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The World Wheat Book

A History of Wheat Breeding

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Mexico: 50 Years of International Wheat Breeding

Sanjaya Rajaram and Martin van Ginkel

Wheat is the most widely grown and consumed food crop worldwide. It is the staple food of nearly 35% of the world's population and demand for wheat will grow faster than for any other major crop. The forecasted global demand for wheat in the year 2020 varies between 840 (Rosegrant *et al.*, 1995) and 1,050 million tonnes (Kronstad, 1998). To reach this target, global production will need to increase 1.6 to 2.6% annually from the present production level of 560 million tonnes. Increases in harvested grain yield have provided about 90% of the growth in world cereal production since 1950 (Mitchell *et al.*, 1997), and by the first decade of the 21st century most of the increase needed in world food production must come from higher absolute yields (Ruttan, 1993). For wheat, the global average grain yield must increase from the current 2.5 t/ha, to 3.8 t/ha. In 1995, only 18 countries world wide had average wheat grain yields of more than 3.8 t/ha, the majority located in north-western Europe (CIMMYT, 1996).

The formidable challenge to meet this demand is not new to agricultural scientists who have been involved in the development of improved wheat production technologies for the past half-century. For all developing countries, wheat yields have grown at an average annual rate of over 2% between 1961 and 1994 (CIMMYT, 1996). In western Europe and North America the annual rate of growth for wheat yield was 2.7% from 1977 to 1985, falling to 1.5% from 1986 to 1995. Recent data have indicated a decrease in the productivity gains being achieved by major wheat producing countries (Brown, 1997). In western Europe, where the highest average wheat grain yield is obtained in the Netherlands (8.6 t/ha), yield increased from 5 to 6 t/ha in five years, but it took more than a decade to raise yields from 6 to 7 t/ha. Worldwide, annual wheat grain yield growth decreased from 3.0% between 1977-1985, to 1.6% from 1986-1995, excluding the USSR

(CIMMYT, 1996). Degradation of the land resource base, together with a slackening of research investment and infrastructure, has contributed to this decrease (Pingali and Heisey, 1997). Production constraints affected by physiological or genetic limits are hotly debated. However, future increases in food productivity will require substantial research and development investment to improve the profitability of wheat production systems through enhancing input efficiencies. Due to a continuing necessity for multi-disciplinary team efforts in plant breeding, and the rapidly changing development of technologies, three overlapping avenues can be considered for raising the yield frontier in wheat. These are: continued investments in conventional breeding methods; use of current and expanded genetic diversity, and investigation and implementation of biotechnology assisted plant breeding.

In this presentation we attempt to give an overview of the International Maize and Wheat Improvement Center's (CIMMYT) international wheat breeding programme, and describe emerging strategies, which might be applied in the future.

Conventional wheat breeding

It is likely that gains to be achieved from conventional breeding will continue to be significant for the next two decades or more (Duvick, 1996), but these are likely to come at a higher research cost than in the past. In recent surveys of wheat breeders (Braun *et al.*, 1998; Rejesus *et al.*, 1996), more than 80% of respondents expressed concern that plant variety protection (PVP) and plant or gene patents will restrict access to germplasm. This may have deleterious consequences for future breeding success, since Rasmusson (1996) stated that nearly half of the progress made by breeders in the past can be attributed to germplasm exchange. Regional and international nurseries have been an efficient means of gathering data from varied environments and exposing germplasm to diverse pathogen selection pressures, while providing access and exchange of germplasm. Breeders utilize these cooperative nurseries extensively in their crossing programmes (Braun *et al.*, 1998). However, the number of cooperatively distributed wheat yield and screening nurseries has been greatly reduced during the past decade. Today, only CIMMYT and the International Centre for Agricultural Research in Dryland Areas (ICARDA) distribute international nurseries for spring wheat, with the National Wheat Improvement Programme of Turkey, CIMMYT, ICARDA and Oregon State University distributing international winter wheat nurseries.

Investments needed for breeding efforts increase with increasing yield levels. Further progress to develop higher yielding cultivars is reduced with every objective added to a breeding programme. Though the list of important traits may get longer and longer, little if any, assistance has been provided by economists to prioritise breeding objectives. Considering that a wheat breeding programme like CIMMYT's allocates around 60% of its resources to durable resistance breeding, it is obvious that there is need for research in this field. Due to high costs, we see durable resistance breeding as one of the first fields where transformation should be applied by breeders through introgression of one or more genes controlling disease resistance.

Breeding for wide adaptation

CIMMYT's breeding methodology is tailored to develop widely adapted, disease resistant germplasm with high and stable yield across a wide range of environments. The impact of this approach has been significant. The total spring bread wheat (*Triticum aestivum* L.) area in developing countries, excluding China, is around 63 million ha of which 36 million ha or 58% are planted to varieties derived from CIMMYT germplasm (Byerlee and Moya, 1993; Rajaram, 1995). During the period of 1966 to 1990, 1,317 bread wheat cultivars were released by developing countries, of which 70% were either direct releases from CIMMYT advanced lines or had at least one CIMMYT parent (Byerlee and Moya, 1993). For the period from 1986 to 1990, 84% of all bread wheat cultivars released in developing countries had CIMMYT germplasm in the pedigree. Simultaneously, the use of dwarfing genes has continued to increase over time, regardless of the type of wheat. More than 90% of all wheat varieties released in developing countries are semi-dwarfs. By the end of 1990 these varieties covered 70% of the total wheat area in developing countries (Byerlee and Moya, 1993). The continuous adoption of semi-dwarf spring wheat cultivars in the post-Green Revolution period from 1977-1990 resulted in an additional wheat production in 1990 of about 15.5 million tonnes, valued at about 3 billion US$. Of this amount 50%, or 1.5 billion US$, can be attributed to the adoption of new Mexican semi-dwarf wheat cultivars (Byerlee and Moya, 1993). In 1990, an estimated 93% of the total spring bread wheat production in developing countries, excluding China, derived from semi-dwarf spring wheats, which cover about 83% of the total spring bread wheat area in developing countries (Byerlee and Moya, 1993).

The cornerstones of CIMMYT's breeding methodology are: targeted breeding for each mega-environment (ME) within an integrated breeding programme, the use of a diverse gene pool for crossing, shuttle breeding, selection for yield under optimum conditions, and multi-locational testing to identify superior germplasm with good disease resistance. In this paper we would like to present some of the recent developments at CIMMYT's wheat programme.

Targeted breeding – the mega-environment concept

To address the needs of diverse wheat growing areas, CIMMYT introduced in 1988 the concept of mega-environments (ME) (Rajaram *et al.*, 1994). A ME is defined as a broad, not necessarily contiguous area, occurring in more than one country and frequently transcontinental, defined by similar biotic and abiotic stresses, cropping system requirements, consumer preferences, and, for convenience, by a volume of production. Germplasm generated for a given ME is useful throughout it, accommodating major stresses, but perhaps not all the significant secondary stresses. Within a ME millions of ha are addressed with a certain degree of homogeneity as it relates to wheat. By 1993 12 MEs were defined, six for spring wheats (ME1-ME6), three for facultative wheats (ME7-ME9) and three for winter wheats (ME9-ME12). Details for each ME are given in table 1.

Use of a diverse gene pool to maintain genetic diversity

Broad-based plant germplasm resources are imperative for a sound and successful breeding programme. Utmost attention is given to the genetic diversity within the CIMMYT germplasm to minimise the risk of genetic vulnerability, since it is grown on large areas and is widely used by Nation Agriculture Research Stations (NARS). We also believe that the use of genetically diverse material is mandatory for future increases of yield potential and yield stability. The parental group of lines considered for crossing in any year consists of 500-800 lines. Twice a year around 30% of the parental stocks are replaced with outstanding introductions. About 2,000 out of 8,000 crosses a year are made to these introductions. In addition, commercial varieties from NARS, and non-conventional sources such as durum wheat and alien species, are used to incorporate desired traits by recombination or translocation. The introductions are mostly used as female to preserve cytoplasmatic diversity.

The most recent example for the potential impact of generating new diversity is the reconstitution of bread wheat by the CIMMYT wide crossing programme by crossing durum wheat (*Triticum durum*) with the D-genome donor *Triticum tauschii*. Lines derived from backcrosses to bread wheat showed substantial morpho-agronomic variation, resistance to Karnal Bunt (*Tilletia indica*) and scab (*Fusarium graminearum*) and a TGW of up to 53 g (Villareal, 1995). Yield potential is close to that of bread wheat, and grain yield of the best synthetic wheat reached 7.7 t/ha (table 2). Some synthetic wheats also express the following traits: resistances to *Helminthosporium sativum* and *Septoria tritici*, tolerances to drought, heat, waterlogging, and frost at flowering.

Other sources exploited for new variability are:

– winter wheats continue to be crossed to spring wheats to combine elite, unique but distinct linkage blocks of desirable genes;

– landraces for very specific traits not available in better backgrounds, such as resistance to *Diuraphis noxia*;

– durum wheat is crossed to bread wheat to increase grain size. The six highest yielding lines derived from this programme outyielded their bread wheat parent by 5 to 20% in yield trials in Cd. Obregon, Mexico;

– *Triticum dicoccoides* (emmer wheat) as source for resistance to stripe rust, leaf rust, powdery mildew, *Septoria* spp. and Wheat Streak Mosaic Virus, tolerance to drought, high protein content and higher yield potential.

Table 1 ■ Classification of mega-environments (MEs) used by the CIMMYT Wheat programme .

ME	Latitude (degrees) [1]	Area (million ha)	Moisture regime [2]	Temperature regime [3]	Growth habit	Sown [4]	Major breeding objectives [5,6]	Representative locations/regions	Year breeding began at CIMMYT
Spring wheat									
1	Low	32.0	Low rainfall, irrigated	Temperate	Spring	A	Resistance to lodging, SR, LR, YR	Yaqui Valley, Mexico Indus Valley, Pakistan Ga,getoc Valley, India Nile Valley, Egypt	1945
2	Low	10.0	High rainfall	Temperate	Spring	A	As for ME1 + resistance to YR, *Septoria* spp., sprouting	North African Coast, Highlands of East Africa, Andes, and Mexico	1972
3	Low	1.7	High rainfall	Temperate	Spring	A	As for ME2 + acid soil tolerance	Passo Fundo, Brazil	1974
4A	Low	10.0	Low rainfall, winter dominant	Temperate	Spring	A	Resistance to drought, *Septoria* spp., YR	Aleppo, Syria; Settat, Morocco	1974
4B	Low	5.8	Low rainfall, summer dominant	Temperate	Spring	A	Resistance to drought, *Septoria* spp., *Fusarium* spp., LR, SR	Marcos Juarez, Argentina	1974
4C	Low	5.8	Mostly residual moisture	Hot	Spring	A	Resistance to drought, and heat in seedling stage	Indore, India	1974
5A	Low	3.9	High rainfall/ irrigated, humid	Hot	Spring	A	Resistance to heat, *Helminthosporium* spp., *Fusarium* spp., sprouting	Joydepur, Bangladesh, Londrina, Brazil	1981
5B	Low	3.2	Irrigated, low humidity	Hot	Spring	A	Resistance to heat and SR	Gezira, Sudan; Kano, Nigeria	1975
6	High	5.4	Moderate rainfall/summer dominant	Temperate	Spring	S	Resistance to SR, LR, *Helminthosporium* spp., *Fusarium* spp., sprouting, photoperiod sensitivity	Harbin, China	1989

Table 1 ■ Classification of mega-environments (MEs) used by the CIMMYT Wheat programme *(continued).*

Winter/Facultative wheat								
7	High	Irrigated	Moderate cold	Facultative	A	Rapid grain fill, resistance to cold, YR, PM, BYD	Zhenzhou, China	1986
8A	High	High rainfall/ irrigated, long season	Moderate cold	Facultative	A	Resistance to cold, YR, *Septoria* spp., YR, PM, *Fusarium* spp., sprouting	Edirne, Turkey	1986
9	High	Low rainfall	Moderate cold	Facultative	A	Resistance to cold, drought	Diyarbakir, Turkey	1986
10	High	Irrigated	Severe cold	Winter	A	Resistance to winter kill, YR, LR, PM, BYD	Beijing, China	1986
11A	High	High rainfall/ irrigated, long season	Moderate cold	Winter	A	Resistance to *Septoria* spp., *Fusarium* spp., YR, LR, PM	Temuco, Chile	1986
11B	High	High rainfall/ irrigated, short season	Severe cold	Winter	A	Resistance to LR, SR, PM, winter kill, sprouting	Lovrin, Romania	1986
12	High	Low rainfall	Severe cold	Winter	A	Resistance to winterkill, drought, YR, bunts	Ankara, Turkey	1986

1. Low= less than about 35-40 degrees.
2. Refers to rainfall just before and during the crop cycle. High= >500 mm; low= < 500 mm.
3 Hot= mean temperature of the cooloes month > 17.5 degrees; cold= 5.0 degrees.
4. A= autumn, S= spring.
5. Factors additionnal to yield and industrial quality. SR= stem rust, LR= leaf rust, YR= yellow (stripe) rust, PM= powdery mildew, and BYD= barley yellow dwarf.
6. Futher subdivided into (1) optimum growing conditions. (2) presence of Karnal bunt. (3) late planted, and (4) problems of salinity.

Source: *Adapted from Rajaram* et al., *1994*.

Table 2 ■ Grain yield and TGW of two crosses of bread wheat with synthetic wheats in yield trials at Cd. Obregon, Mexico in 1993.

Entry	Grain yield (kg/ha)	1,000 KW (g)
Chen/*T. tauschii*//BCN	7,740 a*	53a
Cndo/R143//Ente/Mexi/3/*T. tauschii*/4/Weaver	6,830 b	52a
Bacanora 88 (BW check)	6,770 b	40b

* Means within columns followed by different letters are significantly different at the 0.05 level of probability.

Source: Villareal, 1995.

Shuttle breeding between Cd. Obregon and Toluca

Young and Frey (1994) provide two factors which influence the success of a shuttle programme: a) the use of a germplasm pool encompassing genotypes with broad adaptation and b) the use of selection environments eliciting different responses from plant types. They further state the wheat breeding programme of N.E. Borlaug met these conditions.

When Borlaug started the shuttle breeding approach in 1945 the only objective was to speed up breeding for stem rust resistance. Since then, segregating populations have been shuttled 100 times between the two environmentally contrasting sites in Mexico, Cd. Obregon and Toluca (for a detailed description of the two locations see Braun *et al.*, 1992). We would like to stress this point since the discussion of breeding for wide versus specific adaptation has not come to an end (Ceccarelli, 1989, 1996, 1998). We believe comparisons between breeding methodologies for different species should not only consider selection parameters like heritabilities but also the breeding investments into the respective crop. At CIMMYT alone more than 200,000 crosses have been made since 1945 and today, more than 4,000 advanced spring wheat lines are annually screened worldwide. We are of the opinion that such a large scale testing and crossing programme using a diverse gene pool will most likely have higher chances of identifying widely adapted germplasm. The process will break undesirable genetic linkages and pyramid desired genes unlike programmes which restrict the genetic diversity in the crossing programme and test the germplasm in a narrow environmental range. The wide acceptance of CIMMYT germplasm by NARS and by farmers supports this approach. This is stated without disparaging other approaches.

One of the important results of this shuttle was the selection of photoperiod insensitive wheat genotypes. Initially, selection for photoperiodic insensitivity was unconscious, since the primary aim of the shuttling of generations between two sites per year, was to speed up the breeding. However, this trait permitted the wide spread of the Mexican semi-dwarf wheats (Borlaug, 1995). Today, this trait has been incorporated into most spring wheat cultivars grown below 48° latitude and is now also spreading to wheat areas above 48°N (Worland *et al.*, 1994).

Selection under optimum conditions and breeding for yield potential

Selection of segregating populations and consequent yield testing of advanced lines is paramount for the identification of high yielding and input responsive wheat genotypes. The increase in yield potential of CIMMYT cultivars developed since the 1960s is shown in figure 1 (Rees *et al.*, 1993). The average increase per year was 0.9% and there is no evidence that a yield plateau has been reached. This genetic progress in increasing the yield potential is closely associated with an increase in photosynthetic activity (Rees *et al.*, 1993). Both photosynthetic activity and yield potential increased over the 30-year period by some 25%. These findings may have major implications on CIMMYT's future selection strategy since there is evidence that wheat genotypes with a higher photosynthesis rate have a lower canopy temperature, which can be easily and cheaply measured quickly using a hand-held infra-red thermometer. If verified in future trials, breeders may be able to use this trait to increase selection efficiency for yield potential. This technique may in particularly useful to select wheat genotypes adapted to environments where heat is a production constraint.

Yield per se, measured under well-managed, high input, high yield potential conditions, is closely associated with good input responsiveness. On the other hand, good input efficiency at low production levels can shift crossover points, provided they exist, to lower yield levels and enhance residual effects of high genetic yield potential. Furthermore, combining input efficiency with high yield potential will allow a farmer to benefit from such cultivars over a wide range of input levels. The increase in N-use-efficiency is shown in figure 2 (Ortiz-Monasterio *et al.*, 1995).

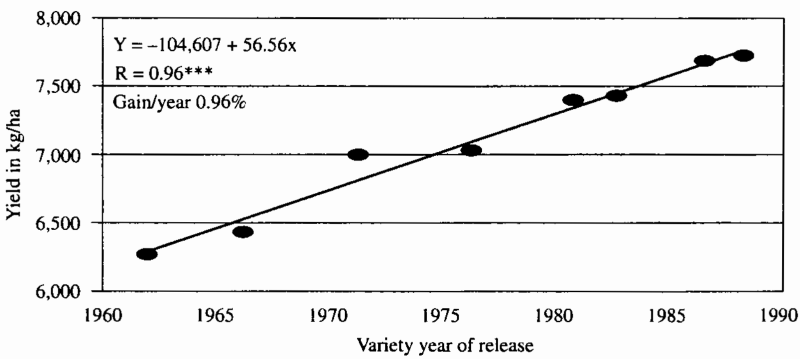

Figure 1 ■ Mean grain yields for the historical series of bread wheat varieties for the years 1960-1989 at Cd. Obregon, Mexico.

Data from Rees et al., *1993.*

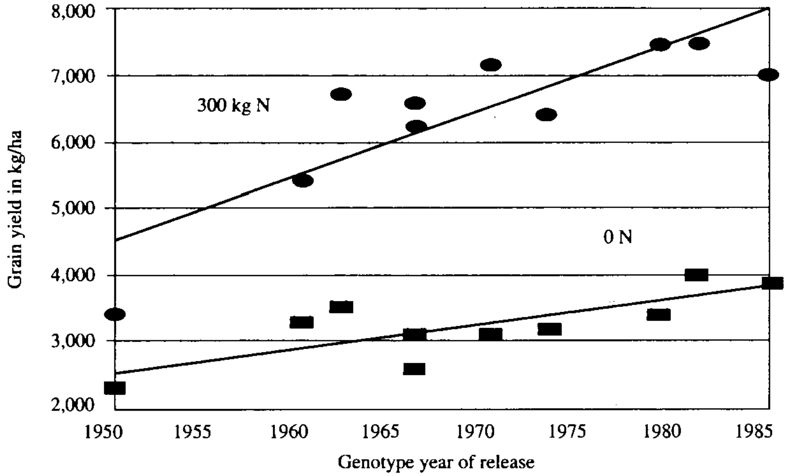

Figure 2 ■ Grain yield of the historical series of bread wheats at Cd. Obregon, Mexico at 0 and 300 kg/ha N applicaton.

Data from J.I. Ortiz-Monasterio et al., *1995.*

Multi-locational testing

Around 1,500 sets of yield trials and screening nurseries consisting of around 4,000 advanced bread wheat lines are annually sent to more than 200 locations covering most major and minor wheat growing areas around the world. Multi-locational testing plays a key-role in identifying best performing entries for varietal release and crossing. Since the shuttle programme (see above) permits two full breeding cycles per year, it takes around five to six years from crossing to international distribution of advanced lines to co-operators. This recurrent selection programme ensures a continuous and fast pyramiding of desirable genes.

Ceccarelli (1989) pointed out that the wide spread cultivation of some wheat cultivars should not be taken as a demonstration of wide adaptation. He argues that a large fraction of these areas is similar or made similar by use of irrigation and/or fertilizer. Therefore, he contends that the term "wide adaptation" has been used mainly to describe geographical rather than environmental differences. If this is true, the genotypic variation should be considerably higher than the GxE interaction in analyses of variances (ANOVAs) of CIMMYT trials. Braun *et al.* (1992) showed that this is not the case. When subsets of locations were grouped on the basis of geographical and/or environmental similarities, the GxE interaction was mostly greater than the genotypic variance. The environmental diversity of sites where CIMMYT's 21st International Bread Wheat Screening Nursery was grown and the diversity amongst genotypes in this nursery were demonstrated by Bull *et al.* (1994). They classified similarities among environments by forming subsets of genotypes from the total data set and compared it with the classification based on the remaining genotypes. Using this procedure they concluded that it was not possible to come to a stable grouping of environments, because little or no relationship existed among them.

Conclusions drawn from trials carried out on research stations are always open to critics who argue that these results do not necessarily reflect farmers' field conditions. However, the wide acceptance of CIMMYT germplasm by farmers in ME 1 to ME 5 (see above) does not support the view that the wide adaptation of CIMMYT germplasm is based on geographical rather than environmental differences.

Strategy for durability of resistance

From its beginning, incorporation of durable, non-specific disease resistance into CIMMYT's germplasm was a high priority since the breeding of widely adapted germplasm with stable yields without adequate long-term resistance against the major diseases would be impossible. The concept goes back to Niederhauser *et al.* (1954), Borlaug (1966) and Caldwell (1968) who proposed the application of general resistance in the CIMMYT programme versus the specific or hypersensitive type of resistance. Very diverse sources of resistance for rusts and other diseases are used intentionally in the crossing programme. The major source for this type of resistance has been proven resistant germplasm from national programmes, advanced CIMMYT lines carrying desired minor genes, germplasm received from CIMMYT's and other genebanks, and material developed in CIMMYT's wide crossing programme.

CIMMYT's strategy in the case of the cereal rusts has been and continues to be to breed for general resistance (slow rusting) based on historically proven stable genes. Accumulating several minor genes and combining them with different specific genes to provide a certain degree of additional genetic diversity can further diversify this non-specific resistance. This concept is also applied to other diseases like *Septoria* leaf blotch, *Helminthosporium* spot blotch, *Fusarium* head scab etc. The following is the present situation of the CIMMYT germplasm regarding resistance to major diseases:

• Stem rust (*Puccinia graminis* f. sp. *tritici*) resistance has been stable after 40 years of utilization of the genes derived from the variety Hope, and losses due to stem rust have been negligible since the late 1960s. The resistance is based on the gene complex Sr2, which actually consists of Sr2 plus 8-10 minor genes pyramided into three to four gene combinations (Rajaram *et al.*, 1988). *Sr2* alone behaves as a slow rusting gene. Since there has been no major stem rust epidemic in areas where CIMMYT germplasm is grown, the resistance seems to be durable. Recently virulence has been reported to the major gene *Sr31* located on the 1B/1R translocation common in many modern wheats. However, proper combining of the above mentioned minor slow rusting genes will be able to avert this temporary breakdown in some materials.

• Leaf rust (*Puccinia recondita* f. sp. *tritici*) resistance has been stabilized by using genes derived from many sources, in particular the Brazilian cultivar Frontana (Singh and Rajaram, 1992). No major epidemic has been observed for almost 20 years. We estimate that more than 20 such minor genes should be present in different CIMMYT spring wheats. Very likely more will be identified in other sources. A total of 3-4 partial resistance genes including *Lr34* give a slow rusting response, and such combinations have been the reason for the containment of leaf rust epidemics in the developing world during the last 15 years wherever the varieties carry several of these minor genes. About 60% of the CIMMYT germplasm carry one to four of these partial resistance genes. *Lr34* is linked to *Yr18* as well as to a morphological marker leaf tip necrosis which makes the gene particular attractive for breeders (Singh, 1992a, b). CIMMYT continues to look for new sources of partial resistance.

• Stripe rust (*Puccinia striiformis*). Slow rusting genes like *Yr18* have been identified (Singh, 1992b); however their interaction is less additive than for leaf and stem rust. More basic research is needed to understand the status of durable resistance in high yielding germplasm. The breakdown of *Yr9* in the Andean Region of Latin America, West Asia and North Africa and the present yellow rust epidemics underline the need for the release of cultivars with accumulated durable resistance.

• *Septoria tritici*: Initially all semi-dwarf cultivars developed for irrigated conditions were susceptible to *Septoria* leaf blotch. Today more than eight genes have been identified in CIMMYT germplasm and two to three genes in combination provide acceptable resistance. Future activities will concentrate on pyramiding these genes and spreading them more widely in the CIMMYT germplasm (Jlibene, 1992; Matus-Tejos, 1993).

• Karnal bunt (*Tilletia indica*): More than five genes have been identified and most of them are partially dominant. Genes providing resistance to Karnal bunt have been incorporated into high yielding lines (Singh *et al.*, 1995). Just 2-3 such genes provide high levels of protection.

• Powdery mildew (*Erysiphe graminis* f. sp. *tritici*). CIMMYT's germplasm is considered to be vulnerable to this disease. The disease is absent in Mexico and the responsibility to transfer resistance genes has been delegated to CIMMYT's regional breeder in South America.

Adaptation of recent CIMMYT cultivars

CIMMYT's breeding strategy has resulted in the development of widely grown varieties, such as Siete Cerros, Anza, Sonalika, Seri 82 which at their peak were grown on several million hectares. Seri 82 was released for irrigated as well as rainfed environments. Reynolds *et al.* (1994) reported that Seri 82 was the highest yielding entry in the 1st and 2nd International Heat Stress Genotype Experiment. Seri 82 can be considered as the first wheat genotype truly adapted to several MEs, in particular to ME1, ME2, ME4 and ME5. A comparison between Seri 82 and Pastor, a recently developed CIMMYT cultivar, demonstrates the progress made in widening adaptation during the last 10 years. Figure 3 shows the performance of Pastor (= Pfau/Seri//Bow), in CIMMYT's 13th Elite Spring Wheat Yield Trial. In 50 trials grown in all six ME's, Pastor yielded only in eight trials significantly (P = 0.01) lower than the highest yielding entry. This figure also demonstrates that Pastor has no tendency for a cross over at any yield level. While we do not deny that such a crossover may exist for some cultivars, Pastor and Seri 82 are clear examples that it is possible to combine abiotic stress tolerance with high yield potential. Figure 4 shows the yield difference between Seri 82 and Pastor. In only 16 out of 50 trials did Seri 82 have a higher yield than Pastor. The latter cultivar proves that breeding for wide adaptation continues to produce superior genotypes.

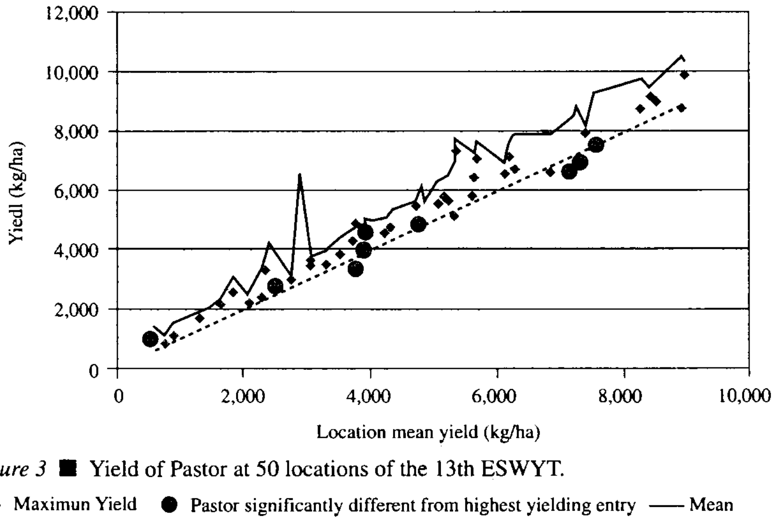

Figure 3 ■ Yield of Pastor at 50 locations of the 13th ESWYT.

---- Maximun Yield ● Pastor significantly different from highest yielding entry —— Mean

Breeding for drought tolerance

There has been a large transformation in the productivity of wheat due to the application of Green Revolution technology. This has resulted in a doubling and tripling of wheat production in many environments, but especially in irrigated areas. The high yielding varieties of semi-dwarf stature wheats have continuously replaced the older tall types at a rate of 2 million hectares per year since 1977 (Byerlee and Moya, 1993).

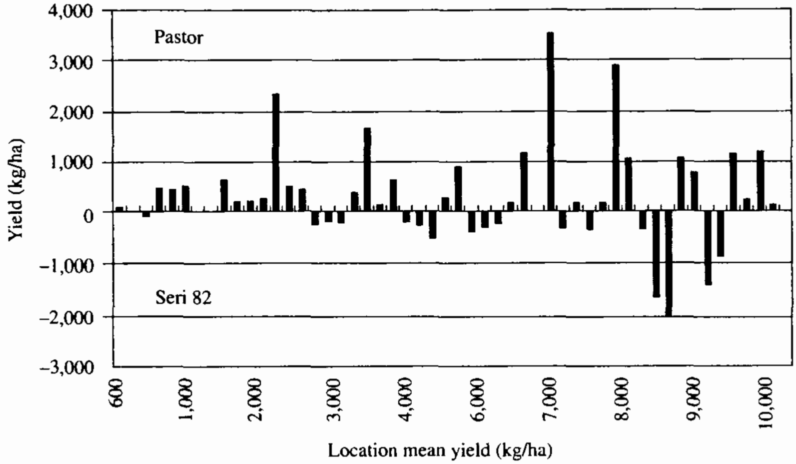

Figure 4 ■ Yield difference between Pastor and Seri 82 at 50 locations of the 13th ESWYT.

There is a growing recognition that the dissemination, application and adoption of this technology has, however, been slower in marginal environments, especially in the semi-arid environments affected by poor distribution of water and drought. The annual gain in genetic yield potential in drought environments is only about half that obtained in irrigated, optimum conditions. Many investigators have attempted to produce wheat varieties adapted to these semi-arid environments, but with limited success. Others have criticised the Green Revolution technology (Ceccarelli *et al.*, 1987) for failing to adequately address productivity constraints in semi-arid environments, although their own recommended technology has had limited impact, in particular in farmers' fields. This criticism is in clear contrast to the actual acceptance of semi-dwarf wheat cultivars in rainfed areas, since most of the 16 million ha increase in the area sown to CIMMYT semi-dwarf wheats in the mid 1980s occurred in rainfed areas. By 1990 more than 60% of the dryland area in developing countries was planted with semi-dwarfs (Byerlee and Moya, 1993).

Here we wish to outline why CIMMYT wheat germplasm has had considerable adaptive success in semi-arid environments. We also wish to draw conclusions regarding an effective methodology for a breeding programme addressing drought prone areas. While doing so, we do not intend to belittle any other methodology or approach followed elsewhere, but do wish to forward the adoption by farmers as the decisive criteria of success for any methodology.

Definition of semi-arid environments and description of distinct drought patterns

In table 1 the major global drought patterns observed in wheat production is presented (Rajaram *et al.*, 1994; Edmeades *et al.*, 1989). Though respectively dealing with spring (ME4A), facultative (ME9) and winter wheat (ME12), the common factor of these three mega-environments is that they are all characterized by sufficient rainfall prior to anthesis, followed by drought during the grain-filling period. In South America, the Southern Cone type of drought (ME4B) is characterized by moisture stress early in the crop season, with rainfall occurring during the post-anthesis phase. In the Indian Subcontinent type of drought stress (ME4C), the wheat crop utilizes water reserves left from the monsoon rains during the previous summer season. In the Indian Subcontinent even an irrigated wheat crop (ME1) may occasionally suffer drought due to a reduced or less than optimum number of irrigations.

Traditional methodology of breeding for drought stress

The traditional methodology, which has been practised for many years by many breeding programmes and in varying forms, is typified by handling all segregating populations under target conditions of drought. In some cases it also recommends the use of local landraces in the breeding process (Ceccarelli *et al.*, 1987). What is not particularly exhibited by this methodology is any impact on yield, farmers' adoption or final national production. This traditional methodology is based on the assumption that the agroecological situation facing the farmer does not vary in its expression over time. It assumes that responsiveness of varieties to improved growing conditions will not be needed. Also it presumes that below a certain yield level under dry conditions a crossover will always occur, where modern high yielding varieties of a responsive nature would always yield less than traditional landrace – based genotypes. Such crossovers may occur for selected genotypes and one should always be open to the possibility that there are real drought tolerance traits operating at the 1 t/ha and below yield level, that adversely affect high yield potential at the 4 t/ha and higher yield levels. So far at CIMMYT such traits have not been identified. In either case, such crossovers would be restricted to rather harsh conditions. Under such circumstances farmers tend to choose – rightfully so – not to grow wheat at all, but rather other known, more drought tolerant crops such as barley or sorghum, or to resort to grazing practices.

Alternative methodology of combining yield responsiveness and adaptation to drought

At CIMMYT we advocate a open-ended system of breeding in which yield responsiveness is combined with adaptation to drought conditions. Most semi-arid environments differ significantly across years in their water availability and the precipitation distribution pattern. Hence it is prudent to construct a genetic system in which plant responsiveness provides a bonus wherever environmental situations improve due to higher rainfall. With such a system, improved moisture conditions immediately translate into greater gain to the farmer. The following section shows why we believe this can be done.

The tale of the VEERY's

In the early 1980s when the advanced lines derived from the spring × winter cross Kavkaz/Buho//KAL/BB (CM33027) was tested in 73 global environments of the 15th International Wheat Yield Nursery (15th ISWYN) (figure 5), their performance was quite untypical compared to any previously known high yielding varieties. In later tests, we found that these lines, called Veery's, carry the 1B/1R translocation from rye, and that general performance of such germplasm was superior not only in high yielding environments but particularly under drought conditions (Villareal *et al.*, 1995, table 3). From the VEERY cross, 43 varieties were released, excluding those released in Europe.

In addition to the creation of a new class of superior germplasm, there is another important lesson in breeding to be learned here. The Veery's represent a genetic system in which high yield performance in favourable environments and adaptation to drought could be combined in one genotype. The two genetic systems are apparently not always incompatible, although others have claimed that their combination would not be possible. Based on this revelation, it is possible to hypothesise a plant system in which efficient input use and responsiveness to improved levels of external inputs (in this case available water) can be combined to produce germplasm for marginal (in this case semi-arid) environments, that at least maintains minimum traditional yields and expresses dramatic increases whenever the environment improves.

Evidence supporting promotion of this methodology

1. By the mid 1980s CIMMYT – bred germplasm occupied 45% of the semi-arid wheat areas with rainfall between 300-500 mm, and 21% of the area less than 300 mm (Morris *et al.*, 1991), including large tracts in West Asia/North Africa (WANA). By 1990 63% of the dryland areas, in especially ME4A and ME4B, was planted with semi-dwarf wheats (Byerlee and Moya, 1993), many carrying the 1B/1R translocation. This represents clear acceptance by farmers,

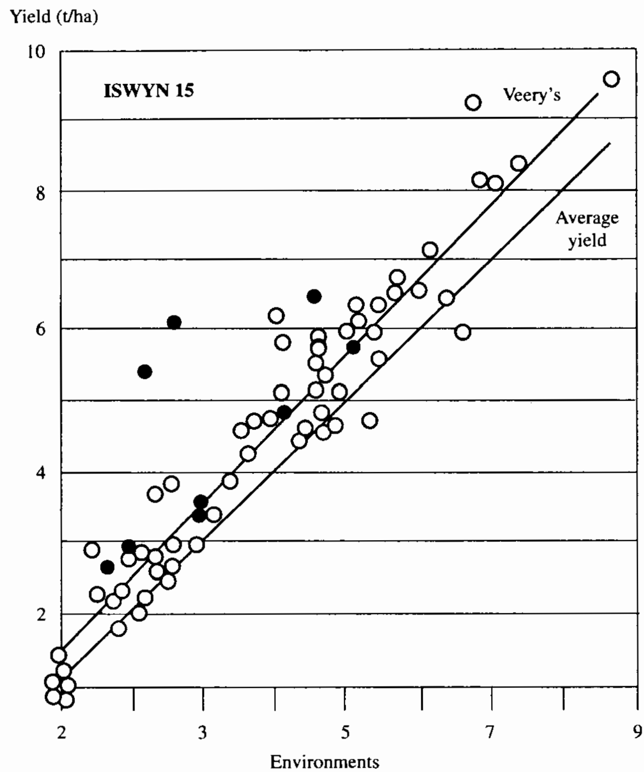

Figure 5 ■ Performance of Veery's in 73 global environments (ISWYN 15).

Table 3 ■ Effect of the 1BL/1RS translocation on yield characteristics of 28 random F2-derived F6 lines from the cross Nacozari 76/Seri 82 under reduced irrigated conditions.

Plant characteristics	1BL/1RS	1B	Mean diff.
Grain yield	4,945	4,743	202*
Above-ground biomass at maturity (t/ha)	12,600	12,100	500*
Grains/m^2	14,074	13,922	152 NS
Grains/spike	43.5	40.6	2.9*
1,000 grain weight (g)	37.1	36.5	0.5*

NS: Not significant.
* Significant at the 0.05 level.
Source: Villareal et al., *1995.*

who widely adopted the new responsive germplasm over their traditional varieties. The positive trend among the final users of our products cannot be ignored. Indirectly, it supports our view that the modern genotypes have adaptation to ME4A and ME4B drought areas while expressing high yields in improved conditions.

2. To support the above assumptions an experiment was conducted (Calhoun *et al.*, 1994; van Ginkel *et al.*, 1998; tables 4, 5) to determine how the most modern and widely (spatially) adapted germplasm compared to commercial germplasm from countries representing the Mediterranean region (ME4A), the Southern Cone of South America (ME4B) and the Indian Subcontinent (ME4C), under conditions artificially simulating those three Mega-environments. The most widely (spatially) adapted CIMMYT lines outyielded the commercial varieties in all artificially simulated environments. The recent adoption trend of CIMMYT germplasm in these difficult marginal environments supports the model of input efficiency/input responsiveness.

Table 4 ■ Wheat genotypes representing adaptation to different moisture environments.

ME1	Irrigation	Super Kauz, Pavon 76, Genaro 81, Opata 85
ME4A	(Mediterranean)	Almansor, Nesser, Sitta, Siete Cerros
Me4B	(Southern Cone)	Cruz Alta, Prointa Don Alberto, LAP 1376, PSN/BOW CM69560
ME4	(Subcontinent)	C306, Sonalika, Punjab 81, Barani

Source: Calhoun et al., *1994.*

Table 5 ■ Grain yields kg/ha of selected wheat genotypes grouped by adaptation and tested under moisture regimes in the Yaqui Valley, Mexico, 1989-90 and 1990-91.

Adaptation group		Full irrigation [1]	Late drought [2]	Early drought [3]	Residual moisture [4]
ME_1	Irrigation	6,636 a	4,198 a	4,576 a	3,032 a
ME_4C	Mediterranean	6,342 b	3,990 ab	4,390 b	2,883 b
ME_4B	Southern Cone	5,028 c	3,148 bc	4,224 b	2,359 c
ME_4C	Subcontinent	4,778 c	3,245 bc	3,657 c	2,704 b

1. received 5 irrigations;
2. received 2 irrigations early before heading;
3. received one irrigation for germination and two post heading;
4. received one irrigation for germination only.
* means in the same column followed by the same letter are not significantly different at P = 0.05.

Source: Calhoun et al., *1994.*

3. The story of Nesser is about an advanced line with superior performance in drought conditions bred at CIMMYT/Mexico and identified at ICARDA/Syria. The cross combines a high yielding CIMMYT variety Jupateco and a drought

tolerant Australian variety W3918A. The performance of Nesser in WANA's ME4A environments has been widely publicised (ICARDA, 1993), and the line is considered by ICARDA to represent a uniquely drought tolerant genotype. However, it was selected at CIMMYT/Mexico under favourable environments, and carries a combination of input efficiency and high yield responsiveness. It performs similarly to the Veery lines in the absence of rust.

Based on the above evidence, our proposed operational methodology is to actively combine input efficiency and input responsiveness.

Application

A breeding scheme is described below to achieve the combination of the two genetic systems. Two contrasting selection environments are alternated, allowing alternate selection for input efficiency and input responsiveness.

- *F1*

Crosses involving spatially widely adapted germplasm representing yield stability and yield potential, with lines with proven drought tolerance in the specific setting of ME4A, ME4B or ME4C. Winter wheats and synthetic germplasm are emphasised.

- *F2*

The individual plants are raised under irrigated and optimally fertilized conditions, and inoculated with a wide spectrum of rust races. Only robust and (horizontally) resistant plants are selected. These may represent adaptation and responsiveness to favourable environments.

- *F3, F4*

The selected F2 plants are evaluated in modified pedigree/bulk breeding system (Rajaram and van Ginkel, 1995) under rainfed conditions or very low water availability. The selection is based on individual lines rather than on individual plants. The progenies are selected based on such criteria as spike density, biomass/vigour, grains/m^2, and others (Van Ginkel *et al.*, 1998) (table 6). This index helps identify lines, which may adapt to low water situations or in other words, are input efficient.

- *F5, F6*

The selected lines from F4 are further evaluated under optimum conditions.

- *F7, F8*

Simultaneous evaluations under optimum and low water environments. Selection of those lines showing outstanding performance under both conditions. Fur-

Table 6 ■ Grain yield and TGW of two crosses of bread wheat with synthetic wheats in yield trials at Cd. Obregon, Mexico in 1993 Genotypic correlation (rg) between agronomic traits and final grain yield, for optimum environment (full irrigation) and reduced water regime (late drought, Mediterranean type) in wheat.

Trait	Moisture regime	
	Full irrigation	Late drought
Days to heading	0.40	0.19
Days to maturity	0.29	0.27
Grain fill period	– 0.32	0.36
Height	– 0.39	0.05
Peduncle length	– 0.46	0.22
Relative peduncle extrusion	– 0.51*	0.25
Spike length	– 0.28	– 0.50*
Spike M^{-2}	– 0.12	0.64**
Grains/spike	0.62*	– 0.42
Grains M^{-2}	0.74**	0.68**
Yield/spike	0.55*	– 0.64**
1,000 grain weight	0.08	– 0.45
Test weight	0.13	0.05
Harvest index (HI)	0.83**	– 0.39
Biomass	0.90**	0.94**
Straw yield	0.52*	0.86**
Yield/day (planting)	0.99**	0.57*
Yield/day (heading)	0.94**	0.44
Biomass/day (planting)	0.86**	0.69**
Biomass/day (heading)	0.74**	0.63**
Vegetative growth rate	0.32	0.63**
Spike growth rate	0.62**	– 0.58*
Grain growth rate	0.17	– 0.44

*, ** indicate significance at the 0.05 and 0.01 probability level, respectively.

Source: van Ginkel et al., *1995.*

ther evaluation in international environments is carried out for purposes of verification.

The proposed breeding methodology is supported in research published in recent years by others, not only on wheat (Bramel-Cox *et al.*, 1991; Cooper *et al.*, 1994; Duvick, 1990, 1992; Ehdaie *et al.*, 1988; Uddin *et al.*, 1992; Zavala-Garcia *et al.*, 1992), where the importance of testing and selecting in a range of environments including well-irrigated ones, has shown to identify superior genotypes for stressed conditions. The methodology aims at combining input efficiency with input responsiveness, by alternating selection environments during the breeding process. This approach results in germplasm that is accepted by farmers because it translates improved environmental conditions into yield gains. The traditional methodology of only selecting under drought conditions, and narrowly relying on the landrace genotypes, does not move yield levels significantly beyond those traditionally obtained, and does not provide the farmer with a bonus yield in the "fat" years.

Future integration of research

Yield stability and yield potential

Traxler *et al.* (1995) analysed grain yield increases and yield stability of bread wheat cultivars released during the last 45 years. In the early period of the Green Revolution, when rapid yield increases occurred, variance for yield concomitantly increased. Since the early 1970s, yield stability has increased at the cost of the rate of increase in yield. However, steady progress was made in developing varieties with improved stability, grain yield or both. For the developing world, yield stability has increased since the beginning of the Green Revolution (Smale and McBride, 1996). While price policy, input supplies and environmental variation contribute more to yield stability than the varietal genotype, the increasing yield stability reflects the emphasis given by breeders to develop germplasm with tolerance to a wider range of diseases and abiotic stresses. Sayre *et al.* (1997) concluded that from 1964 to 1990, yield potential in CIMMYT-derived cultivars increased at a rate of 67 kg/ha per year or 0.88% per year. This data does not suggest that a yield plateau has been reached. In fact, the performance of recently released lines, such as Attila or Baviacora, indicate that yield potential has been further enhanced. Improvements made by breeding for yield stability and adaptation may be illustrated by data for the advanced line Pastor, which out-yielded the hallmark check cultivar Seri 82 in 34 out of 50 locations where the 13th Elite Spring Wheat Yield Nursery was grown (figure 4). The grain yield of Pastor was significantly less than the highest yielding entry at only eight locations (Braun *et al.*, 1996). Results from CIMMYT international nurseries do not suggest that plateaus for yield or yield stability are imminent. Discussion on how to increase the yield potential of wheat often still centres around traits which contributed to the success of the Green Revolution varieties more than 30 years ago, *e.g.* photoperiod and dwarfing genes (Worland *et al.*, 1998; Sears 1998). This emphasises the long-term commitment needed to introduce genes, which may radically alter the conventional phenotype of a wheat plant. This experience may serve as a reminder for those who believe that introducing new genes through transformation, which may effect the adaptation of wheat, will allow the breeder a quick fix.

Plant nutrition

Selection for yield potential and yield stability under medium to high levels of nitrogen has indirectly increased efficiency for nutrient uptake. Recently released

CIMMYT bread wheat cultivars require less nitrogen to produce a unit amount of grain than cultivars released in the previous decades (Ortiz Monasterio *et al.*, 1997). Under low N levels in the soil, N use efficiency increased mainly due to a higher N uptake efficiency (the ability of plants to absorb N from the soil) whereas under high N levels, the N utilization efficiency (the capacity of plants to convert the absorbed N into grain yield) increased. In spite of the increased N-use efficiency of recently – released wheat cultivars, the response to nitrogen of wheat production systems has been observed to be declining in many areas of south east Asia. In Turkey, where zinc deficient soils are widespread, recently, released winter bread cultivars have a higher Zn-uptake and consequently a higher grain yield than local landraces (M. Kalayci, pers. comm.).

Physiology

A recent survey of wheat breeders suggested that research in plant physiology has had a limited impact on wheat improvement (Jackson *et al.*, 1996). However, a strong body of evidence now indicates that physiological traits may have real potential for complementing early generation phenotypic selection in wheat. One of the more promising traits identified is canopy temperature depression (CTD). CTD refers to the cooling effect exhibited by a leaf as transpiration occurs. While soil water status has a major influence on CTD, there are strong genotypic effects under well-watered, heat-stressed or drought-stressed conditions. CTD gives an indirect estimate of stomatal conductance, and is a highly integrative trait being affected by several major physiological processes including photosynthetic metabolism, evapo-transpiration, and plant nutrition. CTD and stomatal conductance, measured on sunny days during grain filling, showed a strong association with the yield of semi-dwarf wheat lines grown under irrigation, in both temperate (Fischer *et al.*, 1998) and sub-tropical environments (Reynolds *et al.*, 1994). In addition, CTD as measured on large numbers of advanced breeding lines in irrigated yield trials, was a powerful predictor of performance not only at the selection site but also for yield averaged across 15 international sites. CTD has been shown to be associated with yield differences between homozygous lines, indicating a potential for genetic gains in yield, in response to selection for CTD (Reynolds *et al.*, 1998). Even more recently, CTD showed genotypic and phenotypic correlation coefficients of 0.6-0.8 with yield under hot irrigated conditions when used to distinguish elite lines.

Genetic resources

Three quarters of the wheat breeders recently surveyed felt that lack of genetic diversity would limit future breeding advances (Rejesus *et al.*, 1996), though genetic diversity was not considered an immediately limiting factor in most programmes. This concern was greater from breeders in developing and former

USSR countries (> 80%) than from higher income countries (59%). Furthermore, in countries where privatisation of wheat breeding programmes has occurred, investments in strategic germplasm development, which may be risky or have importance only in the long term, have declined (McGuire, 1997).

A wide range of opinion has been expressed concerning the abundance of availability of usefully – exploitable genetic variability. Allard (1996) emphasized that the most readily useful genetic resources were modern elite cultivars, since these lines possessed relatively high frequencies of favourable alleles. Rejesus *et al.* (1996) also showed that high yielding cultivars were the parents of choice among breeders. Rasmusson and Phillips (1997) have shown that the assumption that all genetic variability is a result of the inherent exclusive contribution by two parents, *per se*, is not necessarily true considering results from molecular analysis. They discussed mechanisms by which induction of genetic variability may involve altering the expression of genes, the possible mechanisms of single allele change, intragenic recombination, unequal crossing-over, element transpositions, DNA methylation, paramutation or gene amplification. They also stressed the possible importance of epistasis effects, which may have been underestimated in the past.

Introduction of genetic variability from distantly – related wheat cultivars, or related or alien species, has often been specifically aimed at the introduction of simply – inherited traits (*e.g.* genes for disease resistance), but has appeared to be of limited value in quantitative trait improvement. Cox *et al.* (1997) incorporated genes for leaf rust resistance from *Triticum tauschii* into *Triticum aestivum.* With two backcrosses to the recurrent wheat parent, leaf rust resistant winter wheat advanced lines with acceptable quality and equal in yield to the highest yielding commercially grown cultivars were identified. In addition, it has been postulated that since recombination between the D genomes of *T. aestivum* and *T. tauschii* occurred at a level similar to that in an intraspecific cross (Fritz *et al.*, 1995), *T. tauschii* could be considered another primary source of novel genes for wheat improvement.

The number of wheat/rye translocations that have had a significant impact on wheat improvement are actually few in number. The majority of the 1BL.1RS translocations occurring in more than 300 cultivars worldwide can be traced to one German source, and all 1AL.1RS translocations, widely present in bread wheat cultivars grown in the Great Plains of the US, trace to one source, Amigo (Schlegel, 1997a, b; Rabinovich, 1998). Other translocations carry genes for copper efficiency (4BL.5R) and Hessian fly resistance (2RL.2BS, 6RL.6B, 6RL.4B, 6RL.4A; McIntosh, 1993). Chromosome 2R and 7R enhance zinc efficiency in wheat/rye addition lines (Cakmak and Braun, unpublished). Considering the impacts, which have come from the use of wheat/rye translocations, it may be warranted to further exploit these and additional translocations.

While there have been reports indicating a positive effect of 1BL.1RS translocations on yield performance and adaptation (Rajaram *et al.*, 1990), Singh *et al.*

(1998) has determined that, with Seri 82, replacing the translocation with 1BL from cv. Oasis resulted in a yield increase of 3.4 and 5.0% in irrigated and moisture stress conditions, respectively. A further increase in grain yield in disease – free conditions of about 5% was observed in the irrigated trials through the introgression of 7DL.7Ag translocation carrying the *Lr19* gene (from *Agropyron elongatum*). This yield increase was attributed to a higher rate of biomass production in the 7DL.7Ag lines. However, under moisture stress condition 7DL.7Ag lines were associated with a 16% yield reduction, possibly due to excessive biomass production in early growth stages. This would suggest that the effect of the 1BL.1RS translocation is genotype specific and that 7DL.7Ag could be a useful translocation for enhancing the yield potential, at least in irrigated conditions.

Recent efforts to generate newly accessible genetic diversity have involved the reconstitution of hexaploid wheat by producing synthetic wheat. Durum wheat (*T. turgidum),* the donor of the A and B genomes, is crossed to *Ae. tauschii,* the donor of the D genome (Mujeeb-Kazi *et al.*, 1996). Villareal (1995) and Villareal *et al.* (1997) showed that lines derived after two backcrosses to *T. aestivum,* showed increased morpho-agronomic variation, and resistance to Karnal bunt (*Tilletia indica*) and scab (*Fusarium graminearum*). Under full irrigation in north western Mexico, the yield potential of this material was nearly 8 t/ha. When tested under drought conditions for two years, nearly all of the synthetic derivatives had a significantly higher 1,000 grain weight, with grain yield varying between 84 to 114%, when compared with the bread wheat checks. Other traits found to be present in some synthetic wheats and/or their derivatives include resistance to *Septoria* leaf blotch, tan spot, spot blotch, and tolerances to heat, drought, waterlogging, and frost at flowering.

It is likely that in no other crop have more crosses been made, or recombinations occurred to break linkages, than in the case of wheat. The more focused a breeding objective may be, the more restricted a breeder may be in the choice of suitable parents. With increased understanding of the inheritance of a trait, selection strategies may be better targeted. With yield, a complex trait still not well understood genetically or physiologically, the use of genetically diverse material will continue to be a prime genetic source for increasing yield potential. As long as breeders have no other readily accessible tools, genetic diversity and the opportunity for its recombination through crossing will be important to break undesired linkages and increase the frequency of desirable alleles. Future breakthroughs in yield potential will likely come from such genetically diverse crosses.

Hybrid wheat

When farmers or breeders discuss strategies for increasing wheat yields, hybrid wheat is often mentioned as an alternative. However, Pickett (1993) and Picket and Galwey (1997), evaluating 40 years of wheat hybrid development, concluded that hybrid wheat production is not economically feasible because of

a) limited heterotic advantage; b) lack of advantage in terms of agronomic, quality or disease resistance traits; c) higher seed costs; and probably most importantly d) heterosis could be fixed in polyploid plants and consequently hybrids would have no advantage over inbred lines. The use of hybrid crops is usually targeted to higher yield potential environments. Results from South Africa (Jordaan, 1996), however, show that hybrids out-yield inbred lines by 15% at a 2 t/ha mean production potential when narrow row spacing and low seeding rates (< 25 kg/ha) are used. Mean grain yield of hybrids tested in the Southern Regional Performance Nursery (SRPN), across locations in the southern Great Plains, were significantly higher than for inbred lines (Peterson *et al.*, 1997). Bruns and Peterson (1998) calculated mean yield advantage of hybrid wheat at 10-13%, and attributed this advantage, in part, to better temporal and spatial stability and improved tolerance to heat. In contrast, recent reports of hybrid performance in Europe indicate lower levels of heterosis (5 to 12%) (Eavis *et al.*, 1996). Gallais (1989) stated that, provided over dominance is of little importance in wheat, in the long term inbred line development will be more effective than F_1 hybrids. If biotechnological methods can identify increased expression of heterosis by more effective selection of favourable alleles, this impact will likely have equal advantage to inbred and hybrid wheat development. Whether hybrids have a higher absolute yield potential than inbred lines also has to be seen in the light of inbred bread wheat cultivars that already reached grain yields of 17 t/ha (Hewstone, 1997).

Biotechnology

Techniques such as doubled haploids were considered biotechnology 10 years ago, but have became an applied routine in many programmes. The potential of biotechnology has been discussed elsewhere (Sorrells and Wilson, 1997; Snape, 1998). We will rather look at the application of biotechnology in today's breeding programmes. Lack of genetic polymorphism in crops like wheat and soybeans and the consequent problems of identifying molecular markers have been a major limitation to the impact of marker-assisted selection (MAS) in wheat breeding. The identification of a high number of polymorphisms in single sequence repeats (SSR) should therefore greatly enhance the potential to find molecular markers in wheat.

Conventional plant breeders adopt breeding methods which increase their breeding efficiency, but they are conservative when making methodological changes. In a small survey of wheat programmes having unrestricted access to new biotechnological methods, few research programmes, and no main-line wheat breeding programmes, routinely use MAS or quantitatively-inherited trait loci (QTL). Limitation in use is due to the lack of markers for traits of interest, population specificity of a given marker, or their relatively high costs when compared with conventional selection techniques. These limitations may lessen in the next decade.

Modern cultivars are the product of recombinations among the high number of landraces in their pedigrees (Smale and McBride, 1996). Direct use of landraces in contemporary breeding programmes, however, is often considered only as a source for qualitatively inherited traits. Tanksley and McCouch (1997) argue that the lack of success from crosses involving landraces for the improvement of grain yield was mainly due to evaluation on a phenotypic basis, an imprecise indicator of genetic potential. Analysis of QTL has revealed that loci controlling a quantitative inherited trait do not equally contribute to the observed variation for the trait, and often few QTL explain most of the observed variation. In rice QTLs for yield were identified in a wild, low-yielding relative. After introgression into modern hybrid rice cultivars, yield increases of 17% compared to the original hybrid were observed. Based on the observed gains, Tanksley and McCouch (1997) identify the need to more thoroughly evaluate exotic germplasm. Those accessions most distinct from modern cultivars may contain the highest number of unexploited, potentially-useful alleles.

The comparative genetic mapping of cereal genomes has identified a vast amount of conserved linearity of gene order (Devos and Gale, 1997). This observation will likely accelerate the application of QTL in wheat, as well as aid in the identification of genes required for introgression from alien species. Considering the low number of loci tagged today in wheat, the problems related to developing a high-density map for wheat (Snape, 1998) and consequently the limited progress to identify QTL in wheat for yield, we believe that the impact from this linearity on wheat improvement will be significant.

Wheat has been successfully transformed for herbicide resistance and high molecular weight (HMW) glutenins, using both the ballistic and *Agrobacterium tumefaciens* systems (Cheng *et al.*, 1997). Barro *et al.* (1997) inserted two additional HMW glutenin subunits, 1Ax1 and 1Dx5, and observed a stepwise improvement of dough strength. Altpeter *et al.* (1996) introduced 1Ax1 into Bobwhite and increased total HMW glutenin subunit protein by 71% over Bobwhite. However, the affects of transformation are not necessary additive as was shown by Blechl *et al.* (1998) who identified trangenics for HMW glutenins, which also exhibited decreased accumulation due to transgene-mediated suppression.

Conclusion

The challenge to annually produce 1 billion tonnes of wheat within the next 25 years is formidable and can only be met by a concerted action of scientists involved in the diverse disciplines of agronomy, pathology, physiology, biotechnology, breeding, as well as economics and politics. We are optimistic that this target will be met. Today, funds are often directed from breeding towards biotechnology, often due simply to the novelty required for publication. Eventually, transformation may be a valuable technique to alter the performance of a genotype. However, at least during the next decade, the simple decision of a breeder in the field to keep or discard will contribute more to yield increase than any other approach. In conclusion, we agree with Ruttan (1993) who stated that, at least for the next two decades to come, progress through conventional breeding will remain the primary source of growth in crop and animal production.

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