A rich harvest is a tribute to the farmer’s skill and the years of scientific work that have converted triticale from a curiosity to a genuine food crop.

CIMMYT TODAY

WHEAT x RYE = TRITICALE

Intensive triticale breeding at CIMMYT during the past decade has brought this “man-made” crop to the brink of commercial cultivation by farmers in the tropics and subtropics.

TRITICALE, a new and relatively unknown crop, is the product of a cross between the genera Triticum (of which wheat is a member) and Secale (of which rye is member), getting half its name from each parental genus. Created by plant breeders, rather than by the natural processes of evolution, triticale owns the distinction of being the first successful “man-made” cereal grain.

But for millions of food-poor people, the long, patient effort to develop viable triticale and perfect
it as an economic crop is justified by far more than its value as a biological curiosity. In many of the world's least-favored agricultural environments, triticale offers a double hope: yields, nutritional quality and other critical characteristics equal or superior to those of wheat; and the tolerance for drought and poor soil and the resistance to disease typical of rye.

Beyond its immediate potential as a food crop, moreover, triticale's progress from the curiosity shelf to the experimental fields at CIMMYT and other research centers, and now to the threshold of widespread commercial cultivation, encourages the hope that other such intergeneric "wide crosses" will soon follow. The possibility of crossing disparate genera has long appealed to plant scientists as a powerful possibility, at least in theory. From the genetic material that could be combined in wide crosses, breeders might be able to fashion many new high-yielding, high-quality crops custom-tailored for specific human needs and agricultural constraints.

In practice, however, enthusiasm for such speculations was dampened by the empirical evidence that the same differences that make distinct genera attractive candidates for wide crosses also make them sexually incompatible. Indeed, this reproductive integrity is part of the very definition of "genus" in dictionaries and basic biology courses. Wide crosses according to the commonly accepted "laws of nature," are all but certain to be as sterile as mules. The development of fertile triticale, leading to its subsequent improvement as a food crop, suggests that this unbreakable law of nature can at least be bent.

**Ancient history**

The emergence of triticale (pronounced triti-kay-lee) as the first successful crop from a man-made wide cross coincides with the centennial of the wheat-rye hybrid's debut in the scientific literature. A sterile plant grown from a wheat x rye cross was reported by a researcher named Wilson to the Botanical Society of Edinburgh in 1875. In 1884, the *Rural New Yorker*, reporting a replication of Wilson's experiment by a plant breeder named Carmen, published the first illustration of the hybrid, which bore a telltale resemblance to its parents. It was not until 1891 that the first fertile triticale was announced in the literature. Among a population of wheat x rye crosses made in 1888, the German breeder Rimpau found a single spike bearing 15 kernels, of which 12 germinated into fertile plants of uniform phenotype: the first true triticales.

Rimpau's few seeds reproduced with perfect genetic fidelity through generation after generation. Until the 1930's, however, these and other triticales attracted relatively little interest save as taxonomic curiosities and evolutionary dead-ends. Their generally poor appearance and persistently reluctant fertility discouraged interest by practical breeders in the potential of triticale as a field crop.

The most intensive early research on triticales was touched off by a freak occurrence at the Agricultural Experiment Station of Saratov, in southeastern Russia. In 1918, the researchers on the station's wheat staff were amazed to find thousands of unmistakable wheat x rye hybrids in their winter wheat test plots. Evidently the uninvited triticales were the result of spontaneous fertilizations in the previous season between the station's wheat trials and border rows of rye planted, ironically, to prevent cross-pollination among the wheat strains.

Although all the hybrids were male-sterile, incapable of self-pollination, thousands of fertile seeds had been created by spontaneous backcrossing to neighboring wheats and ryes. Later derivatives from these backcrosses proved to be true-breeding and relatively fertile, as well as phenotypically intermediate between wheat and rye. Not until 1931, however, did cytological tests confirm that the hybrids were true amphiploids (intergeneric hybrids) with a diploid chromosome number of 56; and even then the Russians still lacked a convincing explanation of how such amphiploids could have arisen from completely male-sterile plants. An ingenious researcher named Levitsky finally resorted to the theory that the F1 ovules developed asexually with a somatic chromosome number, which was somehow doubled in the first division of the egg cell.

Despite the lack of a firm theoretical base, the Russians at Saratov and elsewhere continued to work on triticale during the 1920's and early 1930's, even conducting preliminary tests of triticale's bread-baking characteristics. Unfortunately, the official establishment of Lysenko's doctrine of heredity, and then the onset of World War II, interrupted the Russian effort. Significant research during this period was also carried on at centers in other European countries, most notably in Sweden, where Arne Muntzing's crucial contributions to the improvement of triticale began in 1931 and continue today. In 1936, among 65 triticales grown from a fertile wheat x rye cross, Muntzing discovered one plant with three heads whose anthers had produced from 20 to 60 percent viable pollen grains. One other plant had a single partially fertile head. Using this pollen for self-fertilization, Muntzing succeeded in obtaining a single seed that germinated into a plant with 56 chromosomes: a new triticale. Thus Muntzing demonstrated "a mechanism of general importance" to explain the spontaneous appearance of fertile triticales in nature making Levitsky's theory of asexual reproduction "superfluous."

Nevertheless, through the middle of the 1930's triticale remained of serious scientific interest mainly to geneticists. Consideration of its potential as an economic crop was forestalled by the hybrid's persistent high degree of sterility and its tendency to set shriveled seed without sufficient endosperm to support seedling growth. Because of these obstacles to research and development, Muntzing re-
A CIMMYT scientist excises the embryo from a seed, left and below, before placing the embryo in a nutrient medium where it will develop leaves and roots. F1 seeds resulting from wheat-rye crosses are deformed and usually unable to supply the nutritive needs of the seedling.

By 4 weeks the leaves and roots have appeared. After 6 to 8 weeks the plantlet is transplanted in soil.
fers to the history of triticale through the mid-
1930's as "the archaic period."

The modern era
The first breakthrough came in 1937 with the dis-
covery in France that a chrysir alcaloid, colchicine,
could induce plants to double their chromosome
number. With this pale yellow poison derived from
the bulb of the autumn crocus, plant breeders could
cure sterility in triticales. Although the colchicine
technique itself required more years of refinement,
it discovery augured the end of the major obstacle
to the development of triticales.

Only a few years later, the colchicine method was
joined by the development of a delicate technique
for excising triticale embryos from their shriveled
seeds and transplanting them to a nutrient culture
medium. Before these two discoveries, would-be
triticale developers were discouraged by the tedious,
usually fruitless search for naturally occurring fer-
tile plants. By 1975, after the refinement of these
techniques, the triticale program at CIMMYT alone
could report the successful production of several
hundred new fertile triticales in only 2 years.

New troubles with triticale
Plant breeders could now produce unlimited num-
bers of wheat x rye crosses with reasonable assur-
ance that their primary triticales would grow into
fertile plants. By the same token, however, they
were then confronted with a long list of inherent
failures in their mature populations. Not the least
of these were the persistent tendencies of the pro-
geny of embryo-cultured chromosome-doubled pri-
marys, to have high rates of sterility and seeds with
shriveled endosperm.

Even triticales that retained their reproductive
vigor exhibited other character deficiencies. Most
triticales, because they derived from European par-
ents adapted to higher latitudes and long days, were
late to mature in the short days typical of the de-
veloping countries for which triticale was intended,
most of which are inside 35 degrees latitude. Some
of the northern triticales needed long days in order
to flower at all. Moreover, the early triticales were
developed from tall, weak-strawed parents, and the
sunlight conditions of the lower latitudes encoura-
ged them to grow even taller and weaker. Espe-
cially under the stimuli of irrigation and fertili-
tization, intended to exploit their full yield potential, the
tall triticales tended to lodge, or fall over, severely
depressing yield.

The early triticales were also narrowly adapted
to specific growing conditions. Their lack of versa-
tility made them inappropriate for wide use in
the developing world, where the plant type most
likely to succeed is one that can tolerate a wide
range of growing conditions and still yield well.
For example, the relatively few, carefully reared
experimental triticales had never been selected in
the field for resistance to the many plant diseases
of the lower latitudes. Once the problems frustrat-
ing the creation of experimental primary triticales
were solved, the disabilities that afflicted triticale
as an economic field crop for the developing world
emerged as an agenda that would challenge plant
breeders for decades to come.

Triticale comes to the new world
The early research and development work on triti-
cale was carried on by individual scientists and
small teams at widely separated institutions in many
countries. The results were reported and shared, if
at all, mainly by the traditional, slow process of
publication in professional journals in a variety of
languages. The rapid and coordinated development
since World War II that has brought triticale to the
verge of economic viability as a new food crop is the
result of a fundamental innovation in agricultural
research in which the contributions of worldwide
networks of collaborating scientists and institu-
tions are focused into a systematic effort by inter-
nationally funded and directed centers. In the case
of triticale, the seeds of this system were planted in
1954, when the University of Manitoba, Canada,
brought together for the first time a large number
of primary triticales from individual researchers and
institutions around the world. From the interna-
tional collection, plus primary triticales of their own
creation, the researchers at the university's plant
sciences department could make an unprecedented
number of eclectic secondary crosses.

An important early result of the work at Mani-
toba was the confirmation of the superior breeding
qualities of hexaploid triticales—hybrids of tetra-
ploid durum wheat x diploid rye, 2n = 42, in com-
parison with the more common octoploids, 2n =
56, the product of crossing rye with hexaploid
bread wheat. The difference of a few chromosomes
was crucial to future progress. As Arne Muntzing
later recalled, "It is possible that the interest in tri-
cale as a potential new crop would have tapered
off entirely if the efforts had been limited to octo-
plloid material. However, this has been successfully
prevented by the enormous development of hexa-
plloid triticales and by the crosses between octo-
ploids and hexaploids."

Even against the stubborn resistance of the octo-
ploid form to improvement, hexaploid triticale was
something of a dark horse. Hexaploids had been
produced by various breeders since 1913: the first
fertile line was reported in 1938. But, according to
Muntzing, the early hexaploids displayed such
poor seed development that researchers were dis-
couraged from further efforts on such an unlikely
prospect. By the mid-1950's, a few dauntless breed-
ers were having better success, among them the
triticale pioneer E. Sanchez-Monge in Spain and
the American J.G. O'Mara at Iowa State University.
It was the latter who provided the Manitoba re-
searchers with their first hexaploid breeding ma-
terial, 10 seeds from an embryo-cultured, colchi-
TRITICALE: FOOD FOR PEOPLE

While great efforts are being made in the experimental fields at CIMMYT and elsewhere to increase the yield and broaden the adaptation of triticale, equal attention is being paid in the laboratory to the nutritional value of the new grain as a food for people and domestic animals. In 1968, assays of triticale at CIMMYT’s Protein Quality Laboratory, under the direction of Evangelina Villegas, indicated protein contents ranging from 11.7 percent to 22.5 percent of total grain weight, with an average level of 17.5 percent. By comparison, the average protein content of wheat is only 12.9 percent. Triticale’s vastly superior showing in these early tests led to premature publicity about a new “super food.”

As Villegas pointed out in 1973, however triticale’s high protein content was linked to its malformed, incomplete endosperm, which exaggerated the higher protein in the germ and the bran. As the size and plumpness of the grains were increased by breeding and selection, the increase of starchy endosperm inevitably diluted the protein percentage of the entire seed.

However, the loss in protein as a percentage of the improved grains was more than offset by the increase in total protein production per hectare. Thus, in 1968, when the best triticale yields were but 2500 kg/ha and the protein content averaged a remarkable 17 percent, total protein production per hectare was 425 kg. By 1973 the protein content had dropped to 13.7 percent, but the best yields were up to 8000 kg/ha, resulting in a total protein production of 1100 kg/ha.

Protein quality, as well as protein quantity, is closely watched. The biological quality of any protein refers to its content of “essential amino acids”—those building-blocks of protein that cannot be synthesized by the systems of humans and other nonruminant animals and must therefore be eaten directly in food. In triticale, as in other cereal grains, the “first limiting amino acid”—the one most lacking—is lysine, therefore the percentage of lysine in triticale protein becomes the index to overall protein quality.

In terms of lysine content, triticale is significantly superior to commercial wheats, in which lysine averages about 3.0 percent of the total protein. In the 5500 triticale lines analyzed by CIMMYT’s protein chemists in 1974, the total protein fraction averaged 13.5 percent, of which 3.7 percent was lysine. By 1972-73, several advanced lines of triticale had a lysine content close to that of quality-protein maize, which incorporates genes for high lysine, while the triticales were far superior to the maize in total protein.

In assessing the protein quality of triticales, the CIMMYT laboratory uses a simple test based on a correlation between lysine content and dye-binding capacity. The same procedure can readily be adopted by protein laboratories in developing areas. In addition, the actual dietary value of triticale has been tested in feeding trials on beef and dairy cattle, hogs, and poultry, as well as laboratory animals. Current feeding trials are being carried out in cooperative programs between CIMMYT and the Instituto Nacional de Investigaciones Pecuarias in Mexico, and with the collaboration of the Instituto de Nutrición de Centro America y Panama in Guatemala.
Borlaug's group and the University of Manitoba were reorganized into a cooperative breeding program.

This alliance, which continued after CIMMYT was founded in 1966, broadened and accelerated the progress of triticale development. Materials tested in the Canadian summer could be selected for significant characteristics and regrown a second time in the same year in the warm Sonoran winter, thus doubling the pace of research. The establishment of triticale nurseries at two CIMMYT stations—Ciudad Obregon, at sea level, and Toluca, at 2600 meters elevation—exposed the triticale to selection under growing conditions more similar to those of the developing world than they could experience in Manitoba. Beyond Mexico, CIMMYT's collaborative relationship with a network of plant breeders, research institutions, and national programs around the world assured that promising experimental varieties from Mexico would be systematically tested under even more varied and realistic conditions. Finally, CIMMYT offered a unique, thoroughly tested collection of wheat breeding materials; an aggressive system for producing and testing new genetic combinations; and a team of trained and field-tested researchers under Borlaug's direction.

In Mexican soil under a Mexican sun the Canadian triticales quickly showed their lack of adaptation to low-latitude growing conditions. They suffered from the short days. They grew too tall. They produced less than half as much grain as the best Mexican wheat. While the triticales equaled or even bettered the wheat in total plant material, their grain yield was depressed by late maturity, lodging and, most significantly, persistent partial sterility and severe shriveling of the seed's endosperm.

The Armadillo accident
Before they had barely begun to work on triticale's manifold disadvantages, the CIMMYT breeders were the beneficiaries of a happy accident. As Borlaug later described it:

I must tell you that the largest and most important step toward making the breakthrough in triticale improvement was executed by capricious mother nature herself, one early dawn March morning in 1967 in Ciudad Obregon, Sonora, while scientific man was still in bed. One promiscuous, venturesome stray wheat pollen grain with a potent and valuable "genetic load" from the nearby wheat breeding plots floated across the road under cover of darkness and fertilized a sad but permissive tall, sterile degenerate triticale plant.

A year later (two generations), scientific men identified several unusually promising plants in a segregating population. The genetic makeup of those plants clearly indicated the value of the illicit stray wheat pollen grain. Its triticale progeny indicated that in the act of fertilization it had dwarfed, introduced partial photoperiodic insensitivity and completely overcome the sterility barrier, which had inhibited progress in triticale improvement for decades.

Borlaug concluded, "This seems to me to be nature's way of telling scientists not to become too arrogant." The CIMMYT scientists had been blessed by a stroke of luck similar to the one that had produced the first field of fertile triticales at Saratov in 1918. The difference was that half a century later in Sonora the CIMMYT triticale team was prepared fully to exploit its good fortune. Happily, the assets of the well-endowed triticale, christened Armadillo, proved to be highly heritable; and the Armadillo hexaploids crossed more readily with wheat and ryes than did the normal hexaploids in the CIMMYT program. As a result, by 1970 practically every triticale at CIMMYT included Armadillo in its pedigree. Armadillo materials were also distributed to the network of breeders and research institutions around the world. By a single cross, breeders could now confer on less-favored triticales Armadillo's legacy of high fertility, improved grain test weight and yield, insensitivity to daylength, one gene for dwarfness, early maturity, and good nutritional quality.

Encouraged by the rapid progress initiated by the Armadillo discovery, the International Development Research Centre in Canada and The Canadian International Development Agency in 1971 provided US$2.5 million for a 5-year program to speed the development of triticale as a crop for food-poor parts of the world.

In worldwide trials at dozens of locations each year, triticale yields have climbed rapidly, and in 1974 exceeded yields of the wheat check varieties.
A new beginning
Like earlier breakthroughs in the history of triticale, the advent of Armadillo solved some problems—or at least indicated that they were solvable—only to bring others to the fore. The prescription that remained for triticale breeders to fill was spelled out in 1971 by Borlaug and Frank J. Zillinsky, who assumed direction of CIMMYT’s triticale program—then newly established as a separate entity from the wheat program—in 1968. “If triticale is to become commercially competitive with other cereal grains,” they wrote, “it must be at least equally productive in grain yield, have adequate resistance to disease infection, desirable grain type, and nutritional quality suitable as feed for animals and a food for humans.” To achieve those goals, the 1970’s at CIMMYT have been a period of intensive effort to compress millennia of evolution into mere generations of painstaking breeding and selection.

Enriching the gene pool
The precondition for overcoming the formidable remaining liabilities of triticale as an economic crop was a gene pool of rich diversity from which more desirable traits might be assembled. “Triticale has lacked the innumerable generations of natural selection...under which the other cereal crops evolved,” noted Zillinsky and Borlaug. “To make up for this lack of natural evolution, it will be necessary to establish populations as genetically diverse as possible....” The development of triticale until 1971, however, had contrived to maintain a very narrow genetic base, just the opposite of the resource the breeders now required.

For example: each new primary triticale must be “handmade” by the delicate, two-stage process of embryo culture and colchicine treatment, and there are inevitably a significant percentage of failures. Accordingly, the number of primary crosses to introduce new germ plasm into the breeding populations has been limited: only about 30 primary hexaploids were available at CIMMYT as late as 1972. In a different way, the wholesale conversion of CIMMYT’s triticales to Armadillo parentage, while it vastly improved the characteristics of most lines, also tended to standardize the genetic stockpile from which the breeders could choose.

To facilitate the diversification of the gene pool by the creation of new primary triticales, CIMMYT’s laboratory scientists have made important refinements in the techniques for culturing embryos and doubling chromosomes. In 1971 only 150 embryos of new crosses could be cultured successfully, and of these only one seedling was successfully treated with colchicine. In 1973, with the improved processes, 125 new fertile primaries were produced; and 84 more the following year. By 1975, CIMMYT’s breeders were able to draw on a bank of some 185 primary triticales.

Meanwhile, the triticale staff has been following several approaches to increase the genetic variation in CIMMYT’s secondary breeding materials. Thousands of crosses have been made between triticales of different pedigrees, triticales and wheats, and triticales and ryes. In some cases the breeders made specific matches between plants; but in others random crosses were encouraged by planting mixed breeding populations in adjacent rows or plots and letting nature take its course.

Many of CIMMYT’s triticales—all of them spring types, due to their Canadian origin—have been crossed with winter wheats, winter ryes, and winter triticales in a cooperative effort with breeders in Canada, the United States, Sweden, Great Britain, Germany, Hungary, and other countries. The conversion of spring triticales into winter types makes it possible to cross them with existing highly improved ryes. The germ plasm of rye land races,


BREAD FROM TRITICALE

The success of triticale will finally be measured not only by its yield in the farmers' fields and its protein quality in the scientist's laboratories, but by its performance in the world's ovens in an almost endless variety of locally preferred bread types. However, even though G.K. Meister, the director of the agricultural station at Saratov, Russia, published preliminary descriptions of triticale's baking properties about 1930, triticale breeders until recently have been preoccupied with the fundamental problems of fertility, yield, and adaptation.

The earliest studies indicated that the light, airy loaves of leavened bread preferred in many of the developed areas of the world could be baked from triticale flour only with the addition of large proportions of wheat flour. The unique contribution of the wheat flour was to produce the elastic substance called gluten, which inflates and stretches during the baking process to produce a cellular, crusted loaf. In 1972, Lorenz et al. demonstrated that the deformed grains typical of triticale resulted in inferior flour protein content compared to that of wheat, despite the original protein superiority of the triticale grain. However, the same researchers also found that triticale flour alone, without the addition of wheat flour, could yield good bread loaves with appropriate adjustments in absorption and fermentation times and mixing procedures. Their experience was confirmed by Tsen et al. and Amaya.

At CIMMYT, however, relatively little effort is spent on producing triticale loaves to meet U.S. or Canadian bread preferences. CIMMYT's mandate is rather to adapt triticale to the food needs of the developing countries, where "bread" has many other names and takes many very different forms.

Nevertheless, satisfactory raised bread can be made from some triticales. Javier Peña and Arnoldo Amaya, CIMMYT cereal chemists recently conducted baking tests on advanced triticale lines that have high test weight (up to 74 kg/ha.). They found several lines that produced loaves with a volume of 785 cc which was similar to the loaf volume of the wheat check. In tests in which chapatis, tortillas, and cookies were made, a number of triticale lines were as good as the wheat check or better. Reports from Ethiopia indicate the enjera, the traditional "bread," can be made successfully from a flour composed of equal parts of triticale and teff, a North African cereal.

collected by CIMMYT in 1972 in Turkey, one of rye's ancestral homes, has contributed still more diversity to CIMMYT's triticale gene pool.

The problem of productivity

The diversified triticale gene pool was CIMMYT's arsenal for an attack on the factors limiting productivity. In their earliest trials in Mexico, triticales had failed to yield even half as much grain as the best locally adapted wheat. By 1969-70, even with the many advantages of the Armadillo genes, Zillinsky and Borlaug reported that "although average yields in triticales have increased substantially, they are not yet competitive with the best commercial dwarf Mexican wheat varieties."

In the 1969-70 International Triticale Yield Nursery (ITYN) grown at the CIMMYT station in Ciudad Obregon, the 10 best Armadillo-crossed competitors yielded an average of 4492 kilograms per hectare, while the top strain reached 4990 kg/ha. The best wheat check, however, yielded 6220 kg/ha—almost 25 percent better than the best triticale—while the wheat average was 5417 kg/ha. Even these results were distorted in favor of the triticales. Out of deference to the inability of the triticales to tolerate the optimum level of fertilization for wheat without lodging completely, the wheat checks were grown with only 60 percent of their recommended nitrogen.

Standing tall

By 1971, among the "several shortcomings which must be corrected to increase yields to a level comparable to the best wheats," Zillinsky and Borlaug identified triticale's tendency to lodge—fall over—as "the most serious limiting factor to higher yields." They warned that "little progress in maximum yields can be expected until a substantial improvement in lodging resistance is obtained." The same problem had plagued many earlier investigators, including Muntzing in Sweden, Kiss in Hungary, and

Today's triticales, left, have much less shriveled seed than triticales in 1971, center, or 1969, right.

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Dr. Kohli, left, gives an open-air class for CIMMYT's first triticale trainees—A. Merezhko, USSR; G. Gebeyehou, Ethiopia, and A. Benbelkacem, Algeria.

The cells of a plucked root tip will reveal, under cytological examination, whether the plant is really triticale or just the result of an accidently self-fertilized wheat.

Homegrown triticale provides the week's bread for a Mexican farm family.
Sanchez-Monge in Spain; but in the lower latitudes of Mexico the triticales tended to stretch still taller on their weak straw until they fell over. Even the Armadillo strains, despite one dwarfing gene inherited from wheat, tended to express the tallness of their rye parent and collapse under the weight of their fuller, more fertile spikes.

As the 1969-70 ITYN demonstrated, triticale's propensity to grow tall and fall down made attempts to increase yields through irrigation and fertilization ironically self-defeating. In later trials against wheat checks, the yields of the best triticales approached the wheat standard at low levels of nitrogen. However, as the nitrogen level approached the 120 kg/ha recommended for the dwarf wheats, the triticales lodged severely and their yields actually fell, while the wheats widened their margin of superiority.

Early attempts to shorten the triticale plant by incorporating additional wheat dwarfing genes were frustrated by the inability to maintain fertility among the dwarf selections. Crossing Armadillo strains with stiff-strawed triticales resulted in only moderate increases in lodging resistance. Since a major obstacle to the expression of the single dwar­fing gene in Armadillo was the tall genotype of rye, a third strategy was to substitute the genes of a dwarf rye called Snoopy. Unfortunately, along with its dwarfing genes Snoopy carried genes for susceptibility to several diseases and other unfavorable traits. Two-gene dwarf hexaploids were finally derived from crosses of hexaploid triticale x bread wheat and octoploid triticale x hexaploid triticale. Introduced in 1971 as Cinnamon, the fertile dwarf achieved significant improvements in yield. By 1975 the best triticales had excellent lodging resistance and the average height of the crop had been significantly reduced. Yield tests demonstrated that triticale could tolerate optimum nitrogen levels.

Shriveled seed
By 1974, Zillinsky reported, "the most important unsolved problem in triticale breeding is abnormal endosperm formation." Instead of the hard, vitreous seed typical of wheat, ripe triticale seed has a wrinkled coat and a deep crease and lacks luster. The practical result is that triticale grain is unattractive to farmers and consumers. The malformed seed also provides a poor environment for the embryo, and leads to a poor germination rate. The shriveled seed is reflected in low test weight (weight

Leafy, forage-type triticales can be grazed or mowed several times a season and later harvested for grain.

Careful daily observation of thousands of triticale lines throughout the growing season is the basis for selecting the lines that advance to international trials.
Crossing a durum wheat with rye leads to hexaploid triticale; crossing bread wheat with rye leads to octoploid triticale. The F1 progeny are haploid and, therefore, unable to self-fertilize. Treatment with colchicine doubles the chromosome number making the plant self-fertile.
Bathing shoots of a new triticale plant in colchicine will double the number of chromosomes in the cells thus making the plant self-fertile.

Will triticale succeed as a new crop? The most critical test occurs when a farmer goes to thresh his first harvest.

On-farm trials conducted by Matt McMahon, CIMMYT triticale agronomist, whets farmers' interest and provides valuable information to researchers.

per unit volume): while the best bread wheats have test weights above 80 kilograms per hectoliter, triticale test weights have commonly ranged from 58 to 72 kg/hl.

Progress in improving grain quality by conventional methods of breeding and selection has been slow. Visual screening for plump seed tends to eliminate genes for desired characteristics such as plant type and dwarfing which are associated with poorly formed grains. In 1969, Ake Gustafsson of Lund, Sweden, attempted to induce grain plumpness by genetic mutation, using mutagenic chemicals and radiation. Although some improvement in seed type appeared in his materials in the third and fourth generations after treatment, mutation proved not to be a general solution to the problem.

The most significant progress in seed improvement resulted in 1972 from a 15-day selection process beginning with 600,000 plants standing in 6000 double rows at Ciudad Obregon. After four stages of elimination by visual inspection, the plump seeds from 2250 highly fertile plants were retained for crossing to the elite lines of triticale. By this tedious process, the CIMMYT plant breeders were able to obtain highly productive triticales with grain test weights as high as 76 kg/hl which had been designated as the triticale standard. Nevertheless, by 1974 the average triticale grain test weight was only 72 kg/hl, representing significant but slow progress from the 1966-67 average of only 65 kg/hl, or the 1970 average of 68 kg/hl. According to Zillinsky, the pace of future improvement in seed
type depends on "the degree of selection pressure placed on the segregating populations, the number of cross-combinations made, and the obtaining of a fortuitous combination of compatible rye and wheat chromosomes."

Disease resistance
Diseases have not appeared as a serious limiting factor in triticale yields, probably because not enough triticale is yet being planted anywhere in the world to trigger serious outbreaks of pathogens. By the same token, Zillinsky notes, information on the inherent resistances and susceptibilities of triticales to diseases is relatively scarce. However, he adds, "wherever the crop is grown, disease symptoms appear, apparently caused by plant pathogens which parasitize wheat and rye species.... As commercial production increases, diseases that parasitize triticales will increase."

In general, European researchers have reported, triticale is superior to wheat in genetic resistance to disease. Since 1971, CIMMYT has been monitoring diseases which infest triticales in Mexico. The Mexico triticales have proved more resistant than wheat to several important diseases, including leaf blotch, powdery mildew, and the smuts. Following the devastation of the Toluca triticale nursery in its first season by stripe rust, a high degree of resistance was obtained by selection from intercrosses with resistant triticale plants and backcrosses to resistant wheats. At least partial resistance to leaf rust has been identified in some stages of certain triticale strains.

On the other hand, triticales lack adequate resistance to certain important pathogens, including Fusarium head blight, Fusarium nivale, bacterial stripe and several virus diseases, and some root-rotting and leaf-destroying organisms. CIMMYT's collaborators at the University of Manitoba are working to develop triticales resistant to ergot, a fungus that does not appear in Mexico but attacks rye in temperate zones, producing highly toxic substances.

The payoff: increased yield
The sometimes dramatic improvements in fertility, lodging resistance, grain type, genetic diversity, disease resistance and other factors achieved at CIMMYT have been manifested in steadily increasing yields, both absolutely and in comparison with wheat standards. In 1968, before the introduction of Armadillo fertility, the best yields for triticale at CIMMYT were about 2500 kg/ha, less than half the top wheat yield of close to 6000 kg/ha. Increased fertility doubled triticale yields in some situations by 1970, and in the 1970-71 INTY trials, the best triticale yielded about 85 percent as well as the best wheat check. By 1972 the best yields for Mexican wheats had increased to 8000 to 9000 kg/ha, while the yield of the top triticale had reached 7000 kg/ha.

The Cinnamon strains with their additional dwarfing genes made their debut in replicated trials in the 1972-73 CIMMYT yield tests in Sonora. While the yield of the top wheat check held steady at 8000 to 9000 kg/ha, the best triticale strains had increased their productivity by about 15 percent to 8000 kg/ha. The top triticale yielded 8352 kg/ha. The yield gap between the best wheats and triticales in Mexico had been closed for the first time.

In the following summer season at the high-altitude CIMMYT station at Toluca, triticale yields again equaled those of the best bread wheats. Of the 150 triticale lines tested at CIMMYT in 1973, about 35 yielded as much as 7000 kg/ha. The following year, 150 of the 600 lines tested met or bettered that standard.

Looking ahead in 1974, Zillinsky said: "Further increments in grain yield in triticales are expected with the introduction of more dwarfing genes and improvements in tillering capacity, grain density, and plant structure. An immediate increase of 10 to 15 percent could be achieved if triticales could produce grain of equal density to wheat. Increasing spike length may also result in yield increases, perhaps compensating for the present deficiencies in tillering capacity."

Adaptation
The assignment undertaken by the CIMMYT-University of Manitoba triticale program was not fully discharged by the achievement of triticale strains that could equal or outperform the best wheats under the carefully controlled conditions at Mexican experiment stations. Rather, the mandate from the Canadian International Development Research Centre in 1971 was specifically for the development of superior triticales so broadly adapted that they could compete with traditional grains in the varied and often marginal agricultural conditions typical of the developing world.

But, as Zillinsky and Borlaug recognized in 1971, "the current strains of triticale appear to be notoriously poor in adaptation." They noted a crippling intolerance for "changes in latitude, elevation, temperature, daylength, availability of moisture and nutrients, and probably many other factors...." The explanation for triticale's poor adaptation was obvious: lack of evolutionary opportunity. "To make up for this lack of evolution," the CIMMYT breeders prescribed, "it will be necessary to establish populations as genetically diverse as possible and have them grown and selected in various environments around the world. The best selections from all possible sources will subsequently be brought together and hybridized to establish a second cycle of diverse material."

"Such a program," they realized, "requires the generous cooperation of many interested scientists around the world." CIMMYT initiated an international triticale testing program in 1969, involving university researchers and public plant-breeding institutions in systematic cooperative exchanges of..."
breeding materials and data. By 1973, international triticale nurseries from CIMMYT were grown in some 48 countries in 212 trials. In the early years, CIMMYT triticale nurseries were sent to all cooperators who would accept them. By 1975, however, 338 trials were grown in 73 countries and CIMMYT was unable to satisfy many additional requests for seed.

The great increase in the range of environments in which the triticales are tested, combined with the great expansion of the diversified gene pool, has resulted in a remarkable improvement in adaptation, as manifested by the ITYN trial results from all locations around the world. In the 1969-70 ITYN, the best triticales yielded only 70 to 75 percent as well as the top wheat. Two years later, the triticales were only 5 percent short, and by the 1973-74 trials, the average yield of the five top triticales had pulled 15 percent ahead of the top wheat in the trials. In Winnipeg, at the University of Manitoba, the top-yielding triticale outyielded the top feed wheat by 18 percent while at the Canadian nursery at Tulelake, California, the best triticale yielded 9890 kg/ha, 21 percent higher than the top wheat.

By 1975, the broadening adaptation of triticale was being demonstrated in a growing number of actual agricultural environments, including the difficult conditions typical of the poorest areas of the world. Kiss in Hungary, Muntzing in Sweden and Sanchez-Monge in Spain reported that triticales have replaced rye to a significant degree in sandy soils. Under similar conditions in the high plateau region of Mexico, triticale have outyielded wheat for 3 successive years.

Triticale has demonstrated an adaptation to acidic, low pH soils in several areas of the world. Such conditions exist in Colombia, Ethiopia, Northern India and Brazil. In each of these countries tricitales have shown yield performance superior to wheat. The resistance of triticale to bunts and loose smut at higher elevations provides an advantage for the crop. Its greater resistance to Septoria tritici is an added advantage in areas where this disease is prevalent—Brazil, Argentina, Ethiopia, and the Mediterranean region. In Brazil it appears more tolerant than wheat to aluminum toxicity. In Kenya and some other locations triticale has outyielded wheat under drought conditions.

The final test
After 10 years of intensive development by the CIMMYT-University of Manitoba program and its many cooperators around the world, triticale's value as a versatile food crop for hungry people in many areas of the world remains a promise on the verge of fulfillment. Although estimates vary widely Zillinsky believes that only 100,000 hectares of triticale are being grown worldwide in the mid-1970's.

Since 1961, a modest production of triticale has been grown in Canada for use in distilling whisky. In Hungary and Spain, where they were certified for release in the 1960's triticale are grown almost exclusively as feed grains in special circumstances where rye does not do well. Argentina has also recently released triticale as a forage crop. Small amounts of triticale have been grown as winter forage since 1971 in the southwestern USA. One Texas manufacturer has marketed triticale bread, cakes, macaroni, and pancake flour in small quantities, but most of the triticale for human consumption in the United States is sold at a premium in specialty stores.

Recognizing the disparity between triticale's original, well-publicized promise and its necessarily measured progress, Zillinsky in 1974 warned that "unethical tactics used in the promotion of seed sales and overenthusiastic reporting have created a distorted image of the crop. Most research scientists agree that it has potential but is not yet ready for general production in competition with adapted varieties of other cereal crops."

Despite Zillinsky's caution, however, by 1975 there were encouraging signs that the demonstrations of triticale's adaptation as a high-yielding crop in a growing number of agricultural environments would soon be translated into widespread commercial plantings. Already in Ethiopia, where 5 years of experimentation with triticale in cooperation with CIMMYT resulted in yields far superior to wheat, one or two promising strains were being multiplied for possible release as commercial crops. Advanced experimental trials in Algeria, Kenya, Turkey, and India suggested that official acceptance of triticale in those countries was not far off. Among the triticale breeders at CIMMYT and the University of Manitoba and their cooperators around the world—workers whose genes for patience are reinforced by the discipline of their calling—there was no doubt that they were close to fulfilling the need, stated by the IDRC, for "a valuable new source of protein and essential nutrients for many people of the developing world."

Summing up at an international triticale symposium at CIMMYT in 1973, L.H. Shebeski, who had initiated the Manitoba triticale program 10 years before, told almost 100 participants from more than 15 countries

In my opinion, over the next 15 years, yields of triticale will improve much more rapidly than those of wheat and should plateau at a level approximately 50 percent higher than those of wheat. This is no idle speculation. . . . With rapidly expanding programs and a quickly widening genetic base, with improved fertility and seed density, with improving world-wide cooperation, the improvements over the next 15 years will greatly surpass all improvements that so far have been attained.

By about 1990, Shebeski concluded, "triticale will have begun to compete seriously with the bread wheats as one of the world's most important food crops."—Anthony Wolff.
TRITICALE'S FIRST CENTURY

1875 Scotland A. Stephen Wilson reports first known wheat x rye cross, resulting in sterile plant.
1888 Germany First fertile wheat x rye hybrid achieved by W. Rimpau.
1918 Russia Thousands of wheat x rye hybrids appear at Saratov research station. F1 plants produce seeds from which true-breeding, fairly fertile, phenotypically intermediate hybrids are derived.
1935 Germany Name "triticale"—from "Triticum" (wheat) and "Secale" (rye)—appears in scientific literature.
Sweden Arne Muntzing begins intensive work on triticale; discovers mechanism of spontaneous fertility in wheat x rye hybrids.
1937 France Pierre Givaudon develops colchicine technique for doubling chromosomes of sterile hybrids, making possible the routine production of fertile triticales.
1940's ? Development of embryo culture technique for growing hybrid embryos from seeds with malformed endosperm.
1954 Canada University of Manitoba, Canada, inaugurates first North American effort to develop triticale as a commercial crop. L.H. Shebeski, B.C. Jenkins, L. Evans, and others assemble world collection of primary triticales.
1964 Mexico The International Wheat Improvement Project of the Rockefeller Foundation makes informal agreement with the University of Manitoba to expand work on triticale.
1965 Canada Rockefeller Foundation makes 3-year grant to University of Manitoba for research on triticale in collaboration with the International Wheat Improvement Project.
1966 Mexico CIMMYT founded; cooperation with University of Manitoba continues.
1968 Mexico Armadillo strain, with almost complete fertility, one dwarfing gene, and superior plant type, appears spontaneously in CIMMYT plots at the Ciudad Obregon station. Becomes progenitor for triticales around the world.
1968-69 Hungary Two secondary hexaploids developed by Kiss in 1965 certified for commercial production and release.
Spain Hexaploid developed by Sanchez-Monge released for commercial production.
1970 Canada Rosner strain, developed at University of Manitoba and used by distillers since early 1960's, becomes first North American triticale released for general use.
1971 Mexico International Development Research Center and Canadian International Development Agency make US$2.5 million grant to CIMMYT-University of Manitoba program for 5-year research effort.
Mexico Debut of Cinnamon line, first two-gene dwarf, to counteract high rate of lodging in triticales.
1972 Mexico CIMMYT begins intensive selection and breeding for grain plumpness with high fertility. Also begins efforts to broaden triticale's genetic base.
1973 Mexico In CIMMYT winter yield tests at Ciudad Obregon and summer trials at Toluca, best triticales yield about as well as top wheat checks.
1974 Mexico Grain test weight of CIMMYT triticales averages 72 kilograms per hectoliter up from 68 kilograms per hectoliter in 1970.
150 of 600 triticate lines tested at CIMMYT yield 7000 kg/ha.
The five highest yielding triticales in trials at 47 world wide locations yielded 15 percent more than the best bread wheat check variety.