New Horizons In Wheat Breeding

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Wheat breeding in its simplest form has probably been practiced for 10,000 years. I had the opportunity two years ago to walk through a Bedouin's wheat field in Israel — we were near the city of Nazareth. It was an incredibly diverse population he was growing — tall and short, early and late types, lax and compact spikes, bearded and beardless heads, both tetraploid and hexaploid genotypes. He explained how he kept some of the grain as seed for next year, always being sure to sample the whole population. Through our interpreter I asked him why he did not select the best plants and retain them as his seed. He responded that some years were not as good as 1985, and he wanted to be sure he had some crop!

All wheats developed prior to 1890 were products of people who practiced the art of plant breeding — simple selection. Crossing of varieties occurred at the end of the nineteenth century. In the first decade of this century, rediscovery of Mendel's laws provided a scientific basis for our wheat breeding by elucidating the mechanism of segregation and the laws of inheritance. In the second decade, Morgan and his colleagues mapped Drosophila chromosomes and thereby explained linkage and recombination of traits. In the third decade, the Russian scientist Vavilov collected germplasm of cultivated species and their wild relatives and established gene banks, which became the forerunners of modern germplasm banks — the backbone of our crop breeding programs today.

Developments in cytogenetics in the fourth decade, considered the golden era of cytogenetics, improved plant breeders' understanding of chromosome structure and function and mechanisms of recombination. The discovery of colchicine in the fifth decade raised hopes of producing new varieties of crops through polyploidy — wheat was crossed with rye to produce triticale. Colchicine has proven a powerful tool in overcoming some of the barriers to interspecific gene transfer. The sixth decade saw the use of x-rays in generating new variability, and this spawned the use of numerous mutation induction techniques. The seventh decade will probably be known for developments in biometrical and quantitative genetics which have helped the plant breeder formulate selection strategies and conduct stability analyses. In vitro techniques developed during the

eighth decade have been extensively used in some crops to obtain homozygosity and fix dominance variance. Opinions will vary on how we will judge the ninth and tenth decades — certainly recombinant DNA technology and other new biotechnologies will be at the forefront.

However, as we reach forward to eagerly grasp new technologies, we need to remind ourselves constantly of what our objectives truly are. We need to remain endproduct driven and recognize the emerging technologies for what they are — exciting tools that may greatly facilitate our task... but tools nevertheless. I was fortunate in being able to start my wheat breeding career at the end of 1965 with a man who had a tremendous clarity of thought. Olaf Johan Olesen, who later became known as Rhodesia's "Great Dane," probably used more art than science in his wheat breeding. He was never too impressed by statistical analyses, but he would spend many hours poring over a pan of seed and picking the "good ones"! He wanted dwarfism in the wheats and a high response to fertilizer and irrigation. The Olesen dwarf, which contains the Rht3 gene, certainly had its limitations - including chlorophyll deficiency, an open seed crease, and a poor response to stress. But it was a start. We added other dwarfing genes and corrected the seed and chlorophyll problems. The lessons I learned from Olesen, and will always hold dear, are that you don't develop varieties by the 'seat of your pants' in an office or at a computer terminal; you don't develop them in a radiation lab or in a petri-dish; you ultimately have to identify those varieties in the field!

The History of Our Spring Wheats

We can learn a lot from examining the origins of today's spring wheat varieties. We hear concerns being raised that the use of wider crosses by wheat breeders today has complicated the separation of the wheat classes. There is some validity in this statement. However, our early wheat breeders showed remarkable ingenity. Marquis wheat was developed in 1907 from a cross between a winter wheat, Red Fife, and an Asian spring wheat, Hard Red Calcutta. A double cross between Marquis x lumillo (a durum wheat) and Marquis x Kanred (a winter wheat) gave us Thatcher. Thatcher has been a parent in a whole array of spring wheat varieties ranging from Newthatch (1944) to Justin in 1962. Newthatch itself had Hope as a parent — and Hope was derived from a cross between Marquis and an Emmer wheat. It is perhaps humbling for those adventurous

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breeders of today to realize that wide crosses have been made for 90 years!

Genetic Gains Through Conventional Breeding

"The Yield Plateau"

Every few years we seem to ask ourselves the question of whether our wheat yields have 'peaked out'. However, we have to take a number of factors into account when we attempt to assess genetic gains:

- Are we looking at actual production yields, or are plant breeders addressing the question to current and potential genetic gains?
- 2. Yield increases must be divided into genetic gains and production gains.
- 3. Of the genetic gains, how much is due to the incorporation of disease resistance?
- 4. What region or array of environments are we referring to when we cite yield increases?

A 1953 publication by Salmon and his co-workers credited improved wheat cultivars with providing 40 percent of the increase in wheat production in the U.S. during the half century ending in 1950. They also pointed out that actual yields and potential yields are usually not the same. When Reitz and Salmon analyzed wheat yield data from the hard red winter wheat region, they concluded that over a 20-year period from 1931 to the early 1950s the gains from new cultivars ranged from 10-30 percent.

The region of testing is important. In Nebraska the yield increases credited to breeding are greater in the more humid eastern half of the state than in the drier western half. It has also been pointed out by Evans that selection for adaptation may result in yield increases but may not represent selection for greater yield potential. He suggested that average annual increases for yield potential of 0.5-1.0 percent had been obtained for many crops. Hueg (1977) indicated that not all of the increased yield attributable to cultivars is due to genetic improvement. He estimated that in Minnesota, of the 51-56 percent increase in wheat yield attributable to cultivars, 26-29 percent resulted directly from breeding for yield, and the remaineder was due to incorporating disease resistance.

Schmidt (1984) used uniform regional nursery data from nine nurseries to evaluate genetic contributions to yield gains. He concluded that genetic improvement had been least in those nurseries grown in harsh climates and greatest in the more productive wheat regions. When he composited the data from all nine nurseries it was found that the annual rate of gain was about 0.74 percent during the period 1958-1980.

Have crop yields peaked out? Some suggest that they have while others suggest that yield increases through conventional breeding will continue but at a slower rate.

Rajaram and Curtis of the International Maize and Wheat Improvement Center (CIMMYT) in Mexico have summarized what they consider to be the major breakthroughs in their spring wheat breeding efforts.

- The introduction of the dwarfing Rht1 and Rht2 during the 1950s raised the yield potential to about 6000 kilograms per hectare.
- Selection of material for increased spike fertility in the 1960s pushed the yield potential up to 7000 kilograms per hectare.
- The 1B/1R translocation in which a piece of rye chromosome was substituted for a piece of the 1B chromosome — was used in the 1970s, and the products have raised yields to 8000 kilograms per hectare.
- The utilization of upright leaf characteristics in the 1980s has raised yield a further 500 kilograms per hectare to 8,500.

The use of Rht1 and Rht2 dwarfing genes controlled lodging, improved harvest index, and increased biomass. Biomass is simply the weight of all the plant's above-ground parts, including the grain. The harvest index equals the grain weight divided by the biomass.

It was the higher rate of partitioning of assimilates into the grain of these semidwarfs that resulted in higher yields.

Most people agree that further selection for increased harvest index will not be productive, and attention has focused on biomass production. Studies at the Plant Breeding Institute have shown the theoretical upper limit for yield to be 13 tons per hectare in the U.K. under prevailing solar radiation, crop growth cycle, photosynthetic rates, and harvest indices. This yield level of 13 tons per hectare has actually been attained under farm conditions with intensive management systems.

Crosses between winter and spring wheat have already demonstrated the potential for improving plant biomass in spring wheat. It is likely that this will continue to be a highly productive area of research in the future. Interspecific and intergeneric crosses offer further promise in increasing yields. Crossing bread wheat to durum wheat is an excellent approach to selecting for higher grain weight. Interspecific efforts due to the existence of close phyllogenic relationships, ease of crossability, and opportunities of a high recombination status offer wheat relatively short-term payoffs (7-10 years). The more distant alien species contributing to intergeneric crosses are likely to fit more long-term goals (15 years). The returns could be quicker if relevant, simply inherited traits are fitted into the program.

Hybrid Wheat

One of the main arguments in favor of hybrid wheat is that if we are indeed approaching a yield plateau, or yield increases through conventional breeding are likely to be slower in the future, then hybrids offer one avenue of bringing about another major yield breakthrough. We have now seen 25 years of hybrid wheat research since Wilson and Ross established the existence of usable cytoplasmic male sterility in 1962 and Schmidt and his coworkers, along with Wilson and Ross, found a suitable restorer line. In the first decade of hybrid wheat research, efforts were directed largely toward perfecting the CMS system, and the two major difficulties encountered were those of securing adequate male-fertility restoration and demonstrating standard heterosis for grain yield. During the second decade, considerable progress was made on improving restoration, and as breeders broadened their germplasm pools, improved levels of heterosis were obtained. Overlapping this period of CMS research was active research on chemical hybridizing agents, or CHAs.

During the past five years we have seen the emphasis change to CHAs as the primary hybrid delivery system. However, the acreage grown to commercial wheat hybrids remains very small. Hard red winter wheat hybrids have demonstrated a 10 percent yield advantage over the best conventional check cultivars in multi-year and location testing in Kansas and Oklahoma. The question is this: Are these yield advantages sufficient given the situation today? Farmers' acceptance of hybrids will be strongly influenced by the extra seed cost per acre, the anticipated yield increase of the hybrid compared with the average on-farm yields of varieties, and the grain market price. So the question arises: What is the future of hybrid wheat?

Hybrid breeding is undoubtedly more efficient than conventional breeding. CHAs have enabled programs to produce and test considerably larger numbers of hybrids than the CMS system would allow. It is also possible to evaluate both the male and female inbreds for general and specific combining ability, since reciprocal hybrids can be made. Hybrids also provide a means of utilizing more exotic germplasm as inbreds. In contrast, crosses with exotic lines suffer inbreeding depression in conventional programs, and recovery of superior genotypes is often more difficult.

I believe that hybrids will tend to be produced for higher yielding areas in the future, such as the irrigation area in the hard red winter wheat region, California, and the Pacific Northwest. There is stronger interest in hybrid wheat in Europe, notably France, at the present time. Most would agree that, providing there is a 15 percent yield advantage, at the present seed costs, seeding rates, and grain market prices, hybrid wheat would offer a 2:1 return on investment for the farmer and an acceptable profit for the seedsman. Consistency of seed set at a level of 60 percent or above in hybrid production blocks has yet to be attained. Also, the question of hybrid purity arises when a CHA is used, and the current sampling procedures and use of electrophoresis practiced in Europe are being challenged, and matters have not been finally resolved. So, in summary, the jury is still out!

Biotechnology

Biotechnology is an ever-growing bandwagon, and in some circles, there has been something bordering on paranoia to clamber aboard for fear of missing out on the potential breakthroughs that will undoubtedly occur in the future.

Cell culture is making available a new, unanticipated source of genetic diversity. It was originally assumed that the plants regenerated from the same clump of tissue would be identical. Yet many of the plants arising from undifferentiated cells in culture are strikingly different from each other and the parent plant from which the culture was derived. The exact cause of somaclonal variation is uncertain. although theories abound. What is clear is that the phenomenon is ubiquitous, occurring in rice, corn, wheat, barley, potato, alfalfa, rape, and other species and affecting many agronomically use traits. At the Plant Industries Division of CSIRO in Australia, Snowcroft and his colleagues are looking for useful variants arising from the culture of wheat. They pay little attention to the plants generated directly from culture, because much of the variation occurring in them is unstable. Instead they look to their progeny to see if the traits are stably transmitted. Research is still at an early stage, and one has to consider that, with all the mutation breeding that has been carried out on wheat, the number of successful end products are few indeed.

To complete the genetic engineering of wheat, it will be necessary to learn how to insert the genes into cells of the plant and obtain a plant with the new genes stably inserted into chromosomes.

Researchers have been attempting various techniques on cereal grains to isolate and grow individual cells, incorporate DNA into those cells, and then regenerate the cells into a plant. Transformation of cells uses such techniques as micro-injection (using a microscopic needle to shoot the DNA into the cell), electroporation (using electrical shock to make the cell take up DNA), osmotic shock (using salt solutions flooded over the cells to make then take up DNA), and bacterial infection. The techniques have met with complete facilure when applied to small grains, except for rice.

However, a potential breakthrough in rye was reported this last January that may improve the chances that biotechnology may assist wheat research. A special preparation of DNA was used that gives plants resistance to kanamycin. They used a normal-sized syringe to inject it into the developing spike of rye plants. The DNA was taken up into the sexual organs (possibly the pollen) and then sexually transmitted to the rye kernels. When the resulting seeds were grown out the scientists found 3 out of 1,000 seeds resistant to kanamycin. The success ratio is considered quite high, and the beauty of this direct injection technique is that it bypasses the laborious steps of trying to grow plant material from single cells following transformation. If it works on wheat we could see glyphosate-resistant wheat in about five years.

Identifying important genes and blocks of genes for plant improvement and discovering ways to insert them into a plant's DNA will continue to be a major research activity.

Before we leave this subject, perhaps we need to clarify the future role of the biotechnologist. I would expect to see him link up as an integral part of the breeding team in much the same way as the plant pathologist is a vital link today. Biotechnology will complement and facilitate current breeding efforts — it will not substitute for the evaluation of

genotypes in the field. A farmer's crop will remain a genotype x environment interaction!

In future there will be increasing pressure to make biotechnology available to developing countries. Given the number of other problems of production that remain to be solved, one might question the need. However, there is real concern that developing countries may miss the race completely if they do not keep abreast of developments in biotechnology, and it is highly probable that funding agencies will respond to this concern.

Plant Variety Protection and Plant Patents

The Plant Variety Protection Act of 1970 made it possible for large and small developers of crop species to keep the flow of improved varieties coming by helping them recover their investments in genetic research. The protection covers a particular genotype — not the genes themselves. Other institutions or companies have been free to use the variety or hybrid in crosses and recover favorable genes in new genetic combinations.

Wheat breeding over the years has depended heavily upon the free exchange of germplasm for cooperative nursery programs, international centers such as CIMMYT, and various germplasm depositories. Not only has this had a very significant effect upon genetic gains, but it has also kept research and development costs — and ultimately seed costs — in line with market realities.

Over 30 years ago, Dr. Emie Sears of the University of Missouri reported on the transfer of resistance to leaf rust from a wild wheat (Aegilops umbellulata) to bread wheat. This work involved using another species as a bridge to facilitate crossing and gene transfer, the doubling of chromosomes, and the use of irradiation. It was the type of innovation that would have many scurrying for patent registration today. Instead, this technique was made available to all, and many of the methods and products of whole chromosomes, chromosome segments, and gene transfer from related genera to common wheat have had a dramatic impact on wheat production in the U.S. and elsewhere.

In the genetic supply industry, innovation must be protected and rewarded if we are to see a continuing investment in research and development. There will undoubtedly be long philosophical arguments over the question of what represents true innovation, and it is becoming increasingly clear that lawyers and administrators are not always in agreement with scientists on this question.

There are numerous genes in wheat that are potentially patenable. Specific examples are genes for reduced plant height (Rht genes), for specific resistance to diseases, and genes for high protein content. One group overseas is even considering patenting the high protein trait from a wild wheat species.

In the future biotechnology will provide many unique processes, and we have already witnessed the insertion of

genes into plants that do not occur within the species or related genera. Such innovation deserves to be patented and protected, and the developer should reap the benefits of their scientific success. There are also legal precedents for patenting genes that occur in nature.

However, a primary concern today is that we are witnessing an increasing trend toward patenting of genes that are not the result of recent innovative research. The bottom line of these events is that in future breeders will have to deal with the issue of patents on material they need to use. Germplasm represents the raw material for plant breeders. Developing countries that are an important source of wild species are closely watching events in developed countries. Some countries have banned the outflow of germplasm while others have imposed selective restrictions. This is a highly sensitive issue, and we need to be strongly aware of the consequences of an over-zealous attitude toward plant patents.

Dealing With Oversupply

A high proportion of the world wheat carryover stocks are at present held a handful of countries — the U.S., the EEC, India, and China. In India and China stocks are held at high levels deliberately for food security reasons. The effect of our U.S. wheat surplus and the farm set-aside programs has had a dramatic effect upon public sentiment toward funding research programs. There is a strong move toward the diversion of public funds to other areas, notably biotechnology, and a number of breeding programs are suffering as a result. This is short-sighted and unfortunate — never has the need been greater to improve our production efficiencies and improve our competitive advantage.

Sooner or later the current world wheat surplus will come to an end. The increasing demand from low-income developing countries shows how vulnerable they would be to higher prices. A series of monsoon failures in Asia or some catastrophe in a major producing country could, once current stocks are reduced to manageable levels, bring a repetition of the world food crisis of the 1970s. We will need to be able to respond rapidly to a changing situation.

Notwithstanding the above, many believe that our markets are likely to be smaller and more specialized in the future. This suggests that breeders will need to place more emphasis on quality. They will also need to work more closely with industry in identifying specific quality niches that can be filled. We will probably see more vertical integration of the industry and contracted production, whereby growers will have to grow specified varieties for the processor. The issue of stability of quality will also need to be addressed in more detail. Cereal chemists do not understand genotype x environment interactions! Recent advances in the application of N.I.R. instrumentation will be important in providing screeing tools for breeder samples.

Where Do We Go From Here?

What then is our profile of a wheat breeder in the 21st century? The first point to make is that variety or hybrid development is a team effort and the product of many

hands. I believe the days of the "rugged individualist" have gone and, in future, the team effort directed toward effective resource management and rapid incorporation of new techniques and emerging technologies will prove successful.

Very often it can be a very simple innovation that can dramatically improve our breeding efforts. For example, the cell indexer or bubble tray has enabled us to handle large populations of single head selections from crosses — nurseries with 1000,000 F3 head rows are a reality today where 20 years ago they were unthought of. Weigh systems on combines with portable data recorders which interface with the computer system via a modem have greatly improved harvest efficiency. Our company has now completed five seasons with these units for yield, test weight, and moisture on our wheat combines. Intelligent use of the computer for the planning of crossing blocks, trait complementation, and nursery management from the time of the initial cross to varietal release has greatly facilitated our task.

Breeders in future will need to respond more rapidly to changing market situations. The concept of waiting 10 years to develop a variety with particular traits may well go by the board under certain circumstances if the company or institution wishes to remain competitive. Hybrids offer increased flexibility and so does anther culture and doubled haploids. Anther culture has been relatively slow to emerge as a routine tool in wheat programs, and work remains to be done to ensure that a wider range of germplasm lines are adapted to the culture medium.

One of the consequences of increased competition in the genetic supply industry is a move toward more specific adaptation. As I mentioned earlier, this is how some of the so-called yield advances are being attained. We have seen in the corn industry and in the soybean industry the move to very closely-defined relative maturity niches. Some are complaining that there are too many wheat varieties on the market today, and buyers have more difficulty predicting quality. I would submit, however, that this is a natural consequence of competition — in the same way as we encounter more bakery products on a supermarket shelf. What we tend to find is that farmers quickly recognize the top varieties, and they tend to occupy major acreage.

Identification of specific market niches will be a challenge in the future. Closer links between the breeder and the end processor seem inevitable. Markets for very high protein wheats or wheats with qualities suited to specified bakery products may well develop. Today Anheuser-Busch not only has a barley breeding program to provide the malting quality they desire — they also have a rice breeding program to provide for one of their major beer adjuncts.

Who will do the breeding in the future? Private or public institutions? I would hope both prevail. The funding cuts in university programs are cause for grave concern, and certainly USDA administrators show little enthusiasm for embarking on any new breeding programs. Companies face the problem of very low margins on varietal wheat seed, and the farmer's grain bin remains a major competitor. This has led to the concept of looking for ways to make a product proprietary by means of seed coatings with microbes that will either cut fertilizer usage or confer a yield advantage. Many strains of free-living, N-fixing organisms have been

identified, and the key will be to identify those with significant effects. Developing countries will still need assistance with germplasm that will yield varieties for local production. The role of breeding at CIMMYT will, I believe, be as important in the future as it has been in the past, providing the current breeding efforts are not tampered with. At a meeting in El Batan, Mexico, a few months ago. Dr. Don Marshall, dean of agriculture at the Waite Institute, University of Adelaide, Australia, remarked that it was an eye-opener for Australian breeders to find that with all their years of effort at the local level, Veery sib from CIMMYT is the top yielder in the national trials.

One reality that cannot escape us as we look toward some high tech solutions in the future is where our wheat is actually grown. In the main it is grown in areas of stress — both biotic and abiotic. To use one illustration — heat stress is one of the limitations on yield in most of the hard red winter wheat region and a significant portion of the spring wheat region. If we look at the maturities of our spring wheats for South Dakota, we have used heat avoidance rather than heat tolerance! Dessication techniques have been used as a screening tool for heat tolerance, the purpose being to determine the capacity of the plant to remobilize and translocate carbohydrate to the grain after loss of wheat canopy.

I have been involved in maximum economic yield studies for some time. It is interesting to note the evolution of our maximum yield groups here in the U.S. Some early enthusiasts sought to superimpose a European management system. British wheats have the luxury of a two-month grain fill. Our HRW wheats are lucky to have 30 days. Those who have grown British wheats in the International Winter Wheat Performance Nursery in, for example, Nebraska or Kansas will know what I mean when I say these wheats have problems.

Breeding will always have to be in phase with our environment, rate-limiting steps will have to be recognized, and techniques used to select for genotypes that overcome these abiotic stresses. Our future lies in improving production efficiencies and lowering the cost per bushel produced by our growers. It is an exciting future, and I believe there will always be a job for those who are willing to blend their scientific knowledge with a willingness to look at plants in the field.

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