

M. Feldman

Development of Triticales in Western Europe

E. SANCHEZ-MONGE

Instituto Nacional de Investigaciones Agrarias, Madrid, Spain

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Abstract The pioneer work on triticales in Europe was done by A. Müntzing, who has been working with octoploid triticales since 1934. However, interest in Western Europe in triticales has been evident only since 1953, when a note on three new hexaploid triticales was presented at the 9th International Congress of Genetics.

Triticales obtained in Western Europe were produced by artificial doubling of the chromosome complement of the hybrid *Triticale* sp. \times *Secale cereale*. Leim studied the genetical control of crossability between hexaploid wheat and rye and obtained evidence of two recessive genes, kr_1 and kr_2 , controlling the high crossability.

In Sweden, the grafting of wheat embryos onto rye endosperm produced plants with increased crossability, although this was not duplicated in other parts of Western Europe.

Duplication of the chromosome number in the F_1 of wheat-rye hybrids has been accomplished by using colchicine applied in various ways. Embryo culture has been also used to increase the success of the crosses.

Breeding programs for the production of secondary triticales were started to use characteristics of the primary triticales, and low fertility and excessive seed shrivelling were partially overcome by selection within lines.

Recent results in breeding in Sweden, Switzerland, France, the United Kingdom, Denmark, and Spain are discussed, as well as the potential of triticales as an agricultural crop.

Résumé En Europe, les premiers travaux sur le triticales ont été faits par A. Müntzing qui travaille sur des triticales octoploïdes depuis 1934. Ce n'est cependant que depuis 1953 que l'Europe de l'Ouest a manifesté un intérêt pour cette céréale, lorsque fut présentée une communication sur trois nouveaux triticales hexaploïdes au Congrès International de Génétique.

Les triticales obtenus en Europe de l'Ouest ont été produits par doublement artificiel de l'ensemble chromosomique de l'hybride *Triticale* sp. \times *Secale cereale*. Leim a étudié le moyen de commander génétiquement l'hybridation blé hexaploïde-seigle, et a obtenu la preuve que l'importance de cette dernière dépendait de deux gènes récessifs, kr_1 et kr_2 .

Le greffage d'embryons de blé sur endosperme de seigle, effectué en Suède, a permis d'obtenir des plants plus facilement hybridables, mais cette expérience n'a été répétée nulle part ailleurs en Europe occidentale.

On est parvenu à doubler le nombre des chromosomes dans les F_1 d'hybrides blé \times seigle en utilisant de la colchicine de différentes manières. La culture d'embryons a également été utilisée pour augmenter le succès des croisements.

Des programmes de sélection destinés à la production de triticales primaires, et la sélection au sein des lignées a permis de compenser partiellement la faiblesse de la fertilité et le ridage excessif des grains.

L'auteur expose les résultats des travaux de sélection récents entrepris en Suède, en Suisse, en France, au Royaume-Uni, au Danemark et en Espagne, ainsi que les possibilités du triticales sur le plan agricole.

IN 1888 Rimpau discovered the first amphiploid between bread wheat and rye. The plant was probably a mixoploid chimaera arising from a 28-chromosome hybrid between *Triticum aestivum* and *Secale cereale*. The plant had a sector that spontaneously duplicated its chromosome number and produced 15 seeds, 12 of which gave rise to a uniform triticales while the other 3 resulted from pollination with wheat. Rimpau described this new cereal in 1891 and Müntzing (1939) confirmed that the somatic chromosome number of the Rimpau triticales was $2n = 56$.

The original concept behind the artificial production of triticales was to combine the bread-making quality and yielding ability of wheat with the vigour and hardiness of rye in a cereal that would have the ability to grow on poor, cold, dry soils. The new cereal can indeed, with special baking procedures, be used for bread making and produces a protein-rich bread. But the main use of triticales in future will probably be for animal feed, whether as grain, green forage, or silage.

The pioneer work on triticales in Europe was done by A. Müntzing, who has been working with octoploid triticales since 1934. But the interest in Western Europe on hexaploid triticales started after a note on three new hexaploid triticales (Sanchez-Monge and Tijo 1953) was presented at the 9th International Congress of Genetics in Bellagio, Italy, in 1953. The idea of working intensively at the hexaploid level in triticales was suggested to us by C. A. Jørgensen when we were examining the large collection of tetraploid wheat genotypes from Spain.

Production of Triticales

The triticales that we designate as "primaries" were obtained in Western Europe by the

artificial doubling of the chromosome complement of the hybrid "*Triticum* sp. \times *Secale cereale*." The crosses between tetra- and hexaploid species of wheat and diploid rye were more easily made by using the wheat species as the mother plant. The intergeneric cross is more easily made with hexaploid than with tetraploid wheats.

At both levels of ploidy, different wheat genotypes show different ability to set seed when pollinated with rye pollen. Some experiments have shown no influence of the rye genotype on the crossability (Krolow 1964). However, the utilization of alloplasmic rye with wheat cytoplasm seems to increase the percentage of germinable seeds in the cross *T. aestivum* \times *Secale cereale* (Vettel 1961).

In a study made by Lein (1943) on the genetical control of crossability between hexaploid wheat and rye, evidence was obtained of the existence of two recessive genes, kr_1 and kr_2 , controlling the high crossability. The dominant Kr_1 reduced crossability to a greater degree than did Kr_2 . The location of these two loci in the wheat genome was investigated by Riley and Chapman (1967). They located Kr_1 on chromosome 5B and Kr_2 on chromosome 5A.

Several attempts have been made to increase the crossability of wheat and rye. The grafting of wheat embryos onto rye endosperm produced plants with increased crossability according to results obtained in Sweden (Müntzing 1956). In other countries in Western Europe no increase in crossability was obtained using this technique with hexaploid (Krolow 1964; Derenne 1960) or tetraploid wheats (Sanchez-Monge 1956a). The heterozygosity of the tetraploid wheat mother plant did not increase the crossability in other experiments (Sanchez-Monge 1956a).

With tetraploid wheats the percentage crossability average seed set obtained by Krolow

(1970) was 13.36% and the percentage of germinated seed in pollinated flowers was 0.15%. In the same experiment the corresponding value to the last figure for hexaploid wheat was 3.07%. My own results with 64 genotypes of tetraploid wheat were 0.6% average seed set and 0.4% seed germination in pollinated flowers (Sanchez-Monge 1956a, b). The inbreeding and selection of self-fertile lines of rye to be used as pollen parents with tetraploid rye did not have any influence on crossability (Sanchez-Monge 1956a).

The duplication of the chromosome number in the F_1 of wheat-rye hybrids has been accomplished by using colchicine applied in different ways:

- coleoptile immersion in the colchicine solution (Müntzing 1939);

- alternative immersion of the washed roots of plants at the tillering stage in weak solutions of colchicine (0.05%) and tap water; the plants were usually put in the colchicine solution during the day and in tap water during the night and the treatment lasted for 4 days (Villax et al. 1954; Villax 1957; Wellensiek 1947);

- the cutting back of a couple of tillers and application of the colchicine solution to them with the use of small vials (Bell 1950; Sanchez-Monge 1956a; Linde-Laursen 1973) or hydrophilous cotton protected with polyethylene (Cauderon and Saigne 1961).

Embryo culture has been also used to increase the success of the crosses (Lupton et al. 1973).

Breeding

Research workers soon realized that the primary triticales were autogamous and vigorous, but they were partially sterile and the kernels were shrivelled. The first six lines of the octoploid triticales that Müntzing (1939) studied showed variability for characters such as vigour, pollen fertility, seed setting, grain shrivelling, baking quality, and winterhardiness. This variability was quickly used by breeders, who made crosses between the primary triticales and started breeding programs for the production of secondary triticales.

The inconveniences of low fertility and

excessive seed shrivelling were partially overcome by selection within lines. However, the results were slow in coming and sometimes contradictory. Müntzing (1972), Ingold et al. (1968), and I (Sanchez-Monge 1969) obtained favourable results, whereas Aufhammer et al. (1961) and others did not find that the selection of plants with the highest seed set was effective.

A much debated question that arose from the production of secondary triticales was that of the relationships between fertility, aneuploidy, and the regularity of the meiosis. Vettel (1960), working with the Rimpau triticales and several mutants, found a negative correlation between the frequency of aneuploid descendants and the fertility of the mother plant. Pieritz (1966) obtained similar results and also showed that aneuploidy is mainly transmitted through the female gamete. Pollen grains with aneuploid numbers rarely functioned and when they did so, the chromosome number only deviated by ± 1 chromosome from the euploid number.

Working with octoploid material showing very high chromosomal instability, Krolow (1962) was able to reduce the aneuploid frequency from 83.3% to only 60.6% by selecting the more fertile plants. Reselection within lines allowed him to reduce the aneuploid frequency to 40.3%. In the same experiment, Krolow found a positive correlation between aneuploid frequency and sterility of the mother plant and between aneuploidy and reduction of tallness. Later experiments (Krolow 1963) confirmed these results.

At the hexaploid level, Krolow (1966) found much lower figures for the frequency of aneuploidy. In the progeny of euploid plants with 42 chromosomes he found 7% aneuploids, mainly with 41 and 43 chromosomes. The progenies of these aneuploids showed a tendency to revert to the euploid number of 42, as the average chromosome number in the progeny of 41-chromosome plants was 41.31, and 42.53 in the progeny of 43-chromosome plants. However, it is easy to show, using Krolow's figures, that in the absence of selection the total frequency of aneuploids tends to increase in such a population.

In crosses between hexaploid triticales it was possible to select, in the F_3 generation, plants with good fertility, 42 chromosomes, and a more stable meiosis than the parents of the cross (Krolow 1969).

It was suggested by Müntzing (1956) that some of the unfavourable characters of triticales could be due to the fact that it is an autogamous species resulting from the integration of the genotype of an autogamous wheat species with the genotype of an allogamous rye species. The genetic contribution of rye would be subject to inbreeding degeneration. He then suggested that inbred lines of rye selected for self-fertility or F_1 hybrids between them be used for the production of triticales.

The results with my own material (Sanchez-Monge 1969), in which high levels of fertility were quickly reached, could be due to the use of self-fertile lines of inbred rye. It is worth mentioning here that the highest values of self-fertility in inbred rye have been obtained from populations coming from the southeastern region of Spain where the wild species *Secale montanum* is also found. It is possible that genes of this later species were introgressed into the cultivated rye.

The work of Riley and Chapman (1957) gives some support to the ideas of Müntzing. Three artificial allooctoploids obtained from *Triticum aestivum* \times *Secale cereale*, *T. aestivum* \times *Aegilops longissima*, and *T. aestivum* \times *Aegilops caudata*, were compared by Riley and Chapman.

The breeding systems of the four species are: *T. aestivum* = self-compatible and autogamous; *Ae. longissima* = self-compatible and usually autogamous; *Ae. caudata* = self-compatible and allogamous; *S. cereale* = self-incompatible and allogamous.

The fertility was highest in the octoploid involving *Ae. longissima* and lowest in the one involving *S. cereale*. The authors suggested that the fertility of an allopolyploid can be affected by the interaction of the breeding systems of the parental species.

The production of secondary triticales from crosses between primaries has been frequently used in Western Europe both at the octoploid (Müntzing 1939, 1956, 1963, 1972; Ingold

et al. 1968; Cauderon 1970) and at the hexaploid levels (Sanchez-Monge 1969; Lupton et al. 1973).

Handling crosses between octoploid triticales has been found to be more difficult than with wheat (Müntzing 1939). The F_1 shows heterosis but in many instances is lower in seed setting and has more irregular meiosis than its parents. Aufhammer et al. (1961) found that the fertility of the progenies was dependent on that of the parents and also on their specific combining ability. In crosses between my hexaploid triticales I have not found any such reductions of seed set in the F_1 in comparison with the parental seed set.

Secondary octoploid triticales are also being produced from other types of crosses. Ingold et al. (1968) have obtained secondary octoploids by pollinating the F_1 of *T. aestivum* \times *S. cereale* with pollen of other octoploid triticales. Some 56 chromosome plants were obtained in this backcross and still more in successive backcrosses. This type of cross has been also used by Vettel (1961) in the production of secondary triticales.

Secondary hexaploid triticales have been recovered from the segregating progenies of the cross between octoploid and hexaploid triticales, the cross being more easily made when the octoploid is the mother plant (Cauderon 1970; Müntzing 1972). Octoploids can also be recovered from this cross, but for this it is better to use the backcross of the F_1 to octoploid triticales, instead of raising the F_2 .

The fact that good types of secondary hexaploids have been obtained from the octoploid \times hexaploid crosses could be due to the existence of differences between the A and B genomes of tetraploid wheats and the same genomes of hexaploid wheats. The cross octoploid \times hexaploid triticales gives opportunity for recombination between the chromosomes of these genomes, and some recombinants may give a better triticales genotype (Müntzing 1972).

In the program of triticales breeding at our Institute we have been using crosses between hexaploid triticales and bread wheat and more recently crosses between hexaploid triticales and durum wheat.

Another interesting approach to the breeding of triticale is the use of induced mutations. By treatment of the seeds with X-rays at a dosage of 16 kr, Vettel (1960) obtained 5.48% mutants in the X_2 progenies. The more frequent types of visible mutations were those of "compact ears" and "lax speltoid ears." Some mutants with improved seed quality were also obtained.

For the improvement of endosperm quality we also started an irradiation program with the assumption that seed shrivelling in hexaploid triticale could be due to an interaction between the cytoplasm (plasmagenes) of wheat and the rye chromosomes, and that a destruction or mutation of the wheat plasmagenes responsible for the unfavourable interaction through irradiation could result in the improvement of the endosperm quality. Potted plants of triticale were emasculated and immediately irradiated in a gamma field with 1500–3000 r. After irradiation the emasculated ears were pollinated using pollen of sister plants of the same triticale line. Five back-cross progenies were recovered with smoother endosperm and the character showed maternal influence in its inheritance (Sanchez-Monge 1968).

The production of decaploid and tetraploid triticales has also been attempted. The decaploid was obtained by Müntzing (1956) by crossing octoploid triticale with rye and doubling the chromosomes of the 35-chromosome F_1 . The resulting decaploid triticale was very unstable, lacked vigour and fertility, and showed a tendency to revert to lower chromosome numbers.

Tetraploid triticales were obtained by Krolow (1973) in the selfed progenies of the cross between hexaploid triticale and rye. In the fifth selfed generation, 97% of plants had 28 chromosomes. These tetraploid triticales have seven pairs of rye chromosomes and the other seven pairs can be a combination of chromosomes of the genomes A and B. The interesting material obtained by Dr Krolow will be evaluated in the near future.

Another possibility that we must explore in the breeding of triticale is that of the production of hybrid seed by means of the use of cytoplasmic male sterility. It is likely that

triticale is more suitable material than wheat for hybrid seed production because pollen production is more abundant and the sterile flowers remain more open for a longer time in triticale than in wheat. The experiments of D'Souza (1972) showed that rye, triticale, and secalotricum (triticale with rye cytoplasm) have bigger stigmas than wheat and longer stigma receptivity. In unfavourable conditions of high temperature and low relative humidity the reduction in the duration of stigma receptivity was less drastic in triticale than in wheat.

The transference of triticale chromosomes to different male-sterilizing cytoplasm has been through back-crosses, using as female parents alloplasmic hexaploid and tetraploid wheats with the cytoplasm of *Aegilops ovata*, *Ae. caudata*, and *Triticum Timopheevi*. For the production of hexaploid triticale with rye cytoplasm, a variety of tetraploid rye was used as female parent (Table 1). No triticale line with rye cytoplasm has yet been obtained that breeds true for male-sterility. Some fertile lines with rye cytoplasm do not compare favourably with their counterparts with wheat cytoplasm (Table 2). The cytoplasm of *Ae. ovata*, *Ae. caudata*, and *T. Timopheevi* are strongly male-sterilizing as far as the hexaploid triticales in our first trials are concerned, and could be used for hybrid seed production if satisfactory restorers can be found. The cytoplasm of *Ae. caudata* is probably the least useful because lower seed set values are always obtained.

Octoploid triticales with rye cytoplasm (secalotricum) compared with the ones obtained in reciprocal crosses by Smutkupt (1968) who found longer ears and culms with rye cytoplasm, but did not consider the identity of the nuclear genotype in the compared lines.

Some Results and Actual Problems

The Swedish octoploid triticales produced by Prof Müntzing and coworkers (Müntzing 1972) have reached yields closely approximating those of the hexaploid wheats used for comparison. The bigger kernels of triticale

TABLE 1. Types of substitution backcrosses.^a

<i>Secale cereale</i> 4n × <i>Triticale</i> ^b (b = 7)
(<i>Aegilops ovata</i> × <i>Triticum aestivum</i> ^b) × <i>Triticale</i> ^{b'} (b = 11, b' = 6)
[(<i>Ae. ovata</i> × <i>T. dicoccum</i> ^b) × <i>T. turgidum</i> ^{b'}] × <i>Triticale</i> ^{b''} (b = 8, b' = 4, b'' = 2)
(<i>Ae. caudata</i> × <i>T. aestivum</i> ^b) × <i>Triticale</i> ^{b'} (b = 12, b' = 4)
[(<i>Ae. caudata</i> × <i>T. aestivum</i> ^b) × <i>T. turgidum</i> ^{b'}] × <i>Triticale</i> ^{b''} (b = 7, b' = 4, b'' = 2)
(<i>T. timopheevi</i> × <i>T. aestivum</i> ^b) × <i>Triticale</i> ^{b'} (b = 16, b' = 4)
(<i>T. timopheevi</i> × <i>T. turgidum</i> ^b) × <i>Triticale</i> ^{b'} (b = 12, b' = 3)

^a b, b', and b'' are the number of backcrosses in the material of INIA.

TABLE 2. Comparison for agronomic characters between triticale lines with wheat and rye cytoplasm.

Character	Wheat vs. rye cytoplasm	
	Line JM-130	Line JM-135
Plant height	5% higher*	4% higher*
Tillering	32% higher*	21% higher*
Maturity date	Identical	Identical
Ears/plant	56% higher**	39% higher**
Spikelets/ear	5.5% higher*	0.9% higher
Flower fertility	2.9% lower	5.8% higher
1000 kernels weight	10.7% lower**	3.2% lower*
Kernel protein content	8.4% higher*	6.3% lower
Grain yield per ha	42.8% higher*	43.6% higher*
Protein per ha	54.8% higher	34.6% higher

*Significant at the 5% level.

**Significant at the 1% level.

compensate for the lower seed setting. The seed quality of some lines is also as good as in the wheats and the crude protein content is always higher in triticale than in wheat.

In Switzerland Ingold et al. (1968) obtained triticale lines with yields 78.3% that of wheat.

Cauderon (1970) reported that in France triticale could become a good cereal for feed grain production either as a winter- or a spring-sown crop, if the problem of lodging could be solved. Yield trials in 1970 with material of Canadian origin showed that triticale gave the same productivity as "Moisson" wheat even with heavy lodging of the triticale plots. Chemical analysis of several lines gave crude protein contents between 17.4 and 22.1% with a lysine content of 2.6–2.9 g per 100 g of protein.

In the United Kingdom the breeding program for triticale at the Cambridge Plant

Breeding Institute was started only 3 years ago (Lupton et al. 1973). The program is aimed to the production of secondary hexaploid triticales by intercrossing their own primary types and also crossing them with other hexaploids from CIMMYT and other origins. Their main problems are winter-hardiness, resistance to ergot, yellow rust, powdery mildew, and glume blotch. They hope to preserve in their material the resistance of rye to take-all and eyespot. Resistance to ear sprouting is also a primary need.

In Denmark Linde-Laursen (1973) has been using octoploid triticales to transfer to wheat the resistance of rye to *Gaeumannomyces graminis* and to powdery mildew. A limited number of farmers have been growing hexaploid triticale lines of Canadian origin but the yields were inferior to those of other cereals. Lodging in these triticale lines was also a problem.

In Spain we have released the hexaploid triticale variety "Cachirulo" and several seed-producing private companies have been buying 12-16 tons of foundation seed from us over the last years. It is difficult, however, to give an estimate of the acreage planted in our country because the seed companies keep the figures of seed multiplication and sales to themselves. With the variety Cachirulo we have no disease problems, although 2 years ago we did detect a small infection with ergot in one field near Madrid. Our variety Cachirulo is, however, far from perfect. It is too tall and can become lodged in rainy years. Also it is a little difficult to thresh. As good attributes we can mention its high fertility and the high protein content of its kernels. The figures obtained by chemical analysis fluctuate between 16 and 25.2% protein depending on maturation conditions, soil type, and fertilization. The average of many trials all over Spain is 20%. The lysine content per 100 g of protein was 3.75 g for a sample with 18.4% protein and 3 g for another with 20.1% protein.

Our present program aims at a reduction in height without loss of fertility, protein, or disease resistance, and also an improvement in the ease of threshing. As donors for short culm character, we have been using a recombination of two different mutants: one obtained after irradiation in our own material, and the other isolated in a segregating population that was sent to us by Prof B. C. Jenkins. The material received from CIMMYT has been also used in the last 2 years.

Utilization

I am convinced that triticale has a great future as an agricultural crop. It can be used in different ways, but seems specially useful for the production of grain for animal feeding. Two years ago we sent samples of 0.5 kg to more than 400 factories that make animal feeds, and that were distributed all over Spain, asking them to make their own chemical analysis and give an opinion. This was unanimously favourable and they are interested in the use of this cereal and in the

manufacture of animal feeds. In two cases the people in the factories did not read the circular letter accompanying the sample carefully and as a result we received orders for several thousand quintals of the crop.

Some experiments have been also carried out at our Institute regarding the utilization of triticale. In one experiment on the feeding of meat poultry (Carballo et al. 1970), based on making isocaloric and isoproteic rations, it appeared that it was possible to use triticale to replace high protein corn in the diet.

Triticale can be used for bread making if special techniques are used and if a protein-rich bread is desired. In another experiment at our institute (Garcia-Olmedo et al. 1970) different products from triticale grain were obtained by experimental milling. The variety used was Cachirulo with 20.8% protein. One of the fractions of shorts obtained (23.9% of the total) contained 25.4% protein. The Buhler flour (63.0%) contained 18.3% protein and by mixing 20% of this flour with 80% of the standard flour used in the bread factories of Madrid, the quality of the bread and, of course, its protein content were highly improved.

Triticale can be used also for silage and the preliminary experiments we have made have given a good product. It can also be used as green forage, as some experiments at the Cambridge Plant Breeding Institute (Rogers and Webb 1972) have shown. In 1971 they obtained 19.4 tons per hectare of dry matter containing 37.5% soluble carbohydrates with a digestibility of 56.5%.

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