IDRC-024e

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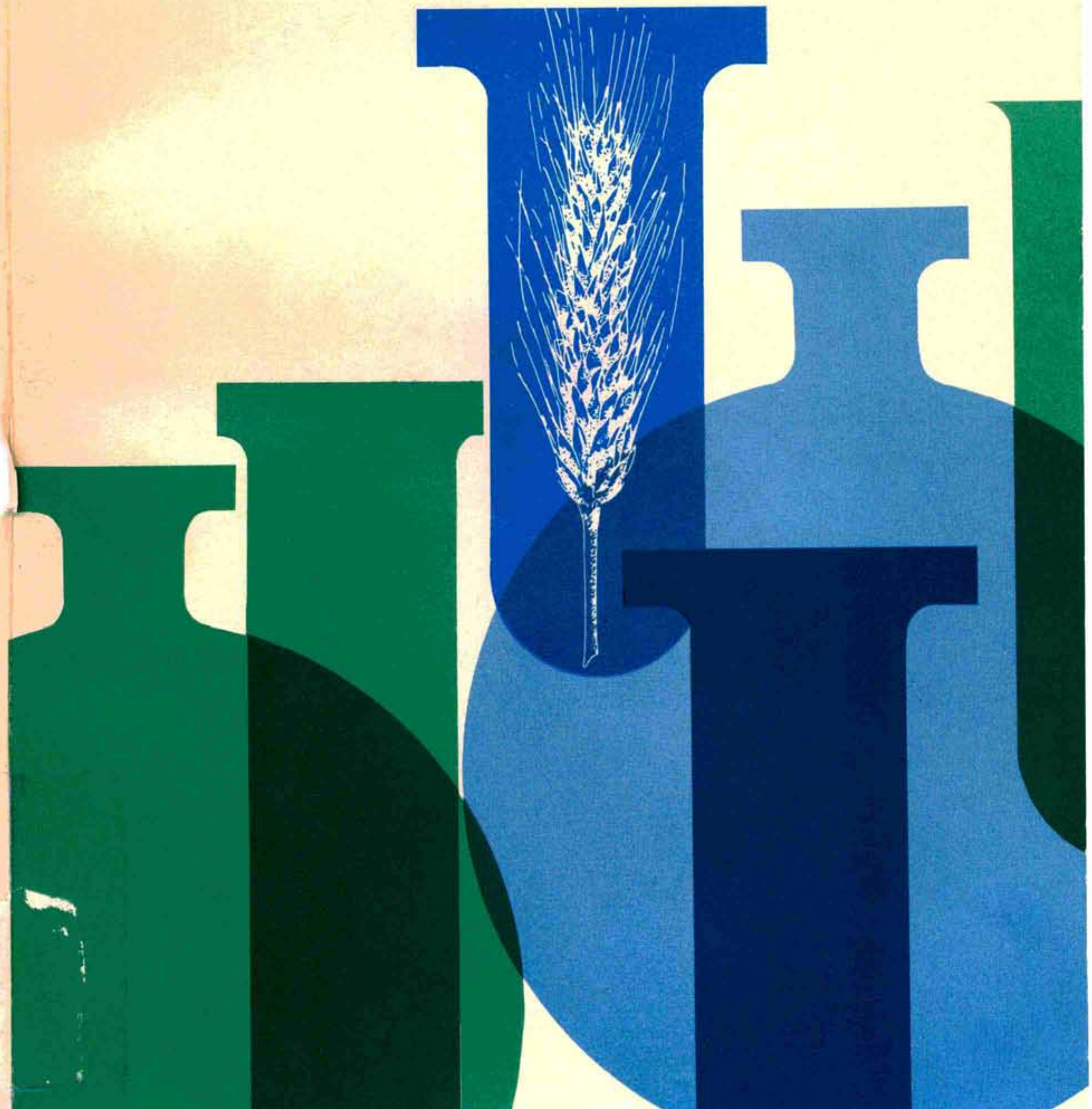
Proceedings of an international symposium
El Batan, Mexico, 1-3 October 1973

Editors: Reginald MacIntyre/Marilyn Campbell



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*The views expressed in this publication are those of the individual author(s) and do not necessarily represent the views of the International Development Research Centre.

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Contents

Historical Review of the Development of Triticale

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Abstract In 1875, a Scottish plant breeder named Wilson was the first to obtain and describe a sterile F_1 triticale hybrid, a cross between wheat and rye. In 1884 the *Rural New Yorker* contained several articles by Carman (an American plant breeder) about crosses between wheat and rye. Most of his crosses were unsuccessful and produced only maternal plants, but also one true F_1 hybrid. The first fertile triticale was not reported until 1888 by a German worker, Rimpau.

Major work on triticale was carried on between 1918 and 1934 at the Agricultural Experimental Station at Saratov in southeast Russia. In 1918 a mass appearance of natural F_1 hybrids between wheat and rye occurred at Saratov, all of which were male-sterile and incapable of self-pollination. Hybrid derivatives were later (1927 and 1928) observed that were more or less intermediate between wheat and rye but were true-breeding and rather fertile.

Meister, in 1928, gave a botanical description of so-called balanced wheat–rye hybrids and designated the new species combination as *Triticum secalotricum saratoviense* Meister.

Cytological analysis was carried out in 1930 and 1931 by Levitsky and Benetz who made a careful study of mitosis and meiosis and stated that the somatic chromosome number in all three families was 56 and therefore the constant intermediate fertile rye–wheat hybrids were definitely amphidiploids of bread wheat and rye.

In 1934, Lebedoff obtained a wheat–rye amphidiploid and was the first to report the occurrence of aneuploidy in such material.

The hypothesis that the wheat–rye amphidiploid must result from an apogamous development of unreduced ovules in the primary hybrids, followed by immediate chromosome doubling, was abandoned in 1936 because of new empirical data of Müntzing. He succeeded in 1935 in getting a seed sample of Rimpau's fertile wheat–rye hybrid. Several seedlings had 56 or ±56 chromosomes and consequently Rimpau's hybrid was obviously an octoploid strain of triticale and the oldest one known. The Rimpau strain had retained a perfect constancy during 45 years of cultivation before the true nature of the new amphidiploid species became known.

The name "triticale" was used for the first time in a paper by Lindschau and Oehler and had been proposed to them by Tschermak.

The archaic period of work with triticale came to an end after 1937 when experimental doubling by means of colchicine had been discovered and new strains of triticale could be produced in unlimited quantities.

The results of more recent triticale research work are also discussed.

Résumé C'est un phytosélectionneur écossais, du nom de Wilson, qui obtint et décrit pour la première fois en 1875 un triticale stérile F_1 hybride, résultant du croisement blé × seigle. En 1884, le *Rural New Yorker* publia une série d'articles de Carman, un phytosélectionneur américain, sur ces mêmes croisements. La plupart de ceux qu'il avait tentés étaient restés infructueux, ne reproduisant que la mère, mais l'un d'entre eux avait donné un véritable hybride F_1. Ce n'est qu'en 1888 qu'un chercheur allemand, Rimpau, a signalé le premier triticale fertile.

La Station Expérimentale Agricole de Saratov, en Russie du Sud-Est, a effectué des travaux essentiels sur le triticale entre 1918 et 1934. Dès 1918, une production importante d'hybrides naturels F_1 entre blé et seigle était intervenue à Saratov, tous mâles stériles et incapables de s'auto-féconder. En 1927 et 1928 on constata la présence de dérivés hybrides plus ou moins intermédiaires entre le blé et le seigle mais se reproduisant en race pure et plutôt fertiles.

En 1928, Meister donnait une description botanique de ce qu'il appelait les hybrides équilibrés blé × seigle, et il baptisait cette nouvelle combinaison d'espèces *Triticum secalotricum saratoviense* Meister.

Levitsky et Benetz effectuèrent en 1930 et 1931 des analyses cytologiques et une étude soigneuse de la mitose et de la méiose, à l'issu de quoi ils établirent que le nombre de chromosomes somatiques des trois familles était de 56, et que par conséquent les hybrides seigle × blé, fertiles et fixés, étaient indubitablement des allopolyploïdes du blé tendre et du seigle.

En 1934, Lebedoff obtint un allopolyploïde blé × seigle et fut le premier à signaler une manifestation d'aneuploïdie dans ce matériel végétal.

L'hypothèse selon laquelle l'allopolyploïde blé × seigle résulte obligatoirement du développement apogamétique des ovules non réduites chez les hybrides primaires, suivi immédiatement d'un doublement des chromosomes, a été abandonnée en 1936 du fait des nouvelles données empiriques obtenues par Müntzing. Il avait réussi en 1935 à se procurer un échantillon de semences de l'hybride fertile blé × seigle de Rimpau. Plusieurs des plantules obtenues avaient 56 ou ± de 56 chromosomes, ce qui prouvait de toute évidence que l'hybride de Rimpau était une souche octoploïde de triticale, la plus vieille connue. Cette souche de Rimpau s'était parfaitement perpétuée durant 45 ans de culture avant que l'on connaisse enfin la véritable nature de cette nouvelle espèce allopolyploïde.

Ce sont Lindschau et Oehler qui ont utilisé pour la première fois dans un texte ce nom de "triticale" qui leur avait été proposé par Tschermak.

L'époque archaïque des travaux sur triticale a pris fin après 1937, lorsque l'on a réalisé le doublement expérimental des chromosomes grâce à la colchicine et que l'on a pu produire en quantités illimitées de nouvelles souches de triticales.

L'auteur expose également les résultats de travaux de recherche plus récents sur le triticale.

In 1875 a Mr Wilson reported to the Botanical Society in Edinburgh that in a series of attempted crosses between wheat as the female parent and rye as the male, he had succeeded in obtaining true hybrids of the kind we are now familiar with.

In 1884 the American plant breeder Carman published several communications in the periodical *Rural New Yorker* about crosses between wheat and rye. Most of his crosses were unsuccessful and gave only maternal plants, but in one instance the cross resulted in a true F_1 plant. This is evident from a picture (Fig. 1) originally published in the *Rural New Yorker* and later reprinted in the *Journal of Heredity* by Leighty (1916). Besides the morphological appearance, the very low fertility was evidence of true hybridity. This was also borne out by the characteristic rye pubescence on the peduncle, which was present in hybrid plants derived from wheat as the female parent.

Triticales first came on the scene thanks to the work of a research team at the Agricultural Experiment Station of Saratov in the southeastern part of Russia. Approximately

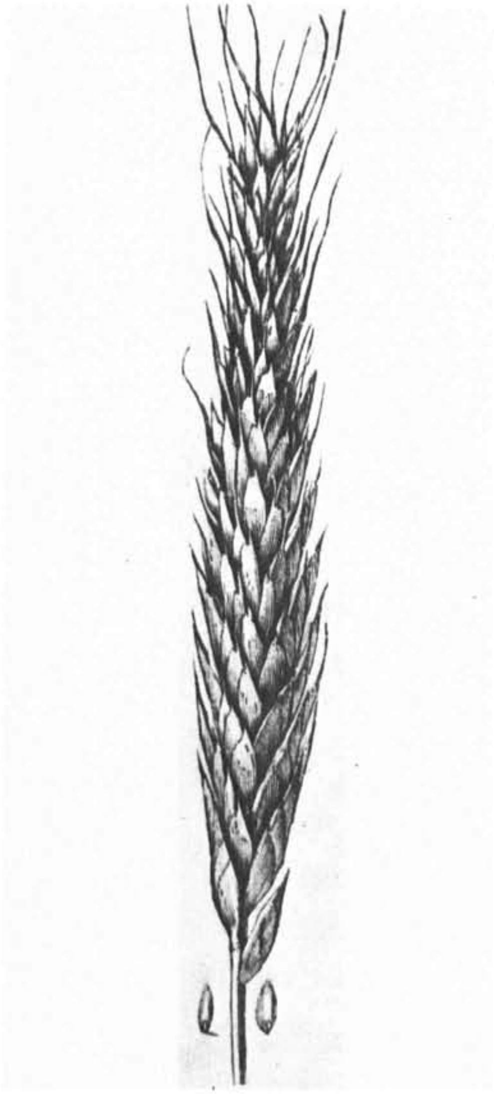


FIG. 1. Wheat–rye. This is the first illustration published of a wheat–rye hybrid, and represents Carman's own work. It appeared as Fig. 339 in the *Rural New Yorker* on 30 August 1884.

during the period 1918 to 1934 the director of the institute, G. K. Meister, and his associates were active in the field of wheat–rye hybridization.

In 1918 an extraordinary phenomenon was witnessed in their experimental fields — a mass appearance of natural F_1 hybrids between wheat and rye in a number of plots of winter varieties of wheat (Meister 1921). In one wheat plot about 20% of the plants were hybrids and altogether many thousands of natural wheat–rye hybrids were observed. They were derived from early flowering wheat varieties that flower rather openly in the dry continental climate of Saratov. Moreover, the wheat plots had been separated from each other by protecting rows of rye, supposed to prevent cross pollination between the wheat varieties. The hybrids were all male-sterile and incapable of self-pollination. Hence, the thousands of seeds collected from the vast number of F_1 plants were generally products of spontaneous back-crosses to wheat or rye.

Hybrid derivatives were later observed that were more or less intermediate between wheat and rye, but in spite of that, were true-breeding and rather fertile (Fig. 2). Such so-called balanced wheat–rye hybrids were suspected to be polyploid as indicated in papers from 1927 and 1928; and in 1930 Tumyakov published a report about fertility and morphology of these "wheat–rye hybrids of balanced type." Meister (1928) gave a botanical description of this material (see Levitsky 1932) and designated the new species combination as *Triticum secalotricum saratoviense* Meister. He also emphasized the importance of the new products for plant-breeding work and even published preliminary results concerning baking properties in this material, which he believed nobody had seen before.

The cytological analysis of this material was carried out by Levitsky and Benetzkaja (1930, 1931) who made a careful study of mitosis and meiosis. They stated that the somatic chromosome number was 56 (Fig. 3) in three different families. Thus, the constant intermediate fertile rye–wheat hybrids were definitely amphidiploids of bread wheat and rye.

Investigations of the mode of meiosis in the pollen mother cells, as well as on the female side, revealed a frequent occurrence of irregularities caused by the presence of univalent chromosomes (Fig. 4*a*). This was observed in all three of the families studied and was therefore regarded to be characteristic of rye–wheat amphidiploids in general.

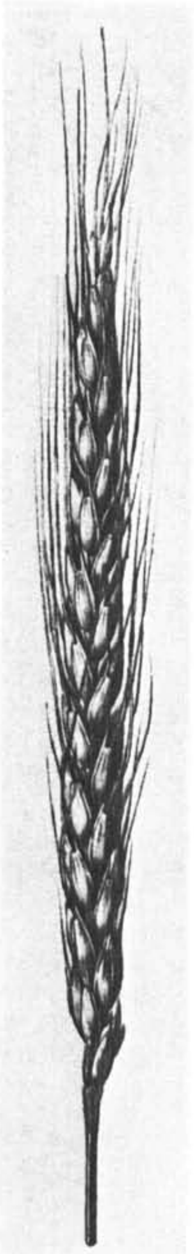


FIG. 2. Later hybrid between wheat and rye, fertile and true-breeding.

This disturbed pairing could not depend on lack of homology, and must therefore be assumed to have had other causes, either a general incompatibility between the parental chromosome sets, or an antagonism between the female cytoplasm and the male chromosome set, which represented another genus.

Levitsky and Benetzkaja also discussed the mode of origin of the amphidiploids and had to base their arguments on the fact that all the primary wheat–rye hybrids at Saratov were completely male-sterile. Under such circumstances they had to assume an apogamous development of F_1 ovules with a somatic number of chromosomes, and that this chromosome set was then doubled in the first division of the egg cell.

This view was reluctantly accepted by other workers writing about the amphidiploid wheat–rye hybrids during 1930–36. Lebedeff (1934), while working at a station in Ukraina, obtained a wheat–rye amphidiploid that was essentially similar to those at Saratov. He was first to report the occurrence of aneuploidy in such material. A few plants had less than 56 chromosomes. Lebedeff, when discussing the reduced fertility of the wheat–rye amphidiploids, pointed out that poor fertility and other disturbances are characteristic of inbred lines of rye. He therefore suggested that such unfavourable properties in the amphidiploids might be avoided by the use of fertile and vigourous inbred lines of rye in the primary cross. He also emphasized the importance of choosing the right varieties of wheat for the primary crosses. He did not believe that cytoplasmic differences between wheat and rye could be important, because backcrossing of primary wheat–rye hybrids to rye had led to quite regular and fertile rye plants in spite of their wheat cytoplasm. Lebedeff also demonstrated the formation of unreduced ovules with 28 chromosomes in primary hybrids. After pollination with rye, a plant with 35 chromosomes had been obtained. He suggested that the occurrence of such ovules should also be utilized for the production of new amphidiploid strains after pollination of primary hybrids with the pollen of already existing amphidiploids. He also outlined other ways for the future breeding of the new material, for which he suggested the name "Tritisecale."

Lebedeff did not publish anything more on his octoploid triticale material. His work may

FIG. 3. *Triticum vulgare* × *Secale cereale*. Constant intermediate rye–wheat hybrid. Somatic plate of an individual from F_1. Chromosome number 56. Enlargement ×2700.

have been stopped by the approach of the Lyssenko regime and the same influence may have also counteracted and stopped the pioneering work carried out by the Meister group in Saratov.

The hypothesis that the wheat–rye amphidiploids must result from an apogamous development of unreduced ovules in the primary hybrids, followed by immediate chromosome doubling, was abandoned in 1936 when new empirical data were published (Müntzing 1936). In 1931 I came to the Swedish Seed Association as head of a new laboratory for chromosome research and induction of polyploidy in cultivated plants. In my program, work with wheat–rye amphidiploids was also included. In the summer of 1935, I had a quantity of F_1 plants representing 15 different cross combinations. In one of these combinations, representing Swedish varieties of wheat and rye, I observed in one of the F_1 plants that single anthers had dehisced and that these anthers contained pollen of good quality. In this plant part of the anthers in three different heads were fertile, whereas the other heads of the same plant were male-sterile as usual. The entire F_1 material available (65 plants) was scrutinized, and in a second plant a single flower with dehiscing anthers was discovered. It belonged to the same cross-combination as the first, partially male-fertile F_1 plant, but in all the other 14 cross-combinations no flowers with dehiscing anthers could be detected.

Pollen samples from the dehiscing anthers (Fig. 4*b*) showed that the percentage of apparently normal pollen grains in these anthers ranged from about 20 to 60%. Measurements revealed that the pollen grains were quite large and therefore probably unreduced. This was verified by using this pollen for controlled self-pollination. From a head thus treated a single kernel was obtained. It germinated and gave rise to a plant with 56 chromosomes, which was the starting point of a new strain of octoploid triticale.

In this case the production of a new triticale strain was made possible either by the spontaneous formation of small somatic sectors with a doubled chromosome number, including anthers as well as ovules, or perhaps

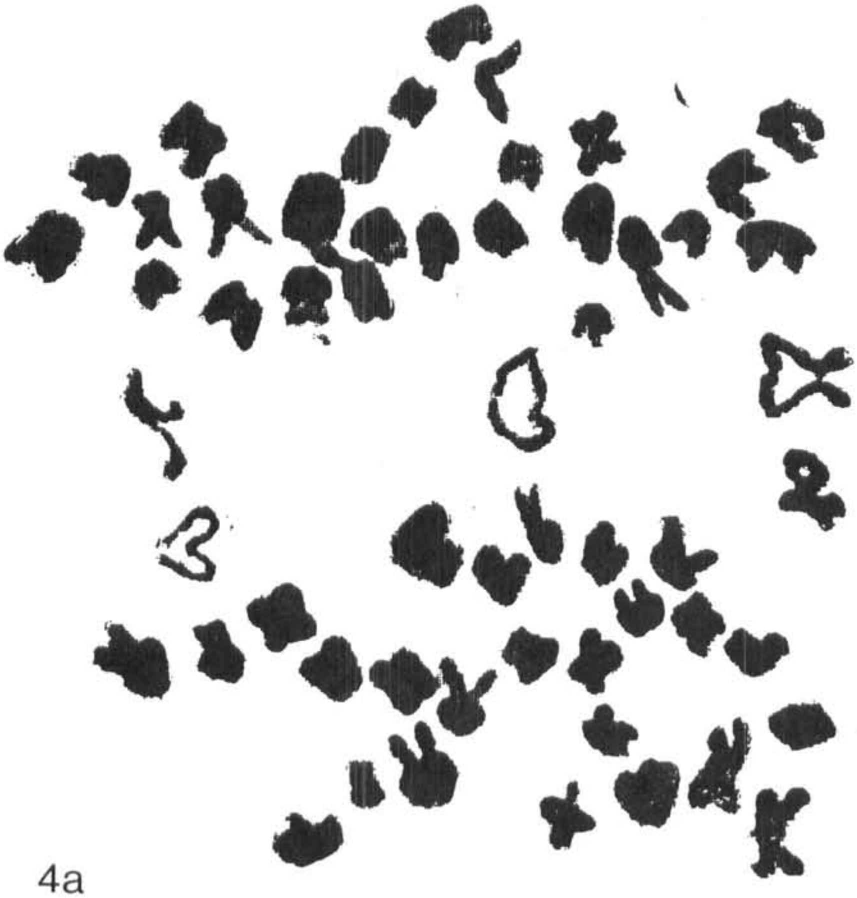
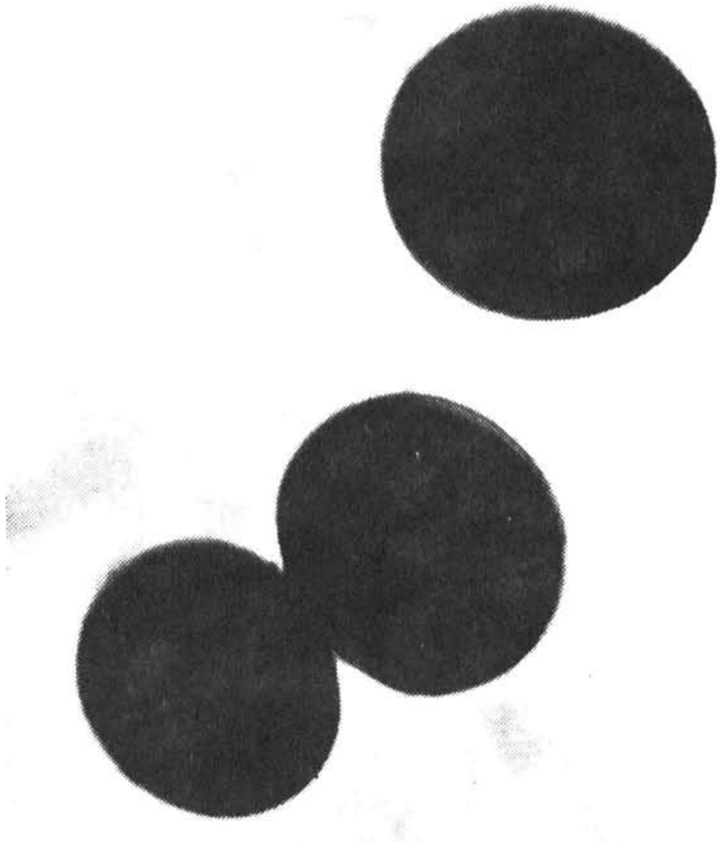


FIG. 4*a*. Meiosis in pollen mother cells showing presence of univalent chromosomes.

even by quite local areas of chromosome doubling leading to single dehiscing anthers, or parts of anthers, with unreduced pollen. Such an occurrence may, of course, easily be overlooked but probably represents a mechanism of general importance that had been at work also in the previous cases of spontaneous origin of octoploid types of triticale. Thus, the rather unlikely hypothesis of apogamous development, followed by chromosome doubling, became superfluous.

Though the octoploid triticale types discovered at Saratov were the first to be scientifically explored, another strain of the same kind had arisen in Germany in 1888. The breeder Rimpau, just like Carman in the United States, made crosses between wheat and rye, and in one of the hybrids obtained, one of the heads produced 15 kernels. In this head there must have been a doubled sector since 12 of the kernels gave rise to fertile plants of uniform appearance (Rimpau 1891). The new constant strain (Fig. 5–7) was at first grown by Rimpau but was shortly afterwards included in the comprehensive material cultivated in a plant-breeding garden in Halle. Guided by serological results that had been obtained with this strain by Moritz (1933), and that indicated the presence of wheat as well as rye proteins, I succeeded, in 1935, in getting a seed sample of Rimpau's fertile wheat–rye hybrid. Several seedlings had 56 or ±56 chromosomes and, consequently, Rimpau's hybrid was obviously an octoploid strain of triticale and the oldest one known. This was also verified by Lindschau



4b

FIG. 4*b*. Pollen samples from dehiscing anthers.

and Oehler (1935). Of particular interest in this case is the fact that the Rimpau strain had retained a perfect constancy during the 45 years of cultivation before the true nature of this new amphiploid species became known.

As far as I know, the name triticale was used for the first time in 1935 in the paper by Lindschau and Oehler. This name had been proposed to them by Tschermak, one of the three rediscoverers of Mendel's laws. Tschermak carried out much hybridization work with cereals and, for instance, succeeded in producing an amphidiploid between tetraploid wheat and *Aegilops ovata* that he named *Aegilotricum* (Tschermak and Bleier 1926). There is reason to believe that the name triticale was coined during verbal discussions between Tschermak and his German colleagues at the Müncheberg Institute for Plant Breeding Research. In their paper Lindschau and Oehler also point out that it would be convenient to distinguish between different strains of triticale by adding the author's name. Thus, "triticale Rimpau," "triticale Meister," etc.

During a 5-year period in the 1930's I had the opportunity of devoting much of my time to work with triticale. The results gathered were reported in a paper published in 1939. Since this paper is characteristic of the status and problems of research in triticale at that time, I shall mention some of the results obtained.

My material consisted of six strains of triticale (Fig. 5–7, 8–10), of which only one

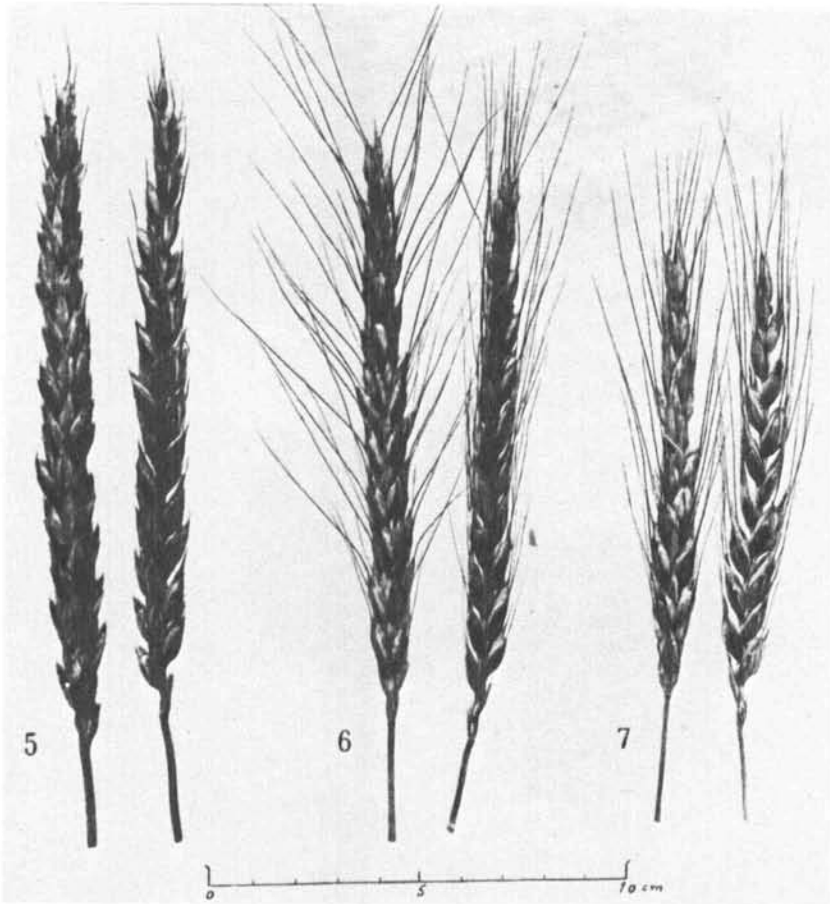


FIG. 5–7. Ears of three of the six constant triticale strains studied. Fig. 5, Triticale A; Fig. 6, Triticale B; Fig. 7, Triticale C. Fig. 5 and 6 represent the types produced by Rimpau; Fig. 7 is of Russian origin. The cross combination most extensively studied is that between strains A and C (Fig. 5 and 7).

represented a union of Swedish wheat and rye and the other strains had been produced in other countries (Germany, Russia, and the United States). The six strains were all partially sterile, but the degree of sterility was different in different strains. The triticales also differed significantly in vigour, in the degree of meiotic irregularity, and in physiological and chemical respects such as winter hardiness, earliness, and baking capacity. A baking test with triticale Meister gave a surprisingly good result, the bread volume being larger than in the best bread wheat varieties available for comparison.

As soon as more than one triticale strain had been obtained, recombination breeding was started, at first by intercrossing triticale Meister and triticale Rimpau. To my surprise, crosses between different triticales succeeded with difficulty, the average seed set being as low as 5%. There were also reciprocal differences in this respect.

Inter-strain hybrids were found to be vigourous. In one of the crosses that was studied in detail, the F_1 plants were taller than the average height of the parents, but were more sterile than the parents and showed a higher degree of nonpairing of the homologous chromosomes at meiosis. In F_2 there was a significant decrease in vigour and, on

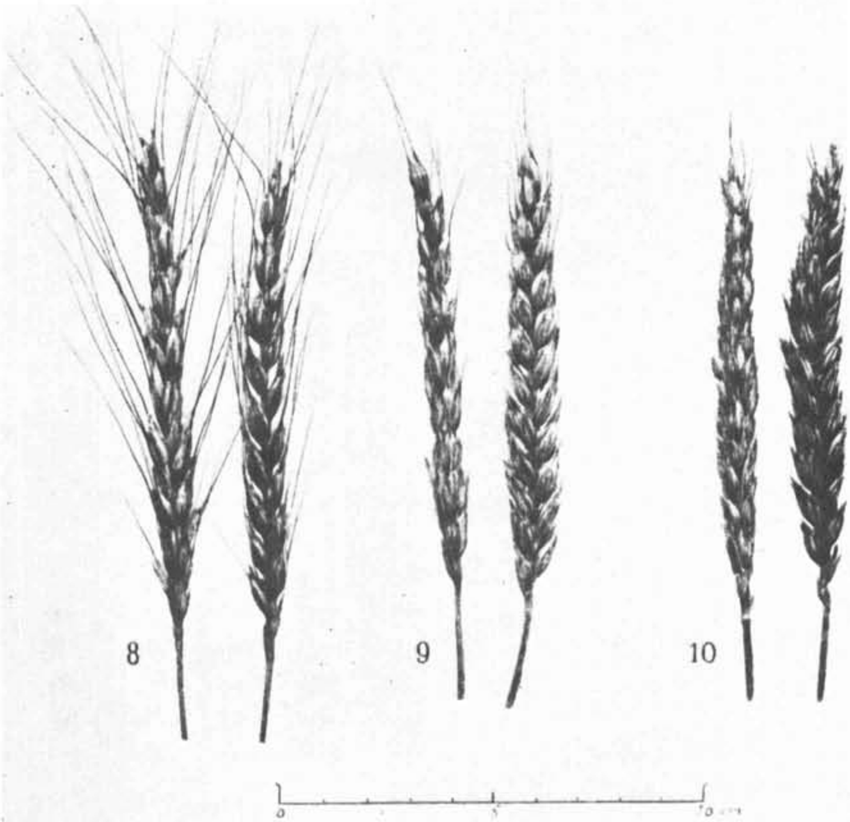


FIG. 8–10. Ears of three of the six constant triticale strains studied. Fig. 8, Triticale D; Fig. 9, Triticale E; Fig. 10, Triticale F. Fig. 8 is of Russian origin, Fig. 9 is the strain of Taylor and Quisenberry, and Fig. 10 represents Triticale Svalof (a combination of "Solvete III" and "Midsomarråg").

an average, the plants were still more sterile than the F_1 plants. However, in later generations fertile recombinants could be obtained that greatly surpassed the parents in yield (Müntzing 1948).

New triticale strains were not only produced by crosses between constant strains already existing, they were also derived from crosses between triticale and bread wheat and selection of new triticale types with recombined wheat chromosomes in the offspring. New triticale strains could also be obtained by pollination of primary wheat–rye hybrids with triticale pollen (Fig. 11–13). In this way, some of the unreduced ovules in the primary hybrids could be picked up by male gametes having the same chromosome number, 28. This method led to new plants with 56 chromosomes that were heterozygous for the wheat as well as the rye chromosomes. A very marked segregation was obtained in the offspring, but this segregation was complicated by chromosomal irregularities.

Unreduced gametes in hybrids between wheat and rye had been utilized earlier — by myself in hybrids between *Triticum turgidum* and rye that, in the absence of triticale strains at that time (1933), were pollinated with hexaploid bread wheat. The result was triple hybrids with 42 chromosomes, carrying the complete haploid genomes of rye and the two wheat species (Müntzing 1935). As is evident from Fig. 14, the morphological appearance of the triple hybrids represented a harmonious union of the three components.

Similar work was later carried out by

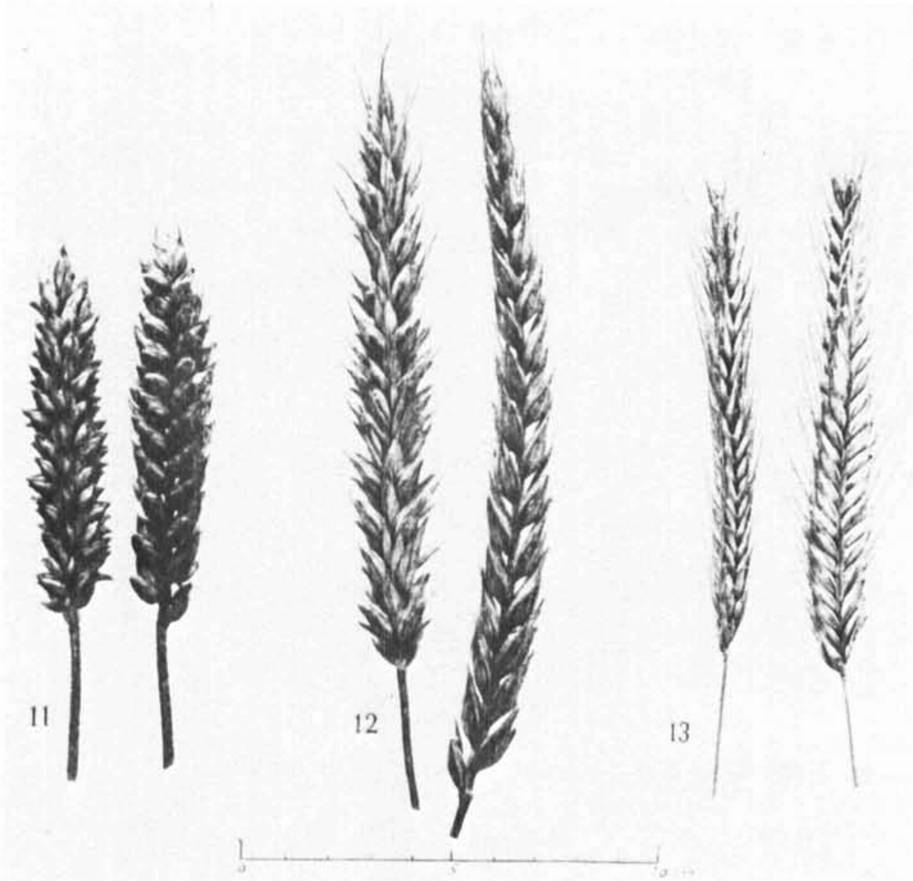


FIG. 11–13. Ears of a new triticale product (Fig. 12) in comparison with ears of wheat (Fig. 11) and rye (Fig. 13). Fig. 11 represents "Solvete III," Fig. 13, "Stalrag," and Fig. 12 two different triticale plants from the I_2 generation of a new triticale heterozygote. This heterozygote arose from pollination of a hybrid between Swedish wheat and rye with triticale pollen. The large ear and kernel dimensions are conspicuous. Fig. 11–13 are directly comparable to Fig. 5–10.

Nakajima (1942, 1951, 1952, 1953, 1958, 1961, 1965) in Japan, and described in numerous publications. To triticale breeders it is of more interest to know that a similar procedure is nowadays successfully used by the Russian breeder Shulyndin in Charkov. By pollination of primary hybrids between bread wheat and rye with hexaploid triticale, Shulyndin (1972) has obtained especially good triticale types. These products he regards as representing a complete synthesis of the three species involved, with the exception that the D-genome of bread wheat has been eliminated.

Recent Work

The archaic period of work with triticales came to an end after 1937 when experimental chromosome doubling by means of colchicine had been discovered and new strains of triticale could be produced in unlimited quantities. However, in many countries, and especially in Europe, World War II seriously hampered research activities. In the Soviet Union, moreover, the Lyssenko regime was a serious obstacle. Nevertheless, some work with octoploid triticale was still continued

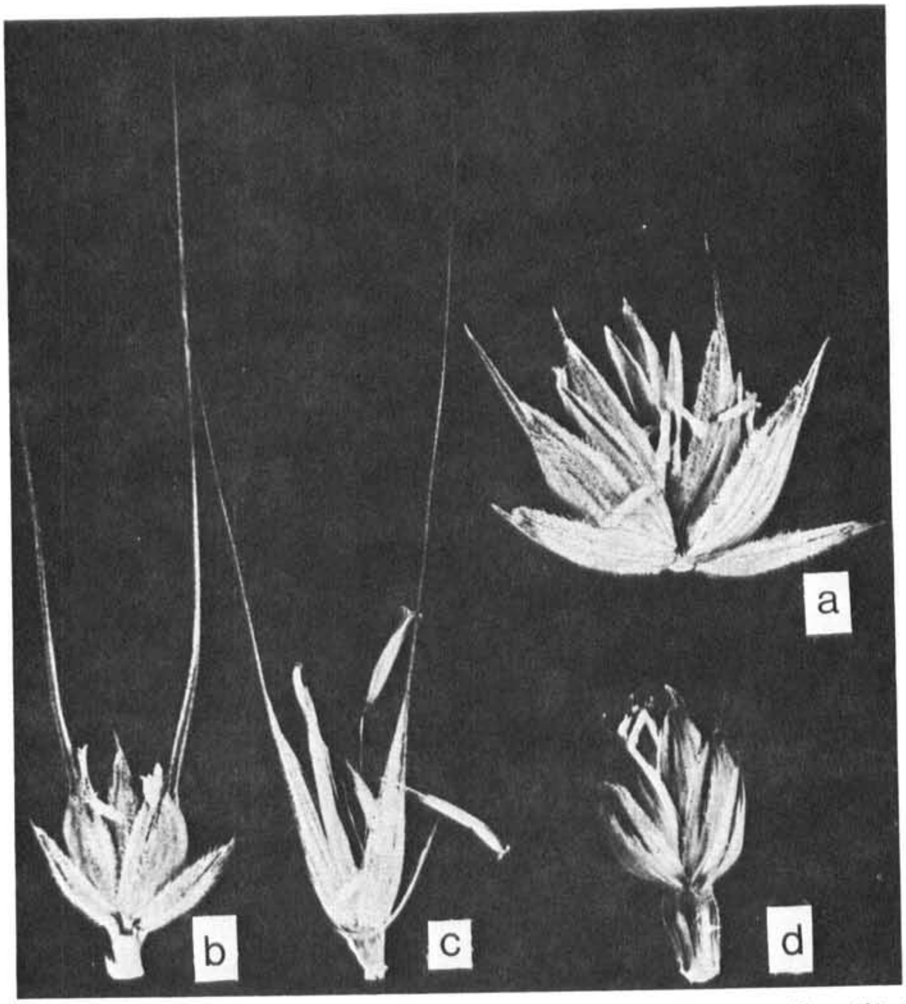


FIG. 14. Spikelets of the triple hybrid (*a*) and the parent species, *Triticum turgidum* (*b*), *Secale cereale* (*c*), and *Triticum vulgare* (*d*). ×20.

and later expanded when conditions became more favourable.

I would like to briefly summarize a few of the results obtained with octoploid triticale during the last few years. It is, of course, easiest for me to base this information on experience gathered from my own material (Müntzing 1948, 1956, 1957, 1958, 1963, 1966, 1970), but special reference should also be made to the comprehensive work by Ingold et al. (1968).

The first primary strains were only theoretical curiosities with a yield much below the level reached by high-bred varieties of wheat and rye. However, breeding work with octoploid triticale led to considerably improved strains that in some field trials, especially on light or sandy soils, gave yields equal to those of bread wheat. Kernel size in these triticale lines was superior to that of wheat, and this fact compensated considerably for the lower seed set of the triticales. Seed quality was also improved to the point of being comparable to wheat. Nevertheless, even the best octoploid strains could not compete successfully with hexaploid wheat.

In part, this was due to lack of sufficient straw stiffness in most of the octoploids, which caused lodging at higher amounts of nitrogen fertilization. Under such circumstances spraying with the chemical CCC increased the straw stiffness of the triticales considerably. It also helped counteract the reduction in yield caused by lodging. No doubt, however, judging from experience made in other countries, a more effective escape from lodging was to breed new material of octoploid triticale with sufficient straw stiffness. Even if this goal could in part be attained, there still remained the main difficulty: an unsatisfactory number of kernels per spikelet, a reduced fertility, the causes of which are not yet entirely clarified.

One main factor, however, is the occurrence of more or less high rates of aneuploidy in the octoploid strains. The correlations between sterility, meiotic disturbances, and rate of aneuploidy have been studied by several workers and were recently discussed in a paper by Weimarck (1973). She concludes that in bulk populations, as well as in progenies of euploid plants, recombined strains are characterized by lower degrees of aneuploidy than primary strains. The recombined strains also have higher fertility and a more stable meiosis than the primary strains. A close relationship was found between somatic chromosome number and fertility, the euploids having clearly higher fertility than the aneuploids. It should be observed, however, that no direct correlation has been found between the degree of meiotic disturbances in a plant and its fertility.

Judging from the results obtained, the present level of aneuploidy in the best octoploid strains (in my material about 30%) can certainly be pushed down still further by recombination and selection, and this must lead to increased productivity.

The economical importance of octoploid triticale is also strongly influenced by kernel quality — not only the degree of shrivelling of the seeds but also the biochemical properties and their relationship to bread-baking capacity. Therefore, in the breeding work during the last decades it became increasingly urgent to pay attention to analytical data gathered by the cereal chemists. It is now not only a question of test weight and raw protein contents, but many other, more sophisticated biochemical variables are involved. A serious weakness in the octoploid triticale types, so far tested, is the enzymatic processes in the kernel and the tendency to pregermination, if the ripening crop is exposed to humid condition before harvest. However, triticale strains react differently to such conditions, and rye varieties that are resistant to pregermination are now available and may be used for the production of new triticales.

A general conclusion in this field of cereal chemistry is also that scales and standards that are well suited for wheat varieties cannot automatically be used for the evaluation of triticales. Test values, which in bread wheat would indicate that the material is entirely unfit for baking, have little significance for triticale. In a recent case quite good triticale bread was prepared from flour having very poor values of alpha amylase, according to wheat standards.

Basic cytogenetic work in octoploid triticale has also led to various important results. By improved technical methods, Pieritz (1966, 1970) succeeded in distinguishing morphologically between wheat and rye chromosomes and confirmed other indirect evidence that in octoploid triticales (in contrast to hexaploids) the univalents occurring at meiosis are predominantly rye chromosomes. The rye chromosomes, therefore, have a tendency to become eliminated in contrast to the wheat chromosomes that are rarely unpaired. Pieritz also showed that there is a strict selection against aneuploidy among the male gametes, whereas all kinds of deviating chromosome constitutions are transmitted by the ovules.

Another cytogenetic phenomenon, observed by various workers, is that in octoploid triticale there are not only meiotic but sometimes also mitotic disturbances, that lead to chromosome deviations in somatic cells (Müntzing 1957). For this reason, the total number of chromosomes in the pollen mother cells may also, in some instances, be higher or lower than it should be. This phenomenon, which also occurs in hexaploid triticale (Orlova 1970), is not unique for triticale but has also been observed and analyzed in various species hybrids (Plotnikowa 1932; Bleier 1934; Lange

1971) and in inbred lines of rye (Rees 1955).

Another finding of interest is that spontaneous reversions to haploidy may sometimes occur in triticale (Müntzing et al. 1963). As a rule, however, this phenomenon is quite rare or entirely absent, but in some strains, reversions to haploidy have been observed more frequently.

It is possible that the interest in triticale as a potential new crop would have tapered off entirely if the efforts had been limited to octoploid material. However, this has been successfully prevented by the enormous development of hexaploid triticales and by the crosses between octoploids and hexaploids. Although this explosion is much more recent than the octoploid story, it may now be worthwhile to look back and point out some of the main features in this phase of the life of triticale.

Hybridization between tetraploid wheat and rye was started about 60 years ago. The first hybrid was probably *Triticum dicoccoides* × *Secale cereale*, which was produced by Jesenko in 1913. The first hybrid between *Triticum durum* and rye was described in 1924 by Schegalow (Plotnikowa 1932). The first amphidiploid between tetraploid wheat and rye was reported in 1938 by Derzhavin. In this case it was a union of *Triticum durum* with *Secale montanum*. Of more interest from the breeding point of view was O'Mara's (1948) amphidiploid between *T. durum* and cultivated rye and Nakajima's (1950) combination of *Triticum turgidum* and rye. A more concentrated effort of producing a broader and more variable material of hexaploid triticale was made by Sanchez-Monge and Tijo (1954) and Sanchez-Monge (1956, 1958) in Spain. This work was primarily made to get triticales of good grain quality as a substitute for a mixture of wheat and rye that is rather widely cultivated in certain regions of Spain. Sanchez-Monge and his co-workers found that it was obviously impossible to obtain, directly, a 42-chromosome triticale with good properties but believed that it would be possible to improve this material by recombination and selection.

That their optimism was justified has been amply demonstrated by the excellent work carried out at the University of Manitoba during the last two decades. This work has represented a successful combination of basic cytogenetic work with intensive breeding efforts and was carried out by such men as Jenkins, Shebeski, Evans, Welsh, and Larter (Larter 1968; Jenkins 1969; Tsuchiya 1969; Larter et al. 1970; Sisodia and McGinnis 1970*a, b;* Tsuchiya and Larter 1971).

The research program carried out by this group and their associates was initiated in 1954. The first material used was the hexaploid *durum* × rye amphidiploid produced by O'Mara. Several additional hexaploid triticales were developed from new crosses, and seeds of other existing wheat × rye amphidiploids, both hexaploid and octoploid, were collected. Many of the best triticale lines from all sources were intercrossed. In the Canadian program more improvements through selection were accomplished in hexaploid triticales than in the octoploids.

Important progress was made through the discovery of light-insensitive, early maturing types, and dwarf and semi-dwarf wheat lines, which were used as a source of shorter and stronger straw in the triticales. These characteristics (light-insensitivity, earliness, short straw, and disease resistance, particularly to stem rust) represented marked improvements over earlier hexaploid triticales. Parallel with the breeding work, quality evaluations of the grains were carried out, and it was also established that grain of the hexaploid triticales is suitable for use in cattle, sheep, and poultry rations. Since these triticales, which lack the D-genome, were not suitable for bread flour, they could instead fill the need for a feed crop in certain areas.

In 1969, one strain, Rosner, was licensed and became recognized as a new crop of commerce in Canada. Results from livestock-feeding experiments, distilling and brewing tests, and also from experimental manufacture of breakfast cereals indicated that triticale had considerable potential as a cereal crop.

A new and very important phase in the history of triticale was inaugurated less than 10 years ago when it was realized that hybridization between octoploid and hexaploid triticale may lead to quite valuable products of recombination. This was clearly realized by Pissarev about 1960 (*see* Pissarev 1966, p. 286–289); and in 1965, Kiss, in Hungary, demonstrated that secondary hexaploids derived from such crosses were superior to primary hexaploids (*see* Kiss 1966*a*, *b*). In the same year similar evidence was obtained in Winnipeg, Manitoba (Jenkins 1969).

Two secondary hexaploid Hungarian triticale varieties were officially registered a few years ago and have been more prolific in Hungarian state trials than any rye variety (Kiss 1971). In comparative trials with wheat, their value was equal to that of the wheat variety Bezostaya 1. Both the new triticale varieties are cultivated for fodder of grains or green matter and have given good results in feeding trials with mice, rats, poultry, and pigs. Baking trials have shown that hexaploid triticale flour may be successfully mixed to 50% with wheat flour. Even without admixture of wheat such triticale flour alone is reported to give excellent and tasteful brown bread. In 1969, about 40,000 acres in Hungary were under cultivation with hexaploid varieties of triticale.

The production of improved secondary hexaploids is now a standard technique used by all breeders of triticale, and Krolow (1969*a*, *b*) has worked out the cytological details occurring during this process. I hesitated to use this technique because so much genome-analytical work seemed to have proved definitely that the A and B genomes of tetraploid and hexaploid wheats were quite homologous or even identical. However, clear evidence that this is not the case was obtained from the University of Manitoba. By an elegant technique, Kerber (1964) succeeded in extracting the AABB part of bread wheat and found that these extracts were dwarf plants that differed in many ways from tetraploid wheat species, and were especially adapted to cooperate with the D-genome of *Aegilops squarrosa*. Later, Kaltsikes et al. (1969) carried out similar extractions.

Conclusion

At the workshop on triticale arranged by CIMMYT and IDRC in Mexico, we became vividly aware of the enormous amount of successful work on triticale that has been carried out here in Mexico by CIMMYT, particularly by Borlaug and Zillinsky.

The work started on a small scale in 1963 and was more firmly established in 1964 as a direct outgrowth of a cooperative breeding program between the University of Manitoba and CIMMYT. At that time a winter-breeding nursery involving most of the Canadian material was sown during November in Ciano. Following harvest, most of the material was returned to Canada for summer plantings, but part remained in Mexico to be sown at Toluca during May. From that time there has been a continuous free, two-way flow and exchange of triticale breeding materials between the Canadian and Mexican programs. Many other centres in the world have also become involved in this international work. In recent years this work has been carried out on a very large scale, and twice as fast as in countries limited to only one generation per year.

In this historical survey I have discussed only one special aspect of the Mexican work that has already been of very great importance and that will certainly have a strong influence on the future of triticale breeding: the origin of the Armadillo types and the block of favourable characters carried by them. In a recent paper by Zillinsky and Borlaug (1971) these characters were specified as follows: (1) a very high level of fertility, never before encountered in any triticale breeding program; (2) improved grain plumpness and test weight; (3) high grain yield per hectare; (4) insensitivity to daylength; (5) earliness; (6) one gene for dwarfness (semi-dwarf F_1); and (7) high nutritional quality.

Since it is highly probable that the Armadillos have arisen following a spontaneous cross to bread wheat, it seems likely that a whole block of linked genes has been incorporated into one of the chromosomes of hexaploid triticale or that a substitution of one or more chromosomes has occurred.

I know that Gustafson and Zillinsky (1973) have obtained evidence pointing in this direction and with the aid of quite new staining methods that make it possible to distinguish each rye chromosome in triticale, and probably soon also most or all of the wheat chromosomes, full clarity about the constitution of the Armadillo types can be expected (Merker 1973).

Thus, the rye genome in the Armadillos may have been weakened but favourably modified by the intrusion of one or more gene-blocks from wheat. If this process will go on still further, the name triticale for such material will become more and more dubious.

However, the species rye has already taken a revenge by invading one of the wheat genomes. In a series of five papers published during the period 1969–72 (Zeller 1969; Sastrosumarjo and Zeller 1970; Zeller and Fischbeck 1971; Zeller 1972; Zeller and Sastrosumarjo 1972), Zeller and his coworkers have demonstrated that rye chromosome No. V, which is known to carry several genes for disease resistance, is present in the commercial wheat variety "Zorba," where it has replaced wheat chromosome No. 1 **B**. The same thing has also happened in another German wheat variety, "Salzmünde Bartweizen." In a third wheat variety, "Weique," the situation is similar but more complicated. In one subline called "Weique Substitution" there is again the same substitution as in "Zorba" and "Salzmünde Bartweizen." In the other subline of Weique there is a translocation between wheat chromosome 1 **B** and rye chromosome V.

The very detailed analyses carried out by Zeller and his associates have also led to the detection of a number of other translocations. Thus, for instance, Zorba is homozygous for a specific translocation and the variety Holdfast for another translocation, involving chromosomes other than those in Zorba.

As is well known, much basic work with substitution and addition lines has already been carried out by many workers, especially Jenkins and Riley. However, as far as I know the recent cases in Germany are the first to demonstrate that such substitutions may arise spontaneously and are present in varieties that are economically prominent due to the presence of such substitutions.

Thus, we may now begin to wonder to what extent wheat varieties will absorb rye chromosomes and triticale varieties will absorb wheat chromosomes. There are probably certain limits to this kind of disorder, and until the ideal reshuffling of chromosomes and chromosome segments has been reached it will probably still be useful to retain the old-concept triticale.

Work with triticale is a wonderful experience and a splendid adventure. It is obvious that by continued interaction between intensive breeding work, basic cytogenetics, and several other sciences, we can really look forward to a future when this crop will become increasingly important for the welfare of mankind.

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