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RESEARCH AND DEVELOPMENT OF A BIOLOGICAL INNOVATION: COMMERCIAL HYBRID WHEAT†

Substantial resources have been devoted to the development of commercial hybrid wheat by both public and private sectors since the late 1940s. In the early 1960s, commercial hybrid wheat development appeared highly promising. By the 1970s, however, this hope had turned into skepticism. Many private and public research organizations had discontinued their commercial hybrid-breeding operations. In the early 1980s, developments in breeding technology prompted a new wave of optimism, and several major seed companies either tested or marketed commercial hybrid seed. Unfortunately, this new optimism has also been muted in the last few years as further technical difficulties have arisen and research budgets have been squeezed. Currently the jury is still out as to whether commercial hybrid wheat will achieve sufficient acceptance among farmers to become profitable. The process by which research and development decisions were made offers important insights into the functioning of U.S. agricultural research systems.

This paper analyzes the history of commercial development of hybrid wheat with particular attention to the interrelationships between the scientific and technological advance leading to the commercial introduction of hybrid wheat; to the complex interaction between the public and private sector research institutions in the development of a biological technology;

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and to the innovation strategies followed by different public and private sector organizations in investing in hybrid wheat research and development and in introducing hybrid wheat into the market.

COMMERCIAL HYBRID BREEDING

Commercial hybrid breeding differs fundamentally from the conventional breeding of self-pollinated crop varieties. It involves different research and development procedures, time frames, and costs than conventional breeding schemes where the development of a new variety begins with a cross made between two genetically different inbred "pure lines."[1] Self-fertilization or backcrossing for five to seven generations follows this initial cross-fertilization. At this point the plant reaches a genetically homozygous or uniform state.[2] It is then ready for seed multiplication for commercial sale. The total length of time required for this entire procedure, i.e., from the initial cross to the last self-fertilization or backcrossing, is four to five years.

However, before this system works efficiently, much time, money, and resources are put into developing good parental and germplasm pools. These two elements are the basis of a sound breeding program because it is from these resources that a breeder achieves his final product. A new germplasm pool takes an average of three years to establish. However, new gene sources are continually added to it. Inbred pure-line parents on average take six years to be developed.

Commercial hybrids are the first generation (F_1) from the crossing of two parents. The parents are typically inbred pure lines, which when crossed produce hybrid vigor (or a heterotic effect) resulting in higher yields than are obtained from conventional breeding schemes.[3] An F_1 hybrid

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[1] A pure line is a line that is genetically pure for all its traits or genes (or homozygous for all its genes).

[2] A homozygous condition means that the individual plant's genome contains little diversity among its genes. Subsequently, the common causal agents of genetic diversity between generations and among full-sib progeny (progeny that have the same parents), segregation, and recombination, do not occur at significant levels. Once this homozygous state is reached, each generation should perform similarly. Therefore, a grower should be able to use the seed from each year's harvest for next year's planting as well as for market purposes, which means a loss in seed sales to the firms.

[3] Heterosis is best defined as "increased vigor or growth of a hybrid progeny in relation" to either of the parents or to the average of the parents (Poehlman, 1979). The parents' genomes must complement each other's best traits for heterosis to occur. Heterosis does not always occur in such crosses. Depending on

usually has dissimilar genes for many of its traits or is heterozygous for its genes. It is this F_1 that is put on the market for commercial sale.

The marketing of the two different varietal types is affected by their genetic differences. Because a self-fertilized plant variety is genetically homozygous, it will not vary significantly from generation to generation. Producers can plant the seed from last year's harvest instead of buying new seed every year from the seed firm.

Hybrids, on the other hand, show significant character differences in succeeding generations characterized by increased non-uniformity in genetic expression in such traits as yield and disease resistance. A final result of this non-uniformity is decreased yields. Consequently, producers must buy new seed each year from a seed firm, a requirement upon which many commercial seed companies depend for their livelihood.

A major difference between the conventional and hybrid schemes lies in the time it takes to develop a market product. Once the germplasm pools are completed, the time of development for the hybrid takes only one to two years (versus four to five years in the conventional scheme). This assumes, however, that the technology for producing commercial hybrids has already been developed.

Given that a hybrid technology is developed and good parental pools are produced, hybrid breeding offers the seed firm many advantages in seed production and marketing. First, money and resources are saved because less development time for a commercial product is needed. Second, market size is increased because its seed must be bought every year. Last, new sources of genes for traits such as disease resistance and drought can be quickly transferred into a commercial product. Demand for such traits can be met rapidly, which is desirable from a marketing point of view.

These advantages are reduced if the conventional varieties are rapidly improved as a result of continuous improvement in parental germplasm pools. Improved conventional varieties increase the acceptable performance level against which a commercial hybrid is measured. How soon a commercial hybrid surpasses the performance of conventional varieties depends on the speed at which they are being improved relative to commercial hybrids. Hybrids must be purchased annually, and farmers will purchase these seeds only if benefits offset the cost. The benefits may not be as large if conventional varieties are a moving target.

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the parents selected for the cross, they may or may not complement each other. Because of the influence of other genetic factors interacting between the parents' genomes, deleterious effects, such as lower yields, may potentially result.

RESEARCH AND DEVELOPMENT

The emergence of an innovation begins with demand. The demand may be created by changes in the economic environment such as in relative factor prices, factor to product price ratios, or factor inputs in the production process of a specific crop. However, other forces such as technological advancements in similar industries, such as hybrid corn, may also create a perception of opportunity. Table 1 lists the major events in the development of hybrid and semi-dwarf wheat varieties from 1948 to 1987. The factors are discussed in more detail in the following sections.

Demand for Increased Yields

Toward the end of the 1940s, the wheat industry witnessed a change in its breeding objectives. Primary breeding objectives evolved from primarily "defensive" to mainly "offensive" for all five classes of wheat (Table 2). Defensive breeding is breeding for drought, disease resistance, or other factors designed to maintain standard yield levels or milling quality. Offensive breeding, on the other hand, emphasizes breeding for yield improvement. Recognition of the need to achieve higher yields set new objectives for the wheat industry.

Three events strongly influenced this change in objectives. First, the success of hybrid corn made plant breeders and farmers aware that yields could be increased more rapidly than in the past as a result of advances in biological science and in breeding technology (see chronology, Table 1, and Appendix A). In 1930, only 1 percent of the corn farmers grew hybrid corn, and corn yields averaged 20 bushels per acre. By 1948, over 80 percent of the corn farmers were growing hybrid corn, and average corn yields had jumped to 40 bushels per acre. Other factors such as nitrogen fertilizer also contributed strongly to this yield increase (Sundquist, Menz, and Neumeyer, 1982).

This increase in corn yield was one of the first major breakthroughs in increasing crop yields. Its success created a perception of technological opportunity. If technology could be used to increase corn yields, then perhaps it might also be used to increase yields in other crops. Wheat yields had remained on a plateau of 10 bushels per acre from 1866 to 1940 (Dalrymple, 1980), and therefore wheat appeared to be a good candidate.

A second development came after an outbreak of a stem rust race, which occurred in the 1950s and caused epidemic yield and quality losses to the wheat crop. It was soon recognized that control measures, such as breeding for resistance to stem rust, had to be undertaken to either maintain yields or attain higher wheat yields. If higher yields could be obtained, an outbreak of stem rust would not be as devastating.

Concomitant to the occurrence of these two events was a sharp reduction in land committed to wheat acreage and an increase in wheat prices. The acreage allotment and crop diversion programs implemented by the federal government after World War II resulted in a large reduction in the land area available for wheat production. Wheat acreage steadily dropped from 83.9 million acres in 1949 to 48.7 million acres in 1970 (Bond and Umberger, 1979). Furthermore, the price of wheat increased from $1.50 per bushel in 1940 to $3.50 and $2.50 in 1945 and 1950 (Hayami and Ruttan, 1985). Increased wheat prices encouraged substitution of other inputs, such as new varieties, fertilizers, pesticides, and irrigation (Binswanger et al., 1978). The effect was to induce a demand for land-saving innovation.

Breeding Strategies for Improving Yields

A new objective now existed for the wheat industry. The pursuit of higher yielding wheat resulted in two separate series of fundamental studies: one opened up the possibility of hybrid wheat production and the other semi-dwarf wheat production. In this paper, the development of hybrid wheat is the main focus.[4]

The concept of hybrid wheat breeding began in the 1950s through the works of Hitoshi Kihara and H. Fukusawa of Kyoto University in Japan. Kihara found a cytoplasmic male-sterile system in an offspring from *Aegilops caudata x Triticum vulgare* in 1951 (see Appendix B). In 1953, Fukusawa discovered a similar system in an offspring of *Aegilops ovata x Triticum durum*. Both the *Aegilops* and *Triticum* species are closely related to cultivated conventional wheat varieties. Both Kihara and Fukusawa came

[4] A feasible mechanism for developing semi-dwarf wheat became available almost concurrently with the change in demand for higher yielding wheat in the late 1940s. In 1946, Samuel C. Salmon from the U.S. Department of Agriculture noticed a short-stemmed wheat variety, Norin 10, at the Morioka Branch Station in Japan. The Japanese were already growing many short-stemmed, or semi-dwarf wheat varieties. Salmon sent Norin 10 back to the department's research facilities at Beltsville, Maryland. Other sources of short-stemmed varieties were introduced in Beltsville within the following year, i.e., Norin 16, Norin 33, Seu Suen 27, and Suweon 92. All of these plants made the production of semi-dwarfs possible by crossing these sources with conventional varieties.

In the early 1950s, Orville A. Vogel and E.H. Everson from Washington State University began to develop a semi-dwarf variety, Gaines, from a cross between Norin 10 and Brevor, a U.S. wheat variety, and then crossed to two additional wheats. Breeding procedures followed a conventional scheme in which the final product was in a homozygous state. In the mid-1950s, extensive varietal yield testing of Gaines commenced, and by 1961 Gaines was released as a commercial variety (Dalrymple, 1980).

Table 1.—Chronology of Principal Events in the Development of Commercial Hybrid Wheat and Semi-Dwarf Wheat Varieties*

Year	Description of event
1948	The success of hybrid corn.
Late 1940s –early 1950s	Outbreak of stem rust wheat 15B.
1949	Wheat acreage reduction programs coupled with increased wheat prices and lower relative input prices.
Late 1940s	Semi-dwarf gene is introduced to United States by Salmon.[a]
Early 1950s	Kihara and Fukusawa[a] discover CMS-Rf system in closely related species of cultivated wheat.
Early 1950s	Vogel, Everson, and Borlaug[a] develop SDW program at Washington State University.
Late 1950s	Testing of SDW varieties begins.
1961	Wilson and Ross[a] from Kansas State University find CMS system in *Triticum timopheevi.*
1961	Gaines, first SDW in the United States, is released.
1962	Johnson and Schmidt[a] from University of Nebraska, and Wilson and Ross find Rf system in *Triticum timopheevi.*
1962	Private sector becomes active and takes over role of leader in development of commercial hybrid wheat.
1968	Bozzini and Scarascia-Mugnozzo[a] at CNEN, Rome, Italy, find male sterile system in wheat.
1969	SDW varieties show increase of 5–50 percent over standard wheat varieties.
1970	Plant Variety Protection Act passes.
1970	Many public sector actors and smaller private actors drop commercial HW programs in favor of SDW program.
1970	All research on male sterile systems in wheat is dropped.
1970	Pollen suppressors technology enters HW development pathway.

Table 1.–Chronology of Principal Events in the Development of Commercial Hybrid Wheat and Semi-Dwarf Wheat Varieties* (*Continued*)

Year	Description of event
1978	DeKalb and Pioneer both release experimental line of commercial HW (via CMS-Rf technology).
1979	Experimental lines are pulled off the market.
1979	Northrup King drops commercial HW program.
1982	DeKalb drops commercial HW program.
1983	Cargill's Bounty, commercial HW (via CMS-Rf technology) begins to perform well in state advanced yield trials.
1987	Rohm & Haas drop commercial HW (via PS technology) program.
1987	Pioneer drops domestic commercial HW program.
1987	Commercial HW development still continues using CMS-Rf and PS technologies.

*HYW, higher yielding wheat; SDW, semi-dwarf wheat; HW, hybrid wheat; CMS, cytoplasmic male-sterility; Rf, restoration factor; and PS, pollen suppressors.

[a]Samuel C. Salmon; Hitoshi Kihara and H. Fukusawa; Orville A. Vogel, Everett H. Everson, and Norman Borlaug; James A. Wilson and William M. Ross; Virgil A. Johnson and John W. Schmidt; A. Bozzini and G.T. Scarascia-Mugnozzo.

across their findings accidently while doing other cytogenetic analysis of these species.

A cytoplasmic male-sterile system consists of separate sterile factors in the cytoplasm and the nucleus. These two factors interact to cause male sterility. Then a plant that typically self-fertilizes is incapable of doing so if a cytoplasmic system is present. The plant can be cross-fertilized without having to hand-emasculate.

Kihara and Fukusawa's interest in continuing their research on these cytoplasmic male-sterile systems was twofold. First, they were curious as to how these systems operated genetically. Second, because hybrid corn and hybrid sorghum were successfully produced by using a cytoplasmic male-sterile system, they thought that a similar system found in wheat might also be used successfully in producing hybrid wheat.

Unfortunately, the cytoplasmic male-sterile system found in the *Ae-*

gilops genus produces deleterious effects in a hybrid, such as reduced hybrid vigor, delayed maturity, pistillody, and poor germination (Sage, 1976). Therefore, the cytoplasmic male-sterile system in these particular *Aegilops* genus was of little value in a breeding program.

Table 2.—Market Class Acreage, Protein Percentage, and Use for the United States

Wheat class	Acreage of total U.S.[a] (percent)	Protein Percent[b]	Use
Hard red winter	59	15	Bread
Hard red spring	13	16	Bread
Soft red winter	12	12	Pastry
White	9	11	Pastry
Durham	7	16	Macaroni

Source: Steve Simmons, 1979, "Agronomy 3010: Adaptation, Distribution, and Production of Field Crops," University of Minnesota, St. Paul.

[a]1972 statistics.

[b]Whole grain.

By the late 1950s, work on finding other cytoplasmic male-sterile systems was underway. By 1957, several programs had been set up across the United States to find and develop cytoplasmic male-sterile lines. In 1961, James A. Wilson and W. M. Ross from the Hayes Experiment Station at Kansas State University presented findings of a new cytoplasmic male-sterile system that did not produce the deleterious effects in the hybrid yielded by the *Aegilops* genus. This new source was found in *Triticum timopheevi*, which is more closely related to cultivated wheat varieties than the aforementioned *Aegilops* genus.

Pursuit of these cytoplasmic male-sterile lines was accompanied by a search for a restoration factor system. A restoration factor system is a genetic system carried by the male parent that restores male-fertility to the resulting hybrid seed. Without this restoration factor system, the hybrid seed is also male-sterile (see Appendix C). Plants from these seeds can only produce via cross-fertilization. Cross-pollination in a plant such as wheat does not occur at a high rate without assistance, for example, hand-pollination. These plants have evolved to rely on reproduction via self-fertilization. Grain fill is low in those plants that have a cytoplasmic male-sterile system but do not have a restoration factor system. It is essential then for a breeder to incorporate a restoration factor system in the male when producing hybrids via cytoplasmic male-sterile systems.

Within a year of Wilson and Ross's finding, Virgil A. Johnson and John W. Schmidt from the University of Nebraska and Wilson and Ross separately discovered a cytoplasmic male-sterile–restoration factor system in *Triticum timopheevi.*

Mechanism for Implementing Breeding Strategies

Higher yielding wheat via hybrid technology now existed. Work to develop a hybrid wheat were carried out for the two wheat classes, Hard Red Winter and Soft Red Winter. Cytoplasmic male-sterile–restoration factor systems were found only in these classes.

Both the private and public sectors were active in the early development of commercial hybrid wheats via cytoplasmic male-sterile–restoration factor systems. However, each sector had different motives for its involvement and level of commitment. The private sector took over the leading role in this pursuit. Public sector researchers had done most of the research to find a mechanism, the cytoplasmic male-sterile–restoration factor system, to produce commercial hybrid wheats.

By 1962, DeKalb was aggressively investing in hybrid wheat research. Other firms, including Cargill, Northrup King, and Pioneer International Hybrid, followed DeKalb's lead and developed their own hybrid wheat programs.

Although DeKalb's move into hybrid wheat influenced other firms, many chose to work on hybrids rather than pure-line varieties because the latter lacked legal protection for proprietary development and marketing of activities. Because of the genetic nature of the hybrid seed, it contains its own built-in trade secret. Other firms and universities have difficulty in copying a hybrid unless they know its parentage. Even then, they would require the inbred lines that serve as parents in their own parental pool before they could make an exact replica.

Despite the private sector's commercial motivation, the public sector was not far behind the private sector in hybrid wheat development. The public sector's interest in hybrid wheat stemmed both from a desire to keep pace with private firms and from a basic interest in the genetic basis of the cytoplasmic male-sterile–restoration factor systems used to produce hybrid wheat. The public institutions that initiated the most extensive hybrid wheat programs in the early 1960s were Washington State University, Kansas State University, North Dakota State University, University of Nebraska, and Texas A&M University.

Between 1962 and 1968, both private and public sector programs conducted basic and applied research on cytoplasmic male-sterile–restoration factor systems found in wheat. More emphasis, however, was given to basic research on the genetics of the cytoplasmic male-sterile–restoration factor systems. The majority of these basic experiments was quite small in scale.

Applied research focused on building germplasm and parental pools for specific use in producing commercial hybrids via cytoplasmic male-sterile–restoration factor technology.

Basic experiments revealed many genetically based problems in using *Triticum timopheevi* as a source of cytoplasmic male-sterile–restoration factor for hybrid production. These problems made restoring complete male fertility in the hybrid difficult. Either no restoration or incomplete restoration occurred instead of complete fertility. Without complete male fertility, grain fill in a hybrid would diminish, and, consequently, yields would be reduced.

Many problems were encountered in developing the cytoplasmic male-sterile female parent and the restoration factor male parent. One of the major difficulties in developing these lines stems from the ploidy level of the common wheat variety.[5] As the ploidy level increases, the number of genes controlling a trait increases. This complexity makes it more difficult to understand and manipulate a genetic system. A common wheat variety contains six chromosome sets; corn, which is a diploid, has two chromosome sets. Consequently, parental development requires much more work in wheat than in corn.

Developing the parents for commercial hybrid wheat production is further complicated by the biological construction of wheat. The parents used in developing the female cytoplasmic male-sterile parent were not closely related but were the only plants available that were capable of producing cytoplasmic male-sterile offspring. Deleterious effects, such as atypical floral morphology or lower yields, resulted.

Developing the male restoration factor parent was complicated by poor anther extrusion and pollen that was viable for only three hours. Poor anther extrusion prevents easy access to the pollen for pollen collection. Short viability time allows little time for successful cross pollination. These traits existed to promote self-fertilization. Breeders had to undo what evolution had accomplished.

By the late 1960s these problems caused many wheat breeders to doubt that commercial hybrid wheat could ever become technologically successful. This doubt was enhanced by two concurrent events. First, the emergence and success of semi-dwarf wheat varieties provided a readily available research alternative. The first U.S. semi-dwarf wheat variety, Gaines, was released in 1961. By 1969, 7 percent of the wheat acreage in the United States was devoted to semi-dwarf wheat varieties. Their yields were 5 to 50 percent greater than conventional varietal yields. Yield increases were due to a combination of short-stemness and heavier nitrogen application (Dalrymple, 1980; Bond and Umberger, 1979). Heavier nitrogen applica-

[5] Ploidy level is the number of sets of chromosomes (genomes) present in an organism.

tions increase grain fill. Short-stemmed varieties could support the heavier heads of wheat plants, whereas the conventional varietal stems could not and lodged subsequently reducing yields.

Second, the passage of the Plant Variety Protection Act (PVPA) in 1970 provided protection to the private sector for its pure-line varieties. The PVPA gave plant breeders "(i) the exclusive right to sell or advertise and to license other persons to sell plants of the registered new variety and/or the reproductive material of those plants; (ii) the right to levy and collect royalties from persons selling or using new varieties registered under the Act" (Butler and Marion, 1983). Pure-line varieties were now protected under law. Farmers could no longer sell their seed to any one else. (The new law could not, of course, prevent them from using one year's harvest for their next year's planting.)

The passage of the PVPA undoubtedly encouraged some firms to place greater emphasis on developing pure-line varieties rather than continuing their hybrid development programs. Actually, many firms found that a number of the parents developed for hybrid production could compete successfully with many of the conventional commercial varieties. These parents were pure-lines, not hybrids. Upon passage of the PVPA, firms could release these parents as pure-line varieties without fear of losing sales because of farmers selling their seed to others.

By 1970 all public sector actors except North Dakota State University elected to drop their hybrid wheat programs. Many of the smaller firms also dropped their programs. The major private sector actors that remained to develop hybrid wheat via cytoplasmic male-sterile–restoration factor technology were Cargill, Northrup King, DeKalb, Nickerson American Plant Breeders, and Pioneer. North Dakota State University, along with the private sector actors, concentrated on Hard Red Spring and Hard Red Winter hybrid wheat research. All work on Soft Red Winter wheat for commercial hybrid production was dropped as the problems encountered in hybrid research were amplified in Soft Red Winter wheat.

METHODS OF COMMERCIAL HYBRID SEED PRODUCTION

In 1970 efforts in further developing hybrid wheat were aimed at revising the old technology and introducing new, and hopefully better, ones to produce commercial hybrid wheats. The three technologies—cytoplasmic male-sterile restoration factor systems, male-sterile systems, and pollen suppressors—are discussed in light of their contribution to the production of commercial hybrid wheat.

Cytoplasmic Male-Sterile–Restoration Factor Technology

Research on hybrid wheat via cytoplasmic male-sterile–restoration factor technology focused on three areas: finding new sources of cytoplasmic male-sterility and restoration factors, building larger and more diverse parental pools, and testing for yield and quality. The first procedure, finding new sources of cytoplasmic male-sterility and restoration factors, was the focal point of the hybrid wheat programs in the 1970s. This basic research effort was rewarded with new sources that were easy to manipulate in a breeding program.[6]

Of all the new sources of cytoplasmic male-sterile and restoration factor systems, *Aegilops speltoides, Aegilops kotschyi*, and *Aegilops variabilis* showed the most potential for providing a new source of cytoplasmic male-sterility and restoration factor and producing high-yielding hybrids. In these three species, both the sterility and fertility restoration systems were complete and controlled by only one dominant gene. Furthermore, the cytoplasm of *Aegilops speltoides* was very similar to that of *Triticum timopheevi.*

During this same period efforts were undertaken to develop parental pools. All cytoplasmic male-sterile and restoration factor systems were further developed, and all parental lines were tested and selected for performance. Testing for yield and quality of hybrids for commercial release began in the mid- to late 1970s. The first Hard Red Winter hybrid varieties resulting from cytoplasmic male-sterile–restoration factor technology were released in 1978 by DeKalb and Pioneer International experimental lines.

The first hybrid releases were premature for several reasons. Further testing of hybrids was required to confirm their environmental stability, as they gave inconsistent yields across environments, and seed stock was impure, more susceptible to disease, and produced lower yields. In addition, not enough seed was available to satisfy market distribution needs. These difficulties prompted DeKalb and Pioneer International to pull their hybrids off the market in 1979.

Unfortunately, the release of the two hybrid varieties and their subsequent recall significantly damaged hybrid wheat's reputation. Many breeders continued to be disillusioned with the continual lack of success of commericial hybrid wheat, and many dropped their commercial hybrid wheat programs. By 1980, Northrup King had suspended all its programs. By 1982 DeKalb had sold its hybrid wheat program to Monsanto after having spent an estimated $24 million on commercial hybrid wheat research.[7]

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[6] Details regarding the sources of cytoplasmic male-sterility may be found in Mukai and Tsunewaki, 1975 and 1979.

[7] Monsanto's purchase of DeKalb's hybrid wheat program indicated that Monsanto was still hopeful that hybrid wheat could become a biological and economic success. Monsanto initially was interested in purchasing the program because of

Since 1981 the hope for a successful hybrid variety via cytoplasmic male-sterile–restoration factor technology has become a reality. Much of the credit goes to Cargill. It produced several hybrid Bounty numbers, which began to top the advanced yield trials in 1981 and continue to do so. For example, in the 1983, 1984, and 1985 Kansas State Advanced Yield Trials, Bounty 203 produced an average yield of 70.8 bushels per acre versus an average yield of 61.1 bushels per acre by Arkan, considered to be a top conventional wheat variety (Table 3). Hybrid wheats produced by cytoplasmic male-sterile–restoration factor technology have also been released by Pioneer International, Nickerson American Plant Breeders, and Hybridtech (Monsanto). Their hybrids have followed Bounty's lead by performing well in advance yield trials.

In 1987, however, due to the depressed wheat economy, Pioneer International dropped its domestic commercial hybrid wheat program. Cargill, Nickerson American Plant Breeders, Monsanto, and North Dakota State University remain active with ongoing commercial hybrid wheat programs Their success now depends on how well commercial hybrid wheat is accepted by farm producers.

The Male-Sterility System

While efforts in the late 1960s were being made to further advance cytoplasmic male-sterile–restoration factor technology, work was also being done on a much smaller scale by these same organizations to develop a male-sterile technology that could be used to create hybrid wheat. This system differs from the cytoplasmic male-sterile system in that the male-sterile trait is determined by genes within the nuclear genome (versus a cytoplasmic-nuclear interaction). A female male-sterile is required for this technology to produce fertile hybrid offspring.

In the mid-1960s, A. Bozzini and G. T. Scarascia-Mugnozza (1968), working at Laboratorio per le Applicazioni in Agricoltura del CNEN, Rome, Italy, found an inherited male-sterile system in *Triticum* genus. Because this system was simply inherited (or controlled by one dominant gene), the technology could be easily managed. At this point several genetically based complications arose in using the cytoplasmic male-sterile–restoration factor systems, and alternative technologies were sought. Ongoing research groups readily took an interest in developing the male-sterile technology, as it not only showed promise but was easily manipulated genetically.

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its own work with gametocides and hybrids. Because Monsanto is principally a chemical company, it needed to form a joint venture with a seed company to produce hybrids using gametocides. However, since joint ventures often end up debating over proprietal rights, Monsanto wanted to own its own seed company. To date, Monsanto has continued developing hybrid wheat using both cytoplasmic male-sterile–restoration factor and gametocide technology.

Table 3.—Advanced Yield Results in Kansas:
1983, 1984, and 1985
(Bushels per acre, not irrigated)

Hybrid name[a]	Firm	16-station average	14-station average	16-station average
Hybrids from CMS-Rf				
Bounty 100	Cargill	66.3	63.0	66.0
Bounty 201	Cargill		67.9	
Bounty 202	Cargill		65.6	66.0
Bounty 203	Cargill		71.3	70.3
Bounty 301	Cargill		64.4	68.9
Bounty 310	Cargill	68.3	65.6	64.4
Quantum H1260	Monsanto		58.7	
Hybrids from PS				
Hybrex 1010	Rohm & Haas	62.1	61.0	
Hybrex 1019	Rohm & Haas		58.9	
Hybrex 1018	Rohm & Haas		59.8	
Top conventional varieties				
Arkan		61.6	60.6	60.8
Hawk		59.9	56.6	59.1
Newton		56.5	57.5	56.1
Tam 105		60.8	61.8	54.8
Tam 107			67.1	57.7
Vona		61.8	56.7	55.8
Agripro			59.6	60.6

Source: Kansas Agricultural Experiment Station, 1983, 1984, 1985, *Performance Tests with Winter Wheat Varieties: Report of Progress*, Kansas State University, Manhattan.

[a]CMS-Rf and PS refer to hybrids produced via cytoplasmic male-sterility–restoration factor and pollen suppressor technology, respectively.

Soon after male-sterile research commenced, inherent problems with this sytem arose and proved much more severe than the problems uncovered during the cytoplasmic male-sterile–restoration factor development. General problems in managing this genetic system stemmed from higher ploidy levels, $G \times E$ interaction, gene instability, polygenetic system, epistasis, and modifier genes. These problems left male-sterile–produced hybrid wheat low-yielding and more susceptible to diseases such as ergot and loose smut (Wilson, 1968). Because of the severe problems associated with the technique, virtually all efforts to develop this system were dropped by the early 1970s.

The Gametocide System

The third line of seed production technology development on hybrid wheat breeding was the use of gametocides, or pollen suppressors. A pollen suppressor is a growth regulator that upon application is translocated to the anther locules where pollen is produced. This in turn causes the sterilization of the pollen. A wheat plant becomes male-sterile without genetic manipulation. Hypothetically, direct lines from conventional wheat-breeding programs could easily be transformed for use in a commercial hybrid wheat program.

While the wheat industry was having problems associated with cytoplasmic male-sterile–restoration factor systems, the technology of chemical induction of male sterility via pollen suppressor in plants emerged. Researchers were optimistic that a chemical could be developed soon for producing male-sterile wheats. The enthusiasm was contagious, and the private sector became active in gametocide research and in fact took the lead. In 1971, Rohm & Haas became the first firm to begin research and development of hybrid wheat via pollen suppressors. Shell and Monsanto followed in 1975 and 1982, respectively.

The results were ultimately disappointing. In 1987, Rohm & Haas decided progress was too slow and continued development of a pollen suppressor was financially too risky. Consequently, they dropped their program. Shell and Monsanto are still developing the pollen suppressor technology although at reduced levels. Their most recent products are far better than any of their predecessors. The resulting hybrid wheats are beginning to attain yield levels similar to those of the conventional varieties and hybrid wheats via genetic manipulation (Lucken, 1982; Kansas State Experimental Station, 1983, 1984, 1985). The major stumbling block is that the 100 percent male sterility needed in the female parent for hybrid production has yet to be attained. Thus seed and self-seed will be produced by the female parent after fertilization. This mixture results in the undesirable traits of nonhomogeneous crops and lower yields.

TOWARD A COMMERCIAL SUCCESS

The path of commercial hybrid wheat's research and development has been difficult. The dramatic change in actors and resources committed to this research reflect this turbulence. In this final section the changes in actors and resources are reviewed, and the potential for adoption of hybrid wheats over the next few years is discussed.

Up until 1960, the public sector did most of the research on commercial hybrid wheat. Kihara, Fukusawa, Wilson, Ross, Johnson and Schmidt were all from public institutions. Its active role was complemented by the private sector in the search for a cytoplasmic male-sterile–restoration factor system. Virtually all wheat programs throughout the world were conducting some research on the subject. But the private sector does not usually pursue a research program unless there is some reasonable probability that a profitable product can be developed. In the early 1960s the probability of successful hybrid wheat development appeared to be low.

Public sector agricultural research institutions invested in wheat breeding despite the uncertainties involved because the research also promised to advance basic knowledge in genetics or in breeding technology. Most programs, however, were funded at very modest levels.

Beginning in 1960, the private sector took the lead in commercial hybrid wheat development. Research was still primarily basic, but now it focused on developing a marketable product: commercial hybrid wheat via cytoplasmic male-sterility–restoration factor technology. Experiments were designed principally to examine how the system worked, however, some parental development was also done.

Although both sectors invested more when a technology to produce hybrid wheat became available, the private sector had relatively more to gain from advances in hybrid wheat development. Until 1961, no legal protection existed that would prevent a farmer from selling his harvested seed to his neighbor.

The public sector did not have to concern itself with having a built-in trade secret. It could divide its resources between commercial hybrid wheat development and semi-dwarf wheat varietal development. This was a desirable strategy because it allowed universities to develop both systems until it was clear which system was best for producing higher yielding wheat.

The principal actors for the private sector at this point were Cargill, DeKalb, Nickerson American Plant Breeders, Northrup King, and Pioneer International. The principal actors for the public sector were Washington State University, Kansas State University, North Dakota State University, University of Nebraska, and Texas A&M University.

Because more money and resources were required for research between 1961–70 than ever before, seed company managment and State Experiment Station Directors, typically the decision makers for the private sector and public sector, respectively, set up strict criteria to measure and evaluate the progress of the programs. Because of the shorter development times involved, progress was checked every two to three years.

By the end of the 1960s, because of the numerous innate problems of cytoplasmic male-sterile–restoration factor systems in wheat, few programs showed reasonable progress. At the same time, semi-dwarf wheat varieties offerred a viable alternative. The Plant Variety Protection Act passed in 1970, making it no longer necessary for private actors to worry about having a built-in trade secret in their product, and they now could invest in pure-line varietal development. Therefore, all public sector actors, with the exception of North Dakota State University, and many small firms, such as Funk Seeds, dropped their hybrid wheat programs, and invested in semi-dwarf wheat varietal development.

This directional change in research and development by small firms and universities did not require a big change in resources. Almost all of these institutes had relatively modest amounts invested in the research and development of commercial hybrid wheat and did not have much to lose by dropping their commercial hybrid wheat programs. In fact, they could take parents being developed in commercial hybrid wheat programs and use them in their semi-dwarf wheat programs.

Cargill, DeKalb, Nickerson American Plant Breeders, Northrup King, Pioneer International, and North Dakota State University continued their hybrid wheat programs. They were joined by two other groups, both of whom introduced a new technology to help develop commercial hybrid wheat. One group from the public sector processed the production of hybrids using male-sterility technology. But due to difficulties with this system, its participation was discontinued. The group from the private sector—Rohm & Haas, Shell, and Monsanto—introduced pollen suppressor technology and the latter two firms continue their work in this area.

Research on the cytoplasmic male-sterile–restoration factor technology and pollen suppressor technology was mainly applied and focused on parental development, gametocide development, and commercial hybrid wheat yield performance. Each one of these three areas was used for measuring research progress which was again reviewed every two to three years.

Innovation development research typically requires more resources as the final testing of the product is carried out. The testing period is often considered the most expensive part of a plant-breeding program. For example, it is usually two to three times more expensive to test a new variety or hybrid than to develop parental lines. Consequently, actors that had already invested quite heavily in commercial hybrid wheat development were not afraid to drop their programs when the likelihood of developing a commercial hybrid wheat looked doubtful. Northrup King and DeKalb both dropped their programs around 1980 before they committed themselves any further to this testing stage. Their decisions were influenced by the slow progress commercial hybrid wheat development made in the 1970s. Pioneer and Rohm & Haas were more optimistic but, due to poor economic conditions, dropped their programs in 1987.

In recent years, some of the hybrids, noteably Cargill's Bounty, have begun to do well in advanced yield trials. However, improved yield performances do not guarantee the economic success of commercial hybrids. At a seeding rate of 50 pounds per acre and a cost of $22.50 per 50-pound bag of hybrid wheat seed (via cytoplasmic male-sterile–restoration factor), the farm producer pays $22.50 per acre for hybrid wheat seed, 2.2 times the cost of conventional seed at 60 pounds per acre, and $6.80 per 40-pound bag, or $10.20 per acre. Commercial hybrid wheats perform less well under averse conditions, such as drought, than conventional wheat varieties do, conditions that occur on an average of once every three years.

The 1985 state yield trials in Kansas, Colorado, Nebraska, Oklahoma, Missouri, and Texas show the top hybrid wheats to yield from −2 to 13 percent, averaging 6 percent more than the top conventional variety in state yield trials (Table 4). These yield advantages are not quite consistent enough to make commercial hybrid wheat a viable alternative to conventional varieties. However, in the opinion of many scientists and administrators, in a few years hybrid wheat's yield potential will be demonstrated.

Table 4.—Yields of the Top Commercial Hybrid Wheats and Conventional Wheat Varieties in Various State Yield Trials
(*Bushels per acre*)

	Top hybrid wheat	Top conventional wheat	Difference (percent)
Kansas	68.9	60.8	13.3
East Colorado (irrigated)	100.5	96.1	4.6
Colorado (dryland)	54.2	53.4	1.5
Nebraska	64.0	57.0	12.3
Oklahoma	66.7	60.4	10.4
Missouri	63.0	57.4	9.8
Texas, Oklahoma Highplains	58.2	59.2	−1.7
Texas Highplains (forage in lb/a)	4,531	4,453	1.8

Source: Cargill, 1986, *Bounty Hybrid Wheat 1986–87 Management Guide*, Minneapolis.

But even this increase may not make it a strong competitor on the U.S. wheat seed market. Absolute yield gains are not very high: 5.25 bushels per acre assuming a 15 percent yield advantage at an average yield of 35 bushels per acre for conventional varieties. These two facts together make commercial hybrid wheat less attractive to the farmer.

Commercial hybrid wheat's largest potential market in the immediate future may be in the European Economic Community (EEC), where average wheat yields are double those in the United States (USDA, 1987). Average absolute yield gains could be 10.5 bushels per acre, assuming an average of 70 bushels per acre for conventional varieties and a 15 percent yield advantage. This gain coupled with wheat prices provide a market more favorable for hybrid wheat seed. A commercial hybrid wheat has already been developed for this market. Some of the same firms involved with hybrid wheat development in the United States, such as Shell and Cargill, are active in this research in the EEC. How well commercial hybrid wheat does in the EEC market as compared to the U.S. market would make an interesting comparative study and opens up questions of policy regarding technological transfer.

The final question is whether or not commercial hybrid wheat is a competitive alternative to conventional wheat varieties. Factors, such as relative input prices, market prices, and how fast hybrid wheat can widen the gap between it and conventional wheat varieties, will help determine its success and where its market will be. This story should be more complete in five years when enough time will have passed for farmers to have gained more practical experience with commercial hybrid wheat.

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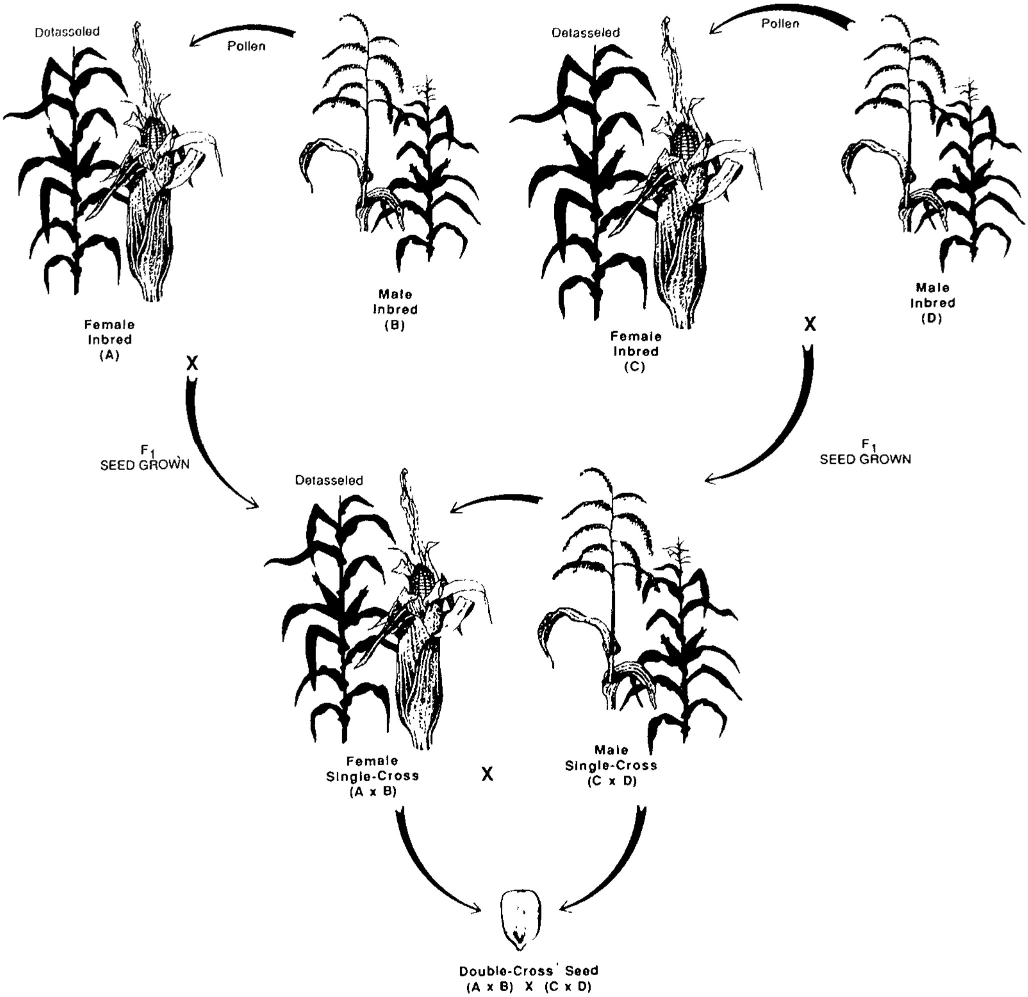
APPENDIX A

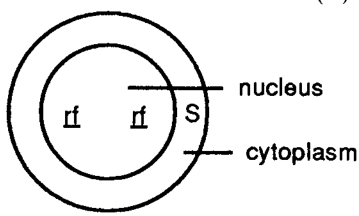
Appendix Figure A1.—Production of Double-Cross Hybrid Corn Seed, 1979



Source: Adapted from S.L. Becker, 1976, "Donald Jones and Hybrid Corn," Bulletin 763, Connecticut Agricultural Experiment Station, p. 8.

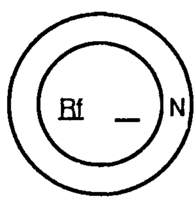
APPENDIX B: COMMERCIAL HYBRID BREEDING VIA CYTOPLASMIC MALE-STERILITY-RESTORATION FACTOR TECHNOLOGY

The following demonstrates how a cytoplasmic male-sterile–restoration factor system works in a diploid plant like corn. In a diploid, two sets of chromosomes (one set of genomes) are present in the plant's nucleus. Cytoplasmic male-sterility results from the interaction of recessive, non-restorer (non-fertile) genes (*rf rf*) in the nucleus and a sterile (S) cytoplasm.



The *rf* genes are contributed by both parents, and the sterile (S) cytoplasm is from the female. Only the female transmits the cytoplasm of a cell to future generations.

Fertility is restored in subsequent generations by crossing the cytoplasmic male-sterile plant with a male plant that has the genetic restoration gene combination along with a (*Rf* _) normal cytoplasm,



The resulting progeny will have the nucleus gene combination, *Rf rf*, which restores the male fertility system within the plant. This restoration ability is essential if the next generation is going to be able to self-fertilize and produce seed. In commercial hybrid breeding, the hybrid plant grown from the hybrid seed self-fertilizes to produce commercial seed.

In a breeding program using cytoplasmic male-sterile and restoration factor systems, A, B, and R lines are developed and maintained. A lines are female parents with *rf rf* and S. Usually the A lines are created through a series of backcrosses between an S *rf rf* female and an N *Rf rf* male in which the female denotes the desired cytoplasm and the male denotes the desired genome that will be found in the A line. All the progeny wil have S cytoplasm; 50 percent will have the genetic restoration gene combination S *rf rf*, and hence will be male-sterile. The other 50 percent of the progeny will be *Rf rf* and male-fertile. The male-fertile plants can be distinguished from the male-sterile plants because the anthers of the fertile plants are normal and those of the sterile plants are shriveled. Fertile males are discarded;

the remaining progeny are crossed back (backcrossed) to the original male. Fertile males in the next generation are selected out again and discarded. This same procedure is repeated until the male-sterile progeny (S *rf rf*) have more than 90 percent of the original male parent's genome transferred into this S cytoplasm.

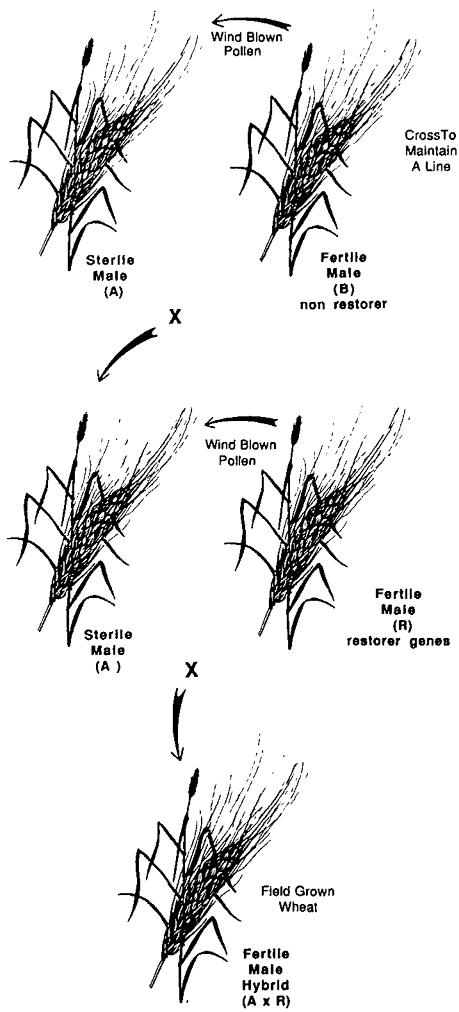
B lines have the genetic restoration gene combination *rf rf* and a normal cytoplasm, N. The genome of the B line is similar to the A line's genome. The main difference between the two lines is that the B line has normal cytoplasm, N, and the A line has sterile cytoplasm S. The B line is used if any maintenance work is needed on the A line, such as increasing disease resistance. After the work is done on the B line, its genome is transferred over to an S cytoplasm through a series of backcrosses. B lines are called the maintainer lines.

The R lines have normal cytoplasm and are male-fertile (N *Rf Rf*). They are the male parents that are used in the final hybrid crossing. They usually are selected to be used as a male parent because they offer such desirable characteristics as higher yields or genetic diversity, and they can restore male fertility to the hybrid by transferring their *Rf* genes to the hybrid progeny. This system works similarly in plants with different ploidy levels than diploids.

APPENDIX C

The male-sterile A-line is maintained by pollination from the B-line, which is genetically identical but is in normal cytoplasm. The hybrid seed is produced by pollinating the A-line from the R-line. The R-line has dominant fertility-restoring genes and combines with the A-line to produce a high yielding hybrid.

Appendix Figure C1.—Scheme for Producing Hybrid Wheat Using Male-Sterility and Fertility-Restoring Genes



Source: Adapted from John M. Poehlman, 1979, *Breeding Field Crops*, AVI Publishing Co., Westport, p. 181.