CIMMYT international wheat breeding

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In the last decade of the twentieth century, when the mainstream debate in agricultural sciences has centred on biotechnology – a new methodology (or even a new science?) – and its application in plant breeding, it is considered both awkward and old-fashioned to reiterate the importance of old but proven methodologies, such as shuttle breeding and multilocation testing. The shuttle breeding methodology is unique to the International Maize and Wheat Improvement Center (CIMMYT); it was proposed 50 years ago and implemented by Norman E. Borlaug (1968), initially accompanied by much criticism, but finally widely acclaimed. This methodology has been responsible for the production of photoperiod insensitive and otherwise widely adapted germplasm. In particular, the shuttle breeding process involving contrasting locations in regard to latitude, altitude and rainfall has proven a most efficient way to introduce and select genes for photoperiod insensitivity. The photoperiod insensitive genes, *Ppd1* and *Ppd2*, abound in CIMMYT's spring wheats, and along with the dwarfing genes, *Rht1* and *Rht2*, resulted in a new plant type, which was not only lodging tolerant (the initial aim), but dramatically higher yielding with high biomass due to pleiotropic effects or close linkage (Hoogendoorn *et al.*, 1988). When superimposed with rust resistance (Borlaug, 1968), the new genetic combination provided adaptation to most irrigated wheat-growing areas of the subtropics.

In the last 15 years, CIMMYT and the Oregon State University Wheat Program have launched a joint shuttle breeding enterprise between Pendleton/Hyslop, Oregon, United States, and Toluca, Mexico, for the selection of widely adapted facultative/winter wheat germplasm derived from spring x winter wheat crosses (Kronstad and Rajaram, 1990). The resulting progenies have shown remarkably wide adaptation in such distinct regions as the Anatolian Plateau in Turkey, Afghanistan, Iran and Uruguay. The original base-germplasm pool, bred only at sites in Oregon, lacked such alleles as *Ppd1* or *Ppd2*, while the shuttle operation permitted a combination of photoperiod insensitivity due to selection at Toluca, plus a high-yield base identified at Pendleton/Hyslop. In addition, resistances were combined.

It should be noted that in the last 20 years, most major wheat breeding programmes in the world have adopted multilocation testing in contrasting environments as an integral part of their philosophy, including those in the Great Plains in the United States, northwestern Europe, East and Southern Africa, West Asia, North Africa, the Southern Cone in South America and the Indian subcontinent. These programmes are cooperative ventures with many contributing components. The widespread adoption of this methodology therefore has led the authors to believe that it has wider application in choosing suitable parents and developing germplasm for release and recommendation to farmers.

CONCEPT OF MEGA-ENVIRONMENTS

CIMMYT has never sought nor proposed a single cultivar for the whole world. CIMMYT defines wide adaptation as the ability of a cultivar to produce high yields in many environments. Such germplasm needs critical and essential diversity or variability for durable-type disease resistance, while carrying certain elements of homogeneity, such as photoperiod insensitivity and semidwarf stature. Uniformity of certain traits should not in and of itself be equated with genetic vulnerability.

The concept of incorporating diversity for disease resistance, combined with homogeneity for those agronomic traits that impart high yields, adaptability and stability, has been CIMMYT's objective since the 1950s when the Bread Wheat Breeding Program was managed by the Rockefeller Foundation/Mexican Office of Special Studies. This was carried out within the framework of a bilateral mission within Mexico. Through the 1960s and 1970s, it was led by CIMMYT with an international mandate and has continued into the 1980s and 1990s, achieving a global focus.

Since 1950, the Bread Wheat Breeding Program has made more than 200 000 crosses, distributed 10 000 advanced lines globally and received recognition and acknowledgement from the world's NARSs (National Agricultural Research System), which released more than 1 500 advanced lines as cultivars to farmers that were grown on roughly 40 million ha in most wheat-growing regions of the developing world.

In 1988, CIMMYT's Strategic Plan proposed the term mega-environment (ME) to subdivide global wheat domains. However, it must be stated that CIMMYT's breeding programme objectives have continually been evolving over the past 50 years, seeking to combine superior agronomic traits with essential and specific abiotic and biotic tolerances in order to address 120 million ha of very diverse wheat-growing conditions. At the time of the proposed ME-based breeding, CIMMYT's Bread Wheat Breeding Program was already strategically and distinctly addressing the issues involving adaptation to such varied environments as irrigated regions, high-rainfall areas, acid soils, semi-arid zones, tropical areas and winter wheat zones. ME delineation is based on water availability, soil type, temperature regime, production system and associated biotic and abiotic stresses. Consumer preferences for grain colour and industrial- and end-use quality are also considered.

Germplasm developed for a given ME will withstand the major stresses present within that ME, but not always the significant secondary stresses. However, an attempt is made to include genetic diversity for additional traits of importance within the ME. How these products are used and distributed within an ME to address the needs of specific agro-ecological niches is the responsibility of the individual NARSs. Emphasis is also given to maintenance of genetic diversity within each ME to counter the threat of genetic vulnerability.

CIMMYT has defined 12 MEs: six MEs focus on spring wheat production areas, three MEs focus on facultative wheat areas and three MEs focus on true winter wheat areas (Rajaram *et al.*, 1995). These are illustrated in Table 6.1. However, in actual fact, the new classification evolved through a long process of exploiting and learning from shuttle breeding and multilocation testing.

Currently, CIMMYT's wheat programme emphasizes the regions of ME1, ME2, ME3, ME4, ME5, ME6, ME7, ME9, ME10 and ME12. All spring wheats are addressed from Mexico, and most winter wheat breeding is done in Turkey, in collaboration with Oregon State University, the Turkish National Program and the International Center for Agricultural Research in Dry Areas (ICARDA). The following traits or genes are considered essential for the different MEs.

Spring wheat mega-environments

ME1 (Irrigated)

'Short dwarf' in stature (*Rht1* and/or *Rht2* with modifiers); photoinsensitive (*Ppd1* or *Ppd2*); high yield potential; input responsiveness and input efficiency; resistance to stem rust (*Sr2* complex), leaf rust (*Lr34* complex) and sometimes stripe rust; better balance of high molecular weight (HMW) glutenins (1 or 2*, 7+8 or 17+18, 5+10); some heat tolerance; lodging tolerance; largely white/amber grain. Typical location is Ciudad Obregon, Sonora, Mexico.

TABLE 6.1
Mega-environments used by the CIMMYT Bread Wheat Breeding Program

ME[a]	Moisture regime	Temperature	Wheat type	Area (%)	Production (*million tonnes*)
ME1 IR	Irrigated	Temperate	Spring	36.1	83
ME2 HR	High Rainfall (>500 mm)	Temperate	Spring	8.5	25
ME3 AS	High Rainfall (>500 mm) Acid Soil	Temperate	Spring	1.9	3
ME4 SA	Low Rainfall (<500 mm)	Temperate/hot	Spring	14.6	20
ME5 TE	Irrigated High Rainfall	Hot	Spring	7.1	12
ME6 HL	Semi-arid	Temperate	Spring	6.2	13
ME7 IR	Irrigated	Cool	Facultative		
ME8 HR	High Rainfall	Cool	Facultative	10.0	23
ME9 SA	Semi-arid	Cool	Facultative		
ME10 IR	Irrigated	Cold	Winter		
ME11 HR	High Rainfall	Cold	Winter	15.0	30
ME12 SA	Semi-arid	Cold	Winter		

[a]ME = Mega-environment, where IR = Irrigated; HR = High Rainfall; AS = Acid Soil; SA = Semi-arid; TE = Tropical Environment; HL = High Latitude.
Source: Rajaram *et al*., 1995.

ME2 (High Rainfall >500 mm of precipitation)

Semidwarf in stature (*Rht1* or *Rht2* and sometimes *Rht8*); photoinsensitive (*Ppd1* or *Ppd2*); *Sr2* and *Lr34* complexes; HMW glutenins (1 or 2*, 7+8 or 17+18, 5+10); better resistance/tolerance to *S. tritici*, barley yellow dwarf virus, stripe rust and scab; sometimes resistance to powdery mildew, *Septoria nodorum*, tan spot, bacterial leaf streak (*Xanthomonas translucens* pv. *undulosa*) and root rots; sprouting tolerance; large, red grain. Typical location is Toluca, Mexico.

ME3 (Acid Soil)

Same characteristics as for ME2, plus tolerance to aluminium and/or manganese toxicity and efficient phosphorus uptake and utilization. Typical location is Cruz Alta, Rio Grande do Sul, Brazil.

ME4 (Semi-arid <500 mm of precipitation)

'Tall dwarf' in stature (*Rht1* or *Rht2* without modifiers); combination of input responsiveness (yield potential) and input efficiency (drought tolerance); *Sr2* and *Lr34* complexes; sometimes stripe rust and common bunt resistance needed; some heat tolerance; some cold tolerance; both white/amber and red grain.

Within ME4, three distinct types of drought or sub-MEs have been identified based on the stage of plant development at which drought is most severe. These are:

- ME4A: Winter rain or Mediterranean-type drought, associated with post-flowering moisture and heat stress typical of the Mediterranean region; late frosts may also occur. Representative locations include

Aleppo, Syria, and Settat, Morocco. Total estimated area is 6 million ha.

- ME4B: Winter drought or Southern Cone-type rainfall, associated with pre-flowering moisture stress; resistances to leaf and stem rust, *Septoria* spp. and *Fusarium* spp. are requirements. Pre-harvest sprouting is also a common problem. Marcos Juarez, Argentina, is a representative location. Total estimated area is 3 million ha.
- ME4C: Continuous or subcontinent-type drought, associated with stored moisture after monsoon rains resulting in receding moisture conditions. A representative location is Dharwar, India. Total estimated area is 2 to 3 million ha and is decreasing.

ME5 (Tropical)

- ME5A: Low-humidity tropics, associated with ME1 characteristics superimposed with high-temperature tolerance; ME5A is targetted for countries such as Sudan and Peninsular India. Typical location is Kano, Nigeria.
- ME5B: High-humidity tropics, associated with ME2 characteristics superimposed with high-temperature tolerance and *Helminthosporium sativum* resistance; sometimes sprouting tolerance is needed. Typical location is Jessore, Bangladesh.

ME6 (High Latitude)

- ME6A: High rainfall, having the same characteristics as ME2, with *ppd1* or *ppd2* allele(s) for photosensitivity. Typical location is Harbin, China.
- ME6B: Semi-arid, having the same characteristics as ME4, with *ppd1* or *ppd2* allele(s) for photosensitivity. Typical location is Akmola, Kazakhstan.

Facultative wheat mega-environments

ME7-8 (Irrigated/High Rainfall)

Moderate level of vernalization requirement (either *vrn1*, *vrn2* or *vrn3*); sometimes rapid grainfill; cold tolerance; most other traits are the same as for ME1 or ME2. Typical locations are Zhengzhou, Henan Province, China and Corvallis, Oregon, United States, respectively.

ME9 (Semi-arid)

Moderate level of vernalization requirement; cold tolerance; sometimes long coleoptile; most other traits are the same as for ME4. Typical location is Eskisehir, Turkey.

Winter wheat mega-environments

ME10-11 (Irrigated/High Rainfall)

High level of vernalization requirement with either *vrn1* + *vrn2*, *vrn1* + *vrn3*, or *vrn1* + *vrn2* + *vrn3*; eyespot resistance needed; most other traits are the same as for ME1 or ME2. Typical locations are Beijing, China and Temuco, Chile, respectively.

ME12 (Semi-arid)

High level of vernalization required; some bunt resistance needed; other traits are the same as for ME4. Typical location is Ankara, Turkey.

Breeding locations in Mexico

Two major locations are used for spring wheat breeding in Mexico, Ciudad Obregon and Toluca. One minor location, at CIMMYT's headquarters in El Batan, Texcoco, is used on occasion for testing.

Ciudad Obregon

Ciudad Obregon is located at 27.5°N, 40 masl, in the state of Sonora. It is a dry, irrigated, low-altitude site, located in a desert climate. Mean rainfall during the wheat crop cycle is about 50 mm. Irrigated yields in the region are high, in the order of 8 to 11 tonnes/ha in experimental plots and 5 to 8 tonnes/ha in farmers' fields. With a reduction in number of irrigations, various kinds of drought stress can be created.

This is one of the two most important breeding and screening sites for the CIMMYT wheat programme. Inoculation of stem rust

(*Puccinia graminis*) and leaf rust (*P. triticina* [syn. *P. recondita*]) by spray applications of susceptible border-mixtures ensures adequate infection of the entire targetted fields. Rust inoculation is carried out in the latter part of January. Spring wheat is grown from November until May.

Toluca

Toluca is located at 19°N, 2640 masl, west of Mexico City in the state of Mexico. This temperate, high-rainfall, high-altitude site is the most important CIMMYT summer cycle location. It is a high-rainfall environment with good disease expression, especially of stripe rust (*P. striiformis*), *S. tritici* and *F. nivale*. Highest yields realized in experimental plots are in the order of 7.5 to 8.5 tonnes/ha. Spray applications to susceptible border-mixtures provide stripe rust and leaf rust infection. Dispersal of infected straw at the tillering stage initiates epidemics of *S. tritici* and *F. nivale*. Individual spikes of selected entries are inoculated with *F. graminearum* (200 000 spores/L) to create scab. Although these diseases are artificially inoculated, they also occur naturally. Bacterial and barley yellow dwarf virus (BYDV) infections are induced in selected populations and occur naturally.

Spring wheats are grown from May until December. When planted in November, winter wheats are exposed to vernalizing temperatures during the winter that are low enough to initiate flowering. Relatively short days compared to those at higher latitudes result in some winter/facultative germplasm maturing late.

El Batan

El Batan is located at 19°N, 2249 masl. This is the administrative centre of the CIMMYT wheat programme, situated to the northeast of Mexico City in the state of Mexico. Irrigation is available during erratic rainfall. Leaf rust develops in epidemic proportions. Stripe rust occurs at irregular frequencies.

GENETIC DIVERSITY

At the present rate of genetic resource utilization in breeding, the variability stored in current advanced lines in most breeding programmes is adequate for the foreseeable future. Only in the case that a rare genetic vulnerability arises, for example, of the magnitude of sudden widespread occurrence of Karnal bunt or extensive wheat blast epidemics in Brazil, should a genetic search of large dimensions be needed.

The CIMMYT Bread Wheat Breeding Program is attempting to thwart epidemics due to well-known pathogens globally through gene accumulation, gene deployment and particularly through providing NARSs access to large-scale, operable genetic variability. CIMMYT's breeding programme products are based on 10 000 simple, annually executed, top- and limited back-crosses, utilizing known variability from spring wheats, winter/facultative wheats, durum wheats, *Aegilops tauschii* (syn. *Triticum tauschii*), rye and *Agropyron* spp. in a mega-environmental setting. Products are made available to NARSs through the following groups of nurseries and trials:

- ME1: International Bread Wheat Screening Nursery (IBWSN), distributed to 100 locations; contains 300 to 450 entries. Elite Selection Wheat Yield Trial (ESWYT), distributed to 100 locations; contains 50 entries.
- ME2: High Rainfall Wheat Screening Nursery (HRWSN), distributed to 50 locations; contains 250 to 400 entries. High Rainfall Wheat Yield Trial (HRWYT), distributed to 70 locations; contains 50 entries.
- ME3: Acid Soil Wheat Screening Nursery (ASWSN), distributed to 30 locations; contains 100 entries.
- ME4: Semi-arid Wheat Screening Nursery (SAWSN), distributed to 70 locations; contains 250 entries. Also, similar germplasm is distributed from ICARDA, Aleppo, Syria.
- ME5: Warmer Areas Wheat Screening Nursery (WAWSN), distributed to

50 locations; contains 200 entries.

• ME6: High Latitude Wheat Screening Nursery (HLWSN), distributed to 20 locations; contains 200 entries.

• ME7, ME8, ME11 and ME12: Favourable Environments Facultative Wheat Screening Nursery (FEFWSN), targetted at the Southern Cone in South America and China.

Several international screening nurseries and international yield trials are distributed from the joint CIMMYT winter and facultative breeding programme based in Turkey to cooperators in ME7 to ME12:

- Facultative and Winter Wheat Observation Nursery (FAWWON);
- Winter Wheat East European Yield Trial (WWEEYT);
- Elite Yield Trial Irrigated;
- Elite Yield Semi-Arid;
- Winter Wheat Observation Nursery Irrigated (WWON-IR);
- Winter Wheat Observation Nursery Semi-Arid (WWON-SA);
- Winter Durum Wheat Observation Nursery.

Special nurseries are described below:

• Special genetic stocks with rare combinations of resistances, yield and quality.

• Also available to NARSs is the variability of unselected and unexploited F_2 segregating populations. In recent years, and specially after the 1988 Strategic Plan, this variability has not been distributed to NARSs in response to their stated preference for advanced lines and CIMMYT's policy to encourage local crossing.

The collected data from international screening nurseries and yield trials are used extensively within the breeding programme to help define and fine-tune objectives and identify parents for crossing. Because of the above-mentioned dynamism of germplasm use and distribution, CIMMYT and the NARSs can be considered well prepared to control any unexpected evolutionary forces in the ever-evolving pathogens. Nevertheless, CIMMYT continues to introgress genetic variability. Because of the dynamism on the pathogen side, and at times due to the shifting nature of gene pool management, advanced lines must contain unexplored variability unwanted today, but valuable in the future. This phenomenon is best illustrated in Australia where CIMMYT germplasm proved valuable on two occasions: first for cereal cyst nematode and second for stripe rust resistance when most Australian cultivars succumbed to stripe rust introduced in 1989. The Brazilian cultivar Frontana has been critical in launching the conquest of leaf rust. Similarly, Chinese germplasm has helped CIMMYT to win the battle against Karnal bunt in Mexico.

MODIFIED PEDIGREE-BULK SELECTION METHOD

With the globalization of CIMMYT's Bread Wheat Breeding Program in the 1980s and the evolution of the concept of 12 MEs, the number of crosses made annually increased dramatically from 2 000 in the early 1970s to 10 000 in the 1980s. The total number of segregating populations (F_2 to F_7) grew from 20 000 lines to 150 000. Similarly, the number of entries in yield trials increased from 1 000 to 5 000 annually. The total hectarage in breeding and testing expanded from 30 ha to 100 ha in the same period.

To accommodate this increase in breeding populations, the methodology of selection was changed from a pedigree system to a modified pedigree-bulk selection approach. The new method allows one experienced CIMMYT breeder to evaluate all segregating populations, in a timely fashion, except for the F_2. Simultaneously, total mechanization of planting and harvesting and the computerization of field books has allowed a limited group of support staff and technicians to carry out all responsibilities. These three major changes introduced in the CIMMYT operation have increased the ability to introgress variability by significantly increasing the number of crosses directed for specific MEs, while keeping the selection programme highly efficient and without sacrificing population size per cross.

The breeding programme in the 1970s traditionally made double crosses and top-crosses in equal proportion. Subsequently, the double cross was eliminated due to poor output, and the limited (one) back-cross was introduced for most MEs, in which a limited amount of variability was allowed compared to top-crosses and double crosses. This strategy permitted the introduction of known genes or traits in a highly productive agronomic background. This practice has begun to be accepted by breeding programmes in developing and developed countries alike.

The modified pedigree-bulk method practised at CIMMYT is described below (van Ginkel *et al.*, 2000):

• F_1: This generation is based on simple cross, limited back-cross or top-cross.

• F_1 Top- or F_1 Back-cross: Outstanding F_1 populations are either topped (three-way) or back-crossed. Top- or three-way crosses are used to extend the variability. Back-crosses are carried out to stabilize variability as the genetic distance between parents becomes greater and are very effective at expanding adaptation and performance.

• F_2: There are 2 000 spaced plants per cross. Individual plant selection is based on agronomic type and disease resistance, and resulting seed is selected based on seed health and grain plumpness.

• F_3: Selected F_2 plant progeny is planted individually as F_3, at a commercial seeding rate of 100 kg/ha in three rows of 2 m per line in order to observe and evaluate competitive ability within the line. The selection of lines is thus based on visual assessment of agronomic performance and disease resistance in a plot rather than on an individual plant. Ten to 15 heads are selected per F_3 line, threshed in bulk and promoted to the F_4 generation after selection for grain characteristics.

• F_4-F_5: Same procedure is used as for F_3.

• F_6: This generation is planted as in F_3, but from five to ten heads are selected and threshed individually from selected F_6 plots.

• F_7: Individual heads are planted, and plots are selected for subsequent complete bulk-harvest.

• Yield Trial: The bulked lines are included in preliminary yield trials and subsequently replicated yield trials before industrial quality tests are carried out. Finally, the superior lines are included in one of CIMMYT's International Nurseries or Yield Trials, classified by ME.

YIELD POTENTIAL

There has been a continuous active involvement of CIMMYT breeders in the evolution of plant types for different agro-climatological conditions. Since the mid-1950s, there has been a continuous rise in wheat yields in Mexico, as presented in Table 6.2. The most modern cultivars of the 1990s yield 2 500 kg/ha more than the original dwarf wheats released in Mexico in the early 1960s. CIMMYT plant physiologists have identified some of the physiological characteristics for this increased yield (Reynolds *et al.*, 1994; Sayre *et al.*, 1995; Waddington *et al.*, 1986).

CIMMYT supports the view of Rasmusson (1996) that hallmark germplasm is paramount to increasing yield potential. Rasmusson was able to increase the yield of barley cultivars in Minnesota, United States, from 4.3 tonnes/ha to 5.2 tonnes/ha based on closely related germplasm. In CIMMYT's programme, measured in Sonora, Mexico, the yields of Kauz and Baviacora cultivars represent similar events to those noted in the Minnesota breeding programme. These two wheats were derived from parents bred in the CIMMYT programme and represented a narrow genetic base.

However, there are cases where a wider genetic base has produced outstanding high-yielding lines, such as Veery, which is a resulting product of a cross involving a Russian cultivar, an Indian line of CIMMYT

TABLE 6.2

Average yields of historical cultivars bred by CIMMYT over a 50-year period as measured in Ciudad Obregon, Mexico, and *Rht* and *Vrn* gene status, reflecting a yield gain of about 100 kg/ha/year

Cultivar	Yield (*kg/ha*)	*Rht* gene[a]	*Vrn* gene[b]
Yaqui 50	4 500	None	na
Pitic 62	6 500	*Rht2*	*Vrn1 + Vrn2*
Siete Cerros	6 500	*Rht1*	*Vrn1 + Vrn2*
Yecora 70	7 000	*Rht1 + Rht2*	*Vrn1 + Vrn3*
Nacozari 76	7 500	*Rht1*	*Vrn2 + Vrn3*
Ciano 79	7 500	*Rht2*	*Vrn1*
Seri 82	8 000	*Rht1*	*Vrn3* (?)
Opata 85	8 000	*Rht1*	na
Oasis 88	8 500	*Rht1 + Rht2*	na
Bacanora 88	8 800	*Rht1*	na
Baviacora 92	9 000	*Rht1*	na

[a]*Rht* status according to Singh *et al*., 1989.
[b]*Vrn* status according to Stelmakh, 1987.

origin and a CIMMYT advanced line. This supports the hypothesis of Kronstad (1996) where he proposes the use of a wider genetic base in the crossing programme.

Unfortunately, most proponents of the use of various physiological parameters and biotechnological tools have not been able to exemplify their theoretical argumentation by producing competitive high-yielding wheat germplasm, either on their own or in collaboration with breeders they were able to inspire. The question remains: What pivotal advice can be given to plant breeders who need to produce germplasm that is continually superior in yield? Based on experiments conducted at CIMMYT and the experiences of its breeders, the following sections will outline the genetic basis of improved yield in CIMMYT bread wheat germplasm, while addressing a number of specific issues.

Dwarfing genes and photoperiod insensitivity genes

The genetic stock Norin 10/Brevor of Japanese/US origin, first utilized by Borlaug in 1954, was primarily employed for the correction of lodging sensitivity by genetically reducing plant height. The dwarfing genes not only provided lodging tolerance but also perhaps pleiotropically affected high yield by allowing more tillers to survive and thus increasing biomass. Through the use of isogenic lines based on the cultivars Maringa and Nainari 60, Hoogendoorn *et al.* (1988) were able to show that yield increased by at least 15 percent when *Rht1*, *Rht2* or *Rht1* + *Rht2* carrying lines were compared to tall cultivars.

A physiologically determinable effect of these genes is an increase in harvest index (HI) (Waddington *et al.*, 1986). Nonetheless, increased HI should be considered a side effect of the *Rht* genes rather than their main effect. Not all combinations of *Rht* genes will produce high yields, and not all cultivars with high HI are actually high yielding. This indicates that other factors are necessary to achieve high yield. Many physiologists have concluded and recommended that the

application of increased HI as a selection criterion would be the most appropriate way to select for high yield. They appear to have ignored the fact that it is much easier to breed directly for *Rht* carrying plant types based on reduced height. A large number of *Rht* genes have been identified, genetically catalogued and otherwise studied. Not all of these affect grain yield. Only *Rht1* and *Rht2* significantly raise yield (Hoogendoorn *et al.*, 1988). *Rht3* does not give any positive effect, nor does *Rht8*. Nonetheless, both *Rht3* and *Rht8* may provide a good degree of lodging tolerance.

Incidentally, photoperiod insensitivity genes (*Ppd1*, *Ppd2*) were introgressed into the CIMMYT breeding programme at the same time as the two dwarfing genes (*Rht1*, *Rht2*) were first utilized. Currently, no isogenic lines are available to study the interaction of these four genes. Nonetheless, circumstantial evidence indicates that the best combinations are either *Rht1* + *Ppd1*, *Rht1* + *Ppd2*, *Rht2* + *Ppd1* and *Rht2* + *Ppd2*. When both dominant alleles of photoperiod insensitivity are combined, yields are generally low. Most current high-yielding lines have only one *Ppd* gene and either *Rht1* or *Rht2*. The *Ppd* gene establishes a proper balance between the vegetative phase and the reproductive phase, including the grainfilling period. Without this optimum balance, the source-sink relationship is somehow biased, and the plant's resources are not proportioned properly to produce high yield.

Spring x winter gene pool exploitation

Following the introduction of dwarfing and photoperiod insensitivity genes, the next group of high-yielding lines at CIMMYT were the product of spring x winter wheat crossing. The first set of semidwarf wheats was hybridized with winter wheats in the late 1970s. Many combinations were very successful, but one spring x winter wheat combination, CIMMYT name Veery, is particularly noteworthy together with its progenies represented by Kauz, Attila, Pastor, Baviacora, etc. These lines differ markedly in plant height, leaf size, maturity, head size, grain size, grain colour, etc. There are studies at CIMMYT and elsewhere indicating that the 1B/1R translocated segment from rye present in Veery and derived from Russian cultivar Kavkaz markedly increases yield (Villareal *et al.*, 1991, 1994a, 1995). On the other hand, there are other studies (McKendry *et al.*, 1996; Moreno-Sevilla *et al.*, 1995a, 1995b) indicating that background effects may be too large and that the 1B/1R chromosome translocation carrying isogenic lines is not always higher yielding than its counterparts.

Besides the 1B/1R translocation, there are other agronomic characters involved in the high-yielding lines derived from spring x winter crosses, such as grains/m^2, and in some cases, spikes/m^2. Spring x winter gene pool recombination has transmitted a higher number of grains through either a higher number of spikes/m^2 or through bigger spikes (Table 6.3) (Villareal *et al.*, 1991, 1994a, 1995). Studies at CIMMYT (Rees, unpublished) have shown that the resulting lines have a rather cool crop canopy relative to the surrounding environment, a higher stomatal conductance and are photosynthetically more efficient.

The authors believe spring x winter wheat populations produce vigorous progenies, tiller profusely, have more surviving spikes, appear robust and keep their leaves healthy for a longer period. This phenomenon is also very common in segregating populations emanating from crosses involving Veery. Thus it is recommended that breeders select for vigorous populations, robust plants, healthy stay-green leaves, many spikes/m^2 and/or bigger spikes to produce a plant type that could be called a Veery ideotype.

Additional contributions of spring x winter crosses

The Veery cultivars and their progenies, such

TABLE 6.3
Means for the 1BL/1RS and 1BL/1BS chromosome translocations in F_2-derived F_6 lines from the cross Nacozari 76/Seri 82 in 1991/92 and 1992/93, Ciudad Obregon, Mexico

Plant characteristic	1BL/1RS	1BL/1BS	F-test[a]
Grain yield (*kg/ha*)	5 605	5 437	*
Above-ground biomass (*tonnes/ha*)	13.9	13.4	*
Harvest index (%)	40.2	39.8	ns
Heads/m^2	351	354	ns
Grains/m^2	14 990	14 778	ns
Grains/head	43.9	41.6	**
1 000 grain weight (*g*)	38.62	38.20	**
Test weight (*kg/hl*)	79.0	78.3	**
Plant height (*cm*)	90.2	93.2	**
Head length (*cm*)	10.5	10.5	ns
Days to flowering	80.0	79.0	**
Physiological maturity (*days*)	121.8	120.6	**
Grainfill period (*days*)	41.8	41.6	ns

[a]Significant at P = 0.05 represented by * and significant at P = 0.01 represented by **; ns = non-significant.
Source: Villareal *et al.*, 1995.

as the Kauz, Attila, Pastor, and Baviacora groups of lines have demonstrated a superior level of abiotic tolerance to a number of stresses (drought, heat, etc.) and improved nutrient efficiencies (N- and P-efficiency). These characters have not been traced to any major qualitative genes, but such an exercise could well provide further opportunities to increase yield. These wheats not only are responsive to good conditions, but also invariably have demonstrated superior performance under low-input conditions. Hence they are also input efficient.

It needs to be determined what kind of genetic control is involved in this multiple stress tolerance. It is clear yield potential *per se* does not completely explain performance under stressed conditions (He and Rajaram, 1994).

Erect versus droopy leaf and closed versus open canopy

Many crop physiologists have debated the role of erect versus droopy leaves on yield potential after the rice cultivar IR8 was created (Evans, 1993). CIMMYT's attempt to produce near-isogenic lines for this trait has not been successful, but random populations were compared with erect and droopy leaves at the F_6 level (Vanavichit, 1990). In general, the erect-leaf types were slightly higher yielding than their droopy counterparts. In current bread wheat lines, there is a great deal of variability in the leaf blade width, leaf area and leaf angle.

It seems likely that the canopy type represented by the line Kauz would be advantageous for the overall efficiency of its canopy rather than having either completely droopy or completely erect leaves. Kauz has an intermediate and dynamic habit, most pre-flag leaves are erect, but the flag leaf is only initially erect and then becomes droopy. This situation provides better penetration of light into the canopy early on and hence higher tiller survival, resulting in a large number of heads/m^2 and consequently more grains/m^2. Subsequently, as the lower leaves start to senesce, the flag leaf becomes droopy and intercepts most of the incoming light without it being lost on the dying lower leaves. Grains are then able to fill properly. The authors propose the support of such a plant type.

Grain size and yield

After having achieved a large number of grains/m^2, the grain size automatically adjusted to a somewhat smaller size, 38 to 40 g/1 000 grains, in Veery, compared to 45 to 50 g/1 000 grains in traditional cultivars, such as Sonalika. This regulatory balance cannot be broken without the introduction of a simply inherited large grain size characteristic of extreme value (more than 60 g/1 000 grains). Perhaps a new balance could then be achieved at 50 g/1 000 grains, while maintaining the desired number of grains/m^2 and hence higher yield. The recently produced *Ae. tauschii* (syn. *T. tauschii*) derived synthetic wheats (Villareal *et al.*, 1994b) offer such a possibility.

Ideotypic approach at CIMMYT

An ideotypic approach has not been possible at CIMMYT due to the complex crossing programme and inherent fear of genetic uniformity or homogeneity and associated phenotypic similarity. Although, if one analyses the germplasm, there are so-called CIMMYT ideotypes. There is a certain commonality in characters across the spectrum, such as reduced height, photoperiod insensitivity, rust resistance and the presence of a certain acceptable level of industrial quality, which is superimposed on two gradations for each of the following characters: semi-dwarfness, maturity, grain colour and two canopy structures. If multiplied, these latter four characters in all permutations would produce 16 wheat ideotypes within the broad CIMMYT ideotype that is destined for irrigated spring wheat production areas (ME1). The 16 ideotypes would be composed of the phenotypic expressions described below.

Height variation

Rht1 and *Rht2* alone give a 90 to 95 cm short semidwarf wheat. The combination of both dwarfing genes would give a 70 to 80 cm short double-dwarf wheat. There are additional height differences due to other minor gene effects. However, for a practical sake, let us define one class of 90 to 95 cm and another of 70 to 80 cm.

Maturity class

Ppd1 and *Ppd2* genes have noticeable individual effects on flowering. The presence of only one of these genes results in an intermediate flowering effect. Together, the effects of these genes are great, making wheat mature very early. Let us consider two classes of maturity: early (120 days) and intermediate (140 days).

Grain colour

Both amber- and red-grained cultivars are needed for ME1. The genetics of grain colour is largely qualitative. However, some minor genes also operate. Only the amber-grained type and the red-grained type are considered.

Closed versus open canopy architecture

There would be two canopy categories based on erect and droopy leaves. Kauz, however, does represent an intermediate, dynamic canopy type, which may even be preferable.

Based on these four morphological characters, the current bread wheat germplasm distributed to irrigated ME1 has 2 x 2 x 2 x 2 = 16 ideotypes. These ideotypes together represent the multiple CIMMYT ideotype for ME1-targetted germplasm. Other features include durable rust resistance, high yield, good spike fertility, good bread-making quality, robust stem morphology and good chlorophyll retention capacity.

Exploitation of Buitre

After 20 years of genetic manipulations and countless recombinations, Ricardo Rodriguez at CIMMYT, under the guidance of Borlaug, was successful in combining various extreme yield components together into one plant type. This unique ideotype has a robust stem, a long head (more than 30 cm, derived from the cultivar Buitre), multiple spikelets and florets, a large leaf area and broad leaves. However, due to some unknown physiological imbalance or disorder, the heads remain largely sterile and resulting grains are mostly shrivelled. In addition, the plants are generally highly susceptible to leaf rust and stripe rust.

CIMMYT has begun to exploit this genetic resource through further hybridization with the most recent advanced lines from the normal breeding programme. The aim is to achieve a balance, with a slightly reduced head size but with head fertility completely restored. In addition, plans are being considered for the exploitation of this ideotype in a hybrid wheat programme. If successful, these genetic stocks offer a possibility of increasing yield 10 to 15 percent above that of Veery descendants.

PROTECTING YIELD POTENTIAL

Many breeding programmes fail to deliver suitable high-yielding cultivars to farmers simply because the cultivar is susceptible to a spectrum of pathogen variability present in an ecological niche. It is absolutely necessary that breeders make simultaneous investment in yield potential, disease resistance, quality and abiotic stress resistance in the region they serve. The CIMMYT breeding programme has invested in the order of 25 to 30 percent of its resources towards improving yield potential, at least 50 percent for disease resistance and the rest for improved quality and abiotic stress resistance. This proportion applies to breeding for ME1. There would be a slightly different proportion for other MEs. This strategy enforces the hypothesis that yield gains must be protected at all costs and through genetic means.

YIELD POTENTIAL AND ADAPTATION TO DROUGHT ENVIRONMENTS

Yield potential may be defined as the efficiency with which a genotype will convert environmental inputs (such as light, water, carbon dioxide and nutrients) into grain output. Yield potential is measured most accurately in a stress-free, non-limiting production system. Duvick (1990, 1992) has termed this potential in corn "the internal physiological ideotype, as distinct from morphological traits". The authors propose that the high yield potential of CIMMYT wheats was instrumental in allowing yield responsiveness when additional inputs were available. Thus, genotypes that are targetted for drought areas should also contain an inherently efficient internal physiological type that would allow them to make use of additional inputs when these are made available. This enhances high input responsiveness.

Around the foundation of the highly effective 'engine', relevant adaptive traits should then be added to enhance input efficiency. The combination of water-efficient and water-responsive traits with yield potential is important in drought environments where rainfall is frequently erratic across years. When rains are sufficient in certain years, the crop must respond appropriately. In short, yield potential provides responsiveness and adaptive traits provide protection of that yield potential under drought conditions.

Wide adaptation and stability over time

Drought intensity and type vary across locations, or 'spatially', and across years, or 'temporally'. On the other hand, cultivars are commonly described as having wide adaptation, defined as the relative ability of a line to yield well consistently across different locations (spatially), or having stability over time, defined as the relative ability of a line to yield well consistently over years (temporally).

Work by Binswanger and Barah (1980) has helped to understand the relationship between both types of variety behaviour. They divide the relevant plant-independent variables into three types:

- Control variables: the experimenter decides on the presence or absence of control variables and determines the degree. Examples are fertilizer, irrigation and protective chemicals. These may vary across locations and years, depending on the experimenter's decision.
- Site variables: these are fixed constraints, such as latitude, soil type, day-length or certain localized endemic pests (e.g. Hessian fly). They vary across sites but not across years.
- Weather variables: these include such factors as total rainfall, its distribution, soil moisture, sunshine hours, cloudiness, temperature, etc. They vary across locations, as well as over years, and do so in a similar manner.

Primarily, weather variables are the cause of drought. Drought therefore varies similarly across locations and years. This similarity allows the use of (spatial) adaptation as a measure of (temporal) stability in dry areas. In order to identify temporally stable, drought-tolerant germplasm, the CIMMYT wheat programme uses multilocation testing, a procedure to gauge spatial adaptation.

It would appear that the impact of the traditional breeding methodology under drought conditions has been limited in delivering superior, widely adopted germplasm to semi-arid environments. However, indications are that the material developed under more favourable conditions during a part of the selection process is superior and finds favour with farmers in dry areas.

The authors propose combining input efficiency (expressed as adaptation to drought) with input responsiveness (expressed as yield potential) in a flexible breeding system. Neither alone will provide superior germplasm for drought-prone areas. Germplasm that carries both genetic systems will result in above-average performance in dry years and greater gain to the farmer in wet years. Shuttle breeding and multilocation testing are used to select and screen such material.

Proposed breeding scheme

- F_1: Crosses are made involving spatially, widely adapted germplasm representing yield stability and high yield, with lines with proven drought tolerance in the specific setting of either ME4A, ME4B or ME4C. Winter wheats adapted to drought environments and synthetic germplasm are emphasized as well.
- F_1Top: Only light negative selection is practised. Samples from all remaining plants are promoted as a bulk to the F_2.
- F_2: The individual plants are grown under irrigated and optimally fertilized conditions and inoculated with a wide spectrum of rust virulence. Only robust and resistant plants are selected. These may represent adaptation to favourable environments.
- F_3: The progenies of selected F_2 plants are evaluated in a modified pedigree-bulk breeding system under rainfed conditions or very low water availability. Selection is based on individual lines rather than on individual plants. The progenies are selected based on such criteria as tiller survival, biomass/vigour, grains/m^2 and others.
- F_4: The progenies of selected lines from F_4 are further evaluated under optimum conditions.
- F_5 and F_6: The process described for F_3 and F_4 is repeated.
- F_7 and F_8: Simultaneous yield evaluations are carried out under optimum and low-water environments. There is a selection of those lines showing outstanding performance under both conditions. Further evaluation in international environments is carried out for the purpose of verification.

The above-proposed breeding methodology finds support in some of the research published in recent years (Bramel-Cox *et al.*, 1991; Cooper *et al.*, 1994; Duvick, 1990, 1992; Edhaie *et al.*, 1988; Uddin *et al.*, 1992; Zavala-Garcia *et al.*, 1992). It should be possible to combine input efficiency and input responsiveness for marginal environments in other crops as well.

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