a prolonged flowering period of female flowers can be expected from selection, or crossing combined with selection.

Qualitative deterioration represented a disturbing possibility in the introduction of hybrid wheat in commercial production. However, investigations made by Johnson et al. (1967), Olsson and Wiber (1968), Schmidt et al. (1970) prove that deterioration in quality need not be feared.

Full restoration of male sterility, furthermore cross-pollination, or more precisely, hundred per cent seed setting have represented so far the most serious problems. The biological and genetic difficulties cause management problems too, since the wide introduction of hybrid wheat is only acceptable if its cultivation is expected to be profitable. As far as the prospects are concerned unfortunately the opinions differ (Lelley 1967*b*; Burca 1969).

Seed-grain production of hybrid maize based on plasmic male sterility has been solved all over the world. The maize is, however, a cross-pollinated plant, and the per hectare seed-grain requirement is 20 kg at a maximum. The wheat, on the other hand, is autogamous, and the per ha amount of the necessary seed-grain is about ten times as much. These two factors explain the difficulties of

seed-grain production and its implications concerning the expenses involved (Lelley 1967*b*, 1970).

A possibility of seed-grain production is when lines A and B are sown in alternating zones and harvested separately. This is feasible though expensive. Another possible method is the mixed sowing of A and B lines substantially differing in thousand-kernel-weight. In this case – though the B lines can be separated by screening – hundred per cent separation is no longer possible. The mixed sowing of the A and B lines of different straw length then separate, earlier cutting of the longer straw A lines seems to be a feasible way, though even in that case no hundred per cent isolation is likely to succeed. To mark line A with a marker gene causing bright colouration in the pericarpium, then after the mixed sowing separating the seed by an electronic colour grader (Barabás 1973), besides being the most expensive method of all, does not solve the problem of hundred per cent separation either, furthermore it is a question what the effect of the cyanidine and poenidine glucoside content of the purple pericarpium will be like (Dedio et al. 1972).

Thus the flowering-biological and technological difficulties of hybrid seed-grain production remain yet to be solved.

Biological and genetic research and breeding work concerning the question of hybrid wheat have become for the last ten years an activity of considerable importance in all countries engaged in wheat breeding. This accounts for the large number of summarizing papers written on this subject (Kihara 1967; Johnson et al. 1968; Heyn 1969; Fedin 1970; Kučera 1971, etc.).

Haploid method is a new possibility of breeding by crossing.

In the case of plants genera reproducible in a vegetative way the F_1 generation, in spite of its genetic heterogeneity, can be maintained as a phenotypically homogenous population. This provides the possibility of fixing the F_1 state, moreover, any subsequent generation of the segregating population can be fixed. This possibility offers the following advantages:

1. The hybrids can be evaluated as once, because there is no need for genetic homogenization.
2. Selection requires a population of lower individual number since the genetic segregation of the subsequent generations will not take place.

These indisputable advantages are up against the drawback that owing to the elimination of genetic segregation the range of possible recombinations is smaller.

For wheat, as a plant of exclusive generative reproduction, hybrid wheat has been known so far to be the only possibility of fixing the F_1 state. In this case, however, the F_2 generation segregates and cannot be used for production. The situation has essentially changed since viable fertile diploid plants both mono- and dicotyledons were raised from plant tissues on culture medium (Shimada et al. 1969; Nitsch and Nitsch 1970; Ternovskii et al. 1972 and Sheridan 1973). Furthermore, tissue cultures have made it possible to raise viable plants from haploid pollen cells, which when diploidized with colchicin develop homozygous diploid offsprings. This so-called haploid method makes the genetic stability of

the F_1 stage possible in plant genera of generative reproduction. By this method homozygous F_1 plants can be produced after crossing whose evaluation and selcction can be performed definitely after one or two generations depending on the rate of reproduction. As opposed to the diploid method the individual number of the population to be selected can be substantially reduced because the heterozygotes are absent. The variability of the redoubled haploids originating from the pollen cells of the F_1 plants is still high, because in the meiosis the chromosomes of the two parents are distributed at random among the pollen cells whereby the possibility of combination for the 21 haploid chromosomes is very high. Thus the redoubled haploid generation raised from the pollen cells of a single plant is genetically highly diversified (Rajháthy 1975; written report).

Nevertheless the haploid method makes it perhaps probable that the hybrid effect manifesting in the yield can be genetically fixed and accordingly this method may replace the otherwise less promising wheat breeding.

At the beginning the attempts to raise haploid plants from the wheat pollen failed (Jones and Netzger 1963; Shaw and Manocka 1965; Matsumoto et al. 1971). Recently the problem has been solved and haploid plants are raised from wheat pollen, too (Ouyang et al. 1973; Wang et al. 1973; Craig 1974). Rajháthy (1975, written report) gives account of haploid plants obtained from pollen culture producing diploid kernels after colchicin treatment. The method is still elaborate but is expected soon to become a routin technique also applicable in the practice of breeding. The haploid method opens new vistas for the work of breeding by crossing.

Among *genome*, *chromosome* and *gene* mutation the latter is the most important one from the viewpoint of practical breeding.

It is of common knowledge that through genome mutation haploids can be produced which, however, are of little practical importance (Pienaar and Niekerk 1973). The practical use of autopolyploidy has not been proved either, since the cultivated wheat is polyploid, and the further increase of the genome number would involve unfavourable consequences. So obviously the amphidiploids with more than 42 chromosomes have not played any role in practice (Zebrák 1962).

Aneuploids, isochromosomes and telocentrics considered as *chromosome mutations* are of great significance in genetic research. Aneuploids are indirectly used in the work of breeding in the case of substitution, addition and translocation, too. The role of different forms of translocation is known and indispensable in distant hybridization.

Artificially induced gene mutation has become an efficient method in the practice of breeding. The general rule that most gene mutations are not favourable and it is a matter of chance whether or not the mutant will be useful applies to the genus *Triticum* too. It depends on the efficacy of the method of selection whether the desirable mutant will be recognized. Success mainly depends on the availability of a method by which a sufficient number of plant can be examined in as short a time as required for the recognition of the mutant in question.

The controllable character of gene mutations has not been proved so far, but there are recent innovations to increase frequency. In the hexaploid wheat where all properties are localized in three homoeologous chromosomes the stock of

genes is, in fact, threefold, therefore it is more difficult to recognize gene mutations but the effect of defective mutants is also lower because the genes are able to compensate for one another. In the tetraploid wheat the situation is less favourable as it contains two homoeologous genomes only. Experiences show that the response given to the mutagenes and the range of mutations, respectively, are to some extent specific of the variety. Furthermore, the responses given by the parents and hybrids to the same mutagene may show some relation (Avakyan 1970).

The mutagene causes molecular changes in the DNA. The organism tries to correct the disorders thus occurring with certain enzymes. A too intensive tendency in correction is disadvantageous from the point of view of breeding. The corrective mechanism is photoreactive, that is, it functions mainly in light though there are also corrective processes acting in the dark. The enzyme that effects the correction is supposed to recognize the fault and correct it on the basis of the complementary thread. However, the possibility of correction is probably a matter of mere chance. It is not therefore clear what the relationship is between mutation frequency, mutagene, variety and corrective tendency (Hanawalt 1972).

The treatment may be *physical* or *chemical* depending on the mutagenes. In both cases the type of the mutant produced depends on chance. However, mutagene, duration of treatment, dose, repeated application and physiologcal state of the medium may all influence the frequency of mutation.

According to Matsumura (1964) by using *fast neutrons* the ploidy level increases the resistance, that is, the diploid wheats become the most sensitive, the hexaploids the most resistant. Otherwise, the fast neutrons cause frequent chromosome breaking. According to D'Amato and Scarascia (1962) the effect of fast neutrons shows a certain specificity of variety, and they are more efficient than the X-rays. Under the influence of fast neutrons sphaerococcoid, speltoid, awned mutants were selected while chromosome breaking and bridge formation occurred in many instances in the meiosis (Borojevič 1965). Bozzini (1965) found the fast-neutron treatment to be successful in selecting for stem solidity too. Martini and Bozzini (1965) even obtained sterile mutants. The property was inherited in a recessive form. According to them the fast neutron treatment exceeds in efficiency the gamma irradiation. Even with a treatment of dry kernel more morphological mutants were obtained than by X-ray treatment. Fast neutron + EMS treatments yielded many dwarf mutants in durum wheat, but the fertility also decreased. Hassan-Khan (1973) isolated early dwarf mutants with high protein content after fast neutron treatment.

The largest proportion of mutation analyses have been carried out with *X-rays*. Ploidy level has an influence on the frequency of mutation with this mutagen, too (Palenzoni 1961). Kao (1965) observed almost four times as high mutation frequency in tetraploid wheats as in hexaploid ones. In the case of repeated irradiation the number of mutations increased further in the tetraploids and remained unchanged in the hexaploids. Scossiroli et al. (1961) used 10 000 and 20 000 r X-ray treatments for durum and aestivum wheats. *T. durum* was more reactive to the larger dose. Scossiroli (1962) observed an extreme variability of internode number, plant height, flowering time, tillering, kernel/spike number and

kernel weight per plant as a response to dry seed treatment at 10 000 r. Borojevič (1963*b*) obtained the largest number of positive mutants both in durum and aestivum wheats with 15 000 and 25 000 r dry seed treatments.

According to Dubinin (1969) the repeated treatment as well as the 10–15 000 r treatment of dry seed of generations F_1 and F_2 were very effective, though in certain cases the parents were found to be more reactive to the treatment than the F_1 generation. F generation showed the highest resistance. Vozvozov (1969) treated germinating seed with doses of 250 to 2000 r and obtained a large number of mutations. Ostrowska (1964) found the dose of 5000 r to be lethal for germinating kernel. With physiologically young embryos treated 6–10 days after fertilization essentially more mutants were obtained by Babayan et al. (1965) than with kernels treated when mature. The number of mutations is higher with an increase in the water content of the kernel, too (Galachalova and Skurina 1963).

Some authors found certain varieties to be more sensitive to X-ray treatment than others. The same dose killed more plants in these varieties than in others.

Gamma-rays produced by cobalt gun are also used to induce mutations. Here too, the tetraploids have been found to be more sensitive to gamma radiation than the hexaploids. Savin (1963) and Yoshizo (1968) pointed out that radiation when applied in a smaller dose had a stimulatory effect on growth while in a larger dose increased genetic variability. Fonstein (1963) when treating the dry seed first with a smaller dose, then that of the M_1 generation with a higher dose of gamma rays found an increase in the resistance to the mutagen. The phenomenon can be explained by selection. When treating dry seed with 5000, 7500 and 10 000 r Tavčar (1962) observed mutation in plant height, spike length, awn length, quality, vegetative period, winterhardiness and rust resistance. Smaller doses resulted in less chromosome aberration and more useful mutants (Tavčar 1965). According to Novy and Urban (1965) 12 500 r is the critical dose of gamma ray. Volodin (1966) obtained 0.55 per cent frequency of mutation with a single gamma ray treatment. After irradiation repeated five times the mutation frequency increased to 12.5 per cent through five generations. According to Savov (1969) gamma ray treatment applied after crossing considerably increased the frequency of mutation. Eiges et al. (1971) obtained the largest number of useful mutants likewise with the 10 000 r dose of gamma radiation. Siddiqui and Haahr (1971) found mutants sensitive and resistant, respectively, to a systemic fungicide. Korotkova (1972) selected higher yielding mutants after gamma-ray treatments. Mujica et al. (1972) produced mutants resistant to stem rust.

Permanent gamma radiation was also used during the vegetative period (Kozhusko 1961): the plants became shorter and so did the spike, and sterility increased. With a large dose sterility suddenly grew. After the re-treatment of subsequent generations the effect was found to decrease in this case, too (Kozhusko 1963). Donini et al. (1964) tried out various doses over 20 h a day. They found that higher than 72 r doses caused total sterility. *T. aestivum* responded with better seed setting than *T. durum* to doses of 20–30 and 52 r, and mutability was higher, too. The largest number of useful mutants were yielded by plants treated after fertilization, during embryogenesis. As a result of observations

made in many cases it has been established that doses higher than 10 r applied on shooting are mostly harmful (Donini et al. 1968).

Of the *radiating isotopes* P^{32} is used most often. Klechovskii et al. (1962) found the DNA content to decrease after P^{32} treatments. Watanabe and Mukade (1962) applied P^{32} in the form of a $Na_2HP^{32}O_4$ solution at doses of 1.0, 2.5, 5.0, 7.5 and 10.0 micro/C per grain. Increasing doses decreased the percentage of survival and increased the frequency of chromosome aberrations. Monosomes, isochromosomes, translocations and deletions appeared. Matsumura et al. (1963) used B^{10} and Li^7 isotopes so that the kernels were germinated in a 0.1 per cent borax solution before the treatment. They obtained various chlorphyll mutations originating from chromosome breakage. Bhatia and Swaminathan (1963*a*) used S^{35} as mutagen. Dubinin et al. (1966) used K^{32} isotope. Swaminathan et al. (1966) treated the seed of *T. turgidum* × *T. aestivum* hybrids with S^{35} isotope at a dose of 10 micro/C. They obtained unusual types of spike and observed pollen sterility which suggested meiotic irregularities. A dwarf mutant of monogenic inheritance was also found. Among the radiating isotopes Cs^{137} too proved efficient.

Some authors carried out experiments with the successive application of different physical mutagens. Bhatia and Swaminathan (1963*b*) treated wheat with X-ray and beta particles. Joint treatment was found to be more efficient than when the two mutagens were applied separately.

Ausländer et al. (1966) made attempts with *ultrasonic* treatment. Kernels soaked over 2 h were exposed to the effect of ultrasound for 30, 50, 60, 70 and 90 sec, respectively. Mutants were not obtained, only an increased intensity of respiration was observed. Albu and Ausländer (1967) found a yield increase after ultrasonic treatment but attributed it to the stimulation of the seed. Accordingly, the ultrasonic treatment does not cause genetic change and is thus likely to have no importance in mutation breeding.

Radiation treatment is regarded by Scarscia-Mugnozza (1969) as a useful complement of the combination breeding. Its importance mainly consists of its being able to change through gene mutations certain characters without modifying the other hereditary properties of the variety or line. The frequency of mutations can be influenced by the intensity, duration or repetition of the treatment, but the intervention does not cause a regular change in the type of mutation. Therefore the success of breeding by inducing mutations depends, in fact, on mere chance. In spite of this it is used more and more often. The relevant literature gives account of numerous successful radiation treatments. Plant height, number of leaves, yielding potential and pathological resistance have been favourably changed in wheat by radiation treatment. Protein fractions and protein content have also been changed. One of the most valuable mutants is Sarbati Sonora (Pal 1969) obtained from Sonora 64 after mutation treatment. Its total protein content and lysine content of protein are higher. Besides those mentioned above early, lodging resistance, better tillering, higher thousand-kernel-weight, pollen sterile mutants as well as mutants with various types of spike, speltoids, compactoids, etc. have been found (Konzak 1966; Grinvald et al. 1967; Savchenko et al. 1971).

According to the opinion of Konzak (1973) the mutation treatment is good among others for obtaining isogenous lines. These lines are useful as crossing partners.

The experiences of the last years have been obtained mainly with *chemical mutagens*. The earliest and most frequently used genome mutagen is colchicin by which the chromosome number can be doubled. It is generally used at a concentration of 1–2.5 per cent, and 0.25 cm^3 of the solution is injected into the tip of the spike that has not yet emerged. In this way the chromosome numbers of pollen cells and egg-cell can be doubled. The colchicin inhibits the premeiotic association of homologous chromosomes, consequently, in metaphasis I abnormal asynapsis and multivalent formation can be observed (Driscoll 1965).

Recently *ethyl-methan-sulphonate* (EMS) is the most widely used mutagen (Shama Rao and Sears 1962). When treating di-tetra and hexaploid wheats Swaminathan et al. (1962) soaked the kernels in solutions of 180, 220, 280 and 400 ppm for 18 h. Chromosome breaking and chlorophyll mutation occurred, in much larger numbers than under the influence of X-rays. Loci close to the centrometer showed particularly frequent mutation. A number of authors observed the effect of the ploidy level in the case of EMS treatment, too. It affected sterility in the first place, but the mutation rate also changed (Gillot and Dommergues 1965). For the treatment $3^0/_{00}$ solution was used. Frequent occurrence of chlorophyll mutants was observed by Rao (1969), too. Kaul (1969) calls attention to a high degree lethality in the case of treating old wheat kernels with EMS. Edwards et al. (1969) found several stem rust resistant mutants in the wheat variety Little Club after 0.5, 0.6 and 0.65 per cent of EMS treatments. Upadhya and Swaminathan (1969) obtained speltoid, vavilovid, turgidum and durum type mutants in *T. piramidale*. Khadr (1970) found mutants cumulative in kernel weight and size after the EMS treatment of crossing derivates. Pinthus et al. (1972) selected herbicide resistant EMS mutants.

EMS is used in combination with other mutagens, too. Chopra and Swaminathan (1966) found the combined use of EMS and NH_2OH more efficient. After a joint application of X-ray and EMS, Prabhakara Rao and Swaminathan (1963) obtained vavilovid mutants. Edwards and Williams (1966) when using EMS treatment alone attained a mutation frequency of about 3 per cent, while when applying EMS in combination with X-ray the frequency of chlorophyll mutation exceeded even 70 per cent. Goud (1967*a*, *b*) obtained an essentially larger number of morphological mutants after the joint use of gamma-ray and EMS. He further noticed that mutations modifying the yielding potential were much more frequent after EMS treatment than under the influence of gamma radiation or fast neutrons.

Besides EMS, many other chemicals have also been put to trial. Khvostova and Mozhaeva (1965) attained a high frequency of mutation and even selected resistant mutants by using *ethylenimine* at a concentration of 0.01 per cent. Eiges (1966*a*) studied the mutageneity of a 0.10 per cent solution of ethylenimine. The rate of mutation changed with the concentration. Eiges et al. (1971) obtained highly valuable mutants in the variety PPG 186 by ethylenimine treat-

ment. Zoz and Makarova (1964, 1965*b*) produced compactoid and speltoid mutants with *nitrozoethyl carbamide* treatment. Salnikova and Zoz (1965) obtained chlorophyll mutants with the same chemical. Pylnev and Orlyuk (1969) gave account of the mutagenic effect on *nitrozoalkyl carbamide*. In addition to ethylenimine Skvarniko et al. (1971) used different concentration solutions of *hydroxylamine diethyl sulphate*, *dimethyl sulphate*, *1-4-bis-diazoacetyl butane*, *nitrozoethyl carbamide* and *nitrozomethyl carbamide* with varying success. Haarring (1962) tested *aluminium chloride*, *morphin ethyl urea*, *calcium chloride* and their combinations. He obtained mutations but their range did not change with the mutagens. Gilbert (1963) made attempts with *diepoxi butane*. According to Zoz (1965) great changes can be expected after treatments with *1,4-bis-diazoacetyl butane*.

In a comprehensive work Brock (1971) evaluated the practical importance of mutation in breeding. This reveals that the role of induced mutation is particularly important in cases when

1. in order to elicit translocation chromosome aberration is induced;
2. by point mutations certain characters are changed if possible in a short time and without disturbing the genotype.

Although the number of mutagens constantly increases, and the different mutagens, doses or the successive application of certain mutagens have been found to exercise a considerable influence on the frequency of mutation, there is no evidence of any connection between the range of mutation, the mutagen or the dose. Thus, the existence of adequate mutation could not be proved. The observation made by Lysenko (1964) that in mutagen treated spring wheat when sown in autumn mostly winter-type mutants are found does not support the hypothesis. Rana and Swaminathan (1967) pointed out that at certain loci the frequency of mutation depended on the mutagen; this suggests that regular studies on the mutagens and their effects may later lead to finding certain correlations which then will make a more systematic use of the mutagens possible. According to Matsumura (1966) with the proper change of doses certain mutants appear more often than otherwise. Skvarnikov (1963) calls attention to the fact that the effect of irradiation can be influenced by the change of temperature, too. Further, it has been revealed that certain loci are particularly sensitive to mutagens. One of them is the Q suppressor. That is why speltoidy and compactoidy are so frequent (Singh 1969). Speltoidy is the consequence of the deficiency of factor Q, while compactoidy results from its duplication (Borojevic 1963).

According to Sobolev (1963) after the mutagen treatment of embryos raised without endospermium the frequency of mutation may increase hundredfold. Recent experiences suggest that the results obtained with smaller doses of mutagens are more favourable for breeding practice. Though, the frequency is lower the disturbance of the genotype become significantly smaller. MacKey (1958) suggested the joint application of small doses of chemical mutagens and X-ray treatment. Safin and Zosimovich (1971) consider the use of small but varying doses of mutagens to be more efficient. Howefer, according to Prihozhenko

(1971) if the same mutagen is repeatedly used over several generations an increasing resistance to its effect may develop which is disadvantageous from the point of view of mutation frequency.

Spontaneous mutation should never be left out of consideration. In breeding work spontaneous mutants have been found to occur in a number of cases. Schmalz (1962*a*) describes a recessive *monococcoid* mutant. Urich and Heyne (1968) found leaf rust resistant, and white spiked spontaneous mutants in the variety Ottawa. Gustafson et al. (1970) observed crosswise striped mutants in the variety Vichita which showed monogenic and recessive inheritance. According to Zoz (1971) the spontaneous mutants are mostly recessive, and so are the induced radiation mutants, while mutants produced by chemical mutagens are mostly dominant. Magni (1969) wrote a comprehensive work on spontaneous mutation in which attention is called mainly to its evolutionary importance.

The haploid method described in detail on page 186 may be of use in breeding by induced mutations too. Until now mainly the double recessive mutants have been used in the practice because from the M_2 generation on they no longer segregate. The dominant mutants have been less utilizable owing to segregation. Even their evaluation is only possible in later generations. Diploidization of haploid plants originating from pollen culture of mutants makes it possible to fix the homozygous state of dominant mutants. By this the haploid method can be used in the work of breeding through mutation.

Induction of adequate variations as a breeding method has been applied so far mostly for producing winter wheat. That is, it could be seen only after a drastic repeated under- or less often overfulfilment of the genetically determined vernalization demands of wheat that winterhardy derivates with hereditarily changed vernalization demand appeared in the population. Truhinova (1962, 1963), Koltsova (1963), Varfolomeeva (1963), Remeslo (1964*a*, *b*) and others recommend a repeated autumn or late autum sowing if spring wheats are to be autumnized. In their opinion when the grain crop of good overwintering plants from the first autumn sowing are sown again in autumn, in the next generation winterhardy plants with a demand of longer vernalization period than in the initial material can be selected with a high probability. Some authors emphasize, too, that with autumn sowing repeated for further two or three years still more winterhardy types with a still longer vernalization phase can be obtained. With a view to a reliable selection thin or single seed sowing is advantageous and desirable and, at the same time, increases the extent of exposure.

Against this Kichigin (1962) underlines that sowing early in autumn is inefficient from the point of view of autumnization. In a stand sown fractionally, every ten days from the 1st of August not a single winterhardy plant could be found. Sowing late in autumn, or at the beginning of winter, on the other hand, was very successful. He too believes that late autumn sowing on two occasions to be sufficient to induce genetic variation.

For alternative wheats Fedorov (1962) and Karapetyan (1963, 1964) advise an early autum sowing. Since they hold the view that from alternative wheats derivates requiring a longer vernalization phase can only be selected after repeated early autumn sowing.

After repeated autumn sowing Hitrinskii (1963) found less frost sensitive lines with a demand for longer vernalization among durum wheats, too. According to Maksimenko (1963) vernalization is equal in effectiveness to the combinative method of breeding. The successes of Mironovskaya 808 are considered by Remeslo (1964) to be the result of adequate genetic variation.

According to the mentioned experiences and attempts made by Rajki (1962*a*, *b c*, 1963), Dionigi (1972, 1973) argued that "pure line" as such does not exist and that a cultivated variety should be viewed as a collection of heterogeneous individuals tending towards modification in successive generations.

Chapter 13 **Selection**

In a population produced by crossing the desired recombination, or in mutant populations the desired mutant, must be found and separated from the other plants. This should take place as soon as possible in order to spare the superfluous reproduction of a heterogeneous population and attain the homozygous state of favourable neocombinations in the shortest possible time.

The selection of visually recognizable morphological characters is simple. Separation of quantitative properties requires, however, objective methods which exclude any error and reduce to the minimum the possibility of favourable recombinations going unnoticed. Selection should thus comprise a screening system separating the desired genotypes in the very first step. In other words, the favourable neocombinations should be recognized in the early generations to attain the homozygous state within a short period of time. A really good method of selection should therefore be simple and quick, making it possible to at once point out individual differences, i.e. suitable for mass examinations.

Possibilities of early selection for the properties listed in the previous chapters are given in Table 23.

The table reveals some deficiencies in the methods of early individual selection.

Table 23.

Property	Method of early selection		
	exists	not quite reliable	does not exist
Yielding potential			+
Germ/m²		+	
Spike/plant		+	
Kernel/spike	+		
Thousand-kernel-weight	+		
Winterhardiness	+		
Drought tolerance		+	
Lodging resistance		+	
Stem rust resistance	+		
Leaf rust resistance	+		
Yellow rust resistance	+		
Powdery mildew resistance	+		
Fusarium resistance	+		
Milling quality			+
Baking quality		+	
Biological quality	+		

There is no method of early selection for yielding ability. Methods for an early individual examination of two yield components are though available, but the separate examination of the components does not give full information about yielding potential. Methods measuring individual climatic resistance are also deficient. The situation is more favourable with the pathological examinations. There is no possibility of early selection for milling quality, and even the early selection of baking quality is not quite reliable.

These deficiencies of the selection methods make breeding work very difficult. It is therefore rightly supposed that for the time being an appropriate recombination can be much easier produced than found with certainly in the population.

In later generations when a sufficient quantity of seed is available examinations shown by the table as "does not exist" can also be performed by indirect or direct methods, but by that time an essentially reduced number of strains should be left from the population, as each strain must be sown to a plot of several m^2 in size. With thousands of strains this cannot be carried out. Thus, by the time a reliable picture is obtained of the yield potential, drought tolerance, lodging resistance, milling and partly baking quality of the genotypes, when a few hundred lines are left from the original combination population only. Unfortunately, we cannot say for sure that they are the best ones regarding the mentioned properties, because perhaps the best lines might have been discarded long before their real value was recognized.

It is therefore an open question when selection for the individual characters can be, or worth being made. For properties of simple transmission selection can already be made from the F_2 generation, especially if they are recessive. In the case of dominant characters the double recessives segregating in later generations must be sorted out. A repeated negative selection is therefore necessary. For polygenically determined properties selection is only worth while when their genetic segregation have become moderate. This can be expected only in later generations. For properties whose realization is considerably influenced by environmental factors selection can only be made under controlled conditions when the likely modifying effects can be reduced to a minimum. If it is impossible, then the disturbing modifying effect has to be eliminated mathematically. This can be done only with strains of higher individual number.

The reliability of transmission and heritability of quantitative characters can be calculated. The h^2 value expresses the heritability in percentage or decimal, that is, it shows the percentage to which the manifestation of characteristics depends on the genetic information, and on environmental factors, respectively.

The h^2 value can be calculated by the formula:

$$h^2 = \frac{\text{selection progress}}{\text{selection differential}} = \frac{R}{S} = \%$$

For example, if the heritability of shorter straw is calculated, and the mean value for the parental population is 120 cm, the procedure will be the following. All plants shorter than 110 cm are selected from the population. They are averaged for height: the result is, e.g. 106 cm. The difference between the mean

values of 120 and 106 is the selection differential, i.e. S = 14 cm. The kernels of the selected plants are sown next year the average height of the new population recorded. It turns out to be no longer 106 cm; it is 111 cm. The difference between the mean values of parental and filial populations, the selection progress, has thus been reduced to 9 cm. $h^2 = R/S = 9/14 = 0.64$, that is 64 per cent which means that the property in question was hereditary in 64 per cent and dependent on environmental factors in 36 per cent (Sváb 1973).

In the practice of breeding heritability is a firm basis to decide on whether or not selection is worth being made early. The closer the value of heritability is to 100, the higher the efficiency of selection will be, and the probability that the derivate considered desirable during the trial is in fact a better recombination and not only the more favourable environmental conditions make it appear better than the parents.

Heritability data presented in the previous chapters (Chapters 9, 11) prove that the important quantitative characters are of different heritability, and the results published on the same property are not identical either. This can be explained by the different methods used for the examinations, and it can be supposed that in a different genetic background the genes have not the same effect. If the heritability of some property reaches or exceeds 50 per cent, the practice of breeding may consider an earlier selection to be justified. If the h^2 value is lower than 50 per cent, selection should be postponed until a later generation, because in the case of an early individual selection the property will be highly modifiable, or the range of variation wide owing to the influence of a large number of genetic factors. The breeder must thus wait until in consequence of a nearly homozygous state variability decreases and the variance analysis of a strain of higher individual number can decide whether a really useful neocombination has been obtained.

The number of heritability tests is not sufficient yet to show its real importance, but it can be seen from the accumulated data that while of the *factors determining yield potential* early selection for two is technically possible, on the basis of heritability it is justified only for one, for the *thousand-kernel-weight*. Early selection for *kernel/spike* is less efficient. The heritability of *productive tillering* is so low that early selection is quite uncertain.

The heritability of *winterhardiness*, *drought tolerance* and *stability* does not make early selection reasonable either.

Pathological resistance is mostly of high heritability. Individual selection can thus be started already in the F_2 generation.

For *milling* and *baking* quality as well as for *Italian paste* quality it is better to make selection again in later generations.

As to protein content, Haunold et al. (1962) found a heritability of 54–69 per cent. For this property selection can thus be made early.

When starting selection even if for visually determinable characters the number of loci determining them and the course of inheritance should be known. For dominant characteristics selection can practically be made already in the F_1 generation, but with view of the segregation of double recessives selection for such characters should better be made in later generations. It is important to know, however, that whether the absence of dominant properties from the

pollen partner in the F_1 generation suggests spontaneous selfing. Such plants must be sorted out already from the F_1 generation. Selection for monogenic recessive characters can be reliably made from the F_2 generation. For multigenic morphological characters selection is again made in later generations.

Of the *morphological features height* is the most conspicuous one. Since height is determined by an extremely great number of loci, results of examinations concerning the course of inheritance are not utilized in the practice of breeding.

Dwarfness originating from the variety Norin 10 is determined by two partially recessive additive genes (sd1, sd2) (Allan 1970). Most of the dwarf- and semi-dwarf varieties received the dwarf character from this variety. Another known source of dwarfness is the winter wheat variety Tom Thumb. In this variety, the property in question is determined by a partially dominant gene localized in chromosome 4A (Morris et al. 1972). Dominant dwarfness is found in the variety Olson too. Selection for the two recessive genes present in Norin 10 can be made already in the F_2 generation. The same applies to dominant dwarfness, but in this case a negative selection should be made in the later generations.

Other important morphological features are the *awned and the awnless character*. In semi-dwarf wheats special emphasis is laid on the awned spikes, since the awns are very useful in making up for the reduced assimilating surface. The awnless character may be developed by three dominant inhibitors, though according to Sears (1953) they are mostly two and only less frequently three in number. The so-called *hooded-character* is determined by the Hd gene in chromosome 4BS. The two inhibitors determining the awnless character are

B1 (tipped) in chromosome 5AL,
B2 (tipped) in chromosome 6BL.

These inhibitors cause awnless spike in different combinations.

The gene formula of totally awned wheat is Hd b1b2. The awnless character of Chinese Spring is caused by two genes only: Hd and B2, that of the variety Federation by genes B1 and B2. The spike is awnless in the case of HdB1 gene present, too (McIntosh 1973). Against these genes recessive awn promoter genes may be active. Eight such promotors have been found so far and marked as a1–a8. Their effect is varying, and they may cause shorter or longer awns in different degrees (Tshunewaki and Kihara 1961). According to the ratio of dominant suppressors and recessive promotors there are awnless, tipped, short-awned and long-awned spikes. The awned character is highly heritable. Selection can be made already in the F_2 generation, moreover, if the seed parent is awned and the pollen parent awnless it can be seen already in the F_1 generation which of the plants are not hybrids.

The *colour of awn* generally agrees with that *of the glumae*, the two are transmitted together. The two combined give the colour of the spike.

The red colour of the spike (colour of glumae) depends on two dominant genes:

Rg1 in chromosome 1BS (Unrau 1950),
Rg2 in chromosome 1BL (McIntosh 1973).

If the pollen donor has red spikes, selection can be made already in the F_1 generation, otherwise repeated re-selections are required.

The *black colour of the spike and glumae*, respectively, is determined by a dominant gene in the tetraploid wheats. Its symbol is Bg, and has been localized in chromosome 1A (McIntosh 1973). This gene is otherwise epistatic to the Rg genes, meaning that when crossing Rg × Bg, the F_1 generation will always be black-spiked (Sikka et al. 1961). Therefore, the hybrid derivates can be recognized already in the F_1 generation if the pollen donor is black-spiked. In the later generations the non-black-spiked derivates will always be homozygous.

Hairy glume is a characteristic morphological feature. This property as a dominant marker has been used in genetic studies (Sheybani and Jenkins 1961). Its symbol is Hg and is located in chromosome 1AS (Tsunewaki 1966).

The *pubescent peduncle* is a property introduced in wheat from rye. In rye its gene is found in chromosome 5R. In wheat its symbol is Hp. It is dominant and is located on the beta arm of chromosome 4A. This character is also an important marker (Driscoll 1963).

The *pubescent node* is likewise determined by a dominant gene, located in chromosome 5AL and marked by the symbol Hn (Gaines and Carstens 1926). If this is used as a marker gene and is found in the pollen donor selection for it can be made already in the F_1 generation.

The red grain colour is determined by three dominant genes with additive effect. Their symbols are:

R1 in chromosome 3D (Sears 1944),
R2 in chromosome 3A,
R3 in chromosome 3B (Metzger and Silbaugh 1970).

The intensity of the colour depends on the effect of dose. McIntosh (1973) divided the varieties into red-kernel groups determined by 1, 2 and 3 genes. In case of need selection for this character can even be started in the F_1 generation.

There is a gene known to cause the *purple colour of the pericarp;* it has been transferred from tetraploid to hexaploid wheat (Coop 1965; McIntosh et al. 1967; Bolton 1968). In tetraploid wheat the purple colour of the pericarp is determined by one or two dominant genes. In some varieties the property is transmitted by two dominant genes, and complementation has also been observed. It can be of any importance only as a marker. Bread wheats should not have kernels of this colour (Dedio et al. 1972).

How the *waxiness of leaf and stalk* is transmitted is not quite clear. Two dominant genes, B1 and B2, have been detected, but there is a recessive gene causing waxiness, too (w1). According to Matsumura (1951) there are also inhibitor genes which eliminate waxiness; their symbols are: I1 and I2. That is why in the inheritance of waxiness extraordinary cases sometimes occur. Selection for the property can only be made in later generations (Driscoll and Jensen 1964*b*).

The *colour of the coleoptyle* may be red, green and light green in wheat. The red colour can be determined by two dominant factors: P1 and P2. Selection can be started already in the F_1 generation but in the later generations it must be repeated.

The colour of the mature stem can be red and light yellow. The red colour is determined by a dominant gene marked Pc. It was located in chromosome 7BS (Law 1966*a*, 1967). Selection can be started in the F_1 or F_2 generation.

Hairy leaf blade is a partially dominant character of monogenic heredity in *T. timopheevi;* the gene has no symbol as yet (Lelley 1953*a*). In other cases two dominant genes were observed (Murti and Lakhani 1958). These genes are in chromosomes 4A and 5A. This character can likewise be stabilized by repeated selection only.

Hairy auricle is transmitted by a dominant gene localized in chromosome 5B (Woo and Smith 1962).

The *red colour of the auricle* is determined by three dominant genes: Rc1, Rc2, Rc3, found in chromosomes 7A, 7BS and 7DS (Kuspira and Unrau 1958).

The *colour of the anther* can be yellow or reddish. The red colour is determined by a dominant gene.

The gene of the compact type of spike is, according to Unrau (1950), in chromosome 2D.

The gene of the speltoid type is found in chromosome 5A. This gene is supressed by the Q-factor (Sears 1944).

The gene of the *vavilovid type of spike* is located in chromosome 5AL. This property too is supressed by the Q-factor, therefore, it only appears with speltoidy. It causes elongation in the axis of the spikelets. The gene is, recessive (Singh et al. 1957).

The *sphaerococcum shape of the kernel* in hexaploid wheats is determined by an incomplete dominant gene (Schmidt et al. 1963). However, a recessive gene has also been pointed out in chromosome 3D (Schmidt and Johnson 1966).

Hereditary sterility appearing at the tip and base of the spike, respectively, is caused by a recessive gene each. In the fertility of the florets in the spikelets the Q-factor has a part too; in case of sterility it is always absent. Fertility on the second and subsequent florets is caused by the Bs gene located in chromosome 5D (Frankel et al. 1969).

Three types of gene configuration exist:

hexaploid	QQ	BsBs	fertile,
spelta	qq	BsBs	fertile,
speltoid		bsbs	base of the spike is sterile.

The *branching spike* originates from *T. turgidum.* It is generally a monogenic character though there are experiences of its polygenic inheritance, too. In some cases the environmental conditions even change the course of realization.

Selection for visually comparable morphological characters of relatively simple heredity depends thus on the conditions of dominance. It may start in the F_2 generation. For dominant characteristics a reselection should be made in later generations.

There are some visually selectable properties which are inherited in a complicated way being determined by many genes or because various modifying genes

also play a role in the changed genetic background. Selection for these properties is only possible in later generations when further major segregation is no longer expected.

Spike density is a polygenic characteristic influenced by minor genes and inhibitors.

Tendency to early tillering, as a multigenic property is likewise inherited in a complicated way and should be selected for again in a later generation.

Both *heading time and the time of ripening* are multigenic features. They may be inherited in a dominant or recessive form, selection should therefore be postponed to later generations.

Polygenic hereditary is shown by the *coleoptyle length* which is determined by genes at least in 10 chromosomes.

Tendency to lodging is determined by genes in 18 chromosomes. The *glassiness of kernels* is once of mono-, then of multigenic character. The inheritance of the *morphological characters of leaf blade* is so complex that almost every chromosome contains determinants. The *size of the anther* is polygenically determined, its course of heredity is not yet known (Sharma 1944).

The *length and branching of roots*, the *number of adventive roots* are also specific of the variety, i.e. genetically determined. According to Sears (1954) the greatest influence on the properties of the root is exercised by chromosome 3D. Otherwise, as to the transmission of the characteristics of root only a few data are available.

Among the visually non-selectable quantitative characters the *vernalization demand* is worth mentioning separately. It is determined by four genes: Vrn1, Vrn2, Vrn3, Vrn4 (Pugsley 1972); in winter wheats all of them are recessive. Of the genes the first one is epistatic over the others. The extent of the vernalization demand depends on the number of recessive genes.

In the transmission of the *photoperiodical demand* sometimes one, at other times two genes have been observed to be active; their symbols are Ppd1, Ppd2. Day-length indifference is generally dominant. According to Piech (1969) in the crossing of Sonora 64 × Resque day-length indifference showed an intermediary transmission.

In the crossing derivates sometimes certain anomalies occur which disturb proper selection. We discussed *hybrid necrosis* in detail earlier (see page 173). A less frequently occurring chlorophyll defect is *virescene* caused by recessive genes (v1a, v1b and v2a, v2b). Chlorophyll defect is only caused by the simultaneous presence of both genes. The genes are found in chromosomes 3A and 3B. The normal quantity of chlorophyll is dominant (McIntosh 1973).

Grass-clump dwarfness is a special abnormity. This phenomenon is caused by four complementary genes: D1, D2, D3, D4, all are dominant. Their chromosomal location is 2Dα, 2BL, 4BL and 2D. The normal growth of wheat is determined by d1, d2, d3, d4 (McIntosh 1973).

To know the linkage conditions of genes is an advantage in the work of selection (Table 24).

In the case of incomplete BC and BC, multilineal and convergent breeding method selection should be repeated after each crossing from the F_1 or F_2 genera-

tion. These methods are most efficient when working with dominant monogenic properties. Selection for recessive characteristics prolongs the process.

After *mutagenic* treatments a two-way selection is made. In the M_1 generation selection is made on the basis of lethality or viability. From lethality and viability conclusion can be drawn on the intensity of the effect of the mutagen, and possibly on the special sensitivity of the variety to the mutagen. Appearance of desirable mutants can only be expected from the M_2 generation onward, actual selection is therefore started in this generation and occasionally repeated later. Mutants left unnoticed in M_2 may be found in M_3 or in the M_4 generation. Double recessive mutants no longer segregate. For dominant mutants, however, reselection should be made.

In carrying out selection every plant breeder employs his own method, i.e. adapts the methods considered correct on the basis of his genetic knowledge to the conditions of the given area of region. Accordingly various schools of selection developed. Quisenberry (1967) describes in detail the methods of selection proved good in the United States and Canada. The English wheat breeding methods are described by Palmers (1970). Techniques used in Sweden are discussed by MacKey (1962) and Fajersson (1963). Forlani (1954) and Antoniani (1962) treats the Italian hexaploid wheat breeding, while Cillis (1963) reports on the methods of durum wheat breeding in Italy. Techniques used in the German Federal Republic are discussed by Wienhues (1959) and Udashin (1968). Wheat breeding methods in Yugoslavia are described my Martinič (1968), those in Poland by Rüebenbauer (1962). Hänsel (1969) gives account of wheat breeding in Austria, Lelley (1973*a*) in Hungary, the methods used in the Soviet Union are discussed by Kirichenko (1962*b*) and Pisarev (1964), those employed in Bul-

Table 24. Major genes in the same linkage group (chromosome) (after McIntosh 1973)

1A chromosome:	Hg-Bg-Pm3a
1B chromosome:	Rg1-Rg2-Bt4-Bt5-Bt6
1D chromosome:	Lr21
2A chromosome:	Pm4-Sr21
2B chromosome-L arm:	Sr9a-Sr9b-Sr16-Sr19-Sr9d-D2-Sr20
2B chromosome-S arm:	Ne2-W1-D2
2D chromosome alpha arm:	Sr6-Lr15-Lr2a-D1-D4-W2-Lr22
3B chromosome:	vla-
4A chromosome:	Hp-Lr12-Lr16-Sr23
4B chromosome:	Sr7a-Hd
5A chromosome:	q-Bl-Hn
5B chromosome:	Ph
5D chromosome:	Lr1-Pm2
6A chromosome alpha arm:	Sr8
6A chromosome beta arm:	Sr8-Sr13
6B chromosome L arm:	B2-Sr15-Lr9-Lr3
6B chromosome S arm:	co
7A chromosome:	Pm1-Pm2-cn-Sr22-Sr15-Lr20
7B chromosome L arm:	Sr17-Pm5-Lr14a-Pc
7B chromosome S arm:	Pc
7D chromosome:	Lr19-cn-Rc3

garia by Popov et al. (1969), Reeves (1964*a*) reports on the breeding methods of Australia, Joshi (1968) and Udashin (1972) on those used in India; wheat breeding in Mexico is described by Borlaug (1968), that in New-Zealand by Coop (1970).

As to the number of combinations the opinions differ. Some believe in a large number of complicated combinations (Borlaug 1968), others consider a smaller number of more carefully prepared combination better. Hänsel (1969) uses the so-called "bulk-crossing" method, where the pollen donor "bulk" stock is produced by a very careful preparation, to be used to pollinate the flowers of the mother variety or variety mixture. This is the inter-cross period, followed by the selfing of the F_1 generation which he calls "selfing-period". The method is recommended mainly for recognizing transgressions.

Wheat breeders unequivocally emphasize that in carrying out crossing a high percentage of seed setting should be endeavoured in order to obtain the largest possible amount of F_1 seed.

The F_1 seed should be sown under ideal conditions (Roy and Murty 1967, 1970). Irrigation should be when necessary provided for. In the case of crossing winter × spring wheat the F_1 generation should be protected from cold (Pugsley 1971). Low winterhardiness and short demand of vernalization are mostly dominant, the first generation is therefore superfluously thinned by an intensive frost (Gotsov 1969). According to Kozlov (1965), the irrigation of the first generation is very advantageous not only from the point of view of a faster rate of propagation, but also with a view to a many-sided evaluation of the material. The modifying effects should be reduced to a minimum in order to facilitate the recognition of genotypic changes (Allard and Bradshaw 1964; Hmelev 1970).

If the necessary conditions are provided the F_1 generation can be raised in a greenhouse during winter, which in the case of crossing spring wheats does not cause any difficulty and years can be saved thereby. With winter wheat the operation is more difficult. The seed-dormancy period should be interrupted early, artificial vernalization carried out and artificial illumination used to satisfy the photoperiodical demand (Bekseev 1962; Lisovski et al. 1969; Dergachev and Surin 1971). Mac Dowall (1972) pointed out that the growth coefficient was in connection with the intensity of light. Winter generation is much easier to raise in phytotron with the necessary environmental conditions automatically adjusted (Pintilie 1971). When raising wheats in greenhouse the *right intensity of light and reduced temperature at night* are particularly important requirements. At a constant temperature the development of the plants is abnormal, the stalks may weaken so much so that they cannot even support an empty spike.

After raising in greenhouse the seed of the F_2 generation should also be treated in order to interrupt the seed dormancy, and the vernalization demand should be satisfied. In this way two generations can be raised in one year from winter wheat, too. Raising in greenhouse has the disadvantage that reliable phenotypic observations can hardly be made in the F_1 generation even if the parents are also sown, because the changed conditions modify the phenotype. Dominant markers can be recognized in greenhouse as well.

The seed of the F_1 generation should be sown in the field one by one because in this way

1. the extent of the heterosis effect can be determined, which gives some information on the prospective result of the combination (Busch et al. 1971),
2. on the basis of the dominant characters of the pollen partner plants that do not originate from crossing can be isolated;
3. distinction can be made between properties of dominant as well as of intermediary transmission;
4. the ratio of propagation is higher.

For a precise comparison a 10×30–10×50 cm single row sowing is most suitable (Fig. 37).

An artificial infection of the F_1 generation gives information only on dominant resistance genes. If the dominant resistance was a characteristic of the pollen donor, on this basis possible out-cross derivates or plants originating from selfing can be sorted out. If the transmission of a dominant resistance gene is the aim, artificial infection of the F_1 generation is indispensable with the back-cross method, because from then on only resistant derivates should be used as recurrent partners.

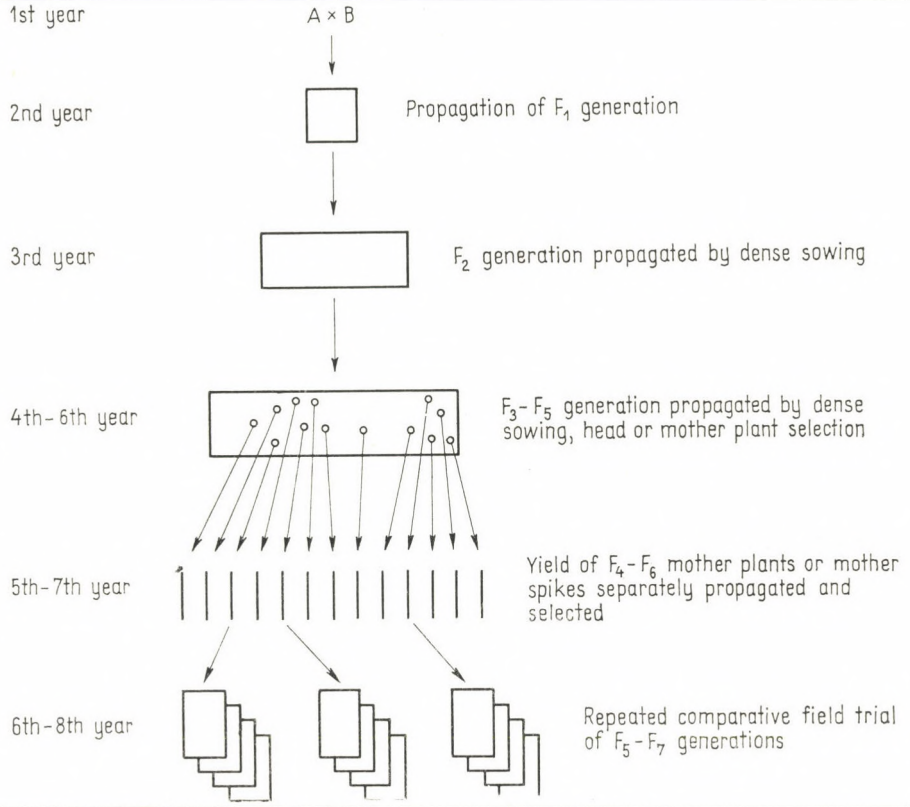
The treatment of subsequent generations depends on the method of selection. Gill et al. (1973) obtained good results by making spontaneous allogamic fertilization possible for the members of the F_2 and F_3 populations.

Bulk-method consists in essentials of reproducing the crossing generations from F_1 to F_x in dense stand without selection. Individual selection or head selection begins in that generation in which the necessary homogeneity has set in. This can be expected in the F_6-F_8 generation. After the first selection pedigree breeding of the selected plants is effected on such a way as to enable the earliest possible starting of a multiserial comparative field trial (Baker and Leisle 1970). The selected plants are propagated by hill-sowing or single-seed drilling followed by a densely sown repeated comparative trial (Table 25). In the bulk method, the beginning of selection depends on the complexity of inheritance of the properties in question. With complicated heredity selection for polygenic properties can be started in the F_6-F_8, for di- to tetragenic properties in the F_4-F_5 generations (Slatkin 1970). The bulk method can be efficiently used to detect transgressive derivates, too. It is used in various forms. Properties, like kernel size, thousand-kernel-weight, whose selection can be carried out with mechanized mass methods are particularly easily recognized by the bulk method (Derera et al. 1973).

To be successful it is desirable that the individual generations should be grown under excellent agricultural conditions (Konovalov 1969). Sen (1964) evolved a mathematical method to forecast the prospective frequency of the different combinations in the next generation. On the basis of a forecast like that the beginning and intensity of selection can be decided.

Individual selection or *pedigree breeding* opposes the bulk-method. Early and continuous individual selection begins in the F_2 generation with the

Table 25. Bulk-method

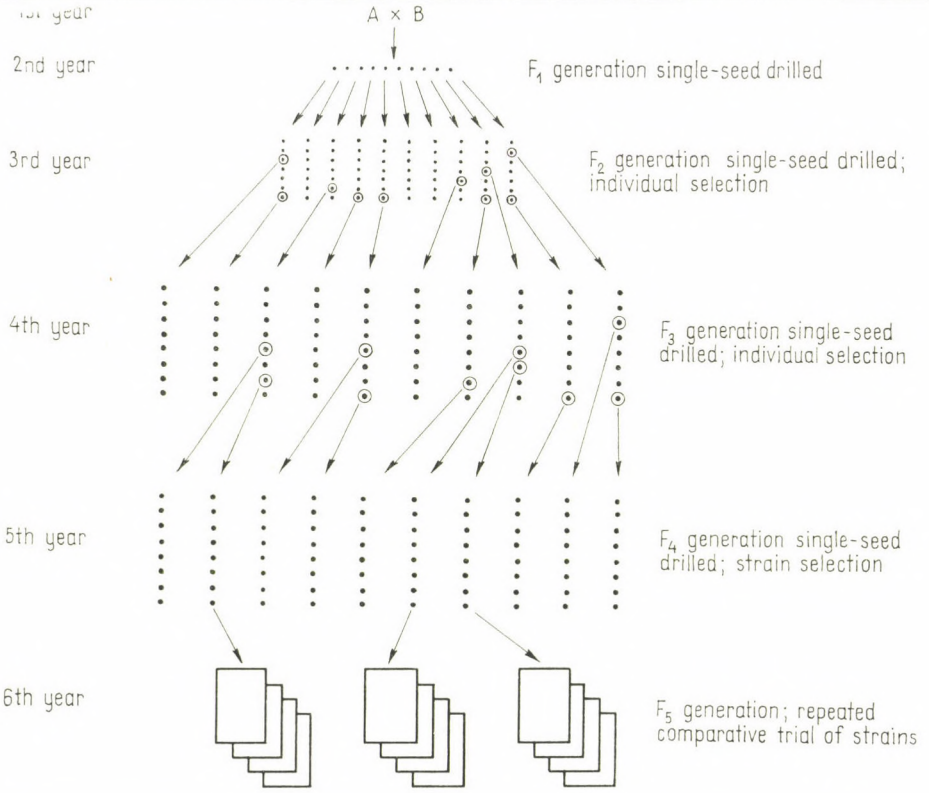


heritability and dominance conditions of the properties taken into consideration. If the F_2 generation is sown with single-seed drill, winterhardiness, pathological resistance, some quality characters and all morphological features can be evaluated at once and the yield components can be analyzed, too. Due to a rapid reproduction, successful selection can be made for all important characteristics in the F_3-F_4 generations (Briggle et al. 1968).

Table 26 shows a sketch of pedigree breeding based on individual selection. In the case of individual selection five years after crossing all values of the population can be assessed. If the F_1 generation is raised in winter in greenhouse then four years after crossing all the economic qualities can be evaluated through multiserial field trials of the strains. The method is highly suitable to detect the transgression and a comparative trial in the fourth of fifth year may definitely reveal the yielding ability of the selected lines, too. Collective yield potential cannot be shown earlier.

Various sowing methods and plot systems have been tried out with a view to determining the collective yielding potential at an early date. Visual selection was found in fact to be unreliable (Krull et al. 1966; Townley et al. 1973). In selection for yield potential the morphological characters are useful, though they give no information about the actual yielding ability. Selection for the length

Table 26. Individual selection



and width of the flag leaf is of considerable help, but does not reveal the actual property (Stoskopf 1967; Smoček 1969*a*). MacKey (1968) pointed out the percentage shares of stalk and leaves in the nutrient supply of the kernel, but nor are those data reliable enough to be utilized in selection. Donald (1968) determined the so-called ideotype of spring wheat which proved to be a useful starting point in selection but does not give information on the actual yield potential. The mathematical method elaborated by Pesek and Baker (1971) gives faint directions only for the comparison of observed and expected crop results.

Many authors have recently studied the roots of wheat plants (Kirichenko et al. 1964; Nefedov 1967; Merfert 1967; Pinthus 1967; Kirichenko et al. 1968; Jachenko and Danichuk 1969). These attempts while yielding partly positive, partly contradictory results have opened a new way possibly leading to the elaboration of a method that will help in solving the problem of individual selection for yield potential. Titova and Grodzhinskaya (1964) likewise tried to approach selection for yield potential when measuring the intensity of the growth process. The method is, however, to elaborate and its reliability has not been proved either. Medunec (1964) tried to draw conclusion on yield potential from the growth of the total volume of the mother plant. Owing to difficulties in application the method has not gained wide acceptance.

About collective yield potential final information is given by the result of repeated comparative field trials. The ultimate goal of every selection process is the "early testing" of the examined strain. Its preconditions are: quick, reliable and continuous selection, quick reproduction and a properly mechanized field trial system (Mihailov and Karaivanov 1965; Lelley 1973*a*).

Finally, it is a question whether selection and testing of strains under different conditions is desirable from the point of view of deciding the yield potential. Selection made under varying ecological conditions is advantageous giving information first of all on adaptability. According to Martinič (1973) the examination of adaptability should be started as soon as sufficient amounts of seed are available. The economic value ultimately represented by the variety in commercial production will be decided in practice. According to Pinthus (1972), however, there is a method of forecasting it. He has set up such a regression function by which – in his opinion – the prospective yield surplus of the variety, and the practical use of the breeding work can be forecasted.

The results of genetic and biological researches increase the efficiency of selection. In spite of this the result is often unreliable, and so subjective insight plays also some role (Mettin 1970; Shebeski and Evans 1973). The success of breeding depends on the recognition of valuable neocombinations, recombinations or mutants. Properly chosen and applied methods of selection decide the result but experience and even good luck are not negligible factors either (Schmidt et al. 1973).

Chapter 14 **Mechanization**

With the exception of the BC method mutation and combination breeding is carried out with equally large numbers of population of high individual number each. For this reason operations of soil preparation, sowing, harvesting, seed cleaning, weighing, counting and testing should be performed for many trials of different kind and dimension. In winter wheat breeding, on account of the long vegetative period, much less time is available for these operations than in the case of spring wheat. Breeding sites should thus be equipped so well as to enable the perfect accomplishment of the necessary work. The extension, intensity and efficiency of the breeding work also depend on the equipment.

Successful wheat breeding can only be carried on in an equalized good quality soil, because selection for the modern idiotypes that satisfy all demands can only be made in good soil, on an up-to-date agrofon.

The operations of soil preparation for the trial plot are known; there is a wide range of different size of soil cultivating machines. They make the garden-like soil preparation of the wheat nursery and the lay-out operations possible before sowing. It is a basic requirement that the soil structure of the seed-bed should allow a uniform depth of sowing, single-seed drilling if necessary, and uniform coming up. Because of this last requirement it is very important that the possibility of sprinkling irrigation should be provided for.

With the lay-out operations care must be taken that the paths between the plots should be wide enough for the turning machines carrying out sowing, care of plant and harvesting. Narrow paths slow down the work of machines and hinder their utilization. To avoid leaving too large areas uncultivated it is a good practice to sow a part of the paths later with crops of short vegetation period which are soon removed and do not disturb the operations.

The importance of studying the wheat collection is a well-known fact. The best opportunity is offered by single-seed sowing. In many wheat nurseries the F_1 seed is sown by single-seed drilling in one-row plots (Fig. 36), both the mutagen treated M_1 seed and the grain crop of the mother heads or mother plants. The mechanization of one-row single-seed sowing had not been solved for a long time. In many places even today this operation is still performed by hand because no machines precisely performing the task is available. Mechanisms suitable to sow to the last seed a few scores of kernel (F_1, M_1) were not available either. It was for this purpose that in 1970 the first two wheeled cart-drill was constructed (Fig. 37) (Lelley 1973*a*) for single row plots. Magazines filled in advance with 25, 50 or 100 kernels are put in the machine. Plant space can be adjusted to 5–10 cm, row width modified at will. Daily performance is 20–25 thousand kernels. A magazine

Fig. 36. Bird's-eye view of a wheat nursery with 1-, 5- and 10-row plots. Width of paths adapted to mechanical operations (Photo by P. Lelley)

is filled in about one minute by means of a device constructed for this purpose. Several hundreds of magazine belong to a machine.

In the one-row plots of the variety collection scattered sowing can be used too. In this case individual evaluation cannot naturally be carried out. This method requires again a sowing machine by which small lots can be distributed to the last kernel. Such a machine is the Improved Test Plant and Garden "Corn-seeder" (Fig. 38) manufactured by the Kraftsman Machine Co. (Winnipeg, Manibota) firm (Cherewick 1954). It is a hand-operated machine, the seed-grain is distributed by a distributor cone and a partitioned rotary disc. Another larger sowing machine mounted on a small tractor by which four rows can be sown at the same time each to a different strain works on the same principle. In the first machine the row distance can be adjusted at will, in the second it can be increased over 20 cm only with certain components dismounted then only three or two rows are sown.

The "Seedmatic 6" self-propelled sowing machine (Fig. 39) manufactured by F. Walter – H. Wintersteigen K. G. serves likewise for sowing one-row plots. It supplies six one-row plots in a single course, the system of seed-grain distribution is in principle the same as above. To the individual micro-plots the seed-grain is portioned out automatically from the magazines filled in advance. Row space is adjustable, the length of row can be varied between 0.7 and 2.0 m. The lowest number of kernel sown per metre is about 25–30. The kernels are distributed in the rows, though rather evenly, at random, i.e. they are not at the same distance from one another.

The F_1 and M_1 seed-grain generally ir also sown in one-row plots of a siz similar to that in the wheat collection. Considering that in the M_1 generatiou individual evaluation is indispensable, the M_1 seed should be sown one by one. If the F_2 generation is to be raised in greenhouse, the F_1 seed of the different combinations, since it is mostly available in a very small number, perhaps a few scores only, is sown in culture pots by hand. For the time being such small lots of seed can be sown one by one precisely and completely in the field only with the one-row single-seed hand drill (see Fig. 37) described by Lelley (1973*a*).

Wide-spaced mother plants generally produce several hundred kernels each. These larger lots are sown either by scattered sowing or by single-seed drilling depending on the method. The bulk method is well suited by scattered sowing. For sowing mixed strains a wide range of plot-drills are available, e.g. the SD 3–8R self-propelled six-row plot-drill (Fig. 40) made by F. Walter – H. Wintersteiger K. G. It is manufactured with two types of magazine. One distributes seed-grain for all six rows simultaneously, in the other type, each furrow splitter has a separate magazine, that is, each row can be sown to a different strain.

When pedigree breeding is aimed at the grain yield of each mother plant has to be sown separately. In this case too the method of sowing may be either scattered or single-seed drilling.

For larger lots consisting of several hundreds of kernel the mechanized single-seed drilling has been solved. A single-seed drill working on the principle of vacuum-compression was constructed by Coop (1961). The machine sows six rows, each row can be sown to a different strain; the row space is about 40 cm. The single-grain drill described by Lelley (1964*b*, 1973*a*) works on a similar principle. This machine sows seven rows at the same time; the row space is 50 cm, the plant space can be varied between 10 and 30 cm (Fig. 41). A vacuum compression single-seed drill is described by Quisenberry (1967), too. The machine sows three rows at a time. All three single-seed drills can be mounted on a tractor; they are of very high capacity. They have proved good in sowing one or several row plots to larger strains. A quick, precise and easy-to-carry out single-seed drilling provides much greater possibilities for individual selection (Lelley 1973*a*).

If it is for head selection then kernels obtained from the individual spikes are sown either one by one, or in hills, or in one-row plots of scattered sowing.

Hill-sowing is carried out in different ways. The simplest and least labour consuming way is suggested by Maksimchuk (1962). By this method unthrashed spikes are planted at a certain distance from one another, in this way thick bunches of plants, hills are produced. Schmaltz (1963) questions the usefulnes of the method. A better solution is to scatter the thrashed kernels of the individual heads into circular hills of 30 cm diameter by means of a sowing funnel, or in a 50 cm long row with a simple hand seeder devised specially for this purpose (Fig. 42). According to Schmaltz (1963) the latter method is more suitable for evaluation and comparison than the former one.

The Seedmatic 6 type drill (see Fig. 39) in which the seed-grain is automatically changed is also suitable for sowing the grain yield of individual heads in one-row short plots (Hoeser et al. 1969). With this equipment 0.7–2.0 m long rows can be sown.

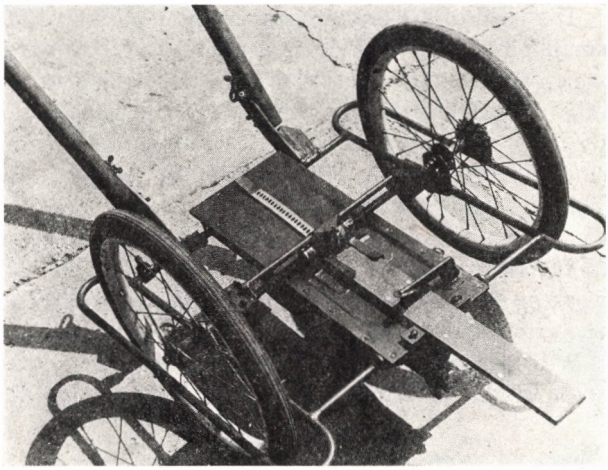


Fig. 37. "Lelley" one-row single-seed drill. Wheat kernels are discharged through the opening of a belt coming out of the oblong, flat magazine (Photo by P. Lelley)

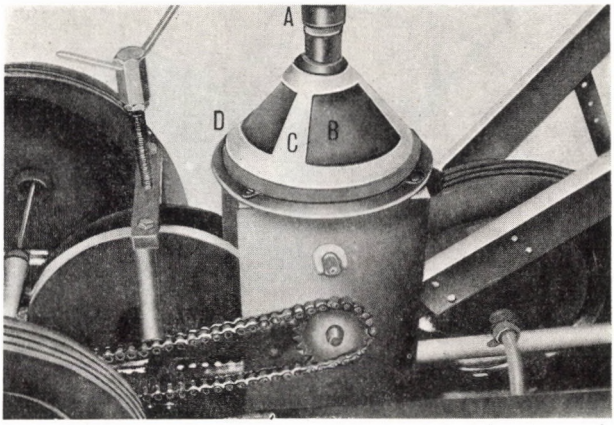


Fig. 38. One-row scattered sowing machine. Seed-grain is distributed by a cone shaped mechanism (Kraftsman Machine Co., Winnipeg)

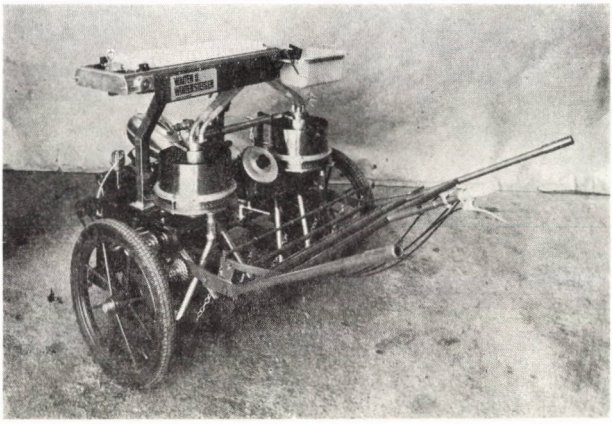


Fig. 39. Seedmatic 6 type self-propelled six-row plot-drill (F. Walter—H. Wintersteiger KG., Ried/I., Austria)

The yield of a 1 m long one-row plot is about 100 g. With this quantity of seed small plot trials with several replications are performed. Sowing machines by which several-row plots can be sown with seed of this quantity work on two different principles. One of them is the principle of Øyord. The amount of seed precisely measured out in advance is poured into a fixed distributor in which a smooth surface cone evely distributes the seed over a horizontal ribbed disc. The disc rotates in synchron with the speed the machine advances at, and the seed drops from between the ribs through an opening into the pipe that leads to the furrow splitter. The Øyord (1972) small plot sowing machines (Fig. 43) work on this principle; the distributing mechanism supplies 1, 2 or 3 furrow splitter with seed-grains.

With the other principle each furrow splitter is attached with a separate magazine (Fig. 44). The magazines are of the same capacity, when fully filled con-

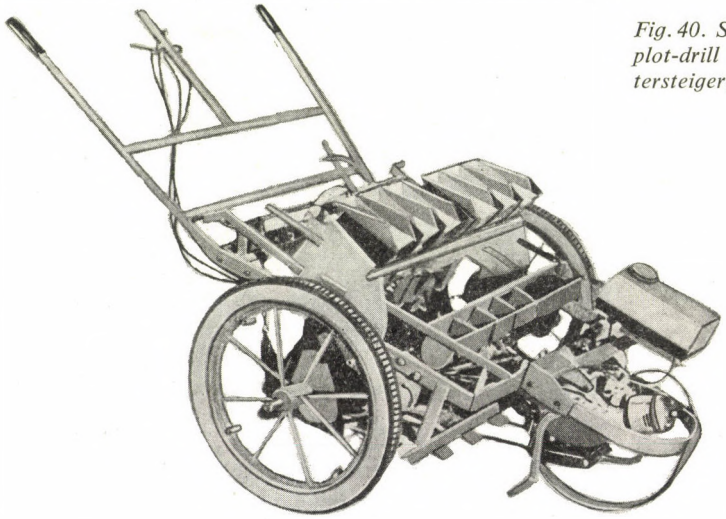


Fig. 40. SD3-8R self-propelled plot-drill (F. Walter—H. Wintersteiger, KG., Ried/I., Austria)

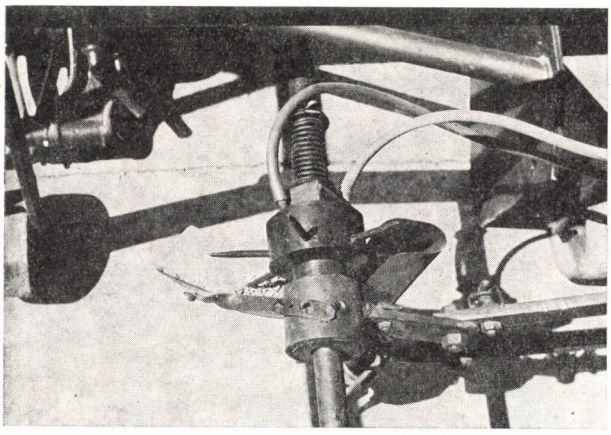


Fig. 41. Feeding mechanism of a tractor-mounted seven-row vacuum-compression single-seed drill. Kernels are picked up by the revolving needles (Photo by P. Lelley)

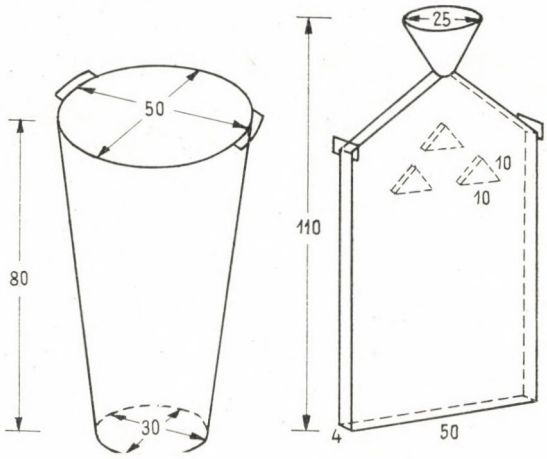


Fig. 42. Hill-sowing funnel and a hand device for sowing 50 cm rows (after Schmalz 1963)

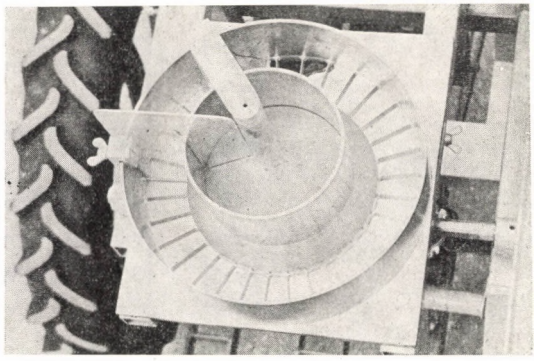


Fig. 43. Øyord's grain distributing cone and disc. Seed-grain is directed by the revolving ribs to the furrow splitter (Photo by E. Øyord)

tain the same volumes of seed. In the course of sowing the kernels are pressed out by constrained movement from the magazines and pass into the shoes. Since the capacity of the magazines cannot be changed they have to be filled up to the brim. The required amount of seed per row can be precisely adjusted by mixing it with sterilized wheat kernels to fill the superfluous space (Fig. 45) (Lelley 1973*a*).

As long as the yield of a strain is small the seed-grain must be used economically. Therefore, besides sowing as many wheat kernels per plot as planned and distributing them evenly between and within the rows it is important that the magazines should be wholly emptied. This is desirable mainly to avoid mixing and accelerate the drilling work, but also because in this way only as many seed-grains have to be poured into the magazines as will actually be sown. Machines working on the principle of Øyord or Weihenstephan and Lelley meet these requirements.

The SC-701 and SC-711 type four-row self-propelled drills (Figs 46 and 47) were designed to sow small plots. The principle of grain distribution is similar to that in the Øyord machines (Dyck 1972). They are suitable to sow 6 m long plots; the row distance is 23–30 cm. In the United States and Canada the com-

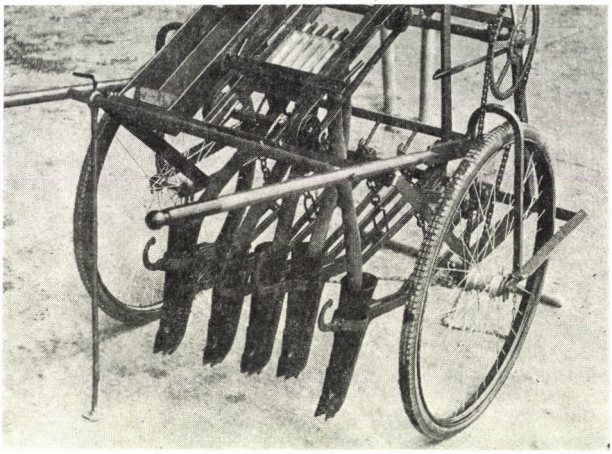


Fig. 44. Five-row precision plot-drill. Seed-grains travel from the magazines to the shoes through constrained motion (Photo by P. Lelley)

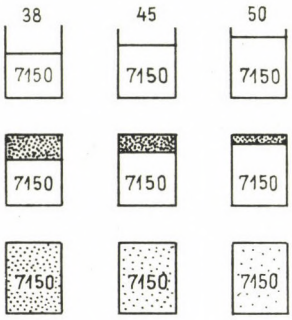
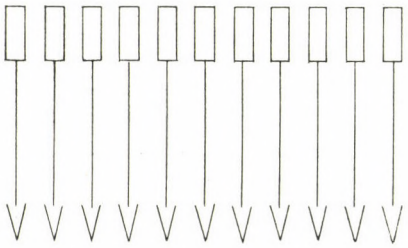


Fig. 45. Sketch of adjusting the amount of seed by mixing it with sterilized seed; 7150 germinating kernels have to be sown of each of three samples of 38, 45 and 50 thousand-kernel-weight, respectively. The black spots indicate the sterilized kernels added to the sample (Photo by P. Lelley)



parative trials of strains are usually sown with such drills in four-row plots with a number of replications. In the evaluation, however, only the two middle rows are taken into consideration.

The yields of larger strain amount to several kg. With a quantity of seed-grain like that, 10–12 row wide and 10–15 m long plots are mostly sown in replicated field trials. The 10–12-row plot drill used for this purpose has a single grain box, the seed-grain is forwarded to the shoes by toothed cylinders. The amount of seed-grain can be adjusted with the working surface of the toothed cylinders or by the number of rotation. Most sowing machines of this type are rather difficult to clean, and the amount of seed-grain cannot be adjusted quite accurately

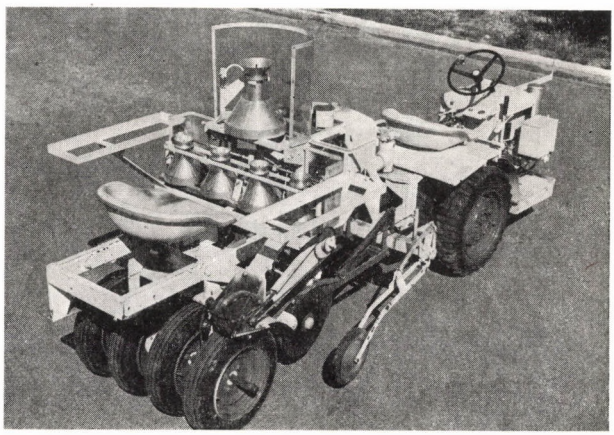


Fig. 46. SC701 type four-row plot-drill described by F. B. Dyck (Res. Sta. Swift Current Sask.; Photo by F. B. Dyck)

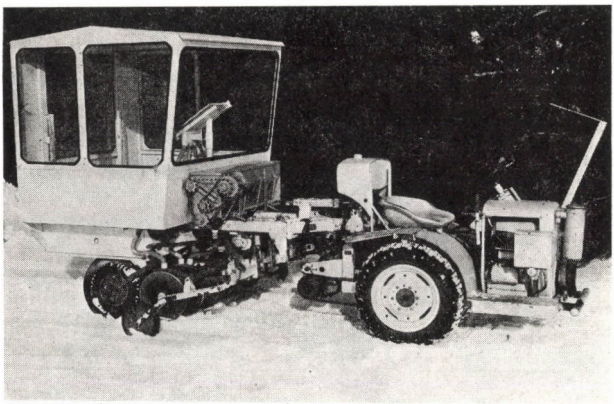


Fig. 47. SC701 type American grain-drill equipped with a closed cabin. The filling apparatus has been modified (Photo by F. B. Dyck)

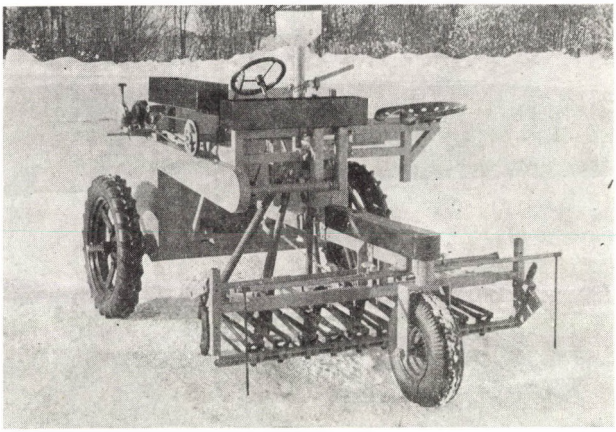


Fig. 48. Øyord system ten-row three-wheeled self-propelled plot-drill. Besides seed-grain, fertilizer can also be distributed with it (Photo by E. Øyord)

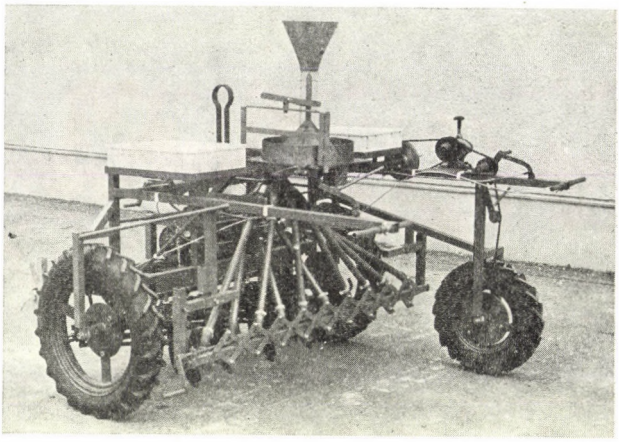


Fig. 49. Tractor-drawn Øyord system plot-drill with adjustable working width. It distributes fertilizer, too (Photo by E. Øyord)

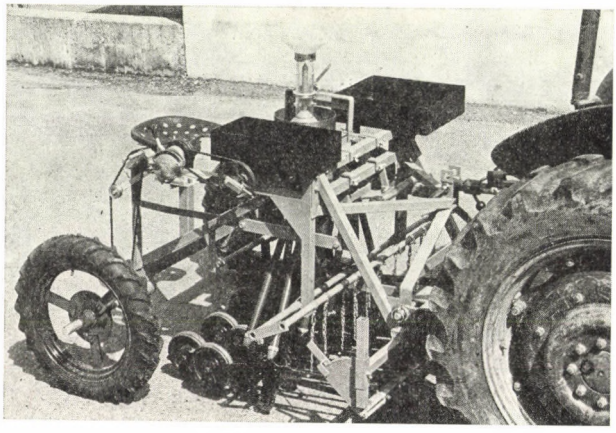


Fig. 50. Øyord system tractor-mounted plot-drill. It distributes fertilizer, too (Photo by E. Øyord)

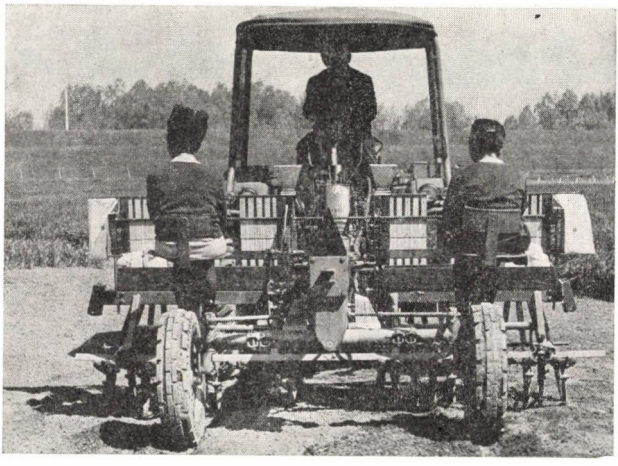


Fig. 51. Two times 10- or 11-row tractor-mounted twin-plot drill, with precision seed-grain distribution (see Fig. 45) (Photo by P. Lelley)

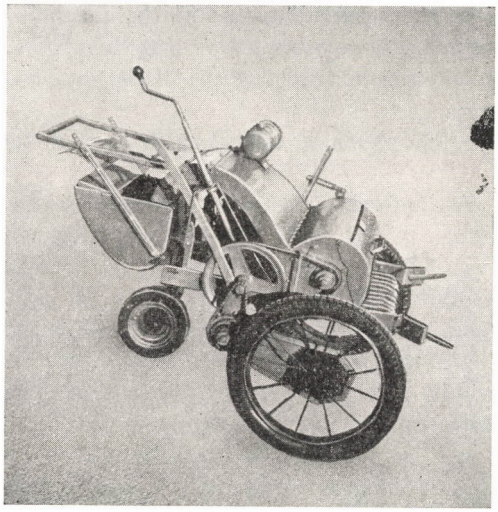


Fig. 52. Poynter Pneumatic Stripper Harvester Model 403 type small combine with a cutting width of 60 cm for harvesting 3–4-row plots. It collects the crop in a container (Poynter Products Pty. Ltd., Bullen, Australia)

either. The larger types of the Øyord system sowing machines (Figs 48, 49 and 50) can be adjusted more precisely, are easier to handle and quite simple to clean (Øyord 1972). They are self-propelled or mounted on a tractor. They entirely sow the amount of seed-grain measured out in advance. A twin-drill operated by a new principle (Fig. 51) is described by Lelley (1972*b*). The machine supplies two plots at a time each with 10–11 rows, the length of the plot is 10–15 m; each shoe has a separate grain box. The seed completely emptied; the amount can be adjusted by mixing the lot with sterile wheat kernels (Lelley 1972*b*) (see Fig. 45).

Trials sown with well-constructed sowing machines suitable for the purpose give more reliable results. At the same time the cost of lay-out decreases, sowing time will not be lengthened which favourably influences the evaluation of the trial. It is therefore a basic requirement that an institution engaged in wheat breeding should be equipped with the most skillful machines from the one-row single-seed drill to the plot-drill of several rows.

Concerning further operations of the trials chemical weed control is among the most important ones. Machines of producing farms can be used for the application of chemicals, but there are smaller apparatuses constructed specially for spraying trial plots (Lush and Mayesh 1972).

Harvesting is very important from the point of view of breeding work. Plots of different shape and size require different types of machine. There are, however, general requirements that concern all harvesting machines:

1. The plot should be completely harvested without any loss of spike and kernel.
2. The yield should be thrashed out fully and without breaking.
3. The machine should be easy to clean which is important partly to avoid mixing, but in the case of smaller plots is not indifferent for the amount of yield either.

4. The crop discharged by the machine should be as clean as possible. In the case of smaller harvesting machines, however, emphasis is laid on the quick and perfect cleaning of the machine rather than on the cleanness of the crop.

5. The machine should easily turn in the smallest possible place.

A combine suitable to harvest one-row or other small plots is described by Finlay et al. (1972). It is self-propelled with a maximum cutting width of 60 cm; (Fig. 52) the operator walks behind the machine. Handling requires three persons; its daily performance is 800 plots, 10 m in length and maximum 60 cm in width each. The crop is discharged by the machine in a relatively clean state. Hergert (1972) describes another small combine constructed specially for cutting the two middle rows of four-row plots used in North America (Fig. 53). It is likewise self-propelled and cuts two rows at a distance of 17.5 cm from one another at a length of 3–6 m. The operator follows the machine on foot. The superficially cleaned crop is blown into a sack together with the glumes. This combine is suitable to harvest one-row plots too, and can thus be used to cut single-seed drilled variety collections or strain propagations. It is easy to clean.

A small combine described by Poynter (1972) serves again the purpose of harvesting small size plots. It is a self-propelled machine with a cutting width

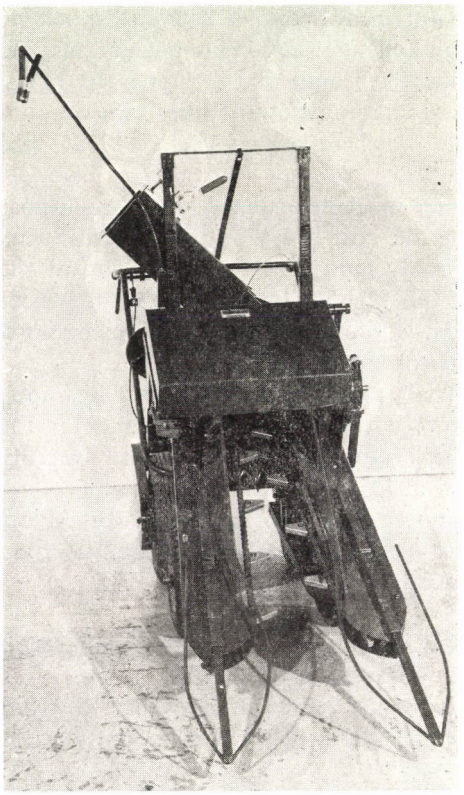


Fig. 53. "Vacuum-Blower-Harvester" made for harvesting two-row plots. It is applied to cut the two middle rows of four-row plots (row space: 17.8–23 cm) used in America. It blows the impure thrashed crop into a sack (Engineering Res. Serv. Res. Branch, Ottawa; photo by G. B. Herger)

Fig. 54. "Hege 125" type self-propelled plot combine with a cutting width of 125 cm (Hege Saatzuchtmachinen, Waldenburg/Würt., Austria; photo by Hege)

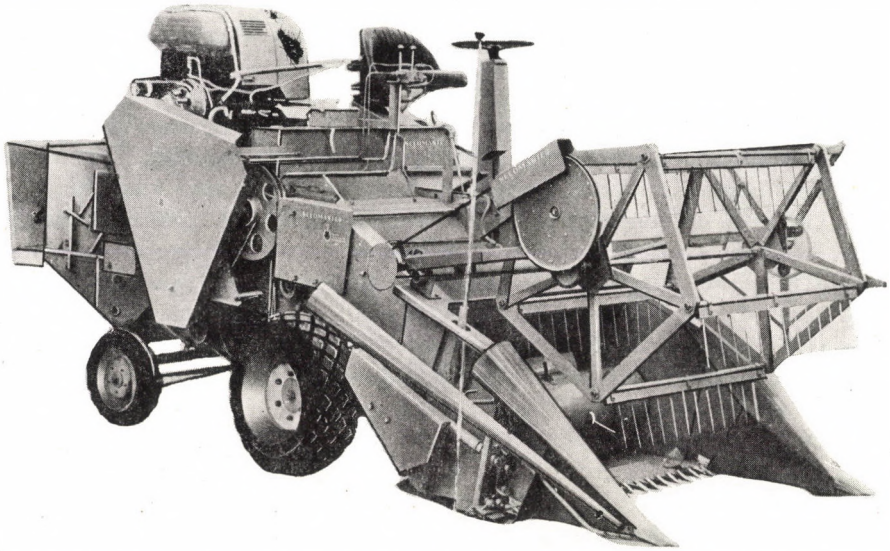


Fig. 55. Seedmaster 125 plot combine (F. Walter—H. Wintersteiger KG., Ried/I., Austria)

of 70 cm, the operator walks behind it. The combine is easy to clean, the kernels together with the glumes are blown into a container.

Graeme and Quick (1972) give information on various types of self-propelled combine constructed to harvest larger plots. Of them Chain PS-50 and Cereal Plotcombine with their cutting width of 140 cm belong to the largest ones. All of them are readily cleaned; the yield is delivered almost perfectly cleaned into

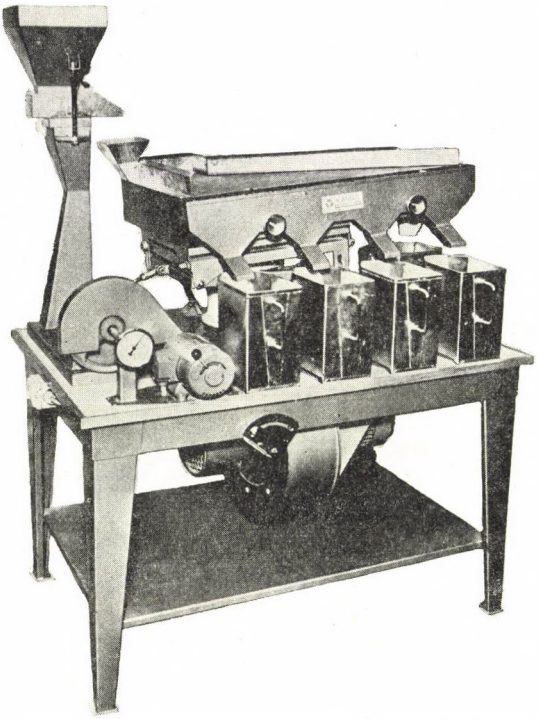


Fig. 56. Kamas Selektor (Kamas, Malmö, Sweden)

container. The driver sits on the machine. Walter et al. (1972) likewise describe a self-propelled small combine with the driver sitting on the machine. The cutting width of the combine is, however, not more than 70 cm. The crop when thrashed is almost clean. Of the combines made in Europe the Häge 125 type self-propelled combine (Fig. 54) is simple to handle and easy to clean, its improved variation is Häge 125-B. The latter has a cutting width of 125 cm and produces almost perfectly clean kernels (Hoffmann and Kühl 1972). The Seedmaster 125 type combine (Fig. 55) made by the firm F. Walter–H. Wintersteiger K. G. is also self-propelled, the driver sits on the machine, the cutting width is 125 cm. In spite of its larger size and weight it is easy to clean.

There are various types of cleaning devices available for the further cleaning of grain samples obtained from the combines by which the impurities can be completely removed. The cleaning apparatus should work quickly and reliably with no loss of grain; it has to be easily cleaned as a precondition of a quick change of samples. This purpose is served among others by the selector (Fig. 56) made by the Swedish firm Kamas Industry AB (Malmö) as well as with the grader (Fig. 57). In both apparatuses cleaning takes place by screening and air flow. A simpler but similarly efficient solution is the laboratory air grader (Fig. 58) made by the Labor Instrument Works (Hungary) where the crop is cleaned with air current only. With this apparatus mixing is yet more easily avoided.

Individual spikes or individual mother plants are thrashed with special spike thrashers. They too have to thrash entirely and without loss, should be easy to

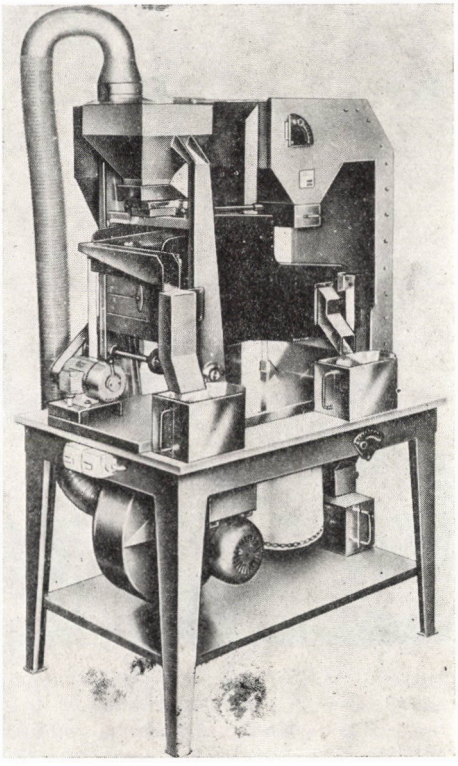


Fig. 57. Kamas air-blast (Kamas, Malmö, Sweden)

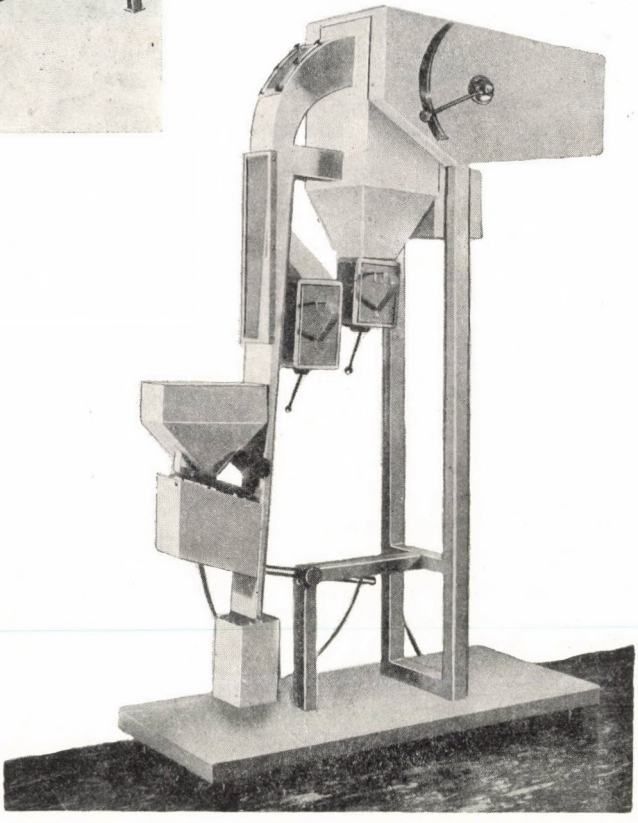


Fig. 58. "Labor air grader" (Labor Instrument Works, Budapest, Type QB-125)

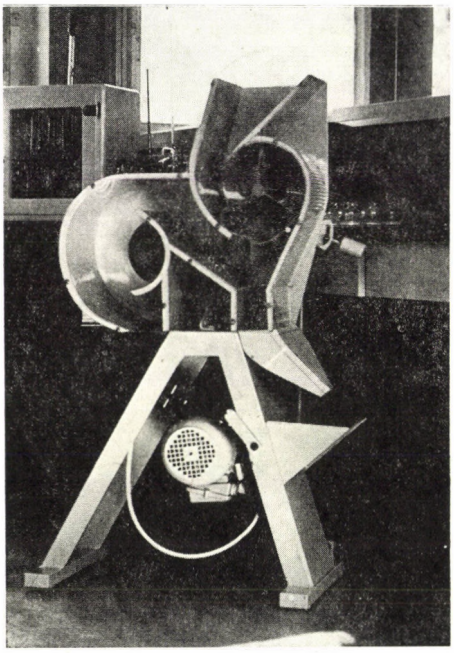


Fig. 59. Labor-Aer (Grain) thrasher LD 180-ST-4, for thrashing individual spikes or mother plants (F. Walter—H. Wintersteiger KG., Ried/I., Austria)

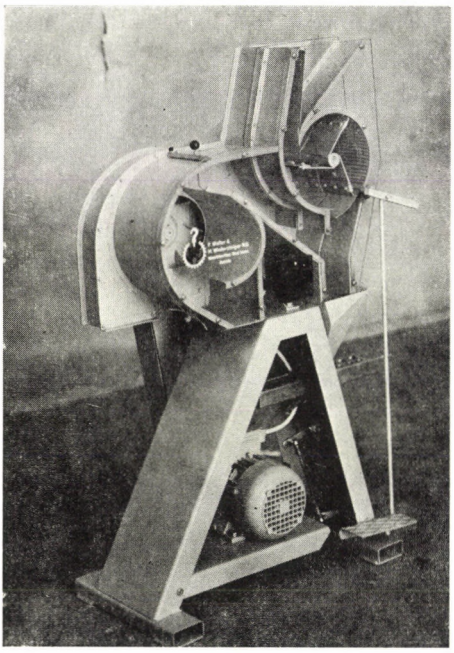


Fig. 60. "Seedboy" laboratory spike thrasher. Suitable for the simultaneous thrashing of two spikes separately. Kernels are collected in small plastic containers (F. Walter—H. Wintersteiger KG., Ried/I., Austria)

clean, and it is important that the kernels should not be injured. The Labor-Airthrasher (Fig. 59) made by F. Walter—H. Wintersteiger K. G. (LD 180, ST 4) fully meets these requirements. The whole process can be visually checked because one wall of the machine is made of transparent material. The air-blast is built in, so the crop comes out clean. The beaters are made of rubber thus the kernels do not suffer injury.

The Seedboy spike thrasher (Fig. 60) is similar but two spikes can be thrashed separately and simultaneously. This thrasher is at the same time an appliance of the Seedmatic 6 type grain-drill. It can be complemented with automatics so that the kernels from each spike pass into separate plastic containers. From these containers the Seedmatic 6 (see Fig. 39) automatically sows separate short rows.

The machinery of laboratory operations includes highly sensitive Roman balances of different types from a precision of 1/100 g to an upper weighing limit of several kilogrammes.

A special equipment of the wheat breeding laboratories is the grain counter (see Fig. 8) which besides the determination of thousand-kernel-weight can be used to determine the number of kernel per spike, and occasionally to count the number of kernels to be sown into the individual micro-plots. There are strict prescriptions for the grain counters. Since besides accuracy, quickness is also

an important precondition. The performance ranges between 300 and 600 kernels counted in one minute according to the different types machine. The essence of the grain counters is vibration conveyance and photoelectric counting. A frequent fault of the machines is inaccuracy in the case of uneven grain size. This is a great fault because the grain yield of wide spaced mother plants, especially of those with a high number of spikes, is mostly uneven, and it is grain counting of mother plants that gives the biggest amount of work. A high capacity electronic grain counter is described by Zachow and Herzberg (1968). Experiences obtained with grain counters are summarized by Eimer (1972).

Observations made at the breeding site can be recorded by a portable tape recorder. In this way surveying will be more simple and reliable. From the tape recorder the text can be written down on a typewriter (Quisenberry 1967).

For the mechanical processing and evaluation of experimental data Martynov and Bobylev (1971) developed a system to which the Minsk-22 or Mir-1 computer can be used. Evaluation of experimental data by computer besides speeding up the operations and making them more exact helps in disclosing much more detailed and manifold relations.

Laboratory and outdoor mechanization of breeding work has recently made a great progress. Important role was played in this by the International Association on Mechanization of Field Experiments (IAMFE) which co-ordinated this significant though not sufficiently appreciated field by organizing international conferences. In the present competition of wheat breeding up-to-date mechanization is just as indispensable as genetic or biological research.

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