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Ricardo Rodríguez
Marco A. Quiñones L.
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Ignacio Narváez

CIMMYT

CENTRO INTERNACIONAL DE MEJORAMIENTO DE MAIZ Y TRIGO
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MEXICO

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londres 40, méxico 6, d. f., méxico.

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Ricardo Rodríguez[1]
Marco A. Quiñones L.[2]
Norman E. Borlaug[2]
Ignacio Narváez[3]

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[1] Ing. Agr., Cereals Department, National Institute for Agricultural Research, Mexico.

[2] Respectively, Biologist and PhD, Wheat Department, CIMMYT, Mexico.

[3] PhD, Cereals Department, National Institute for Agricultural Research, Mexico; at present commissioned to CIMMYT and assigned with Ford Foundation as Consultant on wheat improvement in West Pakistan.

THE PROBLEM

There is no general overproduction of wheat in the world today. However, since the termination of World War II a few countries, such as the U.S.A., Canada, Australia and Argentina, either temporarily or over a period of years, have been accumulating "surplus" stock. These "surpluses" frequently have been burdensome to the national economies of these countries. Simultaneously, a shortage of wheat exists in many countries of the world which traditionally use wheat as an important part of their diet. Countries such as China, India, Pakistan, U.S.S.R., Brazil, and many smaller countries, would like to purchase additional wheat, but are frequently, because of limitations in purchasing power, unable to import more than a portion of the quantity they need. In order to reduce the economic drain resulting from wheat purchases, many importing countries are currently making a serious effort to increase their domestic wheat production through the development of research and extension programs designed to modernize production methods. These decisions are made in order to keep their food deficit from becoming worse.

The world population will double within the next 35 years, assuming an overall population increase of 2 per cent per year. Many areas of the world that are most in need of food have populations that are increasing at the rate of more than 3 per cent per year. Such populations will double within 20 to 25 years. Where will the food come from to feed this exploding world population?

There are groups within countries temporarily plagued with "food surpluses" who would curtail agricultural research as a remedy for overproduction. Such action, if carried out, would in the long run be disastrous both to the nations involved and for the world in general. Anyone who looks toward the future food needs of the world, soon realizes that every effort must be made toward increasing knowledge and improving the materials and methods for increasing food production potential.

The cereal crops are unique in that they can simultaneously provide a large part of the caloric and protein requirements of the human diet. As the world population soars it will become necessary to substitute an increasing proportion of the world protein requirements now supplied by animal protein, from cereals. It will be necessary in the future to both improve the nutritional quality of cereal proteins and to expand their production.

The development of commercial hybrid wheat varieties is one way of increasing wheat production.

CYTOPLASMIC STERILITY AND POLLEN FERTILITY RESTORER GENES

Their utilization for the production of commercial hybrids of small grain plants

The development of commercial corn hybrids in the 1930s and their subsequent rapid, widespread acceptance by the American farmer revolutionized the production of corn in the U.S.A. It is estimated that U.S.

farmers currently plant 12,000,000 bushels of hybrid seed corn each year. Open-pollinated varieties of corn have now essentially disappeared from U.S. farms.

The development and widespread use of hybrid corn varieties, which utilize hybrid vigor, has directly contributed to raising corn yields by 20 to 25 per cent above those of the best open-pollinated varieties grown under the same conditions. Corn hybrids, moreover, indirectly have been potent catalysts in improving other cultural practices, *i.e.*, heavier and more widespread use of fertilizers, better control of weeds, more adequate and uniform plant populations, and more efficient mechanization, etc., each of which also has contributed to increasing yields and reducing costs per bushel.

Corn is a cross-pollinated plant, with the male (tassel) and female (ear) flower parts separated in different parts of the plant. Consequently it was not necessary to await the development of a male sterile (cytoplasmic sterile) and fertility restorer (pollen fertility restorer) system before large quantities of hybrid seed could be produced. Commercial hybrid corn seed was produced in enormous quantities in the U.S.A. for more than two decades by hand detasseling of the female line to prevent selfing, and simultaneously assure cross-pollination by pollen from the male line. Cytoplasmic sterility and the corresponding fertility restorer genes were discovered in corn in 1951. During the past decade its use has increased very rapidly, and currently about two-thirds of the total production of hybrid corn seed in the U.S.A. employs the use of a cytoplasmic male sterile and pollen fertility restorer system.

In order to appreciate the nature and magnitude of the problems and the techniques and methods needed to develop hybrid seed of normally self-pollinated crop plants such as wheat, rice, barley and sorghum, it is first necessary to understand the mechanism of normal seed production in these plants.

All four of the above cereals have small flowers that are borne in large numbers on spikes or panicles. Each individual flower contains both male and female parts enclosed within a set of protective glumes. The anthers in which the pollen is produced, and the ovary which, following fertilization, develops into the seed, are both present in each flower. The enclosure of the female and male flower parts within the same set of glumes results in nearly complete self-fertilization in such plants.

In order to produce a single hybrid wheat seed it is necessary to perform a series of delicate, exacting, properly-timed and tedious hand operations with a pair of small forceps. The first of these involves removal of the immature anthers (emasculation) from the flowers which are to be used as the female in making the cross. The second operation involves the transfer of pollen from mature anthers of the variety chosen as the male parent, to the receptive female flower part (stigma) of the previously emasculated flower of the variety to be used as the female parent. The individual seed which subsequently develops from such a complex and costly manipulation, when pollination and subsequent fertilization is successful, will develop into a single hybrid wheat plant when planted. It is obvious that such a technique cannot be used to produce commercial quantities of hybrid wheat seed.

Sorghum was the first self-pollinated field crop in which the use of cytoplasmic male sterility and pollen fertility restorer genes were employed to produce a commercial hybrid. This system of sterility and restoration of fertility was first discovered in 1950. The first commercial hybrids employing this technique were grown in 1955. Today nearly 100 per cent of the cultivated sorghum area of the U.S.A. is sown with hybrid seed. Essentially 100 per cent of the hybrid sorghum seed production depends upon the utilization of a system of genes controlling cytoplasmic sterility and their counterparts for the restoration of pollen fertility.

THE TOOLS WITH WHICH HYBRID WHEAT VARIETIES ARE BEING BUILT

Heterosis or hybrid vigor

Farmers throughout the world have obtained great benefits from the use of seed of improved pure line varieties of self-pollinated crop plants, such as wheat, rice barley, oats and soybeans.

There are no true hybrid wheat varieties grown on a commercial basis anywhere in the world today. The term "hybrid wheat" is frequently used incorrectly when referring to "pure line improved varieties," which have been developed by a process of repeated selections through several segregating generations following the hand hybridization or crossing technique referred to above. Through this procedure the desirable characteristics controlled by chromosomal genes present in the two different parents can be combined in a true breeding improved variety. Nevertheless, since such a variety is developed only after repeated reselection over six to eight generations following the hybridization, there is no possibility of utilizing hybrid vigor in such a variety. It is "hybrid" only in the sense that two distinct parental ancestors were used in its formation.

The success of true hybrid varieties depends upon the effective utilization of hybrid vigor (heterosis) to produce higher crop yields, than that present in either parent. Hybrid vigor is the stimulus in yield which results in the progeny grown from seed produced by crossing two varieties of unlike genetic makeup. Hybrid vigor is at its greatest level only in the first generation following the cross. Consequently it is not possible to regrow seed produced by the commercial hybrid crop, without greatly reducing yields, since hybrid vigor of any magnitude is restricted to the first generation following the cross.

Only recently has it become possible to utilize heterosis in the self-pollinated crop of sorghum for the production of hybrids. It appears that if the research now underway is successful, wheat may soon become the second self-pollinated field crop where hybrids will be used. The discoveries that made hybrid wheat a definite commercial possibility are explained below.

Cytoplasmic sterility and pollen fertility restoration

Dr. H. Kihara, a Japanese scientist, first reported cytoplasmic sterility in wheat in 1951, which was about the same time cytoplasmic sterility was reported in corn and sorghums. He found cytoplasmic sterile plants in the progeny obtained from crossing "goat grass," a wild relative of wheat, with a common bread variety, *i.e.* (♀ *Aegilops caudata* x ♂ *Triticum vulgare*). Dr. H. Fukasawa, also a Japanese scientist, in 1953 found cytoplasmic sterile plants in segregates from a cross of a different species of goat grass with durum wheat (♀ *Aegilops ovata* x ♂ *Triticum durum*).

In 1955 Fukasawa reported that he was able to restore pollen fertility to a cytoplasmic male sterile derivative containing the cytoplasm of *Aegilops ovata* by crossing it with a species of wild emmer (*Triticum dicoccoides*).

In 1958 Dr. Kihara reported he had developed both cytoplasmic male-sterile and pollen fertile lines from the cross ♀ *Triticum timopheevi* x ♂ *Triticum dicoccum* (emmer).

Although the scientific basis and principles for hybrid wheat development was laid by the aforementioned discoveries, there were too many adverse side effects in the plant materials used in the *Aegilops* studies to serve as a sound basis upon which to develop a commercial hybrid wheat. Nearly a decade passed without much research effort devoted to finding better tools for making a commercial hybrid. Kihara's report in 1958 based on *T. timopheevi,* however, brought the possibilities of finding the right tools a lot closer.

The right tools were finally found in late 1961. Drs. J. A. Wilson and W. M. Ross working at the Kansas Experiment Station at Fort Hays, isolated stable cytoplasmic bread wheat lines from a cross employing *Triticum timopheevi* as the female parent and employing the winter habit bread wheat variety Bison as the male, *i.e.* (♀ *Triticum timopheevi* x ♂ *Triticum vulgare* variety Bison). Sterile plants from this cross repeatedly used as the female parent were back crossed several times resulting in cytoplasmic male sterile Bison lines.

Eight months later Drs. J. W Schmidt, V. A. Johnson, and S. D. Maan working at the Nebraska Agricultural Experiment Station found that they could restore the fertility to the Bison cytoplasmic male sterile line developed at Kansas by crossing it with a *Triticum timopheevi* bread wheat derivative. Shortly after, Dr. Wilson confirmed similar results on restoration of pollen fertility.

Prior to 1962 only a few scientists were engaged in research on hybrid wheat. The discoveries in Kansas and Nebraska triggered off a lot of interest in research in this field. At the present time at least 15 states in the U.S.A. are actively engaged in research to produce commercial hybrids. Research on wheat hybrids is also being done in Canada by the University of Manitoba and the Canada Department of Agriculture. The Kansas and Nebraska Agricultural Experiment Stations have also distributed cytoplasmic male sterile and pollen fertility restorer stocks to scientists in many countries.

The Mexican hybrid wheat research program was begun in 1962. Within the past few years it has grown into a large, aggresive effort. At the present time about 20% of the overall wheat research effort is dedicated to the development of hybrids. A summary of the results of some aspects of this research is given below.

Considering the economic importance of the cytoplasmic-male sterility and pollen fertility restorer systems in the production of commercial hybrids of maize and sorghum, surprisingly little is known about its fundamental nature and mode of action. The best hypothesis that can be advanced to explain this system is presented in the following paragraphs.

The nature of the cytoplasmic male-sterility and restorer system in self-pollinated crop plants

Apparently the production of normal anthers and fertile pollen in wheat plants results from the harmony and balance that exists between specific chromosomal genes (the unit carriers of heredity that are arranged in linear order on the thread-like chromosomes in the nucleus), and between the little understood "non-chromosomal genes", located in the cytoplasm outside of the nucleus. When the genes in these two independent but interacting systems are in equilibrium and balance, anthers develop normally and fertile pollen is produced which results in normal seed production. Apparently in certain wheats there are "defective or mutant non-chromosomal genes" which inhibit normal anther and pollen production. If, however, the corresponding corrective dominant fertility restorer genes are present in the chromosomes of the nucleus, the adverse effect of the "defective non-chromosomal genes" is not expressed and the plant produces normal anthers and pollen. Amazingly, such "non-chromosomal genes" adversely affect only anther and pollen development; they have no adverse effect on the development of the female parts of the same flower (i.e. the stigma and ovary), and consequently when pollinated with fertile pollen they produce seed normally.

In recent years geneticists and plant breeders have developed ingenious techniques for throwing out of balance the equilibrium or harmony that exists between the defective cytoplasmic "non-chromosomal genes" and the corresponding corrective chromosomal genes. Through a system of crosses and backcrosses the two component parts of these two systems are separated. One component, the cytoplasm with its defective "non-chromosomal genes" is diverted and incorporated into the cytoplasmic male sterile line, which eventually will become the female parent in making the final hybrid. The second component, the dominant pollen fertility restorer chromosomal genes are transferred into a commercial variety which will become the male parent in making the cross to produce the hybrid seed.

When the cross is made to produce the hybrid seed, the two components of these two independent but interacting systems are brought back together and into harmony once again, thereby resulting in restoration of pollen fertility in the hybrid seed.

The procedures involved in the development of an experimental single cross hybrid wheat variety, *i. e.* ♀ Penjamo 62 x ♂ Crim, is diagrammed in Figure 1. The source of the cytoplasmic sterility which is used in this case is from *Triticum timopheevi*. This diagram shows the steps that are involved in developing and in selecting the genotypes affecting cytoplasmic male sterility and pollen fertility restoration, assuming that fertility restoration is conditioned by two dominant chromosomal genes.

RESEARCH

Description of the procedures used in developing a hypothetic hybrid

Triticum timopheevi is being used almost exclusively in the Mexican Program as a basis for developing cytoplasmic male sterile lines, and pollen fertility restoration lines.[1] This species apparently contains defective mutant "non-chromosomal genes" that adversely affect anther development and pollen fertility. *T. timopheevi* possess at least two dominant chromosomal genes which counteract the effect of the non-chromosomal gene (s) in its cytoplasm, resulting in normal pollen production and fertility. When *T. timopheevi* (a tetraploid with 14 pairs of chromosomes) is used as a female parent in a cross with a bread wheat variety (*T. vulgare*) such as Penjamo 62 (a hexaploid with 21 pairs of chromosomes) which does not possess the chromosomal genes for pollen fertility restoration, the F_1[2] plants will be highly sterile, because of both aneuploidy and cytoplasmic male sterility. When such F_1 plants are used as the female parents and back crossed to Penjamo 62 for several generations, or are self-pollinated, the aneuploids can be eliminated by selection. Within the F_2 of the single cross or back crosses, hexaploid, cytoplasmic male sterile plants will appear as well as a few completely fertile hexaploid plants. Most of the population will consist of plants with varying intermediate degrees of fertility.

Developing the female parent for the hybrid (The cytoplasmic male sterile line)

One of the cytoplasmic male sterile plants referred to above will be converted into a line which will be used as the female parent in the production of the hybrid seed. This is accomplished by planting the cytoplasmic male sterile plant (which produces little or no functional pollen) between several rows of the parent variety Penjamo 62^N [3] which has normal pollen but does not possess in its chromosomes the genes for "permanently" restoring the fertility to the cytoplasmic male sterile lines. Nevertheless, the airborne pollen from Penjamo 62^N fertilizes the ovaries of the cytoplasmic male sterile plant and thereby produces seed. When the resulting seed

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[1] Several different sources of *T. timopheevi* cytoplasmic sterility have been used in the Mexican program. These includes: 1) a sterile line received through the courtesy of The DeKalb Agricultural Association; 2) a sterile line received through the courtesy of the U. S. Department of Agriculture, and 3) cytoplasmic sterile lines developed directly from *T. timopheevi* by the Mexican scientists.

[2] F_1, F_2, F_3, etc., are symbols used to designate the first generation, etc., after each cross.

[3] Symbols used to indicate the fertility status of line or variety:

N = Normal pollen production but does not possess the chromosomal genes for restoration of pollen fertility to cytoplasmic sterile lines.

MS = Cytoplasmic male sterile line.

R = Line carrrying chromosomal genes capable of restoring pollen fertility to cytoplasmic male sterile line.

A cytoplasmic male sterile spike of Huamantla Rojo, showing tips of exerted stigmas.

Sexual organs of the flower of a wheat plant with normal fertility (above), and of a plant with cytoplasmic male sterility (below). Note especially the difference in shape and development of the anthers.

Anthers from plants with normal fertile pollen (top row) and deformed anthers from plants showing different degrees of cytoplasmic male (pollen) sterility (bottom 3 rows). The anthers in the bottom row are from plants that are completely male sterile.

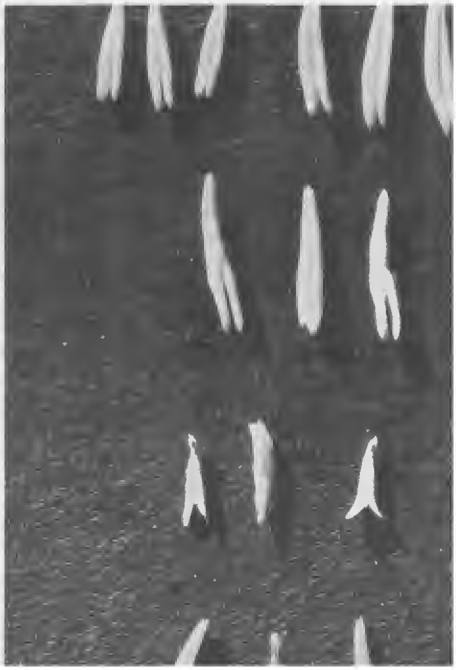
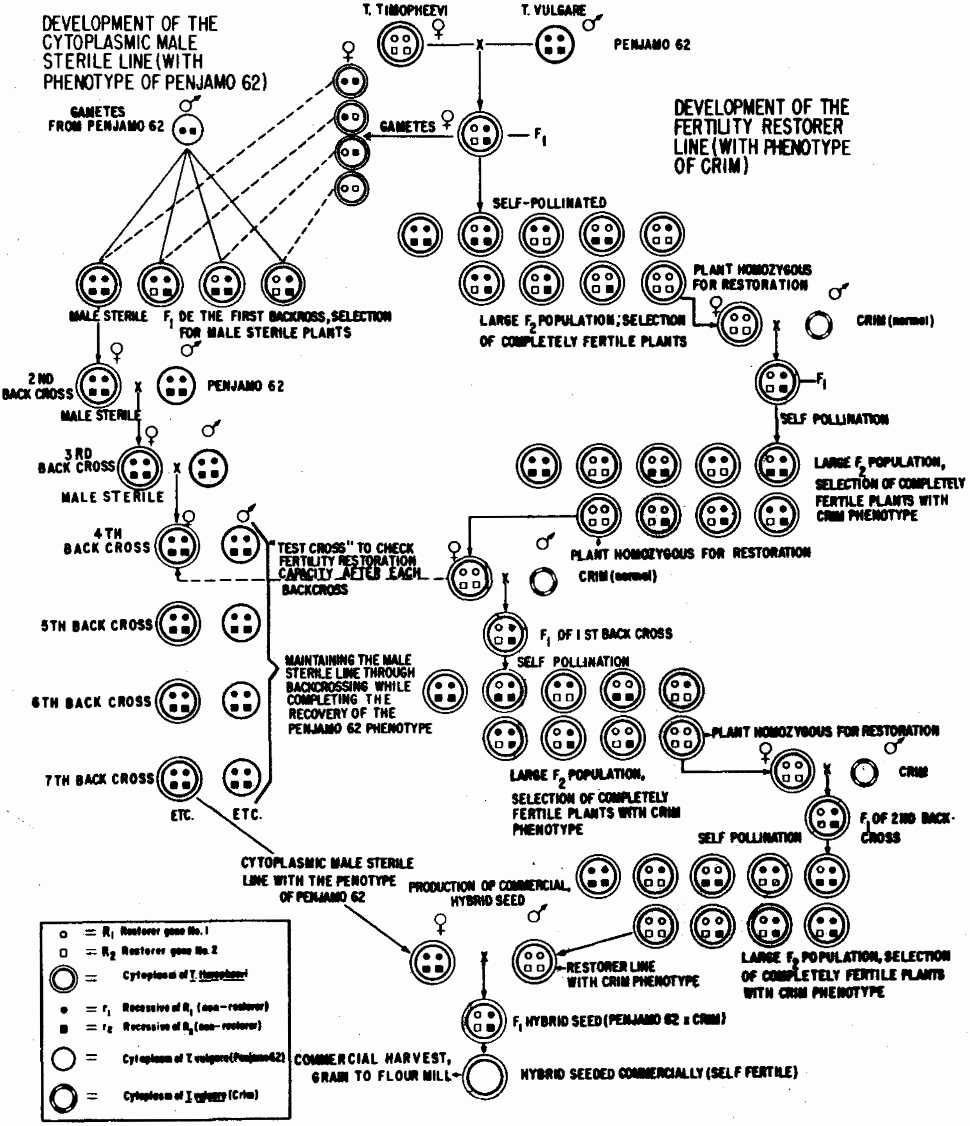


FIGURE 1.

DIAGRAM OF THE CYTOPLASMIC STERILITY—FERTILITY MECHANISM NECESSARY FOR THE DEVELOPMENT OF HYBRID WHEAT

(Example: Penjamo 62 x Crim, assuming two genes required for complete fertility restoration).



from this male sterile line is replanted, it again gives rise to plants which are all male sterile, but more like the Penjamo 62^N parent in agronomic characters, disease resistance, etc., (phenotype). By repeated replanting of the seed of the male sterile lines between rows of Penjamo 62^N sometimes referred to as the maintainer line, a male sterile Penjamo 62^{MS} line is eventually developed which is identical to Penjamo 62^N in all respects, except that it does not produce pollen. Such a line, designated Penjamo 62^{MS}, is now the potential female parent which can be used to produce a commercial hybrid.

Any number of other different male sterile lines can be developed for potential use in the formation of other hybrids by simply crossing other commercial varieties or improved lines individually into the cytoplasmic male sterile Penjamo 62^{MS} line and backcrossing[4] the resulting progeny to the maintainer variety under consideration. In each case the backcrossing is accomplished by replanting each generation of the male sterile line between several rows of the maintainer variety, which is being converted to the cytoplasmic male sterile parent for use in producing the hybrid.

Through such a procedure a large number of cytoplasmic male sterile lines can be produced. Each one will be identical to its recurrent (backcross) parent in all respects, except that it is pollen sterile instead of fertile. More than 100 cytoplasmic male sterile lines, of widely different backgrounds, are being developed for potential use in hybrids in the Mexican program.

Isolation, spacial separation or bagging to prevent cross pollination with other wheats, is necessary during the process of development and multiplication of the male sterile lines.

Developing the male parent for the hybrid (The fertility restorer line)

Dominant chromosomal genes capable of restoring pollen fertility to a cytoplasmic male sterile line, whose development and description was given above, must be incorporated into the commercial variety that is to be used as the male or pollen parent in making seed of the commercial hybrid. The development of the pollen fertility restorer line, *i.e.* $CRIM^R$ in the experimental hybrid under consideration, is more difficult to accomplish than is that of the development of the cytoplasmic male sterile variety, Penjamo 62^{MS} (Fig. 1).

In the latter case, after the cytoplasmic sterile plant has been identified in the F_2 population the process is essentially automatic. In order to maintain and simultaneously multiply the line it must be grown each generation between rows of the maintainer variety Penjamo 62^N. This process automatically results in recovering the phenotype of the maintainer line, *i.e.* Penjamo 62^N in the male sterile background designated Penjamo 62^{MS}.

However, in developing the pollen fertility restorer line or variety, it is necessary to begin to select the most fertile F_2 plants from the original cross (*i.e.* ♀ *Triticum timopheevi* x ♂ Penjamo 62) or in the progeny of the first backcross. The seed of such fertile plants must be replanted, and

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[4] Hand pollinations are frequently advisable in the first and second backcrosses because of the differences between lines in timing of floral development.

again in the segregates of the next generation the most fertile plants must be reselected. If sufficiently large populations are grown and if sufficient care is used in selecting the plants from a fertility standpoint, individual plants will be identified in the F_2, F_3 or F_4 generation which will have complete restoration of pollen fertility, despite possessing *T. timopheevi* cytoplasm. The next step is to cross such a plant which has complete restoration of pollen fertility, using it as the female parent, to the variety $CRIM^N$. Following the backcross, in each segregating generation only those plants are saved for replanting which have a high degree of fertility. The selection in each generation, moreover, should be made so as to select those plants which most closely approach the phenotype of the recurrent parent, CRIM, but which at the same time possess a high degree of fertility. Each time a plant is recovered which is true breeding for fertility, it should again be backcrossed to the recurrent parent, $CRIM^N$. This procedure of backcrossing and selecting repeatedly in segregating generations for complete fertility, is continued until true breeding lines are recovered for pollen fertility restoration in plant types or phenotypes, *i.e.* $CRIM^N$, that are identical to the recurrent parent, $CRIM^N$.

Test crosses must be made to a cytoplasmic male sterile line, using those plants that are thought to have complete pollen fertility restoration before proceeding to the next backcross. Only those plants that possess the capacity to completely restore fertility to the cytoplasmic male sterile parent in the test cross should be backcrossed again.

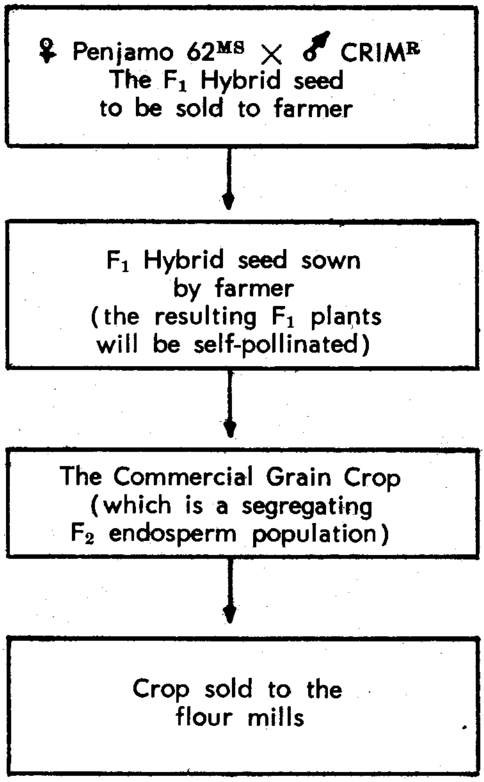
In a system of pollen fertility restoration that is as complex as is that of the *Triticum timopheevi* system where two, three or more genes are sometimes involved, depending upon the varieties under consideration, instead of the single dominant gene system that is available in corn and sorghum, the number of backcrosses should be kept to the absolute minimum which is necessary to recover the phenotype and combining ability of the recurrent parent. Each backcross increases the possibility of losing one of the genes necessary for restoration. In the Mexican program we attempt to recover lines with complete pollen fertility restoration and that are phenotypically similar to the recurrent parent in the single cross or first backcross. To accomplish this it is necessary to grow large F_2 segregating population and to exert strong selection pressure toward recovering fertile plants which most closely approach the phenotype of the recurrent parent in each segregating generation of each backcross. All fertile plants selected in each segregating generation are tested for their pollen fertility restoration capacity by crossing to a cytoplasmic sterile line.

Developing the final hybrid

In producing the seed for a single cross hybrid wheat variety, the cytoplasmic male sterile line, *i.e.* ♀ Penjamo 62^{MS} is crossed with the pollen fertility restorer line, *i.e.* $CRIM^R$ carrying the dominant polen fertility restorers in a true breeding (homozygous) condition. It is absolutely necessary to have all of the essential restorer genes in the homozygous condition in the restorer parent; otherwise in the farmer's commercial fields part of the F_1 hybrid plants will be sterile.

For the hypothetical hybrid we are considering. the manner in which the hybrid will be made is illustrated in Figure No. 2.

FIGURE 2. Making and Utilizing a Single Cross Wheat Hybrid.



Selecting fertile plants (potential restorers of pollen fertility) and sterile plants in a segregating population containing *T. timopheevi* cytoplasm. The selected fertile plants and sterile plants are again crossed to the recurrent parent to develop the male and female parents, respectively, and these will subsequently be used in the production of hybrids.

A cytoplasmic male-sterile line of Penjamo^{MS} *that has again been backcrossed to Penjamo 62*^{N} *by hand pollinations (white shoot bags) to maintain the cytoplasmic male sterile line. Other spikes of this same line (black shoot bags) have been used as the ♀ parent in a test cross, employing hand pollinations, to check the pollen fertility restoration capacity of a restorer line (CRIM*^{R}*).*

The hybrid seed must be produced under isolated conditions to insure pollination of the cytoplasmic sterile line with pollen produced by the restorer line. This will be accomplished under field conditions by planting alternate strips of the cytoplasmic male sterile line which is the female or seed-producing parent of the hybrid, and the pollen fertility restorer line which functions as the male or pollen parent in producing the hybrid. The date of planting of the restorer line CRIM^R must be timed so that it will flower at the same time as the cytoplasmic male sterile line. Only the seed produced on the cytoplasmic male sterile line (*i.e.* Penjamo 62^{MS}) will be harvested and sold as hybrid seed.

Studies on the manifestation of heterosis in wheat

There is no point in developing hybrid wheat varieties unless a high degree of hybrid vigor or heterosis can be effectively and economically utilized.

Briggle, in a survey of the literature in 1963, cites 23 scientists who have published data on heterosis in wheat. These studies in most cases were very limited in scope and application, and were largely of an academic nature. In many cases they relate to heterotic effects on plant height, maturity, tillering, seed size, and weight of the above ground plant parts. Only a few of them relate to heterosis in grain yields. Moreover, nearly all of the early studies were based on a few individual plants and frequently they related to experiments performed under greenhouse conditions. The few experiments done in the field were of a limited nature, based on single rows of F_1 plants with few or no replicates. The magnitude of heterosis that was reported ranged all the way from zero to more than 100 per cent increases over the yield of the parents.

With few exceptions, these early studies are meaningless as a basis for determining the feasibility of commercial hybrids. Frequently in the early studies two unimportant varieties were crossed and the progeny resulting from such crosses were studied for heterosis. The magnitude of increase in grain yield over that of the highest yielding parent entering the cross, therefore, has no relationship to the possible development of an acceptable commercial hybrid. Before large heterotic effects can be of economic significance they must be superimposed upon the yield base of the highest yielding commercial variety available in the region for which the hybrid is being developed.

Even though the early studies demonstrating heterosis were largely of an academic nature and of little practical value for orienting research designed to develop hybrids, they have been supplemented by the observations of wheat breeders who have observed many cases of heterosis while working in broad, aggressive breeding programs. In the past twenty years we have observed more than 26,000 F_1 populations in the Mexican wheat breeding program. We have noted outstanding cases of heterosis in many of these crosses but until two years ago when our hybrid research program was initiated we had made no effort to measure the heterotic effects quantitatively.

The combination of many interacting economic and technical factors will determine the ultimate economic feasibility of hybrid wheat. The most important consideration is whether the increase in yield due to heterosis will be sufficiently great to offset the higher costs of hybrid wheat seed. The costs of producing hybrid wheat seed will likely be high.

There are many other scientific and technical problems such as the incorporation into the hybrid of acceptable milling and baking quality, a high level of disease resistance and desirable agronomic type which also must be achieved before hybrids will become realities. The latter are all attainable through research if the aforementioned problem of the relative benefits from heterosis and hybrid seed costs can be brought into favorable economic balance.

Distribution and magnitude of heterosis in wheat

During the past two years 51 F_1 generation experimental wheat hybrids have been made and evaluated in the Mexican program for grain yield, straw yield, maturity, height, for resistance to lodging, shattering and disease, and for milling and baking quality. All of the F_1 hybrid seed was made by hand pollination. The yield tests were all conducted under irrigation at the Centro de Investigaciones Agrícolas del Noroeste (CIANO) at Ciudad Obregón, Sonora, Mexico. The land prior to planting was fertilized with 140 kilos of nitrogen per hectare. Four irrigations were applied.

During 1963-64 the 25 experimental F_1 hybrids, their parent varieties and commercial check varieties, were included in yield tests. They were sown in an experiment using a lattice design with four replicates. The individual plots of F_1 hybrids, parents and check varieties consisted of 100 F_1 seed sown in a 5 meter row with a spacing between plants within the row of 5 centimeters. The distance between all rows in the experiment was 30 centimeters. This seeding rate is the equivalent of about 18 kilos per hectare. A border or guard row was sown using the semi-dwarf commercial variety Pitic 62 on either side of the F_1 hybrid, parent, and check variety rows, employing the same spacing as used in the F_1 hybrid, parent and check variety rows. A ½-meter row of space planted Pitic 62 was also sown at ends of each plot to reduce border effect. The planting was made on November 25, 1963, and harvested between April 25 and May 10, 1964, depending upon the maturity of each hybrid or variety.

The experimental hybrids evaluated during 1963-64 were crosses between different varieties and lines within the Mexican breeding program. It was felt that if we found usable levels of heterosis between wheats within the Mexican program, it would be possible to find high levels of heterosis with greater frequency when crosses are made between wheats of different countries.

During 1963-64, 23 of the 25 hybrids studied produced grain yields which significantly outyielded the highest yielding check variety, Huamantla Rojo, which yielded 5883 kilos per hectare. Huamantla Rojo produced much higher grain yields in these experiments than is obtained under farm conditions where it never yields more than 4500 kilos per hectare, because of its susceptibility to lodging. In these experiments the guard or border rows of the semi-dwarf variety Pitic 62 supported Huamantla Rojo and prevented it from lodging.

The highest yielding hybrids, Huamantla Rojo x Lerma Rojo 64, and Huamantla Rojo x Sonora 63, yielded 7576 kilos per hectare. Five of the experimental hybrids outyielded Huamantla Rojo by 1500 kilos or more per hectare, whereas 12 of the hybrids surpassed Huamantla Rojo by 1000 kilos or more per hectare.

The degree of heterosis, expressed in the percentage of yield of the highest yielding parent entering the hybrid, varied from 109 to 146 per cent. Of the hybrids studied, 17 yielded more than 120 per cent, six yielded more than 130 per cent and three yielded more than 135 per cent more than the highest yielding parent entering the cross.

The yield and calculated heterosis of seven of these hybrids is presented in Table 1.

There were no adverse effects from diseases, lodging nor shattering during 1963-64.

The heterosis studies during 1964-65 included two yield tests totaling 20 F_1 hybrids. These hybrids generally involved a cross between a Mexican variety and either a Canadian, U.S.A. or Argentine variety. The hybrids,

TABLE 1. The Yield Performance of Seven Experimental Hybrids Selected to Represent the Range of Heterosis Encountered in Two Experiments Involving Twenty-five Experimental Wheat Hybrids Grown at CIANO, Ciudad Obregon, Sonora, during 1963-64.

	Grain Yield in kilos per hectare			(1)	(2)
HYBRID	**F_1 hybrid**	**♀**	**♂**	**%**	**%**
Experiment 1-H					
♀ ♂					
Yaqui 54 × P 4160	6563.3	4212.6	4467.3	46.9	11.5
Huamantla Rojo × Lerma Rojo 64	7576.0	5882.6	5878.0	28.7	28.7
Huamantla Rojo × Sonora 63	7574.6	5882.6	5172.0	28.7	28.7
Yaqui 54A × Sonora 64	5443.3	4212.6	4541.3	19.9	— 2.5
(3) Huamantla Rojo = 5882.6 kgs/ha.					
LSD 5% = 441.20 kgs/ha.					
LSD 1% = 588.33 kgs/ha.					
Experiment 2-H					
♀ ♂					
Nainari 60 × Lerma Rojo 64	6800.7	4728.1	4873.3	39.5	38.4
Nainári 60 × Nadadores 63	6632.5	4728.1	4855.5	36.5	35.1
Lerma Rojo × Sonora 63	6253.3	4766.6	4594.8	31.1	27.3
(3) Huamantla Rojo = 4911.8 kgs/ha.					
LSD 5% = 482.66 kgs/ha.					
LSD 1% = 643.55 kgs/ha.					

(1) % that F_1 hybrid outyields the highest yielding parent entering the cross.
(2) %that F_1 hybrid outyields the highest yielding check variety in the experiment.
(3) Highest yielding variety in the test.

parents and check varieties were planted in a randomized block design with eight replicates. Rows were 2½ meters long with 50 seeds sown per row with a spacing between rows of 30 centimeters (18 kilos/hectare). Eight replicates were used in all cases. The double dwarf wheat variety Sonora 64 was seeded in the border or guard rows, employing the same spacing. These experiments were sown on December 2, 1964 and the hybrids, parents, and check varieties were harvested as they ripened, covering the period between April 20 and May 15, 1965.

A very serious epidemic of leaf rust developed during mid-March, especially on Sonora 64 and its hybrids, as well as on the varieties Sonora 63, Lerma Rojo 64A, Lerma Rojo and 8156, which undoubtedly adversely affected yield on these materials.

Among the 20 F_1 hybrids studied in the two yield tests, 13 of them produced more grain than the highest yielding check variety, Huamantla Rojo, which yielded 5747 and 6233 kilos per hectare in yield experiments 1 and 2 respectively. In experiment 1 the highest yielding hybrid, Penjamo 62 x CRIM, yielded 7313 kilos per hectare, or 1567 kilos per hectare (27 per cent) more than Huamantla Rojo. Five of the hybrids outyielded the check variety by more than 1000 kilos per hectare and eight of the hybrids outyielded it by more than 500 kilos. The degree of heterosis or increase in grain yield expressed in percentage of the highest yielding parent entering the hybrid ranged from 107 to 138 per cent.

In the second experiment the highest yielding hybrid was Pitic 62 x Canadian line CT 244. It yielded 8017 kilos per hectare compared to a yield of 6233 kilos for Huamantla Rojo, the highest yielding check variety. Only four of a total of nine hybrids in this experiment outyielded Huamantla Rojo. All of the hybrids yielding less than the check variety Huamantla Rojo had Sonora 64, which is very susceptible to leaf rust, in their pedigree, and were apparently seriously damaged by this rust.

The yield and calculated heterosis of six of these hybrids is presented in Table 2.

Studies of heterosis in advanced generation of hybrids

The price of F_1 hybrid seed will be high. If farmers could replant the seed harvested from the F_1 hybrid without sacrificing too much in hybrid vigor, this practice would greatly enhance the economic possibilities of commercial hybrids. Experiments have been made during the past year in Mexico to explore this possibility.

During 1964-65, the yielding ability of the F_1, F_2 and F_3 generations of six different hybrids were studied at CIANO. In these experiments the three generations were space planted in 5 meter rows with a distance of 5 centimeters between plants in the row and 30 centimeters between rows (18 kg/ha.). The guard or border rows of Sonora 64 were space planted in the same way.

TABLE 2. The Yield Performance of Six of the Best Experimental Hybrids Selected to Represent the Range of Heterosis Encountered in Two Experiments Involving Twenty Experimental Wheat Hybrids Grown at CIANO, Ciudad Obregon, Sonora, Mexico, in 1964-65.

HYBRIDS	Grain Yield in Kilos/hectare F_1 hybrid	♀	♂	(1) %	(2) %
Experiment No. 1					
♀ ♂					
Lerma Rojo 64A × Selkirk	7033.3	5080.0	2586.6	38.4	22.4
Penjamo 62 × Crim	7313.3	4986.6	5293.3	38.2	27.3
Buck Bolivar × Pitic 62	7013.3	4720.0	5093.3	37.7	22.0
(3) Huamantla Rojo 5746 kgs/ha.					
		LSD 5% = 548.9 kgs/ha.			
		LSD 1% = 724.2 kgs/ha.			
Experiment No. 2					
♀ ♂					
Pitic 62 × CT 244	8017.3	5366.7	5166.7	49.4	28.6
Pitic 62 × Crim	7186.6	5366.7	5313.3	33.9	15.3
Pitic 62 × Pembina	6273.3	5366.7	3026.7	16.9	— 0.6
(3) Huamantla Rojo 6233.3 kgs/ha.					
		LSD 5% = 472.8 kgs/ha.			
		LSD 1% = 624.0 kgs/ha.			

(1) % that F_1 hybrid outyields the highest yielding parent entering the cross.
(2) % that F_1 hybrid outyields the highest yielding variety in the experiment.
(3) Highest yielding variety in the experiment.

The yield of the F_2 generation dropped from 18 to 22 per cent below that of the F_1 hybrid. Further loss, though of less magnitude, generally occurred in the F_3 generation. These data are presented in detail in Table 3.

Apparently much of the yield depression is the result of reduction in capacity to tiller, with a secondary adverse effect attributable to the reduction of fertility in the third and fourth florets in many of the spikelets.

TABLE 3. Comparative Grain Yields of the F_1, F_2, F_3 Generations of Six Hybrids Grown at CIANO. Ciudad Obregon, Sonora, Mexico, during 1964-65.

HYBRID	Grain Yield in Kilos/hectare Generations F_1	F_2	F_3
Huamantla Rojo × Nadadores	7085.3	5710.4	4326.2
Huamantla Rojo × Lerma Rojo 64	7095.7	5590.1	5281.3
Huamantla Rojo × Andes (E)	6560.5	5198.9	4506.1
Huamantla Rojo × Sonora 64	5835.1	4973.7	5133.1
Huamantla Rojo × P4160	6838.7	5303.0	4256.7
Yaqui 54A × P4160	5792.4	4042.6	4655.9

LSD 5% = 593.20 kgs/ha.
LSD 1% = 799.80 kgs/ha.

Hybrid between tall varieties and dwarf varieties —carrying the recessive Norin genes— grow nearly as tall as the tall parent. Lodging therefore again becomes a problem. Observe the difference in height of the tall hybrids and the dwarf variety Sonora 64.

General view of hybrid wheat yield nursery. Many experimental hybrids produced by hand pollination are compared for yield to identify combinations with maximum heterosis.

There are also many other disadvantages, in addition to loss in yield, that would be encountered in attempting to grow advanced generations of such hybrids. These include wide segregation in plant maturity and height, in resistance to diseases, in grain texture, and in milling and baking quality.

After studying 45 F_1 experimental hybrids during the past two years at a very low rate of seeding, it becomes apparent that heterotic responses of from 15 to 30 per cent are quite common in wheat. Some hybrids have shown less, whereas a few have shown more than 40 per cent increase above that of the highest yielding parent. In all probability the magnitude of heterosis that can be found in wheat is similar to that which currently is being utilized in corn and sorghum for the production of commercial hybrids. After two years of research, we are convinced that the magnitude of heterosis encountered in wheat is sufficient to make the production of hybrids feasible if hybrid seed production problems can be solved. The utilization of advanced generations of F_1 hybrids to reduce seed costs does not appear promising on the basis of our information.

Our yield experiments involving experimental hybrids have all been made at a low rate of seeding (18 kilos per hectare) because of the costs involved in producing hand pollinated hybrid seed. It is highly possible that higher yields would have been obtained with some of these same hybrids if higher rates of seeding had been used.

INDUSTRIAL QUALITY CONSIDERATIONS IN HYBRID WHEAT DEVELOPMENT

Industrial quality considerations were of no importance in the development of hybrid corn and sorghum, since both of these cereals are used primarily as feed grains. The situation will be entirely different in the development of hybrid wheat since this cereal is used almost entirely for human food. The milling and baking industries, which depend upon wheat as their raw material, are complex businesses. Large expenditures are made in quality control research each year in order to produce uniform flours and bakery products which will satisfy industrial and consumer demands. Within the past three decades in most wheat exporting countries it has become standard policy to evaluate the milling and baking quality characteristics of all new experimental wheats in cooperative tests in governmental and industrial laboratories. Only those experimental wheats which meet the requirements of industry, as well as the farmer, are multiplied and released for production.

Can hybrid wheats be produced which will meet these quality requirements? In a recent article Wilson and Villegas have shown that the cytoplasm of *Triticum timopheevi* does not adversely affect several of the grain and dough handling characteristics which they studied in male sterile lines, in restorer lines and in experimental hybrids. In all probability, therefore, there should be no unsurmountable quality problems in hybrid wheat development if the breeding programs are properly organized to take into consideration the quality aspects.

All grain harvested from a pure line wheat variety is identical, from a genetic standpoint. This will not be the case with the commercial grain harvested from an F_1 hybrid wheat variety. Such grain will be a segregating F_2 endosperm population. Consequently, there could be considerable variability in both physical and chemical properties between different kernels of such a population. The milling, dough handling, and baking characteristics manifested by such grain will therefore be the average value for this heterogeneous population. Variability in the endosperm population from a quality standpoint can be minimized by employing parents of similar quality characteristics in making a hybrid.

During the past two years the 45 F_1 hybrids and six advanced generation hybrids that were evaluated for heterosis in the Mexican program were also evaluated for quality.

These tests included determinations of grain weights, texture, and protein content of the grain of experimental hybrids, parents and check varieties, produced under the same conditions. Gluten strength was determined by employing the Micro Pelshenke whole meal fermentation test, and the sedimentation test. Physical dough properties were evaluated using the Mixograph and Alveograph. All grain samples were ground on the Buhler Mill after proper tempering. The bake test employed was the standard U.S.D.A. test, employing the pup-loaf. All flour samples were baked with optimum bromation.

The quality characteristics of eight of the most promising experimental F_1 hybrids are compared with their parents and with a control sample of Gold Medal (Full Strength) Flour in Table No. 4[5].

The results of the studies of a number of quality characteristics of the hybrids can be summarized as follows:

1. Grain Characteristics

a) *Test Weight*: All of the experimental hybrids produced grain of high test weight. In the past, in pure line breeding it has been impossible to recover high-yielding lines with high grain test weight from certain varieties such as Pitic 62 and Gabo. In a number of promising experimental hybrids in which Pitic 62 was involved as one of the parents, the grain produced by the F_1 hybrid plants was of high test weight. The use of F_1 hybrids in this specific case provides a means of overcoming the undesirable linkage which exists between the low grain test weight and high yield of Pitic 62.

b) *Grain Texture*: In hybrids developed from a cross between two lines of different textures, the grain from the F_1 hybrid plants is intermediate in texture between that of the two parents. The grains in an F_2 endosperm population of a hybrid developed from crossing a very soft and a hard-textured variety, will vary greatly in texture. It will be difficult to properly temper or condition such grain for milling. Improper tempering will reflect in low flour yields and generally poor milling performance.

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[5] Quality evaluations were made by F. C. Chacón, A. A. Amaya and Miss E. Villegas.

Several of the most promising experimental hybrids indicated in Table 4 have shown deficiencies in milling which are probably due to difficulty in properly tempering an endosperm population of such widely different texture.

2. Gluten Strength

a) *The Pelshenke Value*: The Pelshenke value, which is a crude measure of gluten strength, of a hybrid developed by crossing a parent with weak gluten and one with strong gluten is generally closer to that of the weak parent. The Pelshenke value in the hybrids studied was more variable than was the sedimentation value.

b) *Sedimentation Value*: The sedimentation value for hybrids developed from crosses involving a weak gluten parent and a strong gluten parent were intermediate between the two parents with only one exception.

3. Dough Handling Properties

a) *Mixograms*: The mixogram score of hybrids developed by crossing a strong (gluten) wheat and a weak (gluten) wheat was intermediate between that of the two parents, with a tendency to be somewhat closer to the strong parent. The mixing time of the hybrid is also intermediate between that of the two parents.

b) *Alveogram*: The "W" value of the alveogram, which is an overall measure of gluten strength, in hybrids is intermediate between that of the strong and weak parent.

4. Baking Characteristics of Hybrids

a) *Loaf Volume*: When the doughs from the hybrids were baked with optimum bromation the loaf volumes obtained followed the expected values based on the sedimentation value, alveogram, and mixogram scores. Some of the experimental hybrids produced larger loaves, with better texture and color than either of the parents. Among this group were the following hybrids:

1. Lerma Rojo 64 X Selkirk.
2. Sonora 64 X Crim.
3. Buck Bolivar X Crim.

Some wheats of inferior baking quality produced hybrids with baking quality that was as good as or better than the good quality parent. This group includes the following parents and hybrids.

1. Pitic 62 (Poor baking quality) X Crim.
2. Pitic 62 (Poor baking quality) X CT 244.
3. Penjamo 62 (Poor baking quality) X Buck Bolivar.
4. Penjamo 62 (Poor baking quality) X Crim.

5. Milling Characteristics of Hybrids

A considerable number of the experimental hybrids were inferior to either of the parents in milling characteristics. This was probably due to improper tempering, resulting from the wide differences in texture in different kernels in the F_2 endosperm population. These difficulties can probably be avoided if parents with similar grain texture are used in making the hybrids.

TABLE 4. **The Grain, Milling and Baking Characteristics of Eight Experimental Hybrids and Their Parents Produced Under Irrigation at Ciudad Obregon, Sonora, Mexico, during the 1964-65 Crop Cycle.**

HYBRID OR PARENT VARIETY	Yield of Grain in kgs/ha.	Grain Test Weight kgs/hectoliter	Grain Texture Pearling[1] Index	Grain Pelshenke Value[2] in Minutes	Milling Behavior	Flour Protein %	Sedimentation Value	Mixogram
LERMA ROJO 64A × SELKIRK	7033	81.9	41.5	36	Fair	10.9	32	5
LERMA ROJO 64A	5080	83.7	50.5	37	Fair	10.9	22	2
SELKIRK	2587	75.3	22.5	63	Excellent	10.7	44	7
PENJAMO 62 × CRIM	7313	82.2	30.0	38	Poor	10.8	35	4
PENJAMO 62	4987	82.7	33.0	32	Poor	9.6	20	1
CRIM	5293	81.3	23.0	140	Excellent	11.6	56	8
PENJAMO 62 × BUCK BOLIVAR	6760	83.5	29.0	44	Fair	10.2	32	7
BUCK BOLIVAR	4720	83.2	28.0	150	Good	12.3	55	7
BUCK BOLIVAR × CRIM	5713	82.5	26.0	105	Good	12.9	56	7
BUCK BOLIVAR × PITIC 62	7013	83.1	30.5	43	Fair	10.4	34	7
PITIC 62	5093	81.0	30.5	33	Poor	8.6	19	2
PITIC 62 × CT-244	8017	81.9	30.0	41	Poor	10.1	—	6
CT-244	5167	80.2	22.5	159	Very good	12.2	48	7
PITIC 62 × CRIM	7187	81.5	29.5	46	Poor	10.9	38	5
SONORA 64 × CRIM	5833	82.1	25.0	100	Excellent	10.3	55	8
SONORA 64	3693	80.3	26.0	100	Excellent	11.0	54	8
GOLD MEDAL FULL STRENGTH FLOUR	—	—	—	—	—	12.2	49	7

TABLE 4. (Cont.)

HYBRID OR PARENT VARIETY	Mixing Time Minutes and Seconds	Water Absorption	P/G[3] Value	W[4] Value	BAKING PERFORMANCE				
					Loaf Volume	Internal Loaf			General Baking
						Score	Texture	Color	
LERMA ROJO 64A × SELKIRK	2:10	65	2.9	229	955	100	Excellent	95 cream —	Excellent
LERMA ROJO 64A	1:10	65	2.6	147	725	70	Fair	90 yellow	Fair
SELKIRK	2:40	63	5.0	268	865	90	Good	90 cream	Very good
PENJAMO 62 × CRIM	2:00	67	4.7	323	835	95	Very good	95 cream	Very good
PENJAMO 62	1:10	60	6.0	145	700	95	Very good	95 cream +	Poor
CRIM	4:00	67	6.8	600	765	100	Excellent	95 cream +	Excellent
PENJAMO 62 × BUCK BOLIVAR	2:20	64	9.2	318	875	100	Excellent	95 cream +	Excellent
BUCK BOLIVAR	3:20	64	9.4	358	1020	100	Excellent	95 cream +	Excellent
BUCK BOLIVAR × CRIM	3:10	64	6.7	441	1025	100	Excellent	95 cream +	Excellent
BUCK BOLIVAR × PITIC 62	2:20	64	8.5	295	870	95	Very good	95 cream +	Very good
PITIC 62	1:40	63	5.5	155	725	85	Good	70 yellow	Poor
PITIC 62 × CT-244	2:20	63	7.0	341	910	100	Excellent	100 cream	Excellent
CT-244	4:00	71	8.5	467	950	100	Excellent	95 cream +	Excellent
PITIC 62 × CRIM	2:10	66	6.2	303	910	100	Excellent	95 cream	Excellent
SONORA 64 × CRIM	5:10	60	8.3	493	810	100	Excellent	100 cream	Excellent
SONORA 64	4:50	63	4.7	531	855	100	Excellent	95 cream +	Excellent
GOLD MEDAL FULL STRENGTH FLOUR	—	—	5.8	288	1055	100	Excellent	100 cream	Excellent

[1] Hard textured wheats have lower pearling indexes than soft wheats.

[2] Wheats with strong gluten generally have Pelshenke (doughball fermentation) value of 100 minutes or more.

[3] Measure of tenacity of dough.

[4] Measure of overall strength of gluten. Wheats with W values of 400 and above are considered strong varieties suitable for "carriers" for weaker wheats.

AGRONOMIC CONSIDERATIONS

Dwarfness and lodging resistance in hybrids

The development and distribution of high-yielding semi-dwarf and double-dwarf Mexican wheat varieties (*i.e.* Pitic 62, Penjamo 62, Sonora 63, Nadadores 63, Lerma Rojo 64, Mayo 64 and Sonora 64) greatly reduced lodging, while simultaneously permitting heavier fertilization, thereby resulting in phenomenal increases in grain yields. The use of semi-dwarf and dwarf varieties has been directly responsible for increasing the national average of grain yield in Mexico by 1000 kilos per hectare during the past three years. The impact of these varieties has been so great that they have taken over more than 95 per cent of the area cultivated to wheat in Mexico in four years' time. The sources of dwarfness in all of these varieties are the "Norin genes", whose action is inherited as recessives.

During the past two years all of the highest yielding F_1 experimental hybrids have been the result of crosses between Mexican dwarf varieties and conventional tall-strawed varieties. The F_1 plants in all such cases are nearly as tall as the tall parent. Such tall hybrids will lodge badly when grown under commercial conditions, and because of this defect would not be acceptable to Mexican farmers, who are now thoroughly convinced of the benefits of dwarf varieties.

The data presented in Table No. 5, which includes some of the most promising hybrids from both a yield and milling and baking quality standpoint, indicates clearly the nearly complete dominance of tallness over dwarfness in hybrids. Only when dwarfness is introduced through both parents, as in the case of the hybrids Lerma Rojo 64A × Sonora 64, it is expressed in the hybrid.

TABLE 5. Comparison of the Plant Height of Eleven F_1 Hybrids and Their Parents in Experiments Grown at CIANO, Ciudad Obregon, Sonora, Mexico, in 1963-64, 1964-65.

	Hybrid	Height in Centimeters Hybrid F_1	Parent ♀	Parent ♂
1963-64	♀ Yaqui 54A × ♂ P4160	115.0	113.7	94.6
	Huamantla Rojo × Lerma Rojo 64 (E_1)	126.5	132.5	110.0
	Huamantla Rojo × Sonora 63 (E_1)	117.5	132.5	101.3
	Yaqui 54A × Lerma Rojo 64 (E_1)	123.9	113.7	110.0
	Yaqui 54A × Sonora 64 (E_2)	99.9	113.7	87.6
1964-65	Lerma Rojo 64A (E_1) × Selkirk	120.0	95.0	131.3
	Penjamo 62 (E_1) × Crim	119.0	90.0	125.0
	Buck Bolivar × Pitic 62 (E_1)	111.3	122.5	102.5
	Pitic 62 (E_1) × CT 244	120.0	97.5	128.8
	Pitic 62 (E_1) × Crim	120.0	97.5	131.3
	Pitic 62 (E_1) × Pembina	118.8	97.5	137.5
	Lerma Rojo 64A (E_1) × Sonora 64 (E_2)	85.0	95.0	77.5

(E_1) = Semi-dwarf.
(E_2) = Dwarf.

If the Norin genes are to be used to produce dwarf hybrid varieties, it will be necessary to introduce dwarfness into the hybrid through both parents. This will restrict the Mexican hybrid program for the near future to using as parents the dwarf varieties within the Mexican program, since there are no other countries which currently have commercial dwarf spring wheat varieties. This limitation will prevent the direct use of tall-strawed Canadian, U.S.A. and Argentine varieties in the formation of hybrids. Tall-strawed varieties from these three countries must first be converted to dwarf varieties by incorporating the "Norin genes" into them through a backcross program, if they are to be used as parents in hybrids for the Mexican program. Such a procedure will be both time-consuming and expensive.

Resistance to shattering

The Mexican wheat crop is harvested by direct combining under conditions of high temperature and low humidity. Consequently, all commercial Mexican varieties are resistant to shattering. Several of the most extensively grown North American spring wheat varieties, such as the U.S. varieties Justin and Crim, and the Canadian variety Selkirk, shatter badly when grown under Mexican conditions. This weakness is, however, of no consequence when these varieties are grown in their native habitats where most of the harvest is done by swathing followed by combining.

Several of the most promising experimental hybrids that were studied during the 1964-65 season were crosses between Mexican varieties and Crim, Justin and Selkirk. All of these hybrids shattered badly under Sonora conditions. This defect indicates another problem that must be dealt with in developing commercial hybrid wheats. Fortunately, a number of other hybrids which also showed considerable promise did not have this weakness.

Breadth of adaptation of hybrids

Wheat varieties vary widely in their breadth of adaptation. Certain varieties, such as Lerma Rojo, Lerma Rojo 64, Nainari, Penjamo 62, Pitic 62, Sonora 64, Nariño and Bonza which were developed by the Mexican and Colombian breeding programs are insensitive to photoperiodism, are early maturing and yield well over a wide range of latitudes. Some of these varieties yield equally well at the equator, or at 50° N, or 36° S latitudes, and from near sea level up to 10,000 feet elevation, unless adversely affected by disease. There are other highly successful spring wheat varieties such as Selkirk, Thatcher, Justin and Crim, that are extremely sensitive to changes in day length and cannot be successfully grown at latitudes of less than 38°.

It would be highly advantageous to a company engaged in hybrid wheat research to be able to develop hybrids with a high yielding capacity over a wide range of conditions and throughout a large geographic region. This would cut research costs and simplify seed production and distribution.

When Sonora 64 and Selkirk are sown at Winnipeg, Canada (50° N), the former variety is only two days earlier in maturity than Selkirk. However, when they are sown in October at Ciudad Obregón, Sonora, Mexico (28° N), the variety Sonora 64 is 65 days earlier than Selkirk.

It has recently been demonstrated by Jenkins and Borlaug[6] that a single dominant gene controls the insensitivity to length of day response and adaptation of Sonora 64. The F_1 hybrid produced by crossing Sonora 64 with Selkirk is well adapted and high yielding, and only one day later in maturity than the Sonora parent when planted either at 28° latitude in Mexico, or at 50° latitude in Winnipeg.

The rust resistance in hybrid wheats and the eventual possibility of development of multilineal hybrids

Three different commercially important species of rusts, each one made up of hundreds of different physiologic races, attack wheat. All are obligate parasites. The specificity of the pathogenecity of these organisms is extremely great. Certain races, stem rust, for example, tend to predominate throughout a large geographic area on certain wheat varieties which are congenial hosts for these particular races. The race population within a given geographic area over a period of years will be made up largely of races capable of attacking the extensively grown wheat varieties of that region. When a variety of wheat with a new type of rust resistance is distributed and becomes widely grown in the region, it will remain free from rust attack for a number of years, but sooner or later a new race of the rust will evolve, either through hybridization on its alternate host or through mutation, which will be capable of attacking this new variety.

Wheat is a self-pollinated crop and all individual plants in a conventional pure-line variety of wheat are identical genetically for rust resistance. When a new race of rust appears, which is capable of attacking a previously resistant variety, it will spread like wildfire in such a population, and if ecological conditions are favorable it will cause devastating epidemic which may bring economic ruin to a large geographic area. Equilibrium between host and parasite and security of harvest cannot be re-established in that region until a new variety is released which is resistant to the new physiologic race, as well as to all other rust races which are prevalent in the region. The variability in the genus *Triticum* is so great that there has been no difficulty in locating sources of resistance to any given race and developing a variety resistant to it; however, the bigger and more difficult problem is maintaining the desired level of resistance in a variety against all prevalent rust races throughout a geographic area over a long period of time.

In most temperate zones of the world the life expectancy of a commercial wheat variety is limited from 12 to 15 years because of the appearance of new races of the rust pathogen. In the temperate areas of the tropics or semi-tropics, which do not have the benefits of low winter temperatures, the life expectancy of a wheat variety is about five years before it is destroyed by a new race of rust. Ways and methods must be found to introduce both more diverse and more lasting rust resistance into future wheat varieties.

Maize, in contrast to wheat, is an open-pollinated crop plant. In the tropics and semi-tropics, where ecological conditions are favorable for the

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[6] Unpublished data.

FIGURE 3. The Relative Importance of Variability in Commercial Varieties of Cross-Pollinated and Self-Pollinated Crops for Control of Epidemic Airborne Diseases in Temperate and Tropical Zones.

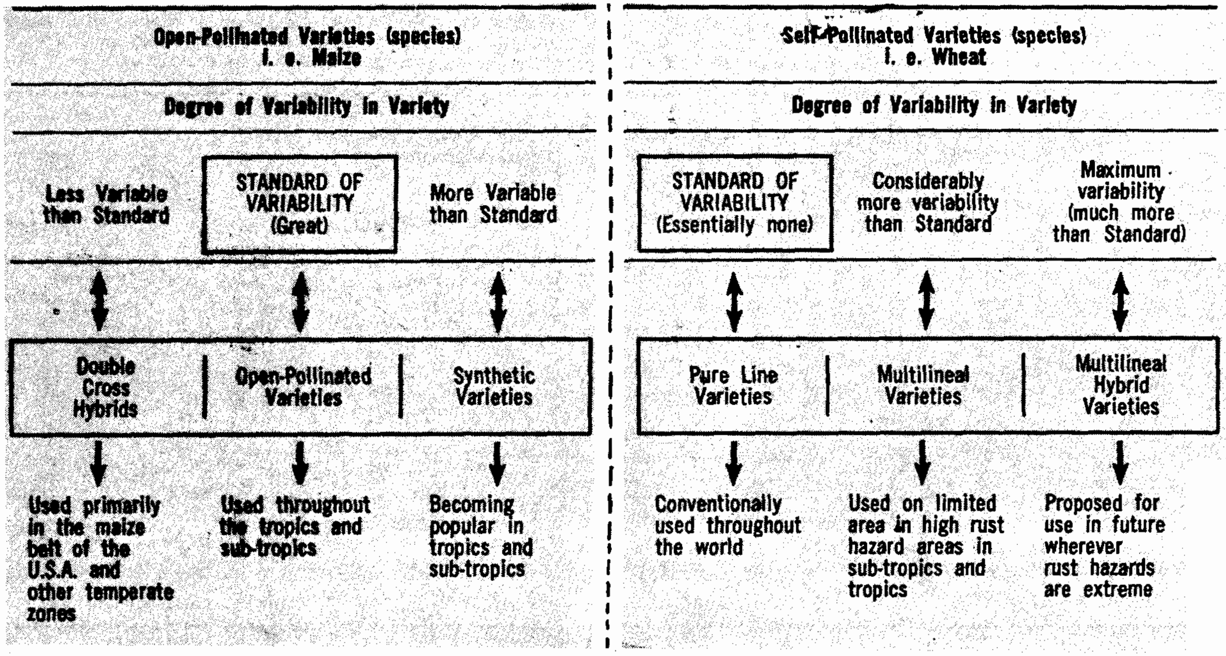
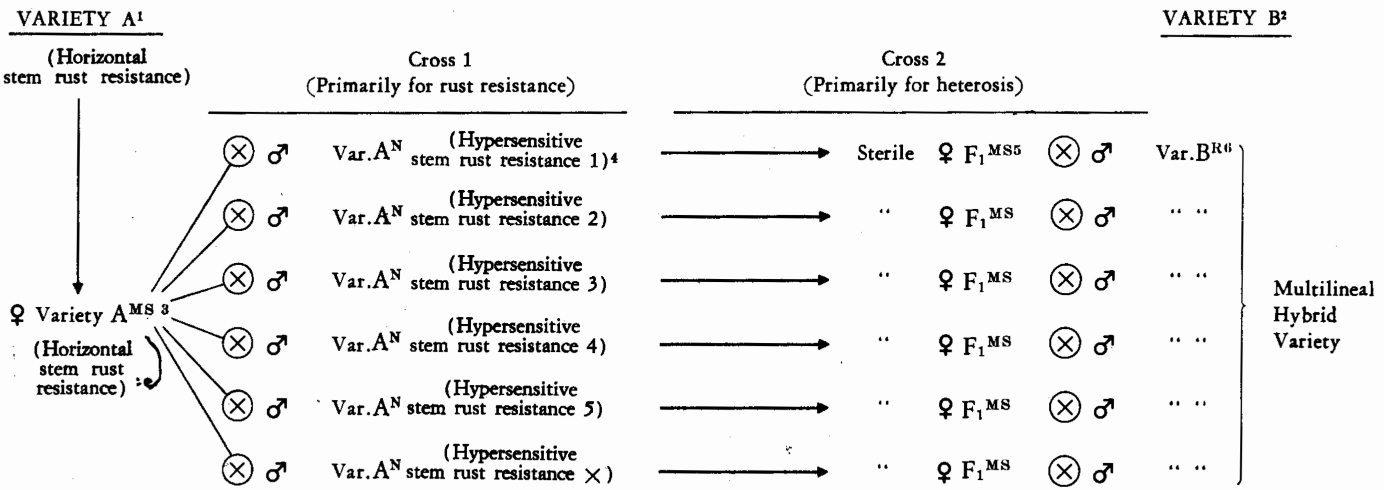


FIGURE 4. Schematic Development of Multilineal Hybrid Wheat Variety with Provisions for a Broad Base of Stem Rust Resistance.



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[1] Variety A — A commercial variety, with horizontal type of stem rust resistance, into which the cytoplasmic sterile will be incorporated and which will be crossed with phenotypically similar but genotypically different lines to obtain stem rust resistance.

[2] Variety B — A commercial variety into which the genes for restoration of fertility will be incorporated, and which when crossed indirectly to derivatives of Variety A as indicated above will provide heterosis in the hybrid.

[3] Variety A^{MS} — Cytoplasmic male sterile modification of Variety A.

[4] Variety A^{N} (Hypersensitive stem rust resistance 1, 2, etc) are multilineal lines phenotypically similar to Variety A^{MS} possessing normal pollination, but not possessing genes for restoration of fertility to the cytoplasmic sterile. Each line is genotypically different for resistance to stem rust (different S. R. genes).

[5] Sterile ♀ F_1 lines derived from first cross.

[6] Variety B^{R} ♂ — Variety B which provides the heterotic yield effect when crossed with Variety A, and also possesses the gene for restoring normal fertility to the cytoplasmic sterile Variety A^{MS}.

development of epidemics of diseases, open-pollinated varieties of maize are nearly always grown. Two different species of rust attack maize, but they never reach the same destructive epidemic proportions that are experienced in pure-line wheat varieties with epidemics of their corresponding rusts, as long as maize is grown as an open-pollinated variety. The tremendous genetic variability from a disease reaction standpoint in an open-pollinated variety serves as built-in protection against epidemics. If, however, maize is grown as a single- or double-cross hybrid in tropical areas, trouble is soon encountered with epidemics of a number of diseases, including the rusts. The lesson to be learned from the so called built-in protection against severe rust epidemics in open-pollinated varieties of crop plants such as maize, in contrast to the destructive epidemics encountered in a close-pollinated crop, such as wheat, is illustrated in Figure No. 3.

The Mexican and Rockefeller Foundation Wheat Improvement Programs have recognized the serious limitations imposed by using the conventional methods of developing pure line varieties of self-pollinated crop plants. They have pioneered the development of multilineal wheat varieties, based upon mechanically mixing together a number of phenotypically similar lines. Two commercial multilineal varieties, Miramar 63 and Bonza 65, with resistance to stripe rust, have been developed and are being grown successfully in Colombia and Ecuador.

One of the most exciting prospects of hybrid wheat development is the possibility of eventually developing hybrid varieties that will be so constituted that they will provide better protection against rust losses, and that this resistance will be of a more stable or lasting nature. This can be accomplished essentially by making every plant in such a hybrid population different for rust resistance, while maintaining a single phenotype for agronomic and quality characteristics. This can be accomplished by developing a multilineal hybrid, based upon backcrossing, using the procedure outlined in Figure No. 4.

The first hybrid wheat varieties will be single crosses. They will in all probability afford a level of protection from rust similar to that being provided by the currently available conventional pure-line varieties. The development of a multilineal hybrid wheat variety cannot be justified until a truly outstanding single cross hybrid has been developed and its value proven commercially. Nevertheless, in the final analysis the better rust control which might result from the development of multilineal hybrids could be one of the greatest benefits that eventually will come from hybrid wheat.

ECONOMIC CONSIDERATIONS

Problems in hybrid seed production

There is still a great scarcity of information on factors affecting the production of hybrid seed costs. During the past three years, however, there has been considerable experimentation conducted in different parts of the world designed to obtain information on various problems of hybrid seed production. Many of these experiments have been designed to obtain information on the percentage of seed set when the two parents are located at different distances from one another. This information is basic to the calculation of hybrid seed production costs.

The majority of these experiments have been largely of an academic nature, however, and usually have consisted of a few emasculated plants located at varying distances from a large plot of the pollinator. In such experiments, where pollen concentration has been high, seed sets generally have been good, often running between 60 to 80 per cent. These types of experiments have contributed very little information of a practical nature, and may actually be misleading.

A few scientists, however, have studied seed set on cytoplasmic male sterile lines sown in plots at different distances from strips of pollinators. Results have been extremely variable with seed set varying from 30 to 80 per cent, even when a proper synchronization was obtained between the flowering of the two parents. Moreover, the apparent seed set, at least in some cases, has been misleading since the so-called male sterile lines have been found to be partially pollen fertile. Where male sterile lines with incomplete sterility have been used, it is impossible to determine what percentage of the total seed set is due to crossing and what part is attributable to selfing.

It has become clear after a number of these studies that accurate and meaningful information will not be obtained until such tests are conducted on semi-commercial field strips, employing cytoplasmic male sterile lines that are completely sterile.

More extensive and accurate information on seed set on stable cytoplasmic male sterile lines grown under semi-commercial conditions is urgently needed as soon as possible in order to obtain trustworthy data on potential hybrid seed production costs.

At the present time no one is able to accurately predict what percentage of seed set can be obtained on cytoplasmic male sterile lines under field conditions. Neither is any one able to foresee the width of strips of pollinator or restorer lines that must be sown in proportion to the cytoplasmic male sterile line. Moreover, no one is currently able to predict the climatic and geographic conditions under which a high seed set can be assured. Until there is more extensive and accurate information on all of these points, it is impossible to predict the future role of hybrids in commercial wheat production.

Within the next two years many different wheat breeders will have developed and multiplied cytoplasmic male sterile lines to a point where they can be evaluated in strips to determine the percentage of seed set. Only then will a realistic picture of seed production costs become available.

The problem of seed costs to the farmer

The widespread acceptance of hybrid wheat by the farmer will depend entirely upon whether the amount of heterosis or extra yield obtained from planting hybrids will offset the higher seed costs, and in addition leave a reasonable increase in income for the additional investment. This balance of additional costs versus income will be different for different wheat producing areas, depending upon the average yield per acre and seeding rate in the area under question.

Although hybrid wheat seed production costs cannot be estimated accurately at present, Dr. L. P. Reitz of the U.S.D.A. (1965 Report of the Wheat Quality Conference) has provided a useful idea for estimating the increases in yield, expressed in the percentage of heterosis that will be required to pay for the increased investment in hybrid seed costs• above those of conventional seed costs. This type of approach to hybrid seed costs also gives some insight into where hybrids will be economically feasible and where they will not.

Dr. Reitz's original calculations are presented in Table 6, as well as extensions to include higher yields and one additional higher level of seed cost. We have incorporated a line to indicate the yield level necessary to compensate for differing levels of increased seed costs per acre, assuming 20 per cent heterosis. The 20 per cent heterosis seems reasonable both in light of the evidence on other crops, as well as on the basis of preliminary heterosis studies conducted in wheat.

It should be pointed out that the additional seed cost inputs referred to in Table 6 do not include the $2.00 per bushel minimum now paid for seed by farmers. The aggregate seed costs per acre therefore include the conventional seed cost together with the additional seed cost input for hybrids as presented in Table 6. A hybrid seed company that can develop an outstanding hybrid will have within reach a very large potential income. If the company can find ways of efficiently producing the F_1 seed of such a hybrid, it could lead to large profits.

The average per acre yields of wheat by continents and selected countries is indicated in Table 7. The table also indicates the additional seed cost input per acre for hybrids that can be compensated for by 20 per cent of heterosis, assuming a commercial grain price of $2.00 per bushel.

Twenty per cent of heterosis will offset somewhat more than $15.00 additional seed cost input per acre in countries such as France, Denmark, Holland and West Germany where per acre yields are high. It drops to a level of $10.00 per acre in Italy and Poland and to a low of $6.00 per acre in Spain. The level of compensation for all of Europe is $10.00 per acre.

Similarly the maximum additional per acre seed input costs that can be compensated for by 20 per cent of heterosis with the average national yield levels encountered in the U.S.A. and Mexico is approximately $10.00, and for Canada $8.00. Where average yields are low, as in India and Pakistan, 20 per cent of heterosis will only offset an additional seed cost input of $4.00 per acre.

National average yields are, however, misleading as a basis for estimating the potential economic feasibility of hybrids. A more realistic basis is a

TABLE 6. The Percentage of Heterosis Necessary to Pay the Additional Cost of Hybrid Seed at Different Commercial Yield Levels.

Commercial Yield Bushel/Acre	Additional Seed[1] Costs per Acre					
	$4.00	$5.00	$6.00	$8.00	$10.00	$15.00
	Heterosis					
	%[2]	%	%	%	%	%
10	20.0	25.0	30.0	40.0	50.0	75.0
15	13.3	16.7	20.0	26.7	33.3	50.0
20	10.0	12.5	15.0	20.0	25.0	37.5
25	8.0	10.0	12.0	16.0	20.0	30.0
30	6.7	8.3	10.0	13.3	16.7	25.0
35	5.7	7.1	8.6	11.4	14.3	21.0
40	5.0	6.3	7.5	10.0	12.5	18.8
45	4.4	5.5	6.7	8.9	11.1	16.7
50	4.0	5.0	6.0	8.0	10.0	15.0
60	3.3	4.2	5.0	6.7	8.3	12.5
70	2.9	3.6	4.3	5.7	7.4	10.7
80	2.5	3.1	3.8	5.0	6.3	9.4
90	2.2	2.8	3.3	4.4	5.6	8.3
100	2.0	2.5	3.0	4.0	5.0	7.5
120	1.7	2.1	2.5	3.3	4.2	6.3
150	1.3	1.7	2.0	2.7	3.3	5.0

[1] Refers only to the additional cost of hybrid seed above the amount now spent on conventional seed.

[2] Commercial grain value calculated at $2.00 per bushel.

└──┐= 20 per cent level of heterosis.

TABLE 7. The Average per Acre Wheat Yields by Continents and Selected Countries Showing the Additional Seed Input Costs That Can Be Offset by a Level of 20 Percent Heterosis.

Continent, Country or Area	Average Yield Bushels/Acre[1] 1962/63	The Maximum additional Per Acre Seed Cost Input that Can be Compensated for by 20 per cent Heterosis[2]
EUROPE	31.4	$10
France	45.7	$15
West Germany	51.8	$15
Denmark	62.7	$15
Holland	68.2	$15
Italy	31.1	$10
Poland	28.9	$10
Spain	16.8	$ 6
NORTH AMERICA	23.7	$ 8
Canada	21.2	$ 8
U.S.A.	25.2	$10
Mexico	28.9	$10
SOUTH AMERICA	20.0	$ 8
Argentina	19.8	$ 8
Chile	22.4	$ 8
ASIA	14.2	$ 6
India	13.3	$ 4
Pakistan	12.2	$ 4
AUSTRALIA	18.6	$ 8

[1] F.A.O. Production Yearbook, Volume 17, 1965.

[2] Assuming a commercial grain price of $2.00 per bushel.

regional approach. The average per acre yield of the farm states of Illinois, Indiana, Ohio and Michigan, that are responsible for the production of the majority of the soft red winter wheat, is 34.5 bushels, whereas the principal producers of hard red spring wheats, namely North Dakota, Montana and South Dakota have an average yield of only 11.6 bushels per acre. Obviously the chances of the economic success for hybrids is greater in the soft red winter wheat region where 20 per cent of heterosis will offset additional seed cost inputs for hybrid seed of more than $14.00 per acre in contrast with the hard red spring wheat region where the same level of heterosis will offset only slightly more than $4.00 per acre.

A changing agriculture will likewise improve the chances for successful use of hybrids. Within the past two years, mainly as a result of the widespread use of dwarf varieties combined with heavier fertilization, the national average yield of wheat in Mexico has risen to 39 bushels per acre. Areas such as Sonora and Sinaloa now have per acre average yields of more than 55 bushels. These areas can afford to increase considerably the money expended for hybrid seed per unit of planted area if high levels of heterosis are assured.

Who will produce the hybrid seed?

The area cultivated to wheat in the world is considerably greater than for any other cereal crop. Moreover, the seeding rate per unit of area is considerably greater in wheat than for such crops as maize or sorghum where hybrids are now used. The wheat seed sown annually in the U.S.A. and Canada alone, is about 70 million bushels, assuming an average seeding rate of one bushel per acre. Nevertheless, a large part of the commercial wheat-producing areas of the world is located in ecological zones where yields are low and where moisture is the factor which primarily limits yield. However, even when these low yielding areas are excluded in calculating the possible hybrid wheat seed market, the potential market remains very large. The hybrid wheat seed market is potentially a huge business. We are all aware of the great impact that the use of hybrid maize and sorghum has had on U. S. agriculture. Private seed companies have played a major role in the development, promotion, production and distribution of hybrids in both of these crops. Without the actual participation of private seed companies in all of these activities it is doubtful that hybrids would have achieved widespread commercial acceptance.

In all probability the production of hybrid wheat seed will be even more beset by technical problems —especially those related to pollination— than in the case of maize or sorghum. Moreover, distribution of larger volumes of hybrid seed will need to be handled and this will require a large and efficient organization. If hybrid wheats become feasible, the only agencies now capable of producing and handling this volume of seed are the private seed companies. Governmental agencies must increase budgets, train personnel, and create greater freedom of operation in order to cope with an undertaking of this magnitude.

Looking ahead in research on hybrids

Much more research is needed to increase our knowledge and understanding of the cytoplasmic sterility and restorer systems in wheat. The male sterility system based on *Triticum timopheevi* cytoplasm is much more complex than the corresponding systems currently being used in the production of commercial hybrids of maize and sorghum.

Most investigators have reported that two genes are involved for complete restoration of pollen fertility in the *T. timopheevi* system. Other scientists have shown that under certain ecological conditions and with certain verieties, at least three genes, and perhaps more, are involved in restoration. A few varieties are very difficult to sterilize when their nucleus is incorporated into *T. timopheevi* cytoplasm. The reason for this phenomena is unknown. Moreover, considerable difficulty has been reported in developing cytoplasmic male sterile lines that remain sterile under a range of different ecological and climatic conditions.

Before satisfactory hybrids can be developed it will be necessary to develop cytoplasmic male sterile lines which remain completely sterile under a wide range of conditions. Such lines exist. Within the past year the Mexican program has been able to isolate lines with complete pollen sterility at Ciudad Obregón, Sonora, which has ecological conditions very favorable for anther and pollen development (28° N and 125 feet elevation). Some of these lines have been equally as sterile at Chapingo, Mexico, at a latitude of 18° N and an elevation of approximately 7400 feet.

The discovery of a single dominant gene for the restoration of pollen fertility for the *T. timopheevi* cytoplasmic male sterile would greatly simplify the development of hybrids.

A dominant single gene which will control plant height also is needed for the development of dwarf hybrids. The recessive Norin genes, which have been used with great success in the development of such commercial varieties as Gaines (U.S.A.), Pitic 62, Penjamo 62, Sonora 64, Lerma Rojo 64 (Mexico), are difficult to use in hybrids. Currently, considerable research effort is being made to find a dominant gene in either natural occurring dwarfs or in mutant populations.

More research is needed to find stigmas, filaments, and anthers that are better suited to hybrid seed production. During the 1964-65 season a preliminary study was made of the variation in flower structure of approximately 200 lines and varieties in the Mexican program. Considerable variation was found in filament length, anther size, and in the manner the anthers were exerted. Unfortunately, in this study no lines were found which were clearly superior in stigma length and exertion. If male sterile lines could be developed with better exertion of the stigma it would result in a higher percentage of seed set and thereby reduce hybrid seed production costs. Much more research effort is justified in this area of investigation.

Within the past two years a vast amount of research effort that was formerly directed toward the development of conventional improved pure line wheat varieties has been diverted to hybrids. Even after hybrid wheat becomes a commercial success, the long time continued success of hybrid breeding programs will depend to a large extent upon the continued production of better basic lines and varieties which can be converted into parents for the production of better hybrids. Continuous aggressive conventional breeding programs producing newer and better lines will, to a large degree, always set the base level of yield, quality, disease resistance, and breadth of adaptation upon which the improvements in future hybrids will be superimposed.

When will commercial hybrids be available to the farmer?

There now appears to be no insurmountable hurdle to the development of successful hybrid wheat varieties for areas where wheat is grown as an intensively cultivated crop. Hybrids will first become economically feasible where wheat is grown in areas of adequate rainfall, or under irrigation, either of which will permit the use of heavy doses of fertilizer, thereby resulting in high yields per unit of area. As increased knowledge permits improvements in the efficiency of hybrids seed production, seed costs will decrease and gradually permit the extension of hybrids to areas of lower per acre yield.

Commercial hybrid wheat varieties are on the horizon, but it is doubtful if there will be any appreciable area of commercial wheat produced from hybrids before 1970.

LITERATURE ON HYBRID WHEAT RESEARCH

Briggle, L. W. Heterosis in Wheat—A Review. Crop Science 3: 407-412, 1963.

Briggle, L. W. Hybrid Wheat—What it Means to Wheat Production. Cereal Science Today. 9: 59-65, 1964.

Crop Quality Council. Hybrid Wheat Seminar Report, 52 pages, 1964 Crop Quality Council, Minneapolis, Minnesota.

Crop Quality Council. Report of the Wheat Quality Conference, pages 36-48. Jan. 27, 1965.

Eleventh Hard Red Winter Wheat Workers Conference. Reports on Progress in Hybrid Wheat Research. Pages 1-20, Fort Collins, Colorado. Feb. 1965.

Fukasawa, H. Fertility Restoration of Cytoplasmic Male-Sterile Emmer Wheats. Wheat Information Service No. 7. 21, 1958.

Kihara, H. Substitution of Nucleus and Its Effects on Genome Manifestations. Cytologia 16: 177-193, 1951.

Kihara, H. Fertility and Morphological Variation in the Substitution and Restoration Backcrosses of the Hybrids, *Triticum vulgare* × *Aegilops caudata*. Proc. 10th International Congress of Genetics, 1958.

Schmidt, J. W., Johnson V. A. and Maan S. S. Hybrid Wheat. Nebraska Experimental Station Quarterly 9: No. 3; p. 9, 1962.

Wilson, J. A. and Ross, W. M. Cross-breeding in Wheat, *Triticum aestivum* L. Frequency of the Pollen-Restoring Character in Hybrid Wheats having *Aegilops ovata* Cytoplasm. Crop Science 1: 191-193, 1961.

Wilson, J. A. and Ross, W. M. Male Sterility Interaction of the *Triticum aestivum* Nucleus and *Triticum Timopheevi,* Cytoplasm. Wheat Information Service 14: 29-30, 1962.

Wilson, J. A. and Ross, W. M. Cross Breeding in Wheat, *Triticum aestivum* L. II. Hybrid Seed Set on a Cytoplasmic Male Sterile Winter Composite Subjected to Cross Pollination. Crop Science 2: 415-417, 1962.

Wilson, J. A. and Evangelina Villegas. Genetic Interactions for the Hybridization of Wheat and their Effect upon Quality. Cereal Science Today. A.A.C.C. Vol II, No. 7, July 1966.