Wheat Yield Potential

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Summary

This paper reviews efforts conducted over the last 50 years to increase yield potential gains while improving adaptation to biotic and abiotic stresses. While percent gains have been similar in irrigated and rainfed areas in absolute figures, productivity has increased considerably more in irrigated areas. The authors underscore the need to develop new germplasm with adaptation to abiotic stresses without sacrificing yield potential, so that farmers benefit in favorable years. A good example is Attila, a line that has been reselected or released in countries with highly contrasting environments. They also emphasize the importance of introducing new genetic diversity. For example, results from Wheat International Nurseries distributed by CIMMYT have shown that cultivars with 1B/1R are better adapted to lower input conditions, and other translocations such as 1A/1R, 7DL/7AG have already shown beneficial effects on yield potential in a range of genetic backgrounds.

Introduction

Wheat is a very important commodity worldwide. It is grown on roughly 200 million hectares with an average total production of 600 million metric tons. Global average productivity is around 2.7 t/ha\(^{-1}\) with high variability among countries and regions. The highest average yields are obtained in Western Europe, with more than 8 t ha\(^{-1}\), in contrast to less than 1 t ha\(^{-1}\) in several countries in Central/West Asia and North Africa (CWANA).

Table 1 lists the wheat area in different regions of the world. The single largest region is CWANA with 52 million hectares, followed by North America with 40 million, South Asia with 37 million, Eastern Europe and Russia with 36 million, East Asia with 29 million, European Union with 17 million, and Australia with 12 million hectares. The largest wheat producing countries are China with 29 million hectares, followed by India with 26 million hectares, and USA with 24 million hectares.

Table 1. Wheat area in different regions of the world.

<table>
<thead>
<tr>
<th>Geographic region</th>
<th>Area (000 ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CWANA (West Asia, North Africa &amp; Central Asia)</td>
<td>52,507</td>
</tr>
<tr>
<td>South Asia</td>
<td>36,899</td>
</tr>
<tr>
<td>East Asia</td>
<td>28,763</td>
</tr>
<tr>
<td>Eastern Europe and Russian Federation</td>
<td>35,963</td>
</tr>
<tr>
<td>North America (USA and Canada)</td>
<td>40,043</td>
</tr>
<tr>
<td>European Union (EU)</td>
<td>17,322</td>
</tr>
<tr>
<td>Australia</td>
<td>12,000</td>
</tr>
<tr>
<td>Global</td>
<td>212,000</td>
</tr>
</tbody>
</table>

World demand for wheat by 2020 is estimated at 840 to 1000 million tons. Yield potential and yield gains are essential to meet this demand, as expanding the wheat area is not feasible. Both China and India will be net importers of wheat by 2020 if their average wheat productivity remains stagnant, as it is now in case of India with 2.7 t ha\(^{-1}\) in the last six years. The African continent in general is the largest importer of wheat grain, followed by the Middle East and North Africa (MENA). However, some MENA countries, such as Turkey, Syria, Egypt, and Iran, have made splendid progress in wheat production and productivity. The prospect for yield gains in the countries of Central Asia remains high, provided they prioritize research and developmental issues.

Yield Potential: Historical Perspectives

Wheat breeding worldwide in the last 50 years has had many priorities, of which yield potential gains, maintenance of biotic resistance, and increased abiotic tolerance, especially manipulation of traits for drought and heat, have been given a lot of attention. In the last 40 years, many researchers have investigated yield potential gains in wheat (Tables 2 and 3). There have been constant increases in yield potential in many geographic regions of the world, both developed and developing countries. One of the most important breakthrougths was the incorporation of dwarfing genes \(Rht1\) and \(Rht2\) in the early 1960s by Dr. N. E. Borlaug and his colleagues. This led to the Green Revolution, especially in the Indian Subcontinent. The genetic gains as a result of international wheat breeding efforts have been spectacular. It is estimated that developing countries in general have benefited due to wheat breeding in the order of an additional US$ 3 billion per year (in 1990 US$) (Byerlee and Moya,
These gains are the result of international breeding efforts led by CGIAR centers and NARS.

Past experience has indicated that the gains in percentage have been similar in irrigated and rainfed areas, but in absolute figures grain yield has increased much more in irrigated areas (Table 2 and 3). The Yaqui Valley of Sonora, Mexico, has constantly realized this gain (Figure 1). Trends similar to those in the Yaqui Valley have also been realized in the Punjab (India), Upper Delta (Egypt), Adana region of Turkey, and supplementary irrigated area of Syria. The case of northwestern India is noteworthy: there was a variety shift 10 years ago from a locally bred variety HD2329 to an introduced cultivar Attila from CIMMYT that was released as PBW 343 by Punjab Agricultural University. The variety PBW 343 now occupies 7 million ha in northwestern India (the states of Punjab, Hariyana, Rajasthan, and U.P.). Based on various experiments (unpublished data), yield potential of PBW 343 increased by ca. 10% over HD2329. The additional economic returns are in excess of US$ 150 million per year in northwestern India. The variety Attila and its various selections are released and registered in Pakistan, Afghanistan, Iran, Turkey, Algeria, Tunisia, and Morocco. The NARS of these countries released these lines based on yield potential gains in their respective regions.

### Table 2. Rate of genetic gain in spring bread wheat yield under irrigated conditions.

<table>
<thead>
<tr>
<th>Environment/location</th>
<th>Period (%/year)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sonora</td>
<td>1962-83</td>
<td>1.1</td>
</tr>
<tr>
<td>Mexico</td>
<td>1962-88</td>
<td>0.9</td>
</tr>
<tr>
<td>Nepal</td>
<td>1978-88</td>
<td>1.3</td>
</tr>
<tr>
<td>India</td>
<td>1967-79</td>
<td>1.2</td>
</tr>
<tr>
<td></td>
<td>1996-91</td>
<td>1.0</td>
</tr>
<tr>
<td>Zimbabwe</td>
<td>1967-85</td>
<td>1.0</td>
</tr>
</tbody>
</table>

### Table 3. Rate of genetic gains in spring bread wheat yield under rainfed conditions.

<table>
<thead>
<tr>
<th>Environment/location</th>
<th>Period (%/year)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ethiopia</td>
<td>1967-94</td>
<td>1.2</td>
</tr>
<tr>
<td>Argentina</td>
<td>1966-89</td>
<td>1.9</td>
</tr>
<tr>
<td>New South (Australia)</td>
<td>1956-84</td>
<td>0.9</td>
</tr>
</tbody>
</table>

The breeding of Attila represents a unique combination of genetic resources from Oregon (USA), France, Mexico (CIMMYT), and India. The original cross was made to combine the yield potential of Veery 5 and the stripe rust resistance of line NdD/P101 from Oregon. Veery 5 had exhibited an outstanding performance in CIMMYT international trials (15th ISWYN) in 73 locations (Figure 2). Its performance in ISWYN 15 was not only excellent in high yielding environments, but superior in poor locations as well. Such cultivars are widely adapted as they combine genes for yield potential with genes needed for adaptation to poor environments. Based on this performance, we developed the hypothesis that varieties can be bred with high yield potential and tolerance to abiotic stresses. The case of Attila proves this hypothesis, as it has been released in countries with contrasting wheat growing environments. The evidence is now emerging that such performance can be also seen in maize hybrids developed in the USA.
Future Research on Yield Potential and Hallmark Germplasm

Rasmusson (1996) proposed the concept of hallmark germplasm in breeding. These germplasm materials are invariably good combiners and show dominant phenotype with positive and useful linkages. Using such lines as parents ensures that the resulting progenies have a high probability for outstanding performance. In the case of bread wheat, Attila and Veery 5 can be classified as hallmark germplasm. At the 7th International Wheat Conference held in Argentina in 2005 several authors presented results related to research on yield potential. Kumari et al. (2005) investigated the variability for stay-green and its association with canopy temperature depression (CTD) and yield traits under terminal heat stress of northeastern India. These authors found a correlation ($r = 0.90$) between LAUD (leaf area under decline) and CTD; LAUD and grainfilling duration ($r = 0.83$); LAUD and grain yield (0.88); and LAUD and biomass ($r = 0.84$). LAUD can be easily used to screen advanced lines. In northeastern India, persistent heat is a major limiting factor for high yield.

CIMMYT researchers Rajaram et al. (1990) were among the first to emphasize the role of the 1B/1R translocation in increasing yield potential in spring wheats. Both Veery and Attilas carry the 1B/1R translocation. Results from International Nurseries distributed by CIMMYT have shown that cultivars with 1B/1R are better adapted to lower input conditions (Figure 2). Foulkes et al. (2005) presented data on wheat varieties from 1972-1995 in the UK and reported a yield potential gain of 1.2% per year. In this study, above-ground biomass and yield were associated with the presence of 1BL/1RS. In a similar study, Zhou et al. (2005) investigated the increase in grain yield for the period from 1970-2000 in the provinces of Hebei, Shandong, and Henan. They reported annual grain yield gains of 0.54%, 0.84%, and 1.05%, respectively, and identified the 1BL/1RS translocation as the main source for this increase in Chinese provinces.

Condon et al. (2005) reported stomatal aperture-related traits to select high yield potential in bread wheats. They proposed that combinations of physiological traits for selection, such as flag leaf stomatal porosity, canopy temperature, carbon isotope discrimination ($A^{13}C$) for photosynthetic capacity, and oxygen isotope (18O/16O) for stomatal conductance, if applied at the right physiological stage, could result in development of lines with 5-10% higher yield potential. Singh et al. (2005) reported on wheat plants with a changed plant architecture, a kernel weight of 45-50 g, number of grains/spike varying from 90-100, semi-dwarf plant height (85-100 cm), with dark green broad leaf and robust stems. They identified the line DL1266-5 as having these characteristics; it produced higher yields than PBW 343 at Delhi. This new architectural type has been dubbed super wheat after super rice. CIMMYT researchers have also developed such types, crossing Tetrastichon (from Yugoslavia), Morocco (from Morocco), Agrotriticum (from Canada), Polonicum (tetraploid branched wheat from Poland) with high-yielding parents from CIMMYT’s spring wheat program.

To summarize the above research findings, translocations have made major contributions to yield potential in wheat. The role of other translocations such as 1A/1R, 7DL/7AG can be significant, provided they are introduced into cultivars with the right genetic background. The right genetic background is necessary for the positive expression of translocations in regards to yield potential in wheat, since these translocations do not always have positive effects on yield. Figure 3 shows 11 interspecific crosses involving the durum variety Cham 5 with species of T. urartu, Ae. speltoides, T. boeticum, and T. dicoccoides. Cham 5 had a yield of 3350 kg ha$^{-1}$ compared to derivatives which had yields from 3650 kg ha$^{-1}$ to 3980 kg ha$^{-1}$ with 300 mm of precipitation. The highest yielding line Cham 5* 3/T.urartu 500529 had an 18% higher yield than Cham 5.

Yield Potential and Abiotic Stress Tolerance

In favorable environments, breeding for increased yield potential and biotic stress tolerance/resistance has been the norm for the last 100 years since Mendelian genetics were rediscovered. Breeders have introgressed genes for disease resistance into high yielding and popular cultivars.
However, the boom and bust cycle of varieties’ performance has continued and is continuing; i.e., high yielding cultivars become susceptible to new races and are withdrawn from cultivation to be replaced with resistant ones.

There has not been a parallel phenomenon in relation to combining yield potential and tolerance to drought, heat, and other abiotic environmental stresses. Breeders developing cultivars for abiotic stress environments have mostly ignored yield potential and focused on stress tolerance. However, there is a need for stress tolerant cultivars with high yield potential in years with high rainfall. In such years, tall cultivars lodge, and yields are further reduced due to disease susceptibility. The Mediterranean region’s agriculture is not completely rainfed. One or two supplementary irrigations providing an additional 100 mm of water is not uncommon in Turkey, Syria, and many Central Asian countries. In such production systems, it is essential to breed cultivars which possess drought tolerance and yield potential. The breeding methodology needs to address the situation. Verry 5 and Attila are excellent examples of adaptation to supplementary irrigation. The ICARDA-CIMMYT wheat breeding methodology has been designed to address the Mediterranean drought situation. Data presented in Figures 4 and 5 show yield performance of experimental wheat lines under natural rainfed conditions and under supplementary irrigation with additional 100 mm of water.

Figure 4 shows the performance of 25 winter wheats grouped as GNR (non-responsive), GNDR (responsive without drought tolerance), GDRL (linear responsiveness with drought tolerance), and GDRQ (quadratic responsiveness with drought tolerance). The categories GNR and GNDR should not be promoted when there are genotypes of GDRL and GDRQ categories. The GDRL types have higher levels of drought tolerance compared to GNR (traditional varieties) and show higher yield potential compared to GNDR and GDRQ.

Figure 5 shows the performance of nine new durum lines compared to check variety Cham 1. The experiment was conducted at Aleppo, Syria, ICARDA, under two water regimes. The graphics give yield and water use efficiency in terms of kg/ha/mm. The variety LC 2504 was not only the highest yielding, but also had highest value for water use efficiency. The check Cham 1 was the lowest yielding and least efficient.
Figure 5. Grain yield (kg ha\(^{-1}\)) and water use efficiency (kg ha\(^{-1}\) mm\(^{-1}\)) of 9 durum wheat experimental lines compared with cultivar Cham 1 in Mediterranean climate. Source: M. Nachit (unpublished, 2004).

References


Association among Durum Wheat International Testing Sites and Trends in Yield Progress over the Last Twenty-Two Years


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Summary

This paper highlights the successes of CIMMYT’s international durum wheat yield trial over the last 22 years, based both on the shuttle-breeding approach and the Center’s global network of NARS cooperators for information feedback. Without this unprecedented global cooperation, none of the impacts (for example, in improving yield under favorable and marginal environments and enhancing disease resistance) would have been possible.

Introduction

Durum wheat currently represents 8-10% of the wheat grown and produced worldwide (FAOSTAT data, 2006). It is, however, concentrated in relatively small geographical areas where it often plays a major role in the food security of urban populations and in the livelihood and nutrition of urban communities. More than 80% of the spring durum cultivars released in the developing world, covering more than 50% of the area planted to this crop, are semidwarf types, either from CIMMYT crosses or from crosses involving at least one CIMMYT parent (Lantican et al., 2005).

The widespread sowing of relatively few, widely adapted cultivars across large geographical areas underscores CIMMYT’s global responsibility to keep providing national agricultural research systems (NARS) with germplasm that can advantageously replace the current cultivars and provide an opportunity for viable diversification of the cultivar base in developing countries. To do that, each year CIMMYT distributes a set of durum wheat nurseries, including the International Durum Yield Nursery (IDYN), a replicated yield trial, to more than 100 collaborators worldwide. Data returned from these yield trials represent a powerful tool to study genotype by environment interactions globally, characterize and classify testing environments, and monitor yield progress over years. Trethowan et al. (2003) analyzed data from 20 years of the Elite Spring Wheat Yield Trial (ESWYT), exploring associations between international testing sites that revealed the importance of several key locations, each representative of large geographical areas with regards to how they differentiate genotype performance. Such analyses performed on data from the Semi-Arid Wheat Yield Trial (SAWYT) allowed Trethowan et al. (2001) to critically assess the global relevance and limitations of CIMMYT’s main drought testing location in Mexico and enabled them to conclude that the testing site effectively predicted genotype performance in the Indian Subcontinent, but failed to do so in areas where other types of drought stress prevail. In durum wheat, Abdalla et al. (1996) used pattern analysis (De Lacy and Cooper, 1990) to classify international testing sites based on five years data of the Elite Durum Yield Trial (EDYT) and concluded that groupings were associated primarily with latitude and water supply. In this study, we used 22 years of data from the IDYN to: (1) explore associations among international testing sites using pattern analysis, and (2) monitor global yield progress over time.

Materials and Methods

All analyses were conducted on grain yield data (adjusted means of two replicates based on an experimental design that has changed over the years) obtained from 827 environments (or location/year combinations), representing 145 locations reporting data from 1983 (14th IDYN) to 2003 (35th IDYN). Only those durum wheat genotypes from crosses made at CIMMYT and produced through at least one round of shuttle breeding in Mexico were included in the study. Only those locations that reported results as complete datasets from at least two years were considered. Associations among international testing sites over years were determined based on how sites differentiated genotypes for yield, using both classification and ordination approaches of pattern analysis (Trethowan et al., 2003). For each of the clusters resulting from pattern analysis, the site that was the “least different” from the other sites (based on the sums of the squared Euclidian distances taken from the dissimilarity matrix for each site versus all other sites in the same cluster) in the cluster was identified as a “key location” or “most representative” site. All years/nurseries included the widely adapted check Yavaros 79, as well as, with very few exceptions, the checks Mexicali 75 and, starting in 1984, Altar 84.

Global yield progress over years was explored through regression analysis using years as the dependent variable.
and average nursery yield or average of the five best yielding genotypes over all reporting locations as independent variables expressed either in t/ha or in relation to the yield of the check Yavaros 79.

Results and Discussion

Association among international testing sites
The pattern analysis placed 44 of the 145 locations into four clusters (at the third fusion level), each including locations that differentiated genotypes similarly for yield (Figure 1). The rest of the testing sites were excluded from the dendrogram due to either insufficient data for all the necessary pair-wise comparisons to be made or to the lack of a consistent grouping trend over years, which prevented the classification of a particular site in a particular cluster. The first group included 14 sites, while the other three consisted of 10 locations each.

The first group included high yielding environments, both irrigated locations (ME1, according to the mega-environment classification used at CIMMYT) in North Africa-Middle East and South Asia (two in Egypt, one in Iraq, four in Northern India, and one in Pakistan) and high rainfall locations (ME2) in Europe (Central Italy, France, Bulgaria, and Serbia), West Africa (Kenya), and CIMMYT’s Toluca station (ME2), one of the two locations used for selecting segregating material as part of the shuttle breeding program. The association between performance in Toluca and that in major irrigated and high rainfall sites worldwide contrasts with the results of Trethowan et al. (2001) and Lillemo et al. (2004) obtained for bread wheat. A poor relationship was indicated between Toluca and international testing sites with regards to performance of bread wheat from either the irrigated or high rainfall programs. This provides a preliminary suggestion that durum wheat may, to a certain extent, classify environments differently than bread wheat, and that generating data on elite durum material at the Toluca station may be justified.

Figure 1. Dendrogram from pattern analysis showing clustering of 44 international testing locations based on yield performance of CIMMYT durum wheat genotypes included in the IDYN from 1983 to 2003.
The second group represents mostly irrigated sites characterized as warm environments (ME5), including five sites in West/South India, one in southern Egypt, one in Ethiopia, and the heat testing site established by CIMMYT in Ciudad Obregon in northwestern Mexico, which uses late planting to generate heat stress through most of the plant growth cycle. However, it also includes a Canadian and a German site, both located at relatively high latitudes where photoperiod sensitivity can be an advantage. Clustering of these two sites with those characterized by high heat may be because the often late spring planting results in plants filling their grain during the hottest time of the year in those environments. Temperature data need to be compiled and related to performance in order to confirm that high temperature is the environmental basis underlying the co-clustering of these locations. If this is confirmed, it would provide support for the relevance of the late planting approach in Obregon as a method to predict performance in hot environments.

Group 3 represents primarily the high yielding irrigated sites (ME1) of northern Egypt (two sites); single sites in India, Pakistan, and Zimbabwe; ICARDA’s rainfed site in Tel Hadya, Syria; and CIMMYT’s irrigated station at Obregon, the other location involved in the shuttle breeding program. The co-clustering to the rainfed location of Tel Hadya and the irrigated Obregon site may appear counterintuitive, but it confirms the results of Abdalla et al. (1996) in durum wheat and those reported by Trethewan et al. (2003) for bread wheat. Interestingly, the simulated drought environment in Obregon (through withholding of irrigation) co-clustered with the full irrigation environment at the same site, indicating that performance under favorable moisture conditions is a good indicator of performance under water-limited conditions, at least under the soil and climate conditions of Obregon.

The last group included all rainfed sites with often highly variable rainfall, mostly in the northern Mediterranean coast (Spain, Portugal, Central Italy, Southern Turkey, and Cyprus), Algeria, and two Chilean sites. This is the only group that did not include a Mexican site for selection or evaluation by CIMMYT, and therefore data generated in Mexico may not be sufficiently relevant for predicting performance at those sites. Since it also includes major durum growing countries, when selecting parents for crossing particular attention should be given to performance at these locations, especially at the group’s key location, the Aegean Agricultural Research Institute in Turkey.

The biplot generated with the principal coordinate (ordination) analysis (Figure 2) supports the overall grouping obtained from the pattern analysis, except that possible overlaps between groups were suggested. For example, both full irrigation and drought environments at the Obregon site, classified in Group 3 in the pattern analysis, were at the limit of quadrants corresponding to Group 1 and Group 3, and could be assigned to either group based on the biplot. This alternative classification makes sense given the similarity between the environmental and production systems of the Obregon irrigated site and the irrigated sites of Group 1. Similarly, the Egyptian, Ethiopian, and the two Indian locations clustering in Group 2 could very well be included in the quadrant corresponding to sites clustering to Group 1. A more in-depth analysis for each individual year and a study of how environmental variables may affect yield at certain locations is needed to more objectively interpret and finalize the classification of durum wheat testing environments.

**Trends in global yield progress over years**

Yield progress can best be assessed when genotype performance is related to a common check present at all locations and years. As shown in Table 1, the use of Yavaros 79 as a reference for estimating yield progress is highly warranted because of (1) the plasticity of its performance and its responsiveness to increasingly favorable conditions (yield ranging from 0.4 to 13.4 t/ha); (2) its overall superiority relative to other widely adapted checks such as Mexicali 75 and Altar 84, as indicated by its overall average yield and the frequency at which it figured among the five best yielding genotypes within a particular nursery; and (3) its better overall stability as determined by regression or the Wricke ecovalence parameters. This is also supported by its well-documented wide adaptation and its status as the most widely grown durum wheat cultivar in developing countries to date.

Regression analysis indicated that from 1983 to 2003 the yield trial means (in t/ha) averaged across all reporting locations (23-45, depending on the year) increased by 1.15% per year. More impressive, the means of the five best yielding genotypes (in t/ha) at each site increased by 3.75% per year. When expressed in percent of Yavaros yield, the five best yielding genotypes at each site increased by 1.43% per year.

To explore trends in yield progress in environments characterized by different yield potentials, we subdivided the environments (regardless of geographical location) into three classes based on their average nursery yield in a given year: unfavorable environments (<2.5 t/ha), intermediate environments (2.5 to 5.0 t/ha), and favorable environments (>5.0 t/ha). Based on the means of the five best yielding genotypes at each site in the same class, expressed in percentage of Yavaros 79 yield, averaged over all reporting sites in the same class, yield increases were observed of 2.08%, 1.36%, and 1.39% per year in unfavorable, intermediate, and favorable environments, respectively. In the locations corresponding to the Central, West Asia and North Africa (CWANA) region, where durum wheat is most important and Yavaros 79 sister lines play a dominating role, yield progress expressed as above was 1.2% per year when all yield levels were considered.
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Figure 2. Biplot from principal coordinate analysis showing clustering of 44 international testing locations based on yield performance of CIMMYT durum wheat genotypes included in the IDYN from 1983 to 2003.

Table 1. Global performance and yield stability parameters of three checks included in CIMMYT’s IDYN from 1983 to 2003.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mexicali 75</th>
<th>Yavaros 79</th>
<th>Altar 84</th>
</tr>
</thead>
<tbody>
<tr>
<td>Environments tested</td>
<td>776</td>
<td>817</td>
<td>737</td>
</tr>
<tr>
<td>Yield range (t/ha)</td>
<td>0.3 – 12.1</td>
<td>0.4 – 13.4</td>
<td>0.2 – 13.0</td>
</tr>
<tr>
<td>Overall mean yield (t/ha)</td>
<td>4.41 a*</td>
<td>4.80 b</td>
<td>4.78 b</td>
</tr>
<tr>
<td>% environments where Yield check &gt; Yield mean top 5</td>
<td>8</td>
<td>22</td>
<td>16</td>
</tr>
<tr>
<td>Stability parameter – Regression slope</td>
<td>0.97</td>
<td>1.02</td>
<td>1.01</td>
</tr>
<tr>
<td>Stability parameter – Deviation from regression</td>
<td>0.064</td>
<td>0.021</td>
<td>0.076</td>
</tr>
<tr>
<td>Stability parameter – Wricke Ecovalence</td>
<td>10.51</td>
<td>8.60</td>
<td>11.53</td>
</tr>
</tbody>
</table>

* Means followed by the same letter are not significantly different at the 0.05 level.

Although these annual yield progress values (1-2%) are common in many national and local breeding programs with a local or regional focus, they can be considered remarkable when obtained by a breeding effort centralized in a single country. As for bread wheat, the international durum wheat yield trial results indicate that the concept of a centralized breeding effort in Mexico based on the shuttle breeding approach and relying on a global network of NARS cooperators for information feedback, has been successful overall. Not only did it initially provide NARS with widely adapted, high yielding semidwarf cultivars to replace landraces in most durum growing countries in the developing world, but it also maintained a steady flow of new genotypes for NARS to select from, resulting in improved yield potential over years (under experiment station conditions).

However, it should be mentioned that this overall positive assessment is based on general trends calculated by averaging results of many, often very different, locations.
Analyses for some individual locations reveal that yield progress over years was not as positive as shown by across-location analyses and was sometimes negative. Again, this calls for a detailed study of environmental conditions and disease pressure at those sites (ongoing) to understand why they failed to show yield progress over time and to then take the appropriate corrective steps. Furthermore, evidence of yield progress from test locations does not necessarily mean that the lines are being adopted by farmers, since this involves many factors other than yield potential.

Interestingly, yield progress was more pronounced in low yielding environments, which is where the majority of the world’s resource-poor rural population lives. A preliminary exploration of the low yielding year/location combinations reveals that these are predominantly rainfed locations in years of low rainfall. However, a formal analysis of actual rainfall at these sites during the low yielding years needs to be conducted before we can reliably conclude that the most substantial annual progress rate occurred in drought-prone environments. Nevertheless, it is safe to suggest that the yield progress achieved through selection of segregating materials and evaluation of advanced lines in favorable environments (irrigated in Obregon and high rainfall in Toluca) has resulted in yield potential progress in favorable environments and in even greater yield increases in unfavorable, possibly drought-prone, environments. However, since performance in dry environments is substantially affected by constraints other than water limitation per se—such as abiotic (micro-element deficiencies or toxicities in soils) and biotic (root and crown rots and nematodes) factors affecting root development and stand establishment—relying on improvement of yield potential alone does not ensure that the germplasm supplied by CIMMYT to national programs will be completely relevant to their needs. Significant and concerted efforts, primarily through partnerships with NARs and advanced agricultural research institutions, to address these constraints through effective breeding strategies are required to enhanced yield stability and translate breeding achievements into improved performance in farmers’ fields.

References

Using Plant Breeding Data to Move from Genotype-by-Environment Interactions to Gene-by-Environment Interactions

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Summary

Genotype-by-environment interactions, especially of the cross-over type for quantitative traits, impede the development of cultivars in plant breeding programs. Progress has been made with self-pollinated cereals to identify and quantify these interactions, usually when the genotypes are cultivars or breeding lines. However, genes influencing traits of interest, such as grain yield or grain quality, are much longer lasting than cultivars, with molecular technologies providing the means of identifying allelic variation. Statistical software and computing power can now make predictions of effects and values of identifiable genes from large, unbalanced data sets for combinations of alleles across many loci.

Using data from southern Australian wheat breeding programs, we have used these technologies to predict genotypic values for the glutenin and puroindoline genes that influence key grain quality traits in wheat (Triticum aestivum L.) and made predictions across 7 glutenin and puroindoline loci for 5,184 combinations of alleles at different flour protein levels. We suggest that the same molecular and statistical technologies that we have used for polygenic inheritance of grain quality can be used for polygenic inheritance of grain yield, but that relationship matrices will be more important to minimize bias. Large data sets, of the type generated by plant breeding programs, will be necessary, and can now be used with these technologies.

Introduction

Genotype-by-environment interactions, especially of the crossover type for quantitative traits, impede the development of cultivars in plant breeding programs. Research over many decades by quantitative geneticists, plant breeders, and biometricians has produced tools for identifying and quantifying these interactions. On the genotype side, the aim of this research has been to assist with the development of stable, elite cultivars, while on the environmental side, the aim has been to better define target production environments. A further objective has often been to develop more efficient methods of evaluating potential cultivars in terms of the numbers and locations of testing environments, replications, and statistical analyses.

Many authors have emphasized identifying repeatable components of genotype-by-environment interactions (Cooper et al., 1996a; Basford and Cooper, 1998). Furthermore, a substantial effort has been made to classify and group environments so that genotype-by-environment interactions are minimized, and genotypic rankings are more consistent (Trethowan et al., 2001; Trethowan et al., 2003). The easiest abiotic environmental components to classify this way are those due to repeatable soil constraints, such as high levels of aluminum, high levels of boron, and zinc deficiency. For these, specific test environments, either field, glasshouse, or laboratory, have been devised, and relatively rapid progress has been made (Fisher and Scott, 1993; Paull et al., 1993; Delhaize and Ryan, 1995; Genc et al., 2002). Nevertheless, many questions still need to be answered. For example, although aluminum tolerance has been shown to be beneficial on acid soils in southern Australia (Scott et al., 2001), it is not known whether aluminum tolerance is detrimental on alkaline soils in the same region. If it is, this would produce a crossover interaction. Likewise, the optimum level of boron tolerance on soils varying widely in boron across relatively short distances is not known.

Due to the unpredictable nature of the Australian environment (Rimmington and Nicholls, 1993; Flannery, 1994), less progress has been made in Australia with constraints due to rainfall and temperature patterns than...
with more easily identifiable abiotic stresses. Nevertheless, progress has been made in understanding and classifying particular environments, and then weighting them in an overall analysis (Cooper et al., 1996b; Podlich et al., 1999; Chapman et al., 2000).

In addition to the difficulties of classifying environments, progress might also be impeded by the temporary nature of the cultivars and breeding lines being assessed. This is because the objective of plant breeding programs is to replace existing cultivars with new ones. Otherwise, the plant breeding program is a failure. Genes are much more permanent than genotypes, with allele frequencies changing as the plant breeding program progresses. By shifting the emphasis from genotypes to genes, predictions of longer-term value to plant breeders should be possible.

Predicting genotypic values

Obviously, the first step in moving from genotypes to genes is the identification of the genes or quantitative trait loci (QTLs) affecting the trait of interest. However, we suggest that the full utilization of this information for quantitative characters requires estimates of the effects of the genes in the target population of environments, either alone or, more often, in combination with other genes. Therefore, in the project that is the topic of this paper, we work with genes already identified and mapped in other projects. Central to our approach is the estimation of genotypic values for alleles contributing to traits of interest. We regard the genotypic value as the expected value of the phenotype in the target population of environments (Eagles et al., 2002c).

This comes from

\[ P = G + A + E \]

where \( P \) is the observed phenotypic value (a number), \( G \) is the effect of the gene (or genes) of interest, \( A \) is due to other genes (random polygenes), and \( E \) is the environmental deviation. Hence, the means from an infinitely large number of observations in the target population of environments in an infinitely large sample of background genotypes would give the genotypic values for the alleles of interest. With this model, the genes are included in the fixed part of a mixed model, while the background, unknown genes, are in the random part (Kennedy et al., 1992). As wheat is an inbreeding species, we are only interested in genotypic values at homozygosity, and we only analyze data where the allelic composition for the genes of interest are known for all cultivars or breeding lines. In animal breeding, \( A \) is a relationship matrix (Kennedy et al., 1992); we will consider the practical implications of constructing these matrices later in this paper.

The usual method for calculating genotypic values is to construct doubled-haploid populations, or special stocks, such as isolines. The statistical analysis of data from these populations is relatively easy; however, the construction of these populations, and their assessment, is often expensive, so that the data sets available to estimate genotypic values are usually small and from a small sample of the target population of environments. The genetic background is usually limited. As discussed in Eagles and Moody (2004), and by Crepieux et al. (2004) in a QTL mapping and detection context, an alternative is to use large data sets assembled as part of plant breeding. These have the advantage of obtaining estimates across large numbers of crosses and being relevant to the breeding populations of interest (Eagles et al., 2002b; Podlich et al., 2004). The disadvantage is that the data are unbalanced with the potential for biased estimates. Unbalanced data can be analyzed using REML (residual maximum likelihood), and biases can be minimized by including lines as a random term in the model or, even better, by using relationship matrices. We have found that these methods allow genotypic values for multiple alleles at multiple loci to be estimated in large data sets.

Bernardo (2002, p. 54) discussed the concept of effects of alleles. He noted that Sir Ronald Fisher used the term average effect of an allele to denote the average deviation from the population mean of individuals that received the allele from one parent, the other allele having come at random from the population. Hence, the average effect depends on the frequency of the allele and other alleles in the population of interest. Although this is useful for selection in populations for which the objective is to improve the mean of a population of individuals, such as a herd of cattle, we consider this to be less useful in breeding plants, for which the objective is to identify a superior genotype (or very closely related genotypes as occurs with \( F_4 \) or \( F_5 \)-derived lines) and multiply this genotype to become a released cultivar. This is the situation with self-pollinated crops such as wheat and barley. New populations of such crops are generated easily and in large numbers by breeders, with segregating allele frequencies often 0.5 (a single cross), or 0.25 and 0.75 (a backcross or 3-way cross). Then, genotypic values of genes and combinations of genes are important for predicting breeding progress. These do not depend on gene frequencies. Interestingly, Fisher (1930) also considered populations in which mating (and thus gene frequencies) is under the control of the experimenter to be different from those where it is not. Researchers with self-pollinated crops, including ourselves, have used the term effect to denote differences between factor levels, such as different alleles of a particular gene. These are especially useful for predicting the genotypic value of a combination of genes.

So far, we have concentrated on predicting genotypic values across a single, large population of environments. However, the same methodology can be used to estimate gene-by-environment effects, and especially to detect when crossover interactions occur. Then, the equation is expanded to
\[ P = G + GF + A + E \]

where GF denotes a gene-by-environment interaction component. In practice, these can be especially useful with repeatable components of the environment (F), which for analysis purposes can be included along with the identifiable genes in the fixed part of the mixed model. An advantage of using genes is that only a few alleles are considered at each locus, rather than the many genotypes often being considered with cultivars or breeding lines. This greatly simplifies the identification of crossover points.

**Genes influencing grain quality**

The major emphasis for breeding wheat and similar crops is improvement of grain yield. However, cultivar acceptance in countries like Australia depends not only on grain yield potential but also on other traits, especially grain quality for target markets. Many lines with high yield potential and acceptable disease resistance are not released because they fail to meet quality standards for classification into higher priced grades. If the combinations of genes required to meet grain quality standards can be identified, crosses can be designed to have a high probability of meeting the standards, and therefore higher selection intensities can be used for disease resistance and grain yield. We expect this to lead to faster progress for grain yield. This might be even more important when breeding for grain yield in complex, water-limited environments, such as those described by Passioura (2006).

We have made the most progress with the genes controlling high molecular weight glutenin proteins (\textit{Glu-A1}, \textit{Glu-B1}, and \textit{Glu-D1}), the low molecular weight glutenin proteins (\textit{Glu-A3}, \textit{Glu-B3}, and \textit{Glu-D3}), and the puroindoline proteins (\textit{Pina-D1} and \textit{Pinb-D1}). These influence dough strength (measured as Rmax), dough extensibility, dough development time, and flour water absorption. Although of importance in itself, the work on grain quality can also be viewed as a method for utilizing polygenic systems with multiple alleles for other traits, such as disease resistance and grain yield.

There are multiple alleles at the glutenin and puroindoline loci. The work of Payne and his colleagues was especially influential in identifying the glutenin genes (Payne, 1987), while the work of Morris and his colleagues was similarly important for the puroindoline genes (Morris, 2002). For prediction purposes, we regard the hardness locus, where the \textit{Pina-D1} and \textit{Pinb-D1} genes are located, as a single gene with three alleles, abbreviated as \textit{Pin-aa} (soft), \textit{Pin-ab} (moderately hard), and \textit{Pin-ba} (very hard). Using estimates of main effects at each locus and significant 2-way epistatic interactions, such as between \textit{Glu-B1} and \textit{Glu-B3} (Eagles et al., 2002b), we can now predict 5,184 genotypes (3 x 6 x 2 x 4 x 4 x 3 x 3) across the \textit{Glu-A1}, \textit{Glu-B1}, \textit{Glu-D1}, \textit{Glu-A3}, \textit{Glu-B3}, \textit{Glu-D3}, and \textit{Pin} loci (see Eagles et al., 2006, for identification of the alleles).

These include most of those present in Australian breeding programs and many that have not yet been evaluated. For example, among these 5,184 predictions is one for \textit{a},\textit{i},\textit{d},\textit{b},\textit{h},\textit{b},\textit{a}, which is the abbreviation for \textit{Glu-A1a}, \textit{Glu-B1i}, \textit{Glu-D1d}, \textit{Glu-A3b}, \textit{Glu-B3h}, \textit{Glu-D3b}, \textit{Pin-ba}, with a current predicted genotypic value of 408 BU for Rmax and 19.7 cm for extensibility, and one for \textit{b},\textit{e},\textit{a},\textit{b},\textit{b},\textit{ab}, with a predicted value of 271 BU for Rmax and 21.1 cm for extensibility. These are the genotypes of the cultivars Diamondbird and Yanac, and their estimated values are 392 BU and 259 BU for Rmax, and 19.8 cm and 21.0 cm for extensibility. The agreement between predicted and estimated values for these two cultivars is particularly close. Our current assessment is that, after adjusting for flour protein, we can account for approximately 65% of the genotypic variance across the southern Australian breeding programs with this 7-locus system for Rmax and approximately 60% for extensibility (Eagles et al., 2006). Hence, 35% to 40% of the genotypic variance cannot be explained by the glutenin and puroindoline genes, suggesting that further gains can be made by the incorporation of other genes into the predictions. The quantitative trait locus on chromosome 2A recently identified by Kuchel et al. (2006) is a likely candidate for one of these genes.

The 5,184 predictions are incorporated into software called a “Cross Predictor,” which allows a wheat breeder to predict the quality profile from potential two-way and three-way crosses in his or her breeding program (Eagles et al., 2004b; Ye et al., 2004; Cornish et al., 2006). Using the properties of the binomial expansion, it calculates the minimum population sizes required for a 95% or 99% probability of obtaining progeny within desired quality ranges, even though there is genetic linkage involved (Ye et al., 2004). This allows the breeder to concentrate on crosses with acceptable probabilities of producing cultivars that can be accepted into high quality classifications and, as mentioned previously, increase the selection intensity for traits such as grain yield and disease resistance.

So far, in our published work, we have made predictions for southern Australia as the target environment and have not considered gene-by-environment interactions. However, if these interactions occur, the target environment may need to be subdivided.

**Subdividing the target environment using flour protein**

Although the original target was all wheat growing environments in Victoria, South Australia, and southern New South Wales, we have now divided the target into low protein environments suitable for wheat in the Australian Soft class and high protein environments in the Australian Hard class. All 5,184 genotypes are still predicted, and all the data available are used to make the predictions, with the calculations made using the VPREDICT directive in GENSTAT (Payne et al., 2003). Spline functions are used...
to allow for a non-linear relationship between the gene effects and flour or grain protein. Currently, predictions are made at 8.5% flour protein for Australian Soft and 11.0% flour protein for Australian Hard.

As an example of the types of predictions obtained and their precision as measured by standard errors, the data for Rmax and dough extensibility used by Eagles et al. (2006) were re-analyzed. Briefly, there were 894 lines classified for glutenin and puroindoline genes that were homozygous and not mixed, from 467 environments (site-year combinations) in southern Australia, with a total of 6,258 observations for both Rmax and extensibility. The same statistical methods based on the REML directive in GENSTAT (Payne et al., 2003) were used, except that in the current analysis, environmental flour protein was included as a spline function and the VPREDICT directive was used to make predictions at 8.5%, 11.0%, and 12.5% flour protein for all 5,184 genotypes. Environmental flour protein was estimated as the mean flour protein in each environment. In this example, epistatic interactions were not included.

Predicted genotypic values for a,i,d,b,h,b,ba, which we previously mentioned, is the genotype of Diamondbird; for a,i,d,b,h,b,ab, which is the genotype of EGA Wedgetail; for a,u,a,b,b,b,ab, which is the genotype of Janz; and for b,e,a,b,b,b,ab, which is the genotype of Yanac, are presented in Table 1. The same combinations of glutenin and puroindoline alleles are found in many relatives of these cultivars.

Table 1. Predictions of means for Rmax and dough extensibility for four genotypes of wheat at three flour protein levels.

<table>
<thead>
<tr>
<th>Flour protein (%)</th>
<th>Genotype</th>
<th>Rmax (BU)</th>
<th>Extensibility (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>8.5</td>
<td>a,i,d,b,h,b,ba</td>
<td>366 ± 10</td>
<td>17.5 ± 0.3</td>
</tr>
<tr>
<td></td>
<td>a,i,d,b,h,ab</td>
<td>355 ± 11</td>
<td>17.7 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>a.u,a,b,b,ab</td>
<td>272 ± 9</td>
<td>17.2 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>b.e,a,b,b,ab</td>
<td>251 ±13</td>
<td>17.9 ± 0.3</td>
</tr>
<tr>
<td>11.0</td>
<td>a.i.d,b,h,b,ba</td>
<td>408 ± 9</td>
<td>20.2 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>a.i.d,h,b,ab</td>
<td>400 ± 9</td>
<td>20.8 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>a.u,a,b,b,ab</td>
<td>321 ± 8</td>
<td>20.9 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>b.e,a,b,b,ab</td>
<td>272 ± 11</td>
<td>21.5 ± 0.3</td>
</tr>
<tr>
<td>12.5</td>
<td>a.i.d,b,h,b,ba</td>
<td>416 ± 10</td>
<td>21.5 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>a.i.d,h,b,ab</td>
<td>411 ± 10</td>
<td>22.3 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>a.u,a,b,b,ab</td>
<td>333 ± 9</td>
<td>22.8 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>b.e,a,b,b,ab</td>
<td>268 ± 12</td>
<td>23.4 ± 0.3</td>
</tr>
</tbody>
</table>

1 Genes in the order Glu-A1, Glu-B1, Glu-D1, Glu-A3, Glu-B3, Glu-D3, Pin.

The standard errors for these predictions are all small (Table 1). Hence, for frequent alleles in this large data set the standard errors are small. However, when the objective is to predict future outcomes, such as from a cross of Diamondbird and Janz, these standard errors are probably less important than whether hitherto unidentified genes are segregating. Therefore, we regard the identification and inclusion of further genes as important for improving the accuracy of our predictions.

The genotype a,i,d,b,h,b,ab had a significantly higher predicted extensibility than a,u,a,b,b,b,ab at 8.5% flour protein, a similar predicted extensibility at 11.0% flour protein, but a significantly lower predicted extensibility at 12.5% flour protein (Table 1). This demonstrates the complexity of interactions possible across flour protein levels. The complexity increases when epistatic interactions are included in making the predictions. The best way to handle such complexity is, we believe, by making predictions from very large data-sets that contain as many combinations of alleles as possible. In practice, especially due to cost considerations, these are only possible from plant breeding programs.

The predictions for the a.u,a,b,b,b,ab genotype at 12.5% flour protein could explain the acceptance of Janz and its relatives into the Prime Hard Classification in northern New South Wales and Queensland. This classification requires high flour (or grain) protein and high dough extensibility. High dough extensibility was predicted for the a,u,a,b,b,b,ab genotype at high flour protein levels (Table 1).
Relationship matrices and the reduction of bias
As mentioned previously, Kennedy et al. (1992) showed that biases in the estimation of the effects of genes in unbalanced data sets are minimized using mixed models, with the gene of interest included as fixed and the remaining polygenic effects included as random in a relationship matrix.

The calculation of coefficients of parentage, upon which relationship matrices are based, requires accurate pedigrees. The International Crop Information System (ICIS, see http://www.icis.cgiar.org and McLaren et al., 2005) has facilitated the assembly of these pedigrees and the subsequent calculation of coefficients of parentage; nevertheless, their assembly is a major undertaking for the hundreds to thousands of lines required to identify gene effects across multiple environments. We have found that more general relational databases, such as Microsoft Access, greatly assist with the assembly of these matrices and their export for statistical analysis by GENSTAT. However, once assembled, relationship matrices have multiple uses. For example, they can be used to predict breeding values (Panter and Allen, 1995; Bernardo, 2002), and especially breeding values corrected for known major genes, such as those providing resistance to rusts, and to therefore enhance the identification of desirable parents for the next cycle of crossing. We are using them for that purpose.

Because not all the pedigrees were available at that time, relationship matrices have not been used for the calculation of allelic effects of the glutenin and puroindoline genes. However, all genes are included in all calculations, and the lines themselves are included as a random effect. Furthermore, the lines come from a wide range of crosses (Eagles et al., 2002a) spanning decades, and the genes account for a relatively high proportion of the genetic variance, so biases are probably small. Furthermore, we have found consistency between estimates made from wheat breeding data and those from designed experiments (Eagles et al., 2002b; Eagles, unpublished). Nevertheless, a current aspect of our work is to assemble the relationship matrices for their inclusion in the estimation of genotypic values for genes influencing wheat quality.

For grain yield, we are using relationship matrices to calculate gene effects. For example, a relationship matrix was used to calculate the effect of the \( Ha2 \) gene in barley on grain yield (Eagles and Moody, 2004; Eagles et al., 2004b). To date, these have been based on Malécot’s coefficient of parentage (Malécot, 1948). Crepieux et al. (2004) have proposed using relationship matrices with plant breeding data to locate and map QTLs for traits of importance. They further suggested using molecular marker information for the development of relationship matrices. We agree that using molecular marker information in the development of relationship matrices has merit, but not at the expense of a major reduction in population size when the objective is to estimate effects and predict genotypic values. Errors in pedigrees are of concern, but characterization of lineages for major genes, especially genes that can be unequivocally characterized, can be used to detect many of these errors.

Genes affecting grain yield
Using breeding data from Victoria, the semidwarf allele of the \( sdw1 \) gene in barley was found to increase grain yield in high yielding environments but decrease yield in low yielding environments (Eagles and Moody, 2004). The crossover point was estimated at approximately 2.0 t/ha. A relationship matrix was not used for those original calculations, but similar results were obtained with the inclusion of a relationship matrix (Eagles and Moody, unpublished). It was possible to classify semidwarf and tall alleles of this gene phenotypically, in a manner not dissimilar to that used by Mendel with dwarf and tall peas (Bateson, 1909). We are confident that there was only one semidwarf allele, as the allele can be traced to Diamant in the pedigrees, but we do not know how many alleles are being classified as tall. Molecular methods might identify several alleles being classified as tall, as has occurred for alleles of the puroindoline genes that produce hard grain (Morris et al., 2001; Cane et al., 2004), but with different properties (Martin et al., 2001; Cane et al., 2004), or with the 7 + 8 bands at the \( Glu-B1 \) locus (Eagles et al., 2004a; Vawser and Cornish, 2004).

In addition to the \( sdw1 \) gene, mapping population studies have identified two other genes, \( eps2 \) and \( Ppd-H1 \), that affect grain weight in barley in southern Australia (Coventry et al., 2003). As grain weight, along with grain number per unit area, is one of the determinants of grain yield, these genes are also likely to affect grain yield. With appropriate molecular methods of identifying alleles of these genes, their effects could be determined by typing lines in breeding programs, assembling coefficient of parentage matrices, and using grain yield data gathered by routine operations of the breeding program in a mixed model analysis. As suggested earlier, the effects are likely to be assessed across a much greater number of other genes and in many more environments than with planned experiments.

As in barley, genes affecting height and phenology have been identified in wheat. These include the \( Ppd \) series of genes influencing photoperiod response, the \( Vrn \) genes and the \( Rht \) genes (Snape et al., 2001; Worland et al., 2001; Ellis et al., 2004; Borojevic and Borojevic, 2005). \( Ppd-1 \) has already been shown to produce a crossover type interaction for grain yield of wheat in Europe (Snape et al., 2001). Genes influencing other physiological traits and likely to influence yield are also being identified (Reynolds et al., 2005). For example, progress is being made toward identifying the genetic basis for carbon isotope
discrimination, a physiological trait associated with grain yield in water-limited environments (Rebetzke et al., 2006). With a molecular means of identifying alleles of these genes, their effects on yield in different environments could be estimated, desirable combinations for particular environments identified, and predictions of outcomes for particular crosses made using software similar to that in the Cross Predictor. Eventually, predictions could be made for particular environment types based on soil, rainfall, and temperature characteristics, enhancing the rate of progress possible in cereal breeding.

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References


Introduction (diversity of wild relatives and alien species of wheat)

Bread wheat has unique evolutionary history among other major cereals. It has three kinds of genomes from three different diploid ancestral species of A, B, and D genomes. The ancestral species of A genome, which is thought to be Triticum urartu Tumanian ex Gandilyan (AA) (Dvorak et al. 1993), and B genome ancestor, which is thought to be closely related to Aegilops speltoides Tausch (SS) (Terachi et al. 1988), hybridized naturally forming tetraploid species of Triticum turgidum L. (AABB) and then tetraploid wheat hybridized again with D genomes ancestor of Aegilops tauschii Coss. (Kihara 1944) forming hexaploid wheat of Triticum aestivum L. (AABBDD). According to molecular and archeological data, the formation of tetraploid is estimated in 100,000-500,000 year ago (Huang et al. 2002) and that of hexaploid is about 10,000 years ago (Hancock 1992). This evolution is well-known among wheat scientist, but it is not so well-known about bottleneck effect on diversity during specification in which only limited population of these ancestral species evolved into hexaploid wheat. Dvorak et al. (1998) reported that genetic diversity of D genome in hexaploid wheat is quite narrow comparing to the diversity of diploid D genome species of Ae. tauschii in a phylogenic tree. Ozkan et al. (2005) also reported that durum wheat originated from one part of the diversity of wild species of T. dicoccoides. (Kihara 1944) forming hexaploid wheat of Triticum aestivum L. (AABBDD). According to molecular and archeological data, the formation of tetraploid is estimated in 100,000-500,000 year ago (Huang et al. 2002) and that of hexaploid is about 10,000 years ago (Hancock 1992). This evolution is well-known among wheat scientist, but it is not so well-known about bottleneck effect on diversity during specification in which only limited population of these ancestral species evolved into hexaploid wheat. Dvorak et al. (1998) reported that genetic diversity of D genome in hexaploid wheat is quite narrow comparing to the diversity of diploid D genome species of Ae. tauschii in a phylogenic tree. Ozkan et al. (2005) also reported that durum wheat originated from one part of the diversity of wild species of T. dicoccoides. Because of its huge diversity, we can expect more number of useful genes in these ancestral species than those in wheat genetic gene pool. In fact, the number of genes has been found and transferred into wheat breeding program from most kinds of wild relatives such as Ae. tauschii, T. monococcum, and Ae. tauschii as well as T. dicoccoides, T. timopheevi, and so on (For review see McIntosh et al. 2003; Tyrka and Chelkowski 2004). Besides the ancestral species, alien species of wheat can also contain much diverse genetic resource for the breeding. The genus Triticum L. belongs to the tribe Triticeae which consists of more than 300 species (Dewey 1984). Even though there are some species which seem to be extremely difficult to be hybridized with wheat, the number of reports is indicating that most of Triticeae species would be hybridized with wheat by normal crossing followed by embryo rescue (Mujeeb-Kazi 1995); therefore, most of Triticeae species can be regarded as potential genetic sources for wheat improvement. Another important thing about these alien species is that there are sources of super resistance/tolerance such as Fusarium head blight whose tolerance is close to immunity (Ban 1997) and salinity whose tolerance is high enough to be able to survive even under salt concentration of sea water (McGuire and Dvorak 1981). The wide cross group in CIMMYT has been working to capture these diverse genetic resources to wheat breeding. This review is aiming to summarize the wide cross activities in CIMMYT for the last twenty years to show its potential for the practical breeding.

The use of wild relatives in CIMMYT

Table 1 shows the list of wild relatives in CIMMYT gene bank. Our interest is to utilize many of these genetic resources for wheat breeding. Historically, however, CIMMYT has concentrated on the use of D genome ancestor of Ae. tauschii. One of reasons is that we can obtain the plants with same genomic constitution of bread wheat (AABBDD) by crossing between durum (AABB) and Ae. tauschii (DD). This artificial synthesized wheat is called synthetic wheats (SH’s), and we can directly put them into breeding program. Embryo culture and chromosome doubling technique is necessary to produce SH’s, but these are already established methodologies. One of interest thing is that the first synthetic wheat developed more than 50 years ago in the analysis on wheat evolution (Kihara 1944; McFadden and Sears 1946) but none was interested in using for breeding. It was prior to the Green Revolution in 1960’s, maybe major impact could be achieved within the diversity of bread wheat itself between eastern and western wheats.

In CIMMYT, the production of SH’s was started in 1986 by Dr. Mujeeb-Kazi about 40 years after the first production. After that time, CIMMYT has produced 50-100 new SH lines each year, accumulating about 1,100 SH of D genome (genome=AABBDD). Also, CIMMYT has also produced about 200 and 50 lines of SH’s of A and B genome (AABBA and AABBS(~BB)) by crossing durum and A or S (~B) diploid species. Newly produced SH’s have usually put on evaluation of useful traits in three different field station in Mexico, namely Obregón (dry area), Toluca...
(temperate area and high land), and Poza Rica (tropical environment). Since the climate of the three stations is quite different each other ranging from dry area to tropical environment, it makes us possible to evaluate different abiotic and biotic stresses (Table 2). Table 3 summarizes the useful traits that we have found in the last twenty years including three kinds of rust disease, FHB, Septoria, Helminthosporium, and drought resistance. The D genome SH’s are quite useful against drought stress. In 2004, about 40% of breeding material in Australia is coming from SH’s related materials (Dr. Trethowan R. personal communication).

Table 1.

<table>
<thead>
<tr>
<th>Species Name</th>
<th>Genotype Constitue</th>
<th>Lines in CIMMYT</th>
<th>Lines used for synthetic wheats</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Triticum turgidum</em> L. subsp. dicoccum (Schrank ex Schübl.) Thell.</td>
<td>AABB</td>
<td>779</td>
<td>24</td>
</tr>
<tr>
<td><em>Triticum turgidum</em> L. subsp. dicoccoides (Körn. ex Asch. &amp; Graebn.) Thell.</td>
<td>AABB</td>
<td>880</td>
<td>3</td>
</tr>
<tr>
<td><em>Triticum monococcum</em> L. subsp. aegilopoides (Link) Thell.</td>
<td>AA</td>
<td>880</td>
<td>120</td>
</tr>
<tr>
<td><em>Triticum urartu</em> Tumanian ex Gandilyan</td>
<td>AA</td>
<td>392</td>
<td>21</td>
</tr>
<tr>
<td><em>Aegilops speltoides</em> Tausch</td>
<td>(~BB) SS</td>
<td>140</td>
<td>34</td>
</tr>
<tr>
<td><em>Aegilops tauschii</em> Coss.</td>
<td>DD</td>
<td>400-600</td>
<td>370-450</td>
</tr>
</tbody>
</table>

Table 2.

<table>
<thead>
<tr>
<th>Field station</th>
<th>Latitude</th>
<th>Altitude</th>
<th>Climatic type/zone</th>
<th>Evaluated traits</th>
</tr>
</thead>
<tbody>
<tr>
<td>Obregón</td>
<td>27.2°N</td>
<td>38m</td>
<td>Dry; Bwh</td>
<td>Leaf rust, Stem rust, drought</td>
</tr>
<tr>
<td>Toluca</td>
<td>19°N</td>
<td>2640m</td>
<td>Temperate; Cwb</td>
<td>Yellow rust, septoria, FHB</td>
</tr>
<tr>
<td>Poza Rica</td>
<td>20.5°N</td>
<td>100m</td>
<td>Tropical; Aw'</td>
<td>Helminthosporium</td>
</tr>
</tbody>
</table>

Table 3.

<table>
<thead>
<tr>
<th>Traits</th>
<th>Number of resistance synthetic wheat of D genome (AABBDD)</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf rust</td>
<td>37 lines</td>
<td></td>
</tr>
<tr>
<td>Strip rust</td>
<td>80 lines</td>
<td></td>
</tr>
<tr>
<td>Kernel bunt</td>
<td>20 lines</td>
<td></td>
</tr>
<tr>
<td>FHB</td>
<td>5 lines</td>
<td>Equal to Sumai#3</td>
</tr>
<tr>
<td>Septoria</td>
<td>20 lines</td>
<td></td>
</tr>
<tr>
<td>Helminthosporium</td>
<td>10 lines</td>
<td></td>
</tr>
<tr>
<td>Drought</td>
<td>35 lines</td>
<td>(40% breeding materials for drought tolerance in Australia)</td>
</tr>
</tbody>
</table>

Once we found the resistance traits, we introduce these into modern varieties of CIMMYT whose process is called pre-breeding. Since SH’s have many undesirable traits of wild Ae. tauschii and its plant type is unacceptable for breeders (Fig. 1), we need to transfer only resistance traits to the varieties leaving behind undesirable traits as many as possible. In many cases, susceptible varieties are employed as current parent to confirm the transfer of the resistance factors. One crossing between SH and modern variety and the selection of progenies are often enough to have synthetic derivative lines which have good plant type of modern variety and resistance traits of SH. One more backcrossing on F1 between SH and modern variety will increase the chance to have lines of good plant type. These SH derivatives have been registered for the distribution (Table 4).

In the last 20 years, CIMMYT has utilized more than 500 accessions of Ae. tauschii as well as 200 and 50 lines Ae. speltoides and T. monococcum (Table 1). However, there are still several hundreds of accessions of diploid and more than one thousand of tetraploids in CIMMYT genebank. More efficient and rapid methodology would be preferable. Trait-Targeted production is one way to select accessions to
Figure 1. Prebreeding activity on synthetic wheat. The leaf rust resistance of SH is transferred to CIMMYT modern variety. The CIMMYT cultivar is susceptible in leaf rust which can be seen from the dried leaves. In contrast, SH shows leaf rust resistance, but has a poor plant type, such as non-uniform height of spikes and openness of stems, when compared to the CIMMYT cultivar. Normal breeding practice (cross of the synthetic and modern variety, followed by selection of progenies) allows us to obtain synthetic derivative lines that have both resistance and good plant type.

<table>
<thead>
<tr>
<th>Pedigree</th>
<th>Registration PI number</th>
<th>Tolerance/resistance trait</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Croc_1/Ae. tauschii (205)/Borlaug M95</td>
<td>PI 610751</td>
<td>Septoria</td>
<td>Crop Sci 40(2):590 (2000)</td>
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<tr>
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<td>Septoria</td>
<td>Crop Sci 40(2):590 (2000)</td>
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<td>PI 610755</td>
<td>Septoria</td>
<td>Crop Sci 40(2):590 (2000)</td>
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<tr>
<td>Altar 84/Ae. tauschii (224)/2*Yaco</td>
<td>PI 610757</td>
<td>Septoria</td>
<td>Crop Sci 40(2):590 (2000)</td>
</tr>
<tr>
<td>Altar 84/Ae. tauschii (191)/Yaco/3/Bagula</td>
<td>PI 610759</td>
<td>Septoria</td>
<td>Crop Sci 40(2):590 (2000)</td>
</tr>
<tr>
<td>Croc_1/Ae. tauschii (205)/Flycatcher</td>
<td>PI 613312</td>
<td>Karnal Bunt</td>
<td>Crop Sci. 41:1652–1653 (2001)</td>
</tr>
<tr>
<td>Croc_1/Ae. tauschii (224)/Kauz</td>
<td>PI 613313</td>
<td>Karnal Bunt</td>
<td>Crop Sci. 41:1652–1653 (2001)</td>
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<td>Altar 84/Ae. tauschii (221)/Yaco</td>
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<td>Karnal Bunt</td>
<td>Crop Sci. 41:1652–1653 (2001)</td>
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<td>Karnal Bunt</td>
<td>Crop Sci. 41:1652–1653 (2001)</td>
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<tr>
<td>Croc_1/Ae. tauschii (213)/Papago M86</td>
<td>PI 613317</td>
<td>Karnal Bunt</td>
<td>Crop Sci. 41:1652–1653 (2001)</td>
</tr>
<tr>
<td>Altar/Ae. tauschii (224)/2*Yaco</td>
<td>PI 613323</td>
<td>Helminthosporium</td>
<td>Crop Sci. 41:1653–1654 (2001)</td>
</tr>
<tr>
<td>Sabul//Altar/Ae. tauschii (224)/3/Yaco//Croc1/Ae. tauschii (205)</td>
<td>PI 613324</td>
<td>Helminthosporium</td>
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<td>Bcn//Sora/Ae. tauschii (323)</td>
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<td>Bcn//Doy//Ae. tauschii (323)</td>
<td>PI 613327</td>
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<td>Crop Sci. 41:1653–1654 (2001)</td>
</tr>
<tr>
<td>Bcn//Doy//Ae. tauschii (895)</td>
<td>PI 613329</td>
<td>Helminthosporium</td>
<td>Crop Sci. 41:1653–1654 (2001)</td>
</tr>
</tbody>
</table>
be utilized. Several reports of target use of Ae. taurchii have been already published focusing on disease resistance (Gill and Raupp 1987; Cox et al. 1994), even though it can not capture the total diversity of species in this way. The easiest way to cover the entire diversity is to select accessions to represent entire geographical regions. Recent advance of GIS system allow us to select them with more specific data set such as precipitations, humidity, soil condition, and so on. The DNA tools are also very useful to see diversity in more detail and more precisely. It is specially the case when there is no information about the accessions and chance of mishandling of accessions which we sometimes encounter.

The use of alien species
Even though alien species is more diverse and possessing much superior resistance, it takes much more time for utilization, requiring additional cytological techniques. One big problem is the absence of homoeologous recombination with wheat chromosomes in natural condition, meaning that we can not eliminate number of undesirable wild traits in alien genome by conventional breeding methodology. Usually we need to produce translocation lines in which only part of alien chromosomes segment are translocated into wheat chromosomes, after the production of wheat-alien F1 hybrids/amphiploids, to eliminate and minimize undesirable traits. Despite of the difficulties, one good translocation has huge impact on wheat breeding. The translocation of rye chromatin, T1BL.1RS, is good example. It was useful because of its multiple disease resistance including three kinds of rust (leaf rust, stem rust, and yellow rust) and powdery mildew (McIntosh 1983) and was so effective that about 50% of CIMMYT varieties had this translocation. Increment of yield also reported at certain background (Carver and Rayburn 1994; Villareal et al. 1998). It has problem on bread making, however, showing that the size of alien fragment needs to be as small as possible. The transfer of useful traits from alien species to wheat has been also reported for improving of disease (For review see Friebe et al. 1995) as well as yield (Singh et al. 1998).

Figure 2. Plant types of F1 and amphiploid between wheat and alien species: (a) Maintenance of various perennial F1 plants. (b) Amphiploid between durum (BIA) and Aegilops variabilis. (c) Amphiploid between durum (CAPELLI) and Ae. triuncialis.

The last 20 years, CIMMYT has produced more than 150 F1 hybrids and 50 amphiploids between alien and wheat. Most of alien sources were coming from genus Aegilops and Thinopyrum. The plant types of all amphiploids are quite different from that of wheat cultivars and not acceptable for cultivation. We have maintained those lines, but some of amphiploids are unstable in their chromosomal number, especially in the case when total chromosome number in one plant exceeds 56 and carefully cytological checking is necessary in every seed increase. Some of amphiploids have been backcrossed with wheat to reduce chromosome number and maintained as partial amphiploids in which chromosome numbers are less than 56 (42 bread wheat chromosome + 14 alien chromosome or 28 durum wheat chromosomes + 14 alien chromosomes) and as disomic addition lines in which only one pair of alien
chromosomes added to wheat. These lines, especially disomic addition lines, are usually more stable than amphiploids and easier to use. All of amphiploids, partial amphiploids, and addition lines can be employed for characterization of abiotic and biotic stresses.

Once we find good resistance sources in any of above lines, we move to produce translocation lines. Our strategy of alien translocation is to focus on traits that we can not find good sources in wheat/relatives to produce impact on the breeding, because we need to spend long time for the production. The available translocation in the world is summarized (Friebe et al. 1995). This information is quite valuable to avoid duplication of work. We have focused on FHB disease which has been serious problem in recent years in the world and we can find only limited resistance sources among wheat/relatives. We have already found several amphiploids which showed resistance equal or better than Sumai#3 (Mujeeb et al. 1984; unpublished data). Among them, we focused on Triticum bessarabicum and Leymus racemosus because of availability of addition lines which we can use to identify chromosomal location of tolerance genes. There is several methodologies available for inducing translocation such as induction of homoeologous recombination between wheat and alien chromosomes by using mutants or alien gene sources of ph1b (Sears 1977) and Ph1 (Chen et al. 1994), induction of centromeric translocation (Sears 1952), use of radiation, gametocidal system (Endo 1988), and tissue culture. Among them, homoeologous recombination has been contributing to produce most number of translocations that have utilized in wheat breeding programs. For T. bessarabicum, we use ph1c mutant to induce homoeologous translocation and have already obtained several translocated chromosomes (Fig. 3). Same attempt had been done on L. racemosus, although we could not have been successful without obtaining any of translocation. It may be coming from far evolitional distance between wheat and L. racemosus. For alternative, induction of centromeric translocation and other methodologies has been underway in this species.

![Image](image.png)

**Figure 3. The Thinopyrum bessarabicum translocation line of wheat. Arrow indicates yellow Th. bessarabicum chromosome fragment translocated into reddish wheat chromatin.**

**Conclusion**

CIMMYT is trying to capture genetic diversity of wild species as many as possible including both of ancestral species of wheat and alien species. CIMMYT has focused on the use of D genome ancestor in the form of synthetic wheats and it has been very successful, providing many useful traits against abiotic and biotic stresses for breeding program. More efficient methodology including DNA tools would be favorable to capture additional sources not only in Ae. tauschii but also in other species. Since some of alien species have superior resistance, CIMMYT is also working on this subject in long term effort.
References


Stomatal Aperture Related Traits and Yield Potential in Bread Wheat

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2 CIMMYT, Apartado Postal 6-641, 06600, Mexico, D.F., Mexico
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Summary

This paper summarizes the results of a project aimed to evaluate the use of physiological traits related to stomatal aperture (such as canopy temperature, leaf conductance, and carbon isotope discrimination) in early generations of the CIMMYT wheat breeding program, to break the barriers to bread wheat yield potential. The results indicate considerable potential in the use of those tools to complement breeders’ visual selection for high yield potential lines.

Introduction

It is forecast that by 2020 the world will need to produce 760 million tons of wheat per year (Rosegrant et al., 2001). This is 27% more than world production in 1997 and indicates that demand for wheat will grow by 1.3% per year worldwide and by more than 1.5% per year in developing countries. Despite this continuing increase in demand, it is expected that the area sown to wheat will change very little and that inputs to maintain high yields, such as irrigation, will actually decline significantly. This scenario indicates an urgent need for accelerating the breeding and release of wheats with increasingly higher yield potential.

Breeding wheats with high yield potential has been a major focus at CIMMYT over several decades (Reynolds and Borlaug, 2006). Published studies of wheat yield potential progress at CIMMYT indicate a steady increase (a little less than 1% per year) from the early 1960s (when GA-insensitive semidwarfing genes were first cemented in CIMMYT wheats) to the late 1980s (Sayre et al., 1997) and extending to the mid-1990s (Reynolds et al., 1999). This steady rate of yield potential gain within the CIMMYT program appears to have been maintained to the present day. For example, data presented at this symposium (Singh, on CD, Euphytica) indicates that the highest yielding advanced lines currently being tested in the CIMMYT program out-yield their recurrent parent by 15%. As it happens, the recurrent parent of these newest, high yield potential lines is Baviacora 92, which was released 15 years ago. Simple arithmetic dictates that this equals a yield potential gain of 1% per year.

The yield gains of up to 1% per year achieved at CIMMYT have been obtained by strategic choice of parents contributing exploitable diversity for improved yield and disease tolerance, followed by visual selection in early generations and empirical selection based on yield trial data in later generations. These tools have served CIMMYT well to continuously raise yield potential (Rajaram and van Ginkel, 1996), but they may be insufficient to enable an acceleration in the rate of yield potential gain to 1.5% per year, or higher. Are there additional tools that could help wheat breeders achieve the boost to yield potential gain that seems to be required if future demand for wheat is to be met? This paper summarizes results of a project aimed specifically at evaluating the use of some of these possible tools – physiological traits related to stomatal aperture – in early generations of the CIMMYT wheat breeding program.

Why stomatal aperture related traits?

Research during the 1990s at CIMMYT revealed a consistent correlation between the historic increase in yield potential among CIMMYT semidwarf bread wheats and changes in stomatal aperture related traits (SATs) (Fischer et al., 1998). The studies by Fischer and colleagues were done on a relatively small number of historically important CIMMYT releases spanning nearly three decades from the early 1960s to the late 1980s. The key finding was that more recent, higher yielding releases had higher stomatal conductance than older, lower yielding releases. They also found that yield progress was reflected in changes in traits functionally related to stomatal conductance, such as canopy temperature depression (CTD) and carbon isotope discrimination ($^{13}C$).

Several other studies, before and since the study by Fischer et al. (1998), have also shown positive associations between grain yield and SATs: for example, yield and CTD and yield and leaf porosity, in warm, irrigated environments (Amani et al. 1996; Reynolds et al., 1994; Reynolds et al., 1998; Gutierrez-Rodriguez et al., 2000); yield and $^{13}C$, in
SATS measured in this study
In the study reported in this paper we measured canopy temperature (CT) or canopy temperature depression (CTD), leaf porosity (POR), and carbon isotope discrimination (13C). Apart from their reported associations with yield, other features of these SATs make them appealing as potentially useful tools to complement conventional practice in selecting for high yield potential. Measuring stomatal conductance using conventional diffusion porometers is a relatively slow procedure poorly suited to the sampling of large numbers of plants or plots, and CT/D and POR provide much faster, alternative ways of assessing variation in stomatal conductance. Both are measured using relatively cheap, hand-held instruments and they are fast: many plots can be sampled in a short time so large numbers of lines can be assessed.

Variation in CT among entries reflects variation in how effectively the canopy is being cooled by transpiration of water from the leaves. Assuming uniform evaporative demand, the rate of transpiration (and therefore CT) is largely a function of how open the stomata are, i.e., the stomatal conductance. A single measure of CT provides an estimate of the average conductance of many leaves, because the infra-red thermometer used to measure CT samples a patch of canopy comprised of many leaves. On the other hand, POR is measured on single leaves, so several leaves need to be sampled in each plot to get an average for that plot. The measurement is fast enough that six to eight leaves can be measured within a minute, whereas a single measure of CT takes about 10-15 seconds. POR is measured using a viscous flow porometer that clamps on the leaf and pushes a standard volume of air through the stomatal pores, in one side of the leaf and out the other (Rawson and Hulse, 1996). Conductance and POR are linearly related over the range of stomatal conductance because the carbon in the sampled dry matter (i.e., summed conductance of both leaf surfaces in the range 500-1500 mmol/m²/s) (Rebetzke et al., 2000). But POR and CT do have at least one disadvantage. Both these “instantaneous” SATs are best measured under stable, sunny weather conditions. Even in Ciudad Obregon, Mexico (a desert environment), cloud-free conditions without strong winds occur less consistently than might be expected.

The third SAT assessed in this study was carbon isotope discrimination (13C), which is a more integrative measure of stomatal conductance than either CT/D or POR. It is a measure of the ratio of the two stable isotopes of carbon (13C:12C) laid down in plant tissue over time relative to the ratio of these two isotopes in the CO₂ on which plants feed. 13C makes up about 1% of the C in atmospheric CO₂ and fractionally less than 1% of total plant C. This is because plants of C₃ species favor the fixation of 12C over 13C, i.e., they discriminate against 13C.

There is subtle, yet highly repeatable, genotypic variation in the 13C of C₃ species such as wheat (Condon et al., 1987). To a large extent, variation in 13C reflects the extent of stomatal limitation on carbon uptake. More precisely, it reflects the balance between CO₂ supply to the leaf interior (as set by the stomatal conductance) and the rate of CO₂ drawdown once inside the leaf (as set by the amount and activity of photosynthetic machinery). The greater the stomatal limitation (i.e., the lower the stomatal conductance) per unit photosynthetic machinery, the smaller the discrimination against 13C and the greater the ratio of 13C:12C measured in dry matter. Leaf or grain dry matter can be used for sampling variation in 13C. This dry matter is dried and finely ground, and only a very small sample is analyzed for 13C:12C ratio using a specialized laboratory instrument, an isotope-ratio mass spectrometer.

Measuring 13C is considerably more expensive than measuring CT or POR, but it can be done on freshly sampled dry matter or on dry matter that has been dried and stored for a long time. Sampling the dry matter can be done at any time, so it is not weather-dependent. Measuring 13C also gives a much more time-integrated measure of stomatal conductance because the carbon in the sampled dry matter is laid down over a period of days to weeks.

Details of the Study
Germplasm
Large sets (n=48-62) of random, F₃-derived, recombinant inbred lines (RILs) from five crosses were sown in three consecutive years under temperate, high radiation conditions at CIMMYT’s irrigated field station at Ciudad Obregon in northwestern Mexico (27 20°N, 109 54°W, 38 m ASL). Lines consisted of random F₃-derived bulks grown between F₁ and F₂ as low density bulks without selection pressure, except for some truncation to remove extremes for phenology and height. Populations studied were from two crosses already known to be varying for SATs among the progeny (Siete Cerros/Seri 82; Quarrion/3*Genaro 81), and three crosses among parents selected from CIMMYT breeders’ crossing blocks on the basis of high yield potential and measurements of SATs (Ures/Jun/Kauz/3/SW89.3243; SSeri1/SW89.3243; SW89.3243/Chil2*Star). All parents were generated by the CIMMYT program except Quarrion, which is an Australian “semi-winter” cultivar with a pedigree strongly based on CIMMYT parents. The populations were grown in three consecutive years (2001-02, 2002-03, and 2003-04), referred to henceforth as the 2002, 2003, and 2004 growth cycles, when the populations were at F₅, F₆, and F₇ (repeated), respectively.
Field trial management
The 5 populations were sown in 8 m² yield plots, consisting of 2 raised beds with 3 rows per bed, and in small plots of 1.6 m² (2 m x 2 rows on one raised bed), simulating breeders’ early-generation observation plots. For both plot sizes, trials were sown with 2 repetitions using randomized lattice designs incorporating repeated checks. Plots were sown in mid to late November each year, anthesis had occurred by early March, and plots were harvested after grain maturity in late April. All plots were sown N-S. Plots received 5-6 irrigations of ca. 100 mm each year, the first either immediately before or immediately after sowing, depending on seasonal conditions. Weeds were controlled by early herbicide application and subsequently by hand. Pests and diseases were controlled with foliar sprays when necessary. Nitrogen (150 units/ha) and phosphorus (25 units/ha) fertilizers were applied to achieve 80-90% of maximum yield potential of 7-8 t/ha (Sayre et al., 1997), while minimizing lodging.

Measurements
Grain yield was measured by machine-harvesting yield plots. Machine-harvested yield data was also collected on the small plots. Data on SATs was collected on small plots to simulate the use of SATs in breeders’ observation plots. A visual estimate of yield potential (1-10 scale) was also taken on small plots in 2003 and 2004.

Leaf porosity (POR) of six to eight flag-leaves per plot was measured using a Thermoline viscous-flow porometer. Raw data from the porometer (counts) were inverted (1/counts) to generate data linearly related to stomatal conductance over the range of counts measured on irrigated wheat plants (Rebetzke et al., 2000). Single sets of data were collected from each plot once in the 2 weeks before anthesis (boot stage) and once in the 2 weeks after anthesis (grainfilling) in 2002 and 2003. Leaf porosity data were collected 3 to 12 days after irrigation and on cloud-free days between 1000 h and 1500 h. Days of high wind were avoided.

Measurements of CT in 2003 and 2004 or, in 2002, CTD (equals air temperature minus canopy temperature, whereby cooler canopies give larger values of CTD) were taken on each small plot using a Telatemp infra-red thermometer pointed towards the north (away from the sun) and downwards at an angle towards the center of the plot. The thermometer was held at an angle to the row direction so that no soil was in the field of view of the thermometer (Reynolds et al., 1998). Measuring CT/D is faster than measuring POR, but CT measurements are more subject to short-term environmental variation due to changes in wind speed and air temperature and humidity. Repeated measures of CT were taken to overcome this problem. Data were collected at least three times per plot both before anthesis (boot stage) and after anthesis (grainfilling). Data were collected 3-18 days after irrigation on cloud-free days between 1000 h and 1500 h. Data from days of high wind were excluded from statistical analyses due to high error variance.

Samples for carbon isotope analysis were collected in 2002 only. Recently expanded leaf material was sampled in early January, near the time of full ground cover. Subsamples of grain were taken after machine harvest. Samples were not collected from Cross 5. Leaf and grain samples were oven-dried and ground finely for isotope analysis. This analysis was done using a Europa ANCA sample preparation system connected to a 20-20 ratio mass spectrometer (PDZ Europa Ltd, Cheshire, UK). Values of 13C were calculated assuming a 13C of air of -8‰ (Condon et al., 1987).

Statistical analysis of data
Data were analyzed using mixed models (REML) after checking for normality and error variance homogeneity. Data transformation was not required.

Results
Variation in yield and SATs
Average yields harvested from the large yield plots were a little over 5 t ha⁻¹ and ranged significantly among genotypes within populations from more than 6 t ha⁻¹ to less than 3.5 t ha⁻¹. Average yields harvested from the small plots used for SAT measurements and the ranges in yield variation among lines within populations were very similar to those in the large plots, consistent with the similarity in the general growth environments at the two plot scales. SATs also varied highly significantly among lines within populations. For 13C, the range of variation was on the order of 1.5 to 2.0‰. The average value for leaf 13C across populations was 18.4‰, a little higher than for grain 13C (17.9‰).

Values of POR also tended to be greater when measured earlier in the season, averaging about 8 POR units at boot stage and 5 POR units during grainfill. Conversely, the range of variation for POR within populations tended to be greater during grainfill (up to 5 POR units) than at the boot stage (2-3 POR units). Because of the physical parameters that determine CT/D, average values of CT/D tend to more strongly reflect ambient conditions (air temperature, humidity, and wind speed) than leaf morpho-physiological state. Nonetheless, averaged across sampling events, there was also highly significant within-population variation in CT/D, on the order of 1 to 1.5 ºC during the boot stage and 1.5 to 2 ºC during grainfill. Among the SATs, values of broad-sense heritability (h²) were similar to those of yield. Heritability was highest for grain 13C, which at 0.75 was similar to that of large-plot yield averaged over three years (h² of 0.72). The other SATs (leaf 13C, POR, and CT/D) had values of h² in a single year that averaged between 0.6 (similar to the average h² of single-year, large-plot yield) and 0.4 (similar to the average h² of single-year, small-plot yield).
Genetic correlations of SATs with yield
The genetic correlations (Rg) between SATs measured on small plots and yield measured in larger yield trial plots are summarized in Table 1, where, for simplicity, data are averaged across populations and years. For the most part, average values of Rg were highly significant (0.4 or greater). When averaged across populations, values of Rg were close to 0.5 for $^{13}$C, measured only in 2002, about 0.6 for POR, measured in 2002 and 2003, and about -0.65 for CT/D, measured over all three years.

The positive values of Rg for yield with $^{13}$C and POR indicate that higher yield was genetically associated with more-open stomata, i.e., higher values of POR and $^{13}$C.

Table 1. Summary of genetic correlations (Rg) between SATs measured in small plots and yield measured in large plots for each of 5 populations of RILs. Values presented were calculated by determining Rg for all available SAT/yield combinations across years, and averaging. Yield was measured over 3 years (2002, 2003, and 2004); SATs as indicated in the table.

<table>
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<th>Cross</th>
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</tr>
</thead>
<tbody>
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<td></td>
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<td>Boot</td>
<td>Grains</td>
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</tr>
<tr>
<td>SSeri1/SW89.3243</td>
<td>0.35</td>
<td>0.31</td>
<td>0.17</td>
<td>0.24</td>
</tr>
<tr>
<td>SW89.3243//Chil/2*Star</td>
<td>nm³</td>
<td>nm</td>
<td>0.60</td>
<td>0.79</td>
</tr>
<tr>
<td>Average Rg</td>
<td>0.51</td>
<td>0.50</td>
<td>0.55</td>
<td>0.62</td>
</tr>
<tr>
<td>No. of years for SATs</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>SAT/year combinations</td>
<td>3</td>
<td>3</td>
<td>6</td>
<td>6</td>
</tr>
</tbody>
</table>

1 For CT/D, all values of Rg were positive for CTD measured in 2002, but these have been assigned as negative to allow averaging with negative Rg values for CT measured in 2003 and 2004.
2 All values of Rg for CT/D are assumed positive for calculating mean values of Rg across traits. The mean Rg for SW89.3243//Chil/2*Star is shown in brackets because it does not include Rg values for $^{13}$C.
3 'nm' indicates that leaf and grain $^{13}$C were not measured for this cross.

The magnitude of genetic correlations varied with population, being on average highest for the Siete Cerros/Seri 82 cross and lowest for the SSeri1/SW89.3243 cross (Table 1). This difference largely reflected variation in how closely different SATs were associated with yield in particular crosses. All SATs showed strong associations with yield for the Siete Cerros/Seri 82 cross. Yield and CT/D were strongly associated for SSeri1/SW89.3243, whereas the associations of yield with POR and $^{13}$C were considerably weaker for this cross. For the Quarrión/3*Genaro 81 cross, POR showed the strongest associations with yield. The reason for these inconsistencies among crosses and SATs is not clear. POR measurements tended to be restricted to the first half of the period between irrigations, whereas some CT/D measurements were taken later in the period between irrigations, when available soil water may have been more depleted. It may be that genetic associations of yield with $^{13}$C were weaker than with CT/D and POR because variation in $^{13}$C reflects not just variation in stomatal conductance but also variation in photosynthetic capacity.

Correlated response of yield to selection based on SATs
One objective of this study was to establish the extent to which genotypic differences in SATs were reflected in genetic gains in yield. This was done by calculating the correlated phenotypic response of 3-year plot yield to selection for the best 25% and worst 25% genotypes based on their average SAT values. To simplify presentation, the results are summarized over crosses and years in Table 2. Despite $^{13}$C showing smaller genetic associations with yield than either CT/D or POR, this was not reflected in
yield gains associated with divergent selection for SATs. Of all three SATs, the correlated phenotypic response of yield was greatest for $^{13}$C, at about 40 g m$^{-2}$. The response was similar for $^{13}$C of leaves and $^{13}$C of grain. POR, measured at either boot stage or during grainfill, and CT/D, measured at the boot stage, were associated with a yield gain of a little over 30 g m$^{-2}$ on average, while CT/D measured during grainfill was associated with a 25 g m$^{-2}$ gain from indirect selection. Interestingly, and in contrast with $^{13}$C, CT/D at grainfill showed, on average, the strongest values of Rg with yield, yet it gave the smallest correlated phenotypic response of yield to divergent selection based on SATs. The yield gains from divergent selection are in the context of average trial yield levels of about 500 g m$^{-2}$, and therefore represent relative yield gains ranging from about 8% for $^{13}$C to 5% for CT/D measured during grainfill.

In these experiments we also measured small-plot yield, which was found to be a better predictor of large-plot yield than any of the SATs. Divergent selection for small-plot yield was associated with an increase of 52 g m$^{-2}$ in large-plot yield (Table 2). This result may reflect the similar layout of the small and large plots sown in this study. Plots at both scales were sown on narrow beds, one 2-m bed for the small plots and two adjacent 5-m beds for the large plots. Breeders’ yield plots are no longer sown as solid stands at Obregon, but on two beds that give access to light, water, and nutrients from a furrow down the center of each plot. This may favor a reasonably strong association between yield measured on observation plots and yield measured in large plots.

### Table 2. Phenotypic response of grain yield in large plots, averaged over 3 years for 5 populations, to positive and negative selection based on traits measured in small plots.

<table>
<thead>
<tr>
<th>Trait</th>
<th>No. of years trait measured</th>
<th>Yield difference$^1$ (g m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small plot yield</td>
<td>3</td>
<td>52.0</td>
</tr>
<tr>
<td>$^{13}$C of grain</td>
<td>1</td>
<td>41.0</td>
</tr>
<tr>
<td>$^{13}$C of leaves</td>
<td>1</td>
<td>38.1</td>
</tr>
<tr>
<td>Visual selection</td>
<td>2</td>
<td>33.2</td>
</tr>
<tr>
<td>CT/D at boot stage</td>
<td>3</td>
<td>31.4</td>
</tr>
<tr>
<td>POR at boot stage</td>
<td>2</td>
<td>30.6</td>
</tr>
<tr>
<td>POR at grain-filling</td>
<td>2</td>
<td>30.5</td>
</tr>
<tr>
<td>CT/D at grain-filling</td>
<td>3</td>
<td>25.5</td>
</tr>
</tbody>
</table>

$^1$ Yield difference equals yield of 25% best-selected lines, based on traits, minus yield of 25% worst-selected lines.

The phenotypic yield response to visual selection (breeders’ score on a 1-10 scale) was also determined in 2003 and 2004. In large plots yield response to divergent selection based on visual score on small plots was 33 g m$^{-2}$, comparable to the yield response based on CT/D measured at the boot stage and POR measured at either stage (Table 2). Since it is routine for breeders to do visual scoring of yield potential on observation plots, at least at CIMMYT, multiple regression analysis was conducted with visual scoring and CT to establish if there was any benefit from measuring CT in addition to visual scoring. (In this case, only the complementarity of CT and visual score was assessed, since visual scoring was not done in 2002, when $^{13}$C and POR were measured). The results of analyses on all five crosses combined over two years indicate that while between 13 and 56% of yield could be explained using either measure, a significantly higher proportion of yield, 26 to 63%, could be explained by combining both measures (Table 3). Using visual scoring alone was most effective for the older of the five crosses, Siete Cerros/Seri 82 and Quarrion/3*Genaro 81. Visual scoring was less effective, compared with CT alone, for two of the three crosses made among elite parents chosen from the breeders’ crossing block at the start of this study, Ures/Jun/Kauz3/SW89.3243 and SW89.3243/Chil/2*Star. Visual scoring and CT were equally effective for the cross SSeri1/SW89.3243.

### Discussion

Each of the SATs evaluated in this study—canopy temperature (CT/D), leaf porosity (POR), and $^{13}$C—can be measured relatively easily in breeding populations. Each was shown to have relatively strong genetic associations with yield under the irrigation regimes and environmental conditions encountered at Obregon. Further, there was substantial response of yield to retrospective selection based on each of the SATs. It would only be in very unusual circumstances (e.g., catastrophic damage to yield plots prior to harvest) that SATs might be used as a substitute for yield-testing of advanced lines in replicated trials. A much more likely scenario is that SATs would be used alongside visual selection to help identify those entries to be advanced to the yield-testing stage. In this study, SATs appeared as effective as visual selection in identifying lines with higher yield potential.
Table 3. Multiple regression analysis of the association between yield measured on large plots and visual scoring (1-10 scale) and canopy temperature (CT) measured an small plots, for 5 populations, combined over 2 years.

<table>
<thead>
<tr>
<th>Cross</th>
<th>Step</th>
<th>Variable</th>
<th>Model r²</th>
<th>F</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Siete Cerros/Seri 82</td>
<td>1</td>
<td>Visual</td>
<td>0.56</td>
<td>79.51</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>CT - boot</td>
<td>0.63</td>
<td>10.93</td>
<td>0.01</td>
</tr>
<tr>
<td>Quarrion/3*Genaro 81</td>
<td>1</td>
<td>Visual</td>
<td>0.24</td>
<td>15.33</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>CT - boot</td>
<td>0.32</td>
<td>5.74</td>
<td>0.05</td>
</tr>
<tr>
<td>Ures/Jun//Kauz/3/SW89.3243</td>
<td>1</td>
<td>CT - boot</td>
<td>0.17</td>
<td>10.21</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>CT - grainfill</td>
<td>0.23</td>
<td>3.50</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Visual</td>
<td>0.26</td>
<td>1.72</td>
<td>0.20</td>
</tr>
<tr>
<td>SSeri1/SW89.3243</td>
<td>1</td>
<td>CT - boot</td>
<td>0.13</td>
<td>8.86</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Visual</td>
<td>0.26</td>
<td>7.02</td>
<td>0.01</td>
</tr>
<tr>
<td>SW89.3243//Chil/2*Star</td>
<td>1</td>
<td>CT - boot</td>
<td>0.17</td>
<td>9.68</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Visual</td>
<td>0.23</td>
<td>4.15</td>
<td>0.05</td>
</tr>
</tbody>
</table>

1 For each cross, the first step in the multiple regression model is attributed to the trait explaining the highest proportion of variation in yield, as indicated by increments in the model r² value. F values for each model step are indicated, along with levels of statistical significance (P).

Multiple regression analysis was used to test the complementarity of visual selection and one of the SATs, canopy temperature. The analysis revealed that substantially more yield variation could be explained by the combination of both CT and visual scoring. This result needs to be explored more comprehensively, but it is supported by data from a preliminary study on CTD conducted by van Ginkel et al. (2004, and p. 134, this volume). In that study it was found that when visual selection by the breeder was complemented by CTD measurements, almost three times more high yielding lines were identified compared with visual selection alone. In addition, incorporating measurements of CTD led to the retention of considerably more lines in the highest-yield cohort. Given that selection in segregating generations must take into account multiple factors, such as disease tolerance, appropriate phenology, etc., if these physiological criteria are to be applied in breeding programs, it would be logical to apply visual selection pressure for simple traits such as agronomic type and disease tolerance in the earliest generations (say, F₂ to F₃) to eliminate obviously unsuitable lines, while selecting for more quantitative physiological criteria such as SATs in later generations, say from F₄ onwards, when lines are more genetically fixed.

An important consideration for the utility of SATs in breeding programs is the resources needed to measure SATs relative to the resources required for other activities. Brennan et al. (on CD, Euphytica) report on a detailed economic assessment of the cost effectiveness of the different SATs used in this study. In summary, the economic assessment found that the two SATs measured using hand-held instruments, CT/D and POR, both had a low cost of measurement (c. 0.2-0.3 US$ plot⁻¹) compared with yield testing (c. 12 US$ plot⁻¹) because of the low cost of the equipment needed for CT/D and POR and because both can be measured by relatively unskilled labor. The analysis indicates a potentially high return to investment from applying these cheaply-measured SATs. In fact, Brennan et al. (op. cit.) calculate that, even though no equipment is needed, the cost of visual scoring is actually a little greater than CT/D or POR, (c. 0.45 US$ plot⁻¹ for visual scoring) because highly-trained staff are required for this task. In contrast to CT/D and POR, the cost of a single ¹³C analysis (c. 10 US$ plot), coupled with other labor and equipment costs means that the per plot cost of measuring ¹³C is at least as great as the cost of a yield plot, so ¹³C is unlikely to be used in routine screening in early generations. Similarly, even though yield measured on small plots was found to be a slightly better indicator of large-plot yield than any of the SATs, the cost of small-plot yield testing would also be prohibitive.

CT/D and POR are considerably cheaper than ¹³C or small-plot yield, but successful collection of useful data sets of both instantaneous traits is dependent on stable, sunny weather conditions. In our experience, CT/D is somewhat more susceptible than POR to fluctuations in wind speed. On days with light, fluky winds, all canopies will tend to warm quite rapidly if there is no wind, because it becomes relatively difficult for the canopies to transpire into the pool of moist air caught in the unstirred boundary layer of air around them. If the breeze picks up, however briefly, there can be large, rapid cooling of canopies as the warm layer of

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moist air is replaced by drier air that promotes rapid transpiration. Changes in CT/D that result from these changes in wind speed, air temperature, and humidity tend to be somewhat uncoupled from stomatal conductance, which can remain relatively constant throughout. Thus POR measurements tend to be relatively insensitive to changes in wind speed, at least until the wind becomes quite strong, for example, sufficiently strong that it becomes difficult to grab hold of the leaf to be measured. The best conditions for measuring CT/D are therefore when there is a relatively stable, relatively gentle breeze, and there are no clouds to cause rapid fluctuations in incoming solar energy. POR measurements also require that there are no fluctuations in irradiance, as stomata open and close quite rapidly in response to changes in irradiance.

When considering the genetic correlation of SATs with yield, there was a tendency for both POR and CT/D to show higher Rg when they were measured during grainfilling than when they were measured during booting, while for $^{13}$C there was no difference between $^{13}$C of leaf and $^{13}$C of grain in Rg with yield (Table 1). However, when considering the correlated phenotypic response of yield to divergent selection based on SATs, there were no consistent differences when comparing SATs at different growth stages, except for CT/D where genetic gains were larger for CT/D measured at the boot stage than CT at grainfill. (Table 2). Overall, these results indicate that SATs measurements are relatively insensitive to stage of development, supporting the conclusion from earlier studies in a warmer environment (Amani et al., 1996).

Physiological basis for the associations of SATs and yield
The physiological traits measured here – CT/D, POR, and $^{13}$C – are all related to stomatal conductance. Genetic variation among lines in stomatal conductance may reflect heritable variation in morphological characteristics such as the size and number of stomatal pores. Such morphology-driven variation in stomatal conductance may be sufficient in its own right to generate variation among lines in the rate of carbon gain that is directly reflected in crop biomass or yield. Thus, variation in stomatal conductance would be reflected as variation in radiation use efficiency (RUE), with higher conductance lines having higher RUE and perhaps higher biomass. Biomass variation was not measured on the populations of RILs grown in this study, so associations between SATs and biomass could not be tested. Fischer et al. (1998) found no association between SATs and biomass in their study of key CIMMYT semidwarf wheats released up to 1988, even though there were strong associations between grain yield and SATs. From a study of the association between $^{13}$C and yield among (mainly) released cultivars, Condon et al. (1987) concluded that, while variation among entries in the rate of carbon gain was likely a contributing factor to the large genotypic variation in biomass and yield they observed, the extent of yield variation appeared too great to be explained simply by the direct effects of conductance on carbon gain.

Variation in stomatal conductance may also reflect variation in the response of lines to a number of physiological and metabolic processes. For example, high stomatal conductance may be indicative of a high demand for photo-assimilates caused by many, rapidly filling kernels (i.e., sink strength) in physiologically well adapted lines. This hypothesis is supported by the observation that SATs may show a higher association with final yield and grain number than with above ground biomass (Condon et al., 1987; Fischer et al., 1998). But the hypothesis seems to be countered by observations of yield-related differences in SATs well before anthesis in the present study and also the study by Fischer et al. (1998), i.e., genotypic variation in SATs was apparent well before large differences in sink strength might have been anticipated. There are several other hypotheses that could explain the relationship between SATs and yield; they are not mutually exclusive, in that their application may vary depending, for instance, on crop growth stage or environmental conditions: (1) high stomatal conductance may reflect an intrinsically higher metabolic capacity before anthesis that sets up a larger grain number which subsequently drives greater demand after anthesis; (2) high stomatal conductance may be indicative of a good vascular system capable of meeting evaporative demand, or (3) high stomatal conductance may reflect a less conservative response to reduced soil water potential or evaporative demand between irrigation events. Hence, there may be genetic diversity among lines for root signalling which can cause reduced stomatal conductance in response to soil water deficits which are not actually limiting potential evapotranspiration or there may be genetic diversity among lines for stomatal response to vapor pressure deficit reflecting hydraulic status of the leaves. As part of the ACIAR-funded project that supported the work reported in this paper, we investigated several of these hypotheses and could not eliminate any of them.

Conclusion
The results of this study indicate considerable potential for the use of SATs in early-generation testing to complement breeders’ visual selection for lines with high yield potential. Further work is required using breeders’ populations and expertise to establish an optimal integration strategy of SAT measurements into full-scale breeding operations. Use of SATs in this way should lead to more effective culling of low yield potential lines, thereby reducing the number of such lines that advance to expensive multi-environment yield testing. This should then mean that high yielding elite lines are identified more readily, at lower cost, freeing resources to allow breeders to sample more crosses and increasing the probability of generating gene combinations for even higher yield. In a companion paper, Reynolds et al. (p. 136, this volume) discuss how such gene combinations
might best be generated, arguing that a promising avenue for generating higher yield lies in improving the balance between source traits and sink traits.

Acknowledgments

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References


Complementing the Breeder’s Eye with Canopy Temperature Measurements

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Summary
This paper focuses on the use of canopy temperature depression during the selection of segregating generations to positively skew gene frequency for yield and adaptation. The study reported here made it evident that the combination of canopy temperature depression with visual selection improves the rate of genetic progress and was the approach that identified lines with the highest yield potential.

Introduction
Canopy temperature depression (CTD) has been studied widely on a range of wheat genotypes under drought stress (Blum et al., 1982; Blum, 1988) and heat stress (Reynolds et al., 1994; 1998; Amani et al., 1996), and impressive correlations with yield in breeding populations were found. Clearly crops with cooler canopies cope better under stress than those with warmer canopies, ultimately resulting in higher biomass and yield. Those plants with cooler canopies are better able to regulate stomatal conductance (Amani et al., 1996; Fischer et al., 1998) leading to cooler leaves compared to ambient conditions.

To some extent it is logical that under stressed conditions, particularly high temperatures, CTD is useful in differentiating genotypes for yield. However, under optimal conditions, without moisture or temperature stress, a cooler canopy has also been shown to be associated with yield progress in a small set of cultivars and is probably associated with improved sink strength (Fischer et al., 1998). This has led to studies to examine the association in populations of random inbred lines under the same conditions with similar results (Condon et al., p. 126, these proceedings). However, a critical question related to application in breeding is to what extent the trait can be used during the selection of segregating generations to positively skew gene frequency for yield and adaptation. The specific aims of this study were to (1) measure the value of selection using CTD in breeding wheat for high yield potential, and (2) determine the extra genetic gain, if any, from integration of CTD measurements with selection using the breeder’s eye.

Materials and Methods
In this study we compared four crosses among four CIMMYT spring bread wheats, differing in yield potential, plant architecture, and CTD: Attila x Babax, Attila x Lucero, Babax x Borlaug F95, and Borlaug F95 x Lucero-M. The materials were advanced using the modified bulk breeding method, in which individual F2 plants are selected and maintained as individual bulks from F3 through F6. At F6, individual spikes are selected and sown separately and new, near homozygous advanced lines are then selected from among these head rows. CTD measurements were first recorded in the F4 generation on two-row 1-m plots, each derived from a separate F2 plant; at the same time, all F4 plots were visually selected independently by the breeder. Measurements of CTD were made two and four times on sunny still days during grainfilling. Earlier and later generations were selected visually by the breeder in accordance with ongoing breeding practices. An unselected bulk of each cross was also maintained and multiplied without selection alongside the selected generations.

This approach resulted in three germplasm flows: ‘Breeder’, ‘Breeder+CTD’ and ‘Bulk.’ The total number of lines per germplasm flow differed at each generation, as the breeder visually selected only the best genotypes within each cross (Table 1). The materials were developed using shuttle breeding between two contrasting locations in Mexico, thereby allowing the advancement of two generations a year. The crosses were made at Ciudad Obregón in northwestern Mexico (27°N, 60 masl), and the F2, F4 and F6 generations were grown at the same location. Alternating generations were planted in the Toluca Valley (19°N, 2,640 masl). The site in northwestern Mexico is an arid, irrigated location with clear sunny skies during much of the crop growth period, which is ideal for taking CTD measurements. All generations were grown on raised beds under well-watered and optimally fertilized conditions.

Yield trials of the resulting near-homozygous lines from all three germplasm flows were carried out at Ciudad Obregón on raised beds under fully irrigated and optimally fertilized conditions during three crop cycles (November-April in 1999-2000, 2000-2001, and 2003-2004). The trial design was a latinized alpha-lattice with two replications, and each
trial plot consisted of two beds, 4 m in length, with three rows sown per bed. One hundred and fifty units (150) of N were applied, 75 days units before planting and the rest at first node. The seeding rate was 100 kg/ha, and the harvested area of each plot was 6.4 m². Yield data from each trial were analyzed using SAS PROC MIXED (183), with genotypes considered to be fixed effects and years, replicates and sub-blocks within replications as random effects. Adjusted means were obtained and used for all subsequent analyses.

Results and Discussion

Fifty percent of the variation in yield under these optimum conditions was explained by cooler canopies ($r^2 = 0.55$ ($P = 0.001$)), when analyzed across all crosses and germplasm flows. Overall, ‘Breeder+CTD’ and ‘Breeder’ selection were superior to ‘Bulk’ in identifying high yielding lines (Table 1). ‘Breeder+CTD’ also identified more high yielding lines based on the 1999-2000 and 2000-2001 crop cycles than ‘Breeder-only’ selection, although this was not consistent across all crosses. This superiority of the ‘Breeder+CTD’ selection likely reflects wider genetic diversity compared to ‘Breeder-only’ selection, as the segregating populations were less severely truncated (Figure 1).

Table 1. Yields of three selection methods of germplasm flows: ‘Breeder’, ‘Breeder+CTD,’ and ‘Bulk’; adjusted means from three years of yield trials.

<table>
<thead>
<tr>
<th>Method</th>
<th>Mean yield (kg/ha)</th>
<th>N</th>
<th>Tukey grouping</th>
</tr>
</thead>
<tbody>
<tr>
<td>Breeder</td>
<td>7311</td>
<td>57</td>
<td>A</td>
</tr>
<tr>
<td>Breeder+CTD</td>
<td>7120</td>
<td>154</td>
<td>AB</td>
</tr>
<tr>
<td>Bulk</td>
<td>6872</td>
<td>25</td>
<td>B</td>
</tr>
</tbody>
</table>

A second positive contribution of CTD to selection was the identification of very high yielding lines. This can be seen in Figure 1, where the upper tail of the ‘Breeder+CTD’ distribution extends beyond that for ‘Breeder.’ Clearly, ‘Breeder+CTD’ allowed very high yielding lines to be identified. However, while the top yielding lines of both methods were statistically similar—not unexpected, given breeder involvement in both—the real impact of CTD was in the identification and elimination of lower yielding lines that would otherwise have entered into expensive yield trials.

Conclusions

Clearly CTD is significantly correlated with yield under well-watered and fertilized production conditions. Although the breeder using visual selection only will make steady progress in raising yield potential, it is evident that integrating CTD in this process will improve the rate of genetic progress. CTD also improves the cost efficiency of wheat breeding, as low yielding genotypes that appear agronomically attractive can be eliminated earlier in the selection process. The only limitations are the need for clear sunny skies if accurate CTD assessments are to be made, and the timing of CTD assessment, as some genotypes differentiate best if measurements are made preanthesis and others postanthesis.

References


Source and Sink Traits that Impact on Wheat Yield and Biomass in High Production Environments

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Summary

For many years, yield improvement reported in wheat was associated with increased dry matter partitioning to grain, but more recently, increases in above-ground biomass have indicated a different mechanism for achieving yield potential. The most likely way of increasing crop biomass is by improving radiation use efficiency (RUE), while there is evidence that sink strength is still a critical yield limiting factor in wheat; this suggests that improving the balance between source and sink (SS) is currently the most promising approach for raising yield, biomass, and RUE. Experiments were designed to establish a more definitive link between SS traits and yield, biomass, and RUE in high yield environments using progeny deriving from parents contrasting in some of those traits. The SS traits formed three main groups relating to (1) phenological pattern of the crop, (2) assimilation capacity up until shortly after anthesis, and (3) partitioning of assimilates to reproductive structures shortly after anthesis. The largest genetic gain in performance traits was associated with the second group; however, traits from the other groups were also identified as being genetically linked to improvement in performance parameters. Since many of these traits are interrelated, principal component analysis (PCA) and multiple regression were adopted with the view to discern these relationships more clearly. The trait most consistently associated with performance traits was biomass at anthesis (BMA). The PCA indicated a fairly close association among traits within this group (i.e., assimilation related traits) while those from the other two groups of SS traits (i.e., phenological and partitioning) appeared to have secondary but independent effects. These conclusions were partially born out by stepwise multiple regression for individual crosses where BMA was often complemented by traits from the two other groups. Taken together the data suggest that the assimilation traits biomass in vegetative stage (BMV) and BMA have partially independent genetic effects in this germplasm and were complementary to achieving improved performance. The identification of a number of SS traits associated with yield and biomass, which both PCA and multiple regression suggest as being at least partially independent of one another, support the idea that additive gene action could be achieved by adopting a physiological trait based breeding approach where traits from different groups are combined in a single background. A second breeding intervention based on these results would be in selecting progeny for BMA and BMV using spectral reflectance approaches since those traits that lend themselves to large scale screening.

Introduction

Raising genetic yield potential of crops remains an important research objective for applied scientists for a number of reasons. Year-to-year variation in yield due to unpredictable weather and biotic stresses can have major economic impacts; food security is still not guaranteed for millions of resource-poor people in both urban and rural areas. There is good evidence—in wheat, at least—that improved genetic yield potential of cultivars have impact in both favorable as well as marginal agro-ecosystems (Reynolds and Borlaug, 2006). The physiological basis of yield improvement in wheat has been reviewed by different workers (Loss and Siddique, 1994; Slafer et al., 1994; Calderini et al., 1999; Reynolds et al., 1999; Fischer, 2007). For many years most of the yield improvement reported was associated with increased dry matter partitioning to grain, while above-ground biomass was not modified (Austin et al., 1980; Kulshrestha and Jain, 1982; Calderini et al., 1995; Sayre et al., 1997). In addition, physiological determinants of biomass, especially radiation use efficiency of the crop, was apparently unchanged (Calderini et al., 1997; Fischer et al., 1998). However, more recently increases in above-ground biomass have been reported (Singh et al., 1998; Reynolds et al., 1999; 2001; Donmez et al., 2001; Shearman et al., 2005) indicating a different

Abbreviations: ANT=days from emergence to anthesis; BM=biomass at harvest; BMV=biomass vegetative stage (approximately Zadoks stage 35); BMA=biomass 5 days after anthesis (Zadoks stage 70); dBMs = growth rate (g/d) between approximately Zadoks 35 and 70; GM2 = grains/m2; GSP = grains/spike; HI= harvest index; MAT=days from emergence to physiological maturity; PCA = principal component analysis; SPI= spike index; SPM = spike mass (g/m2); SPS= spike size (g) shortly after anthesis; SM2=spikes/m2; RGF = relative grainfill duration; RSG=relative spike growth duration; RUE=radiation use efficiency; SM2 = spikes/m2; SS = source and sink; TKW = thousand kernel; YLD=yield of grain at harvest.
mechanism for achieving yield potential. Furthermore, despite the theoretical upper limit of HI, estimated at 0.60 (Austin et al., 1980), there has been no quantum improvement in partitioning since it reached ca. 0.50 in the mid-1980s (Fischer and Quail, 1990). Therefore, the conclusions reached previously by experts that investments in raising wheat yield potential should simultaneously focus on improving source and sink (Richards, 1996; Slafer et al., 1996) seem to be still valid.

The most likely way of increasing crop biomass is by improving RUE (Slafer et al., 1999). Various approaches for raising RUE of wheat has been the subject of review (Reynolds et al., 2000), with genetic modification of Rubisco probably the most recent (Parry et al., 2003; 2007). The theoretical limits to RUE were revised by Loomis and Anthon (1996) and, when applied to the irrigated wheat environment of the current study, suggest that significant increases in RUE are attainable (Reynolds et al., 2000). Furthermore, there is an ever increasing body of evidence that suggests sink strength is still a critical yield limiting factor in wheat (Fischer, 1985; Slafer and Savin, 1994; Abbate et al., 1995; Miralles et al., 2000; Borras et al., 2004; Miralles and Slafer, 2007) and that improving the balance between source and sink is currently the most promising approach for raising yield, biomass, and RUE (Reynolds et al., 2001; 2005; Shearman et al., 2005; Foulkes et al., 2007).

Candidate traits for improving the source/sink (SS) balance come from a number of studies. Bingham (1969) suggested that increasing the relative partitioning of assimilates to the developing spike by anthesis (i.e., spike index) might increase grain set. This was later confirmed by Austin et al. (1980) when they analyzed the physiological bases of wheat breeding improvement in the UK. In addition, works looking at the association between resources available during spike growth stage and the spike index have supported the idea (Fischer, 1985; Slafer et al., 1990; Abbate et al., 1995). Based on examination of the relationship between photoperiod and changes in relative duration of phenological phases, Slafer et al. (1996) proposed increasing the relative duration of spike growth (RSG) through manipulation of genetic sensitivity to photoperiod as a means to reach higher spike mass. Subsequent work by Miralles et al. (2000), in which duration of spike growth phase was increased through manipulation of photoperiod, showed that grain set could be increased in this way.

Another way to increase investment in spike growth would be to increase pre-anthesis RUE and, therefore, biomass at anthesis (BMA), making more assimilates available to increase spike mass. Higher dry matter partitioning to the spikes could also be a complementary alternative. Gonzalez et al. (2005) showed that photoperiod manipulation increased spike index. In addition, 7Ag.7DL translocation lines that showed improved agronomic performance over their recurrent parents and the following SS traits showed superior expression in tandem with yield (12%) and final biomass (9%); BMA (5%), spike mass (15%), and spike index (9%); RSG was not affected (Reynolds et al., 2005). In a subsequent study, BMA was increased artificially with a brief light treatment that increased the rate of biomass accumulation during spike-growth or booting stage (dBMs). The treatment was inevitably associated with increased BMA (21%), but there was a larger increase in spike mass (27%) and substantially increased RUE (10%) during grain filling (Reynolds et al., 2005). Work looking at winter wheat cultivars has also shown that pre-anthesis RUE was positively associated with yield gains (Shearman et al., 2005).

Therefore, experiments were designed to establish a more definitive link between SS traits and yield, biomass, and RUE in high yield environments using progeny deriving from parents contrasting in some of those traits. The SS traits formed three main groups relating to (1) phenological pattern of the crop (RSG and relative duration of grain filling-RGF-); (2) realized assimilation capacity up until shortly after anthesis (biomass at flag leaf emergence - BMVs, dBMs, and BMA); and (3) partitioning of assimilates to reproductive structures shortly after anthesis (spike mass, spike index, and absolute spike size). The specific objectives of the experiments were to study in three sets of random sister lines: (1) which SS traits were best associated with yield, biomass, and RUE; (2) the association among SS traits to indicate which trait combinations may result in additive gene action for agronomic performance.

Materials and Methods

Crop environment

All experiments were conducted at the CIMMYT experimental station near Cd. Obregon, northwestern Mexico (27 20˚N, 109 54˚W, 38 m ASL) during the spring wheat season (late November sowing and April harvest). The site is a temperate, high radiation environment; irrigation, plus appropriate weed, disease, and pest control were implemented to avoid any biotic or abiotic stresses. However, nitrogen fertilizer was applied at a rate (150 kg N/ha) which, in combination with residual soil N estimates, was designed to achieve approximately 80-90% of maximum yield potential (normally 7-8 t ha-1; Sayre et al., 1997) and avoid yield losses associated with lodging.

Phosphate fertilizer was applied at a rate of 25 kg P/ha. Plants were sown as plots 5 m long and 1.6 m wide, consisting of 2 raised beds with 3 rows/bed (20 cm between rows) at a seed rate of 100 kg/ha. Plots were sown in randomized lattice designs with 2 reps on three consecutive wheat cycles. Emergence dates were 5 December 2001, 2 December 2002, and 6 December 2003. These three cycles
will be referred to subsequently as the 2002, 2003, and 2004 growth cycles, respectively. A summary of weather data averaged for five different growth stages in each year is presented in (Table 1). The growth stages consisted of three periods up until anthesis (average date) of approximately equal day-degree length, and two periods during grainfilling of approximately equal day-degree length. The growth stages corresponded approximately as follows: (1) canopy establishment, (2) spike primordia, (3) rapid spike-growth, (4) first half of grainfilling, and (5) second half of grainfilling.

### Table 1. Weather data averaged for different growth stages in three wheat cycles, northwestern Mexico, 2002-2004.

<table>
<thead>
<tr>
<th>Growth stage and year</th>
<th>Air temperature (°C)</th>
<th>Radiation MJ/m²/d</th>
<th>days</th>
<th>day °</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>2002 Cycle</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Growth stage)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 Canopy establishment</td>
<td>24.9</td>
<td>6.4</td>
<td>14.3</td>
<td>26</td>
</tr>
<tr>
<td>2 Spike primordia</td>
<td>26.3</td>
<td>5.7</td>
<td>14.4</td>
<td>26</td>
</tr>
<tr>
<td>3 Rapid spike-growth</td>
<td>24.6</td>
<td>7.5</td>
<td>15.6</td>
<td>26</td>
</tr>
<tr>
<td>4 Grainfill: first half</td>
<td>27.5</td>
<td>7.6</td>
<td>21.7</td>
<td>22</td>
</tr>
<tr>
<td>5 Grainfill: second half</td>
<td>27.9</td>
<td>8.3</td>
<td>23.4</td>
<td>21</td>
</tr>
<tr>
<td><strong>2003 Cycle</strong></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Stage 1</td>
<td>25.2</td>
<td>7.8</td>
<td>14.8</td>
<td>26</td>
</tr>
<tr>
<td>Stage 2</td>
<td>27.7</td>
<td>7.9</td>
<td>15.3</td>
<td>25</td>
</tr>
<tr>
<td>Stage 3</td>
<td>27.2</td>
<td>11.1</td>
<td>15.3</td>
<td>23</td>
</tr>
<tr>
<td>Stage 4</td>
<td>25.3</td>
<td>9.0</td>
<td>20.4</td>
<td>22</td>
</tr>
<tr>
<td>Stage 5</td>
<td>29.1</td>
<td>9.2</td>
<td>24.5</td>
<td>20</td>
</tr>
<tr>
<td><strong>2004 Cycle</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stage 1</td>
<td>26.8</td>
<td>6.0</td>
<td>13.0</td>
<td>26</td>
</tr>
<tr>
<td>Stage 2</td>
<td>23.0</td>
<td>8.6</td>
<td>14.6</td>
<td>26</td>
</tr>
<tr>
<td>Stage 3</td>
<td>24.0</td>
<td>6.4</td>
<td>18.6</td>
<td>28</td>
</tr>
<tr>
<td>Stage 4</td>
<td>27.0</td>
<td>8.2</td>
<td>22.4</td>
<td>22</td>
</tr>
<tr>
<td>Stage 5</td>
<td>30.6</td>
<td>11.7</td>
<td>24.7</td>
<td>19</td>
</tr>
</tbody>
</table>

### Agronomic and physiological measurements

Dry vegetative biomass (BMV) was estimated a few days after the last plots achieved full canopy closure (approximately Zadoks stage 35), and BMA was measured shortly (5 days) after anthesis (Zadoks stage 70) on each individual plot. These cuts consisted of the above-ground tissue from 3 rows of a 50 cm length of the bed, starting at least 50 cm from the end of the plot to avoid border effects. Fresh biomass was oven-dried at 70°C for 48 h for dry weight measurement. The trait dBMs was calculated as BMA-BMV divided by the number of days between their respective harvests. The trait spike index was estimated by randomly selecting 12 normal spike-bearing culms from biomass cuts shortly after anthesis and measuring the dry weight of the spikes and culms separately, spike index being the coefficient of the dry weights respectively. The trait spike size was the average dry weight of the 12 spikes. Trait spike mass was calculated by multiplying BMA by the spike index.

Dates of following phenological stages were estimated visually: 50% terminal spikelet stage (using binocular microscope), 50% anthesis, and 50% physiological maturity by the color of spikes. These values were used to derive two additional phenological parameters: (1) relative duration of rapid spike growth (RSG), i.e., the number of days between terminal spikelet and anthesis stages as a percentage of the number of days between crop emergence and physiological maturity; and (2) the relative duration of grainfilling (RGF), i.e., days between anthesis and maturity divided by days between emergence and maturity. After physiological maturity was reached, yield was measured by machine-harvesting a bordered area of 4.8 m². Prior to that, a random sub-sample of 100 spike-bearing culms was removed from each plot, dried, weighed, and threshed, so that harvest index could be estimated. Using these data and an estimate of individual kernel weight (TKW), yield components were calculated: spikes m⁻², grains spike⁻¹ (GSP) and grains m⁻² (GM2), and final above-ground biomass.
Radiation use efficiency was estimated for biomass shortly after anthesis and for biomass at maturity using the sum of incident photosynthetically active radiation from emergence to the day of the anthesis cut and until date of maturity, respectively, after correcting for predictable losses in light interception using the model presented by Reynolds et al. (2000). However, the correction assumes no genetic effects in early light interception or stay-green at the end of grainfilling. Differences in stay-green were not observed based on visual estimates (not shown); however, observed differences in BMV could have been the result of differences in early light interception. Nonetheless, the fact that growth rate between Zadoks 35 and 70 (dBMs) was highly correlated with estimated RUE shortly after anthesis \((r=0.79)\) suggested that the effects of early light interception were relatively minor and that the estimated RUE values were a reasonable approximation with respect to genetic effects. Canopy temperature was measured on sunny days with an infra-red thermometer on all genotypes on three or four different occasions during boot stage and again during grainfilling, as described elsewhere.

Germplasm

Lines consisted of random F4 derived bulks from three crosses. Cross 1 was Condor/R143/Ente/Mexicali_2/3/A. Squarrosa (TAUS)/4/Weaver /5/Bacanora and 34 sister lines were studied with the parents. Cross 2 was Sonalika/Attila, and cross 3 was Sonalika/Borlaug, for which 23 sister lines and the parents were studied in each cross. Between F1 and F4 generations, the populations were managed as low density bulks without selection pressure being applied. The parents were chosen for high yield potential and for contrasts in RSG, spike index, and BMA (unpublished data).

Statistical analyses

To obtain the proportion of the total sums of squares accounted for by the genotype-by-year interaction for each trait, a combined analysis of variance was conducted with the PROC GLM procedure from SAS (SAS version 9.1.3, 2004), with all the effects, environments (years), reps within years, blocks within years and reps, genotypes and environment-by-genotype interaction (GEI), being considered as fixed effects.

Since the traits were measured in different units, we performed the PCA based on the correlation matrix using the PRINCOMP procedure from SAS, and then graphing the first two eigenvectors associated to the first two largest eigenvalues which accounted for 71% of the total variance. The multiple regression was realized with the PROC REG procedure from SAS using the stepwise selection procedure.

Broad-sense heritabilities \((h^2)\) for each trait were estimated over the three years as follows:

\[
h^2 = \frac{\sigma^2_g}{\sigma^2_g + \sigma^2_e + \sigma^2_{ge}}\]

where \(r\) = number of repetitions, \(e\) = number of environments (years), \(\sigma^2_g\) = error variance, \(\sigma^2_g\) = genotypic variance, and \(\sigma^2_{ge}\) = genotype-by-environment interaction variance. Similarly, the genetic correlation can be estimated as

\[
\rho_g = \frac{\sigma_{gxy}}{\sqrt{\sigma^2_{gx}\sigma^2_{gy}}}\]

between the traits X and Y, \(\sigma_{gxy}\) = genetic covariance between the traits, and \(\sigma^2_{gx}\) and \(\sigma^2_{gy}\) are the genetic variances for traits X and Y, respectively. The genetic covariance was estimated using the statistical property of the sum of two random variables, which states:

\[
\sigma^2_{(x+y)} = \sigma^2_x + \sigma^2_y + 2\sigma_{xy}\]

which can be rearranged and written as

\[
\sigma_{xy} = \frac{\sigma^2_{(x+y)} - \sigma^2_x - \sigma^2_y}{2}
\]

For both broad-sense heritability and genetic correlations, all the variance components were estimated using the PROC MIXED procedure from SAS considering all the terms in the model (environments, reps within environments, blocks within reps and environments, genotypes and genotype-by-environment interaction) as random effects.

Results

Agronomic response of germplasm

A summary of the mean agronomic response of sister lines from each of the three crosses—averaged over three cycles—is presented in Table 2. Crosses 1 and 3 had better yield performance on average, but agronomic parameters for progeny from all crosses were within the ranges to be expected from elite/elite crosses. The maximum and minimum values of any genotype (averaged over three years), considering all three crosses, are presented and support this conclusion, for example, when considering the range for harvest index, height, phenology, etc. As mentioned earlier, these trials were N managed to achieve approximately 80-90% of maximum yield potential and avoid the confounding effects of lodging, which can be considerable and certainly greater than the generally insignificant genotype x N interaction effects among contrasting but relatively high N levels in this environment (Sayre, personal communication).
Table 2. Growth parameters of random sister lines from three crosses averaged across genotypes and three growing cycles, and genotype range represented by max and min 3-year average values considering genotypes from all crosses, northwestern Mexico, 2002-2004.

<table>
<thead>
<tr>
<th>Final harvest</th>
<th>Yield dw g/m²</th>
<th>Kernel dw g</th>
<th>Grains lm²</th>
<th>Harvest Index</th>
<th>Biomass dw g/m²</th>
<th>RUE g/MJ</th>
<th>Spikes lm²</th>
<th>Grains /spike</th>
<th>Height cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cross 1 (n=36)</td>
<td>585</td>
<td>37.9</td>
<td>15,500</td>
<td>0.462</td>
<td>1,270</td>
<td>1.53</td>
<td>293</td>
<td>54.7</td>
<td>96</td>
</tr>
<tr>
<td>Cross 2 (n=25)</td>
<td>508</td>
<td>42.1</td>
<td>12,200</td>
<td>0.466</td>
<td>1,100</td>
<td>1.36</td>
<td>254</td>
<td>49.6</td>
<td>94</td>
</tr>
<tr>
<td>Cross 3 (n=25)</td>
<td>562</td>
<td>44.6</td>
<td>12,800</td>
<td>0.481</td>
<td>1,180</td>
<td>1.43</td>
<td>273</td>
<td>48.3</td>
<td>91</td>
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</table>

<table>
<thead>
<tr>
<th>SE</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>26</td>
<td>422</td>
<td>685</td>
</tr>
<tr>
<td>1.9</td>
<td>32.9</td>
<td>50.5</td>
</tr>
<tr>
<td>931</td>
<td>9,500</td>
<td>19,500</td>
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<tr>
<td>0.013</td>
<td>0.422</td>
<td>0.517</td>
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<tr>
<td>62</td>
<td>910</td>
<td>1,450</td>
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<tr>
<td>†</td>
<td>17</td>
<td>345</td>
</tr>
<tr>
<td>17</td>
<td>200</td>
<td>65.5</td>
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<table>
<thead>
<tr>
<th>Phenology</th>
<th>Pre-harvest</th>
<th>Spikelet</th>
<th>Terminal</th>
<th>Anthesis</th>
<th>Maturity</th>
<th>RSG *</th>
<th>RGF †</th>
<th>Biomass</th>
<th>Biomass</th>
<th>Growth</th>
<th>RUE</th>
<th>Spike</th>
<th>Spike</th>
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<tr>
<td></td>
<td></td>
<td>days</td>
<td>days</td>
<td>days</td>
<td>%</td>
<td>%</td>
<td>g/m²</td>
<td>g/m²</td>
<td>g/m²/d</td>
<td>g/MJ</td>
<td>Spike mass</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cross 1 (n=36)</td>
<td>39</td>
<td>81</td>
<td>120</td>
<td>0.352</td>
<td>0.323</td>
<td>328</td>
<td>818</td>
<td>19.4</td>
<td>1.79</td>
<td>0.317</td>
<td>256</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cross 2 (n=25)</td>
<td>35</td>
<td>75</td>
<td>118</td>
<td>0.331</td>
<td>0.365</td>
<td>244</td>
<td>681</td>
<td>17.8</td>
<td>1.64</td>
<td>0.341</td>
<td>228</td>
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<tr>
<td>Cross 3 (n=25)</td>
<td>37</td>
<td>75</td>
<td>120</td>
<td>0.320</td>
<td>0.374</td>
<td>256</td>
<td>704</td>
<td>18.4</td>
<td>1.70</td>
<td>0.356</td>
<td>247</td>
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<td></td>
</tr>
<tr>
<td>SE</td>
<td>1.6</td>
<td>2</td>
<td>1</td>
<td>0.014</td>
<td>0.014</td>
<td>28</td>
<td>47</td>
<td>1.9</td>
<td>†</td>
<td>0.017</td>
<td>16.8</td>
<td></td>
<td></td>
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<tr>
<td>Minimum</td>
<td>30.0</td>
<td>68</td>
<td>115</td>
<td>0.284</td>
<td>0.267</td>
<td>185</td>
<td>577</td>
<td>15.8</td>
<td>1.42</td>
<td>0.275</td>
<td>196</td>
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<td></td>
</tr>
<tr>
<td>Maximum</td>
<td>44.8</td>
<td>88</td>
<td>124</td>
<td>0.442</td>
<td>0.418</td>
<td>395</td>
<td>917</td>
<td>23.8</td>
<td>2.09</td>
<td>0.397</td>
<td>304</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* RSG = relative duration of spike growth period.
† RGF = relative duration of grain filling period.
† Calculated from means.

Genotype by year interaction (GEI) was significant for all parameters, and the proportion of the total sums of squares from ANOVA that were associated with GEI averaged 13% for yield and 18% for final biomass. Source/sink traits showed values similar to yield or lower, except for dBMs, which averaged 30% and was the highest of any trait. Both yield and final biomass were subject to path analysis to determine the basis of this GEI in terms of the interaction of environmental variables with phenological stage and growth parameters; results will be presented subsequently. For reference, the actual range in duration from emergence to anthesis and relative duration between terminal spikelet and anthesis (as a proportion of the period from emergence to physiological maturity), respectively, were for Cross 1: 78-87 days, and 0.28-0.34; for Cross 2: 68-84 days and 0.27-0.41, and for Cross 3: 68-88 days and 0.27-0.42, considering average values across all three cycles.

Association of source/sink traits with performance traits
A number of different analytical approaches were taken to establish which of the SS traits were best associated with performance traits. Principal component analysis (PCA) was performed across the three cycles of the experiment for individual crosses as well as all genotypes from the three crosses together; PCA was also run for individual years using all genotypes. Genetic correlation was made of yield and final above-ground biomass with SS traits, considering crosses separately and together across years. Phenotypic correlations were made of yield, final biomass, and RUE with SS traits. Stepwise multiple regression was performed for SS traits on yield, final biomass, and RUE.

Considering the PCA across genotypes of all crosses and years (Figure 1), yield, biomass, and RUE can be seen to be associated most strongly with traits associated with assimilation, namely BMV and dBMs and, to a lesser extent, BMA. There was no apparent association with any of the phenological traits RSG, RGF, ANT, and MAT. Of the partitioning traits, only spike mass showed association with performance, spike size (g) and HI showed no association, and spike index showed a negative association. When considering PCA for individual years (combining crosses), the SS traits relating to in-season biomass estimates were consistently associated with performance traits, but when considering individual crosses, BMA showed the most consistent association. For RSG there was a consistent weak association with performance traits in all years, but its relationship with yield varied considerably when considering
different crosses. The trait RGF showed a more or less reciprocal relationship to RSG. For spike index, the overall tendency considering years and crosses was for a weak negative association with yield.

Genetic correlations of SS traits with the performance traits yield and final biomass are presented in Table 3. The SS traits that were most consistently and strongly associated with performance traits were BMA, BMV, and spike mass. Interestingly, although a positive relationship was found between BMA and the length of the emergence-anthesis period, a strong association between BMA and RUE was also found (Figure 1). The trait spike index had a tendency to be negatively associated with yield but was more strongly and consistently negatively associated with final biomass. One of the phenological traits, RGF, was consistently and negatively associated with both yield and biomass; RSG showed more inconsistent results, being negative for cross 1 and positive for the other two. The trait dBMs showed inconsistent genetic correlations with yield and final biomass.

Phenotypic correlations were run between SS traits and three performance related traits—yield, final biomass, and RUE—and generally results were quite consistent with genetic correlations. Spearman correlation coefficients were significant but generally weaker than genetic correlations for BMV, BMA, and spike mass, except that BMV did not show significance for cross-2. For spike index, while the general trend was also towards a negative association with biomass and RUE, results were only significant for cross 3. The phenological trait RGF also showed negative association with performance traits but coefficients were not significant in cross 1, while RSG again showed positive association but it was not significant for any performance traits in cross 1 either. The trait dBMs showed significant positive association with performance related traits in cross 1 only. Phenotypic correlations for spike size (g) were positively associated with all three performance traits for cross 1 only. Phenotypic correlations between performance traits and canopy temperature measured both during the boot stage and during grainfilling were very highly significant.

Stepwise multiple regression was run on performance traits (yield, biomass, and RUE) using all SS traits for the three crosses; results are presented in Table 4. The SS trait BMA was involved with 8 of the 9 regression models and was the first step in 5 cases, while BMV was included in 5 models, in conjunction with BMA in 3 cases. The SS traits related to phenological pattern RGF and RSG were included in 4 and 3 models, respectively. The trait spike size (g) was included in all 3 models for cross 2 but not in the other crosses. The traits spike mass, dBMs, and spike index were included in one model each. When comparing the SS traits that were adopted among the 9 models, no strong pattern emerged except for the fact that more variation was explained for all three performance traits in crosses 1 and 2 than for cross 3, and BMA appeared to be more important in explaining variation in final biomass and RUE than it was for grain yield.

![Figure 1. Principal component analysis of source/sink traits with yield and biomass considering 86 genotypes from three crosses grown over three crop cycles, northwestern Mexico, 2002-2004.](image)
Table 3. Broad-sense heritability and genetic correlations with yield and with final biomass of source/sink traits for random sister lines of three crosses averaged over three growth cycles, northwestern Mexico, 2002-2004.

<table>
<thead>
<tr>
<th>Source/Sink Trait</th>
<th>Broad-sense heritability</th>
<th>Genetic correlation with yield</th>
<th>Genetic correlation with final biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>RSG</td>
<td>RGF</td>
<td>BMV</td>
</tr>
<tr>
<td>All genotypes</td>
<td>0.58</td>
<td>0.95</td>
<td>0.60</td>
</tr>
<tr>
<td>Avg. 3 crosses</td>
<td>0.37</td>
<td>0.92</td>
<td>0.49</td>
</tr>
<tr>
<td>Cross 1</td>
<td>0.12</td>
<td>0.87</td>
<td>0.58</td>
</tr>
<tr>
<td>Cross 2</td>
<td>0.50</td>
<td>0.97</td>
<td>0.40</td>
</tr>
<tr>
<td>Cross 3</td>
<td>0.49</td>
<td>0.91</td>
<td>0.48</td>
</tr>
</tbody>
</table>

Abbreviations used.
RSG & RGF = relative duration of spike growth and grain filling periods, respectively.
BMV & BMA = biomass at full canopy cover & anthesis, respectively.
dBMs = growth rate during spike growth period.
SPM & SPI = spike mass (g/m²) and spike index shortly after anthesis.

An SS trait that has been reported previously as being associated with GM2 in a set of Argentinian cultivars released after 1984 (Abbate et al., 1998) is the grain number to spike dry matter ratio at anthesis. In the current study, the trait showed a similar range of genetic variation (60-100 grains/g) as observed previously and showed a 0.6 correlation with GM2 in crosses 1 and 2 while the association was reciprocal with TKW. However, the trait was not associated significantly with yield, biomass, RUE, or SS traits for any of the crosses.

Discussion

Two of the main objectives of this study were to determine which SS traits were best associated with performance parameters (yield, biomass, and RUE) and to analyze the association among SS traits to ascertain which traits in combination may result in additive gene action. Considering the three main groups of SS traits—phenological pattern; assimilation capacity up until shortly after anthesis; and partitioning of assimilates to reproductive structures—it is clear from the results that the largest genetic gains in performance traits were associated with the second group. However, traits from the other groups were also identified as being genetically linked to improvement in performance parameters. Since many of these traits are interrelated physiologically (and numerically in some cases), analytical procedures, including principal component analysis and multiple regression, were adopted with the view to discern these relationships more clearly.

Interrelationships among source/sink traits

The SS trait most consistently associated with performance traits was BMA. The PCA indicated a fairly close association among traits within this group (i.e., assimilation related traits), while those from the other two groups of SS traits (i.e., phenological and partitioning) appeared to have secondary but independent effects (Figure 1). These conclusions were partially borne out by stepwise multiple regression for individual crosses, where BMA was often complemented by traits from the two other groups, and especially the traits spike size (g) and RGF (Table 4). However, BMV was in fact the trait that most often complemented BMA in multiple regression; the PCA analysis (Figure 1) also suggested a degree of independence. Taken together, the data suggest that the assimilation traits BMV and BMA have partially independent genetic effects in this germplasm and were complementary to achieving improved performance.
Table 4. Stepwise multiple regression of source/sink traits on yield, final biomass, and radiation use efficiency for random sister lines of three crosses averaged over three growth cycles, northwestern Mexico, 2002-2004.

<table>
<thead>
<tr>
<th>Yield</th>
<th>Step</th>
<th>Variables</th>
<th>Model R²</th>
<th>F</th>
<th>Prob&gt;F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cross-1 (n=36)</td>
<td>1</td>
<td>BMA</td>
<td>0.528</td>
<td>38.060</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>SPI</td>
<td>0.616</td>
<td>7.570</td>
<td>0.010</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>RGF</td>
<td>0.650</td>
<td>3.040</td>
<td>0.091</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>dBMs</td>
<td>0.675</td>
<td>2.450</td>
<td>0.128</td>
</tr>
<tr>
<td>Cross-2 (n=25)</td>
<td>1</td>
<td>RSG</td>
<td>0.226</td>
<td>6.700</td>
<td>0.016</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>SPS</td>
<td>0.373</td>
<td>5.150</td>
<td>0.034</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>BMA</td>
<td>0.524</td>
<td>6.690</td>
<td>0.017</td>
</tr>
<tr>
<td>Cross-3 (n=25)</td>
<td>1</td>
<td>BMA</td>
<td>0.161</td>
<td>4.410</td>
<td>0.047</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>RGF</td>
<td>0.228</td>
<td>4.410</td>
<td>0.047</td>
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</table>

<table>
<thead>
<tr>
<th>Biomass</th>
<th>Step</th>
<th>Variables</th>
<th>Model R²</th>
<th>F</th>
<th>Prob&gt;F</th>
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<tbody>
<tr>
<td>Cross-1 (n=36)</td>
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<td>BMA</td>
<td>0.619</td>
<td>55.140</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>RSG</td>
<td>0.643</td>
<td>2.280</td>
<td>0.140</td>
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<td>Cross-2 (n=25)</td>
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<td>BMA</td>
<td>0.389</td>
<td>14.640</td>
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</tr>
<tr>
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<td>2</td>
<td>SPS</td>
<td>0.553</td>
<td>8.070</td>
<td>0.010</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>dBMs</td>
<td>0.706</td>
<td>10.900</td>
<td>0.003</td>
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<tr>
<td>Cross-3 (n=25)</td>
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<td>BMA</td>
<td>0.324</td>
<td>11.000</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>SPI</td>
<td>0.370</td>
<td>1.610</td>
<td>0.218</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>SPM</td>
<td>0.407</td>
<td>1.310</td>
<td>0.265</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>RUE</th>
<th>Step</th>
<th>Variables</th>
<th>Model R²</th>
<th>F</th>
<th>Prob&gt;F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cross-1 (n=36)</td>
<td>1</td>
<td>BMA</td>
<td>0.597</td>
<td>50.370</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>RGF</td>
<td>0.661</td>
<td>6.200</td>
<td>0.018</td>
</tr>
<tr>
<td>Cross-2 (n=25)</td>
<td>1</td>
<td>BMA</td>
<td>0.230</td>
<td>6.860</td>
<td>0.015</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>SPS</td>
<td>0.508</td>
<td>12.460</td>
<td>0.002</td>
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<tr>
<td></td>
<td>3</td>
<td>RGF</td>
<td>0.645</td>
<td>8.110</td>
<td>0.010</td>
</tr>
<tr>
<td>Cross-3 (n=25)</td>
<td>1</td>
<td>BMA</td>
<td>0.150</td>
<td>4.040</td>
<td>0.056</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>SPI</td>
<td>0.275</td>
<td>3.810</td>
<td>0.064</td>
</tr>
</tbody>
</table>

Abbreviations of variables.
RSG & RGF = relative duration of spike growth and grain filling periods, respectively.
BMA = biomass shortly after anthesis.
dBMs = crop growth rate during spike growth period.
SPM, SPI, SPS = spike mass (g/m²), spike index, & spike size (g) shortly after anthesis.

Path analysis of main effects attempts to test assumptions about causal relationships among the variables (Vargas et al., 2007). A parallel analysis reported separately (Reynolds et al., 2007) did not produce any surprises with respect to relationships among yield components, and generally confirmed the predictable relationships among SS traits. For example, BMV showed a relatively high association with BMA and spikes m⁻². Early vigor has been proposed as an important trait for improving yield in wheat (López-Castañeda et al., 1995). The trait dBMs showed high association with BMA and generally negative path coefficients with grains spike⁻¹—presumably reflecting compensation among yield components. Nonetheless, some results were more surprising. The trait RSG also showed a positive association with BMA, confirming the PCA result (Figure 1); this may have been associated with the fact that larger RSG was strongly associated with days to anthesis, which in turn was somewhat associated with larger BMA (see subsequent discussion). The trait BMA showed strong association with both GSP and spikes m⁻² indicating the importance of BMA in forming two major yield components. In the light of the results of this study, RUE was one of the main causes of higher BMV and BMA. Then, BMV favored spikes m⁻² and spike mass (associated with BMA) improved GSP. Fertile florets spike⁻¹ and GSP have been shown positively associated with spike mass (Miralles et al., 2000; Gonzalez et al., 2005). In addition, spike mass was a factor in determining BMA.

However, the trait spike index, which partially defines relative spike mass, was not indicated as being involved in this relationship and, in fact, showed a surprisingly low and...
erratic association with other traits in general. This result was not consistent with other work indicating the importance of spike index in determination of grain number (Gonzalez et al., 2005). Although work conducted on a set of Argentinean cultivars released after 1984, while showing significant genetic variation in spike index (from 28-34%), indicated the trait was not associated with yield or grain number (Abbate et al., 1998). Association between maintenance of large numbers of grains/spike and post-anthesis assimilation rate has been demonstrated in other germplasm (Reynolds et al., 2001; 2005; Shearman et al., 2005), and preliminary evidence for a causal signaling mechanism has been suggested by studies in which abscisic levels in spike tissue at boot stage were found to be lower in genotypes displaying higher grains/spike (Figure 2).

![ABA concentration in spike tissue](image)

Figure 2. Concentrations of abscisic acid in spike tissue of at late boot stage of 7DL.7Ag substitution lines and their recurrent backgrounds, average of three genetic backgrounds, at two field location in Mexico 2002 (ABA was extracted using the methodology of T. Setter, pers. comm.).

Regulation of grain number would be an important trait to ensure seed quality in conditions where post-anthesis assimilation capacity might be reduced by a number of factors such as water deficit, shading by weeds, and loss of photosynthetic tissue due to biotic agents. It is therefore understandable if even modern wheat cultivars have retained apparently excess photosynthetic capacity (Reynolds et al., 2005), since for most of its evolution and in most environments, the crop experiences unpredictable agronomic conditions. However, the genetic capacity to partition more assimilates to spike growth (spike index) resulting in larger numbers of grains per spike and, therefore, a more complete utilization of post-anthesis photosynthetic capacity would appear to be advantageous for wheat in well managed, high yield environments. One reason why different SS traits appear to have variable influence in determining performance traits in different studies may be related to variations in phenological patterns of the lines being studied; this factor will be discussed in the section on comparing genotypes in experimental breeding populations.

**Comparing genotypes in experimental breeding populations**

While the timing of phenological stages such as anthesis can be controlled by choice of genotypes in studies with unrelated fixed lines, experiments aimed at estimating genetic effects of traits employ the random progeny of experimental crosses. In this kind of population data can be confounded by two major factors. The first is that some genotypes may have generally poor agronomic adaptation; however, this can be relatively easily overcome by selecting suitable populations from a range of crosses among contrasting but agronomically elite parents, as was the case in this study. The second confounding factor is genetic variation in flowering date. This is not generally considered to be problematic if the population’s overall maturity class fits the target environment. However, this is almost certainly a false assumption and the most likely reason why, for example, QTL studies frequently identify Ppd loci as those most strongly associated with adaptation to stress environments, as has been the case for drought adaptation studies in rice (Lafitte pers. comm). It is well established in wheat that key developmental processes such as kernel set are determined within relatively narrow developmental windows and can be especially sensitive to environmental conditions (Fischer, 1980; Fischer, 1985; Abbate et al., 1997). Therefore, genotypes growing side by side but which pass through key developmental stages on different dates are likely to trigger different physiological responses at the whole plant level. In summary, the potentially confounding effects of uncontrolled variation in phenology have yet to be fully overcome in studies with experimental populations aimed at identifying candidate traits and genes for crop improvement, though some progress has been reported recently (Olivares et al., 2007). The germplasm in the current study showed a 10-20 day range in days to flowering (depending on the cross) and is likely to have influenced some results. For example, while BMA was strongly correlated with RUE (Figure 1) there was also an association with the duration of the emergence-anthesis period which varied from cross to cross. There was also an association of RSG with BMA, and it appeared that larger RSG was also strongly associated with the duration of the emergence to anthesis period. Nonetheless this is the first study reported which looks comprehensively at the association of SS and performance traits and in spite of variation in phenology some very clear patterns emerge which have the potential to be applied in breeding as will be discussed in the following section.

**Implications for breeding**

Assuming that the genetic backgrounds chosen for this work are representative of other germplasm sources used in breeding for yield potential, these results provide a set of
traits that can be applied in a number of ways. The first intervention would be in crossing, where potential parents can be screened for the SS traits and crosses made between parents with complementary characteristics. The identification of a number of SS traits associated with yield and biomass, which both PCA and multiple regression suggest as being at least partially independent of one another, supports the idea that additive gene action could be achieved by adopting a physiological trait based breeding approach where traits from different groups are combined in a single background (Reynolds and Trethowan, 2007). With reference to a conceptual model developed to identify potentially complementary traits for crossing strategies (Figure 3), the traits identified in this study fit into two main groups: pre-anthesis source traits (including BMV, BMA, and dBMs), pre-anthesis sink traits (including spike mass and spike index), and phenology traits such as RSG and RGF. The importance of post-anthesis assimilation rate probably in response to sink size was also indicated in this study by the strong association of performance traits with canopy temperature (CT) during grainfilling.

Figure 3. Conceptual model of traits influencing yield potential in wheat; traits are considered in groups that affect source or sink strength either before or after anthesis, based on evidence from the literature.

A second breeding intervention based on these results would be in selecting progeny for those traits that lend themselves to large-scale screening. It is fortuitous that BMA was identified in this study as the trait best associated with yield and biomass, since a rapid screening protocol for distinguishing genetic differences in biomass at anthesis and other crop stages such as BMV has recently been tested and validated in the same environment (Babar et al., 2006a). The methodology involves measurement of spectral reflectance indices with a hand-held probe, which also distinguishes between yield (Babar et al., 2006b). The high heritability of both BMA and BMV (Table 3) supports their value as early-generation screening traits. The third way in which the information generated by the current study could be applied to crop improvement would be to identify new and better sources of the SS traits in germplasm collections where the same rapid screening methodologies could be applied at least to screen large collections of accessions for BMV and BMA.

Acknowledgments

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References


Raised Bed Planting Technologies for Improved Efficiency, Sustainability and Profitability

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SUMMARY

The increase in average yield of irrigated spring wheat in farmer fields in the Yaqui Valley, from the early 1950s, when new rust resistant, non-semi-dwarf wheat cultivars were initially extended to farmers, through the development and release of the new, input responsive, high-yielding semi-dwarf cultivars up to the present, has been impressive (2.36% increase per year). However, this rate of yield improvement has gradually been decreasing to the point that there has been a rather modest yield increase in farmer fields since the 1980s. The declining yield increase trend, combined with both very minimal farmer adoption of newly released cultivars in the Yaqui Valley over the past 10 to 15 years and the apparent meagre increase in wheat genetic yield potential (especially for bread wheat) since 1992, as estimated in optimally managed yield potential trials, is troubling. This situation has led to concerns that a possible genetic yield potential “ceiling” has been or is being reached for irrigated spring bread wheat.

An important portion of the wheat yield increase that has occurred in Yaqui Valley farmer fields over the past 55 years can also be attributed to improved, crop management practices that farmers have adopted together with the new, higher-yielding cultivars. If speculation that a genetic yield potential ceiling is being reached proves correct or if continued genetic gains are going to be more difficult and expensive to realize, then one fact is patently clear – farmers now need, perhaps more than ever before, new and appropriate crop management alternatives that can maintain superior yields, reduce production costs, improve input responsiveness and offer farmers long-term, sustainable production opportunities that both protect as well as enhance the natural resource base.

INTRODUCTION

Generally workshops/symposiums that focus on crop yield potential nearly always restrict considerations to genetic yield potential issues even though other factors, especially suitable crop management practices and associated agro-climatic conditions for the defined targeted area/s, also condition the expression of a crop’s yield potential.

Therefore it is enlightening that this wheat yield potential symposium has included a session on “Enhancing the National Resource Foundation” although this is a rather glorified title for providing an opportunity to describe useful and sustainable crop management practices – more succinctly, suitable agronomic systems – that are appropriate for farmer use and which can help assure a more dynamic and sustainable expression of a crop’s yield potential in farmer fields where it really counts.

A Retrospective View of Wheat Yield in Farmer Fields in the Yaqui Valley, Sonora, Mexico and Its Relationship with Yield Potential

There is concern that the “easy breeding” part of increasing yield potential is reaching a plateau for many crop production situations and that further major genetic gains in yield will be hard won and more costly to achieve than in the past. This concern has been expressed for the Yaqui Valley in southern Sonora, Mexico which is the historic, celebrated site associated with the origin of the wheat
“Green Revolution” and which still remains an important irrigated, spring wheat production area in Mexico. It also represents nearly 40% of the developing world’s spring wheat area (Bell et al., 1995) including comparable areas in India, Pakistan, Afghanistan, China, Iran and southeast Turkey, among others.

Fortunately, there exists a reliable data base for the Yaqui Valley that has documented the progression of average wheat yields in farmer fields from the early 1950s when “land races” were being replaced by the new, improved, non-semi-dwarf varieties developed by Dr. Borlaug and his colleagues up through the release of the first semi-dwarf cultivars (both bread and durum wheat) that subsequently followed, to the present.

Figure 1 presents this progression of average wheat yields in farmer fields in the Yaqui Valley from 1951 to 2005. Although the overall increase in yield averaged 81 kg \text{ha}^{-1}\text{per year (2.36\% per year) over this entire time period is commendable}, examination of Figure 1 clearly indicates that the annual increase in yield has been slowing, especially since the mid-1970s. This most certainly has contributed to suspicions that it is becoming “harder” to continue to achieve major, consistent increases in irrigated spring wheat yield potential. And it is very likely that similar, decelerating wheat yield trends (start fast but slow down with time) are occurring for many other production situations (particularly other irrigated spring wheat areas) following the initial replacement of old cultivars with a progression of modern, high-yielding semi-dwarf cultivars.

Table 1 breaks down the rate of yield increase for defined time periods associated with successive eras of cultivar development by breeders from 19951 to 2005. It is of interest to note that the highest annual percent yield increase as well as a high kg \text{ha}^{-1}\text{per year increase occurred from 1951 to 1966, which corresponds to the period when improved, rust resistant, non-semi-dwarf cultivars were being supplied to farmers. Then the time period from 1966 to 1981 represents the initiation of the “grand semi-dwarf cultivar phase” distinguished by the introduction and continued improvement of the new-fangled, semi-dwarf cultivars. Marked increases in annual yields, both on a percentage basis as well on an absolute kg/ha/year basis, occurred during this era.

For the period from 1981 to 1996, the improvement in wheat yields in farmer fields dramatically slowed down, even though a fairly wide spectrum of new and supposedly higher-yielding cultivars was available for farmer adoption. One conjecture put forward by breeders about this “slow down” in yield increase is that it reflects their efforts to incorporate other needed traits (disease resistances and quality factors, among others) into the existing, high-yielding, semi-dwarf genetic platforms and that this breeding effort to consolidate other needed traits may have hindered the breeders’ ability to concurrently continue to select for increased yield potential.

This speculation may explain at least part of observation of low yield gains in farmer fields from 1981 to 1996 (Table 1). But the continuing flat (even slightly negative) trend in farmer yields for the period from 1996 to 2005 does add to the persistent concerns that a “yield potential ceiling” is being encountered. However, when the yield trend for the period from 1981 to 2005 is considered, it presents a slightly better image of the situation indicating a 0.8% annual yield increase (44 kg \text{ha}^{-1}\text{per year). However, it must be pointed out that little of this yield trend can be attributed to genetic gain since there was very little farmer adoption of new cultivars from about 1990 or so to about 2004.
During the era from 1996 to 2005 (and even back to the early 1990s, there was a remarkable reluctance by Yaqui Valley farmers to adopt new cultivars, although new, cultivars of both bread and durum wheat were regularly released. The stagnant, even declining yields from 1996 to 2005 may have occurred primarily because only two cultivars, released in the mid-to-late 1980s (Altar 84, durum wheat and Rayon 89, bread wheat, with Altar 84 predominating), occupied most of the wheat area in the Yaqui Valley during this period. The question to be answered then is “why didn’t farmers replace these two varieties over such a long period”? In addition to the farmer reluctance to change cultivars during this period, there was also a very modest inclination by farmers to adopt new, high yield generating crop management practices.

There are various possible grounds (socio-economic/marketing/trade issues, shortages of irrigation water during the last 5 years, major collapses of leaf rust resistances, especially for durum wheat cultivars, loss of soybean as a crop to rotate annually with wheat due to an newly introduced white fly biotype plus other possible factors) that may explain the lack of farmer interest to adopt new cultivars from the early 1990s to 2005, in spite of the historical readiness of Yaqui Valley farmers to adopt new cultivars almost at the drop of a hat. Therefore, it is quite conceivable that there was truly a lack of attractive, new cultivars available to farmers during this time period that combined adequate increased yield potential with the other required traits.

Part of the declining yields from 1996 to 2005 period may also, however, simply reflect the congruence of some fairly “good years” at the beginning of the era followed by several years at the end of the period with mediocre climatic conditions that limited optimum yield expression (Figure 1).

Figure 2, nevertheless, offers further evidence for negligible increase in genetic yield potential for CIMMYT derived, irrigated spring bread wheat cultivars from 1992 to 2005. It presents data from the bread wheat yield potential trial conducted by the wheat agronomy group at the CIANO station during the 2004/05 crop cycle. In this trial, a historical set of bread wheat cultivars, which were released and adopted by farmers in the Yaqui Valley (and other similar areas around the world) from 1966 until 1992 were compared with newly released cultivars/advanced lines provided by the CIMMYT bread wheat breeders to include in the trial and which “theoretically” represented their best efforts for the Yaqui Valley from 1992 until 2005.

Together these two groups of lines were compared under optimum production conditions in melgas (flat planting with flood irrigation) with fungicide, on raised beds (irrigated by furrows) with fungicide and on beds without fungicide. Figure 2 clearly indicates the marked increase in genetic yield potential for the historical cultivars released between 1966 and 1992 for both melgas and beds with disease control. However, essentially no yield increase was observed for the supposedly superior lines developed after 1992 until 2005. The lack of progress in yield for bed planting without disease control for cultivars released from 1966 to 1992 reflects the erosion in their race-specific leaf rust resistance to new, evolved rust races.

Table 1. Annual rates of increase in average wheat yield in farmer fields in the Yaqui Valley, Sonora, Mexico for defined time periods from 1951-2005.

<table>
<thead>
<tr>
<th>Time period</th>
<th>Periods of Cultivar Development</th>
<th>Yield increase per year (%)</th>
<th>Yield increase per year (kg/ha)</th>
<th>R2 Year vs Yield</th>
</tr>
</thead>
<tbody>
<tr>
<td>1951-2005</td>
<td>From the first improved non-semi-dwarfs to the present</td>
<td>2.36</td>
<td>81</td>
<td>0.857</td>
</tr>
<tr>
<td>1951-1966</td>
<td>Improved non-semi-dwarfs</td>
<td>5.20</td>
<td>110</td>
<td>0.808</td>
</tr>
<tr>
<td>1966-1981</td>
<td>First generation semi-dwarfs</td>
<td>3.00</td>
<td>111</td>
<td>0.569</td>
</tr>
<tr>
<td>1981-1996</td>
<td>Second generation semi-dwarfs</td>
<td>0.15</td>
<td>9</td>
<td>0.011</td>
</tr>
<tr>
<td></td>
<td>Further semi-dwarf cultivar development with modest farmer adoption</td>
<td>-0.43</td>
<td>-23</td>
<td>0.040</td>
</tr>
<tr>
<td>1996-2005</td>
<td>Second generation semi-dwarfs to the present</td>
<td>0.08</td>
<td>44</td>
<td>0.337</td>
</tr>
<tr>
<td>1981-2005</td>
<td>Second generation semi-dwarfs to the present</td>
<td>0.08</td>
<td>44</td>
<td>0.337</td>
</tr>
</tbody>
</table>
Based on these results and especially when combined with the yield trend observed in Yaqui Valley farmer fields in Figure 1 and Table 1, it seems that there should be real concern that a “yield potential ceiling” has been reached, at least for spring bread wheat for irrigated production situations. Therefore, until the breeders can get the irrigated spring bread wheat genetic yield potential “locomotive” back on track again, more resources and efforts to develop and extend new crop management practices to farmers which can increase yield and reduce production costs must be more earnestly emphasized.

**Raised Bed Planting Technologies with Conventional Tillage – The First Step**

Referring again to Figure 1 above, it goes without saying that the wheat yield increase that has occurred over the years in Yaqui Valley farmer fields has been linked with farmer adoption of superior cultivars. But this yield increase has also been combined with the parallel adoption of improved crop management practices. Bell *et al.* (1995) also focused on the Yaqui Valley and utilized the same data set that was drawn on for Figure 1, but for the period 1968 to 1990 (commencing near the initiation of the semi-dwarf cultivar phase). They concluded that during this 22 year period, 28% of the weather-adjusted yield gain was attributed to genetic gains (0.5% yield increase per year), 48% was attributed to improved crop management, mainly increased application of N fertilizer, (0.86% yield increase per year) and the remaining 24% could not be explained (0.43% yield increase per year).

One possible contribution to the unexplained portion of the yield gain from 1968 to 1990 may entail the accelerated rate of farmer adoption of conventional tilled, raised bed planting systems with furrow irrigation which replaced conventional tilled, solid-stand flat planting with flood irrigation (melgas) in the Yaqui Valley (Figure 3a and 3b). This change in planting system for wheat as well as most other crops occurred from the late 1970s up through the 1990s by which time over 90% of Yaqui Valley farmers had adopted the raised bed planting system Aquino (1998). However, in most farmer surveys that have been conducted, increased yield has not commonly been mentioned as a primary reason for changing from planting wheat in melgas to raised beds.

Farmers more commonly tend to justify this shift in planting system based on:

- **Irrigation water savings** – Commonly 15 to over 40% irrigation water savings is observed with raised beds and furrow irrigation as compared to flood irrigation in melgas. Table 2 provides examples comparing yields for bed planting versus melga planting for various crops in a number of farmer fields in northwest India along with the irrigation water saving for raised bed planting;

- **Opportunities to use other weed control strategies besides herbicides** – Raised bed planting of wheat provides the field access opportunity to mechanically cultivate in the furrows which is now a common weed control practice used by farmers for wheat in the Yaqui Valley which, when combined with pre-seeding irrigation, has dramatically reduced the need for herbicide use in wheat by farmers in the Yaqui Valley Aquino (1998). Aquino (1998) further indicated that over 80% of farmers used herbicides in the mid-to-late 1970s when flat planting with flood/basin irrigation was widely used as compared to less than 20% current farmer use of herbicides now that more than 90% of farmers seed wheat in raised beds. In addition, bed planting allows much easier hand weeding in wheat as compared to traditional planting of wheat in solid stands on the flat because the reduced number of well-defined rows on the top of the bed which allows easier differentiation of grass weeds from wheat – a marked benefit for small-scale, resource constrained farmers;
- **New options to reduce tillage** – Many farmers directly seed crops like soybean and occasionally maize after wheat using the same beds without additional tillage. However, following harvest of these crops tillage, normal tillage is used prior to seeding the subsequent wheat crop on newly formed beds (Opportunities to further reduce tillage are more fully discussed below);

- **Opportunities for better fertilizer management, especially N fertilizers** – Raised bed planting also provides enhanced field access opportunities to place fertilizer, especially N fertilizers, when and where the wheat crop can make more efficient use. Figures 4 and 5 clearly indicate the beneficial effects obtained by band incorporation of N fertilizer at 1st node and/or boot stage on both durum yield and grain protein content, respectively. Split, banded N applications at these stages in wheat is greatly facilitated by bed planting;

- **Reduced seed rates** – Table 3 compares grain yield at 100 kg seed/ha versus 50 kg for several bed planted bread wheat genotypes. There was no significant difference in average yield at these contrasting seed rates although there were seed rate by genotype interactions.

- **Reduced lodging incidence** – Average percent plot area lodged over two crop cycles at CIANO for 16 genotypes planted in melgas was 43% versus 21% for raised beds;

- **Better stand establishment and reduction of periodical waterlogging caused by extreme rain events or excessive irrigation due to the drainage opportunity provided by the furrows between the bed.**

Figure 3a. Flat planted, flood/basin planting (melgas)  
Figure 3b. Raised bed planting with furrow irrigation

<table>
<thead>
<tr>
<th>Crops</th>
<th>No of Farmers 2000 to 2002</th>
<th>Yield (kg/ha) Bed (% Water Saved) Melgas</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maize</td>
<td>10</td>
<td>3270 (35.5%)</td>
</tr>
<tr>
<td>Urd bean</td>
<td>10</td>
<td>1830 (26.9%)</td>
</tr>
<tr>
<td>Mung bean</td>
<td>10</td>
<td>1620 (27.9%)</td>
</tr>
<tr>
<td>Pigeon Pea</td>
<td>10</td>
<td>2200 (30.0%)</td>
</tr>
<tr>
<td>Gram</td>
<td>8</td>
<td>1850 (27.3%)</td>
</tr>
<tr>
<td>Wheat</td>
<td>22</td>
<td>5120 (26.3%)</td>
</tr>
<tr>
<td>Rice</td>
<td>20</td>
<td>5620 (42.0%)</td>
</tr>
</tbody>
</table>
The predominant farmer perception has quite correctly characterized raised bed planting as offering opportunities to reduce costs via enhanced input use efficiencies (Table 2 and Figures 3 and 4) and by providing opportunities to employ less costly field operations. The role of raised bed planting as a yield improving technology per se appears to be less well understood, although the reduced lodging associated with raised bed planting can directly enhance yield as well as indirectly augment yield through reduced harvest losses.

Figure 4. Effect of application timing of 225 kg N/ha on average grain yield of six durum wheat genotypes planted on beds at CIANO/Obregon from 1996 to 1999.

The CIMMYT wheat agronomy group has expended considerable effort to compare raised bed versus melga planting to better understand the raised bed planting system for wheat and other crops, its potential use elsewhere as well as to more fully realize the breeding implications for selection of appropriate cultivars for this planting system. Table 3 provides an example of one of these comparisons at a time when all of the included cultivars had been selected primarily by yield testing in melgas. Several interesting aspects can be observed in Table 3 including:

- The average yield for the cultivars was higher for melga planting but there was a significant planting method by cultivar interaction;
- There was no yield difference between 100 versus 50 kg ha\(^{-1}\) seed rate for bed planting but again a significant seed rate by cultivar interaction occurred;
- Cultivars like Yecora 70 and Oasis 86 (two of the few double-dwarf gene cultivars released in the Yaqui Valley) and Super Kauz 88 were decidedly poorly adapted to bed planting due in part to short stature and/or upright growth habit. However, Borlaug 95, a short and upright cultivar, does contradict to a degree this observation;
- Cultivars like 7 CERROS 66 performed equally well on beds at the higher seed rate but yield declined at the lower seed rate;
- BAVIACORA 92 performed equally well across all plantings systems.

Many similar trials have been conducted at the CIANO station under controlled experiment station conditions and have generally supported the premise that yield per se was not “magically” increased by bed planting. However, it became clear that there was a planting method by genotype interaction, which was largely characterized as a one-way interaction. Consequently, it has been rather easy to identify genotypes with high yields in melgas but which were low yielding when planted on raised beds. However, genotypes with high yields on beds were usually high yielding when planted in solid stands on the flat if differential lodging was not a confounding factor.

Figure 5. Effect of application timing of 225 kg N/ha on grain protein content of six durum wheat genotypes planted on beds at CIANO/Obregon from 1996 to 1999.
Table 3. Effect of planting method on bread wheat grain yield

<table>
<thead>
<tr>
<th>Planting Method</th>
<th>Seed Rate</th>
<th>Melga Planting 120 kg/ha</th>
<th>Bed Planting 100 kg/ha</th>
<th>Bed Planting 50 kg/ha</th>
<th>YIELD (kg ha⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>-------------------------</td>
<td>-----------------------</td>
<td>----------------------</td>
<td>----------------</td>
</tr>
<tr>
<td>Cultivar</td>
<td></td>
<td>-------------------------</td>
<td>-----------------------</td>
<td>----------------------</td>
<td>----------------</td>
</tr>
<tr>
<td>7 CERROS 66</td>
<td></td>
<td>8273</td>
<td>8281</td>
<td>7756</td>
<td></td>
</tr>
<tr>
<td>YECORA 70</td>
<td></td>
<td>8177</td>
<td>7688</td>
<td>7434</td>
<td></td>
</tr>
<tr>
<td>CIANO 79</td>
<td></td>
<td>8059</td>
<td>7805</td>
<td>7993</td>
<td></td>
</tr>
<tr>
<td>SERI 82</td>
<td></td>
<td>9671</td>
<td>9393</td>
<td>8948</td>
<td></td>
</tr>
<tr>
<td>OASIS 86</td>
<td></td>
<td>9749</td>
<td>8676</td>
<td>8742</td>
<td></td>
</tr>
<tr>
<td>SUPER KAUZ 88</td>
<td></td>
<td>9763</td>
<td>8644</td>
<td>8581</td>
<td></td>
</tr>
<tr>
<td>BAVIACORA 92</td>
<td></td>
<td>9767</td>
<td>9796</td>
<td>9698</td>
<td></td>
</tr>
<tr>
<td>BORLAUG 95</td>
<td></td>
<td>9741</td>
<td>9391</td>
<td>9255</td>
<td></td>
</tr>
<tr>
<td>MEAN</td>
<td></td>
<td>9150&lt;sup&gt;a&lt;/sup&gt;</td>
<td>8709&lt;sup&gt;b&lt;/sup&gt;</td>
<td>8803&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
</tr>
</tbody>
</table>

Means followed by the same letter are not significantly different by LSD (0.05); The planting method by cultivar interaction was significant at the 0.05 level and the interaction LSD (0.05) was 675 kg ha⁻¹.

Understanding this interaction has allowed CIMMYT wheat breeders to dramatically replace the large areas previously managed for segregating materials and especially for yield trials in melgas over the past 15 years with raised bed planting. The advantage gained by breeders has been a striking reduction in experiment station operational costs (20 – 25% less cost per ha for bed planting compared to melgas – similar to that realized by farmers – combined with the opportunity to reinforce this saving by being able to plant up to 30% more plots per ha as compared to melga planting.

One trial that was conducted over two crop cycles at the CIANO station demonstrated very interesting features for wheat grown on raised beds. Wheat breeders, who had long-term involvement in the CIMMYT bread wheat breeding effort, were asked to identify two groups of genotypes from those that had been sent out to the “real world” in the international trials from the late 1960s to the late 1980s (yield testing under melgas was still the common practice used to identify superior genotypes throughout this period). One group of genotypes included those that had been sent out and ended up being widely used by the NARS cooperators generating positive impacts. The other group of genotypes was also sent out with equal expectations but just did not make it in the real world (but not because of problems like immediate susceptibility to leaf rust, for example).

These two contrasting groups of genotypes were then grown under both melgas and raised beds during the 1999/00 and the 2000/01 crop cycles with similar, optimum production conditions including disease control. Figure 6 presents the average yield performance for the two sets of genotypes when planted in melgas and when planted on raised beds. As can be observed, the performance of both sets of genotypes in melgas was similar with a slight but insignificant advantage for the group of disappointing “real world” performers. However, when the two sets of genotypes were grown on raised beds, the group of successful “real world”, international performers yielded significantly higher compared to the disappointing performers. It seems obvious from this trial that there is some association between stable, high genotypic yield performance across diverse circumstances for genotypes that are good “bed performers”.

Field observations over the years, both on station as well as in farmer fields, have clearly indicated that the “good” bed performers tend to “execute” excellent yields when production conditions are optimum but also produce better yields when production conditions are suboptimal (poor stand establishment, poor weed control, inadequate N and water etc). Therefore it seems likely that as farmers in the Yaqui Valley began to rapidly switch from melgas to raised bed planting from the early 1970s onward, a part of the yield increase that was left “unexplained” by Bell et al. (1995) may be attributed to farmer adoption during this period of cultivars like Nacozari 76, Genero 81 and Rayon 89, all of which were both successful cultivars in different locations around the world as well as excellent bed performers. While raised bed planting clearly provided Yaqui Valley farmers with reduced production costs and opportunities for increased input use efficiency, it may have also provided opportunities for expression of higher yield especially under less than optimum production/management conditions.

Permanent Raised Bed Planting Technologies – The Next Step

The change from conventional tilled melga planting to conventional tilled raised bed planting by farmers in the Yaqui Valley is an example of adoption of an appropriate, new “resource conserving technology”. Raised bed planting, albeit with conventional tillage, provides important opportunities for improved input use efficiency as well as various cost saving management options compared to planting in tilled melgas. However, raised bed planting as currently practiced by farmers in the Yaqui Valley still involves considerable crop residue burning (less in recent years) and tillage (again with some reduction in recent years). It does not, therefore, encompass the broad, basic tenets that characterize Conservation Agriculture (CA) which include:

- Dramatic tillage reductions with the goal to reach as close to zero till as possible across all crops that encompass a system;
- Adequate crop residue retention on the soil surface to reduce erosion and improve soil chemical (especially organic matter), physical (especially soil aggregation) and positive biological parameters (promotion of beneficial organisms);
• Economical options for potential diversification of current, repetitive crop rotations;
• Enhanced, readily perceivable economic/household benefits to encourage rapid farmer adoption while providing realistic prospects for long-term, sustainable crop production.

Figure 6. Comparison of average yields of 17 "good" bread wheat international performers versus 7 "poor" performers when planted in melgas versus beds at CIANO, during the 1999/00 and 2000/01 crop cycles (LSD at 0.05 = 239 kg/ha).

Therefore, over the past 15 years, CIMMYT agronomists (and others in various locations including India, Central Asia, China, Turkey, Australia and the USA) have endeavored to use conventionally tilled, raised bed planting as a “platform” to develop a new surface irrigated production system that complies with the basic CA tenets. This new system is called permanent raised bed planting with furrow irrigation between the beds. CIMMYT agronomists strongly believe that this new system is the logical way to bring CA to most surface irrigated production systems (wheat-cotton, wheat-maize, wheat-oilseed; wheat-legume among many others including rice-wheat).

Progress has been made in various regions/cropping systems to apply zero till planting on the flat, particularly for sprinkle irrigated conditions but also for flood irrigated conditions, including the magnificent example of farmer adoption of zero till wheat planting on the flat with flood irrigation in the Indo-Gangetic Plains (IGP) for the predominant, rice-wheat system. Unfortunately, farmer adoption of zero till for rice in the IGP is still low, reducing the consolidation of improved, beneficial soil affects, although efforts to develop appropriate zero till rice technologies are well underway.

As can be observed in Table 2, there definitely is scope for use of raised bed planting within the rice-wheat system, including planting the rice crop on beds, which can lead to irrigation water saving, better nutrient management, new weed control options and new opportunities for crop diversification within this monotonous cropping system if farmer appropriate technologies and cultivars can be developed.

CIMMYT advocates bed widths from 60 to 90 cm (furrow to furrow) for both tilled as well as permanent raised beds, especially for small-scale farmers using 2-wheel tractors or low hp, 4-wheel tractors. However, in Australia and the USA, it is common to see bed widths up to 2 m or wide for irrigated conditions and even wider beds for rainfed conditions where waterlogging is an issue and the raised beds (tilled and permanent) are mainly for drainage. On many soil types, however, irrigation water use efficiency can go down as bed width is increased which is one main reason CIMMYT agronomists do not recommend beds wider than 90cm except when appropriate for specific cropping situations.

To initiate the permanent bed planting system, a last cycle of conventional tillage to form new beds is carried out, which are then reshaped as needed and reused for successive crops. It is not a zero till system since there is soil disturbance in the furrow bottoms during the reshaping process. But there is no soil disturbance on top of the beds where crops are planted. Therefore permanent raised beds can be categorized as a controlled tillage system. For proper execution, all implement wheels should track in the furrow bottoms essentially providing an automatic controlled traffic system. The controlled implement wheel trafficking restricts compaction to the furrow bottoms, not where the crops are seeded on the bed tops, and in many cases this compaction in the furrow bottoms facilitates the forward and lateral movement of the irrigation water thereby reducing excess downward water infiltration, especially when residues are in the furrow which can retard forward water advance through the field.

The primary objective of permanent beds is to reuse the same bed continuously and indefinitely. For example, the initial raised beds that were formed during the summer of 1992 for one of the CIMMYT long term trials at CIANO (see more below) and the subsequent permanent beds have been continuously reused twice a year until the present (28 consecutive crops). Obviously the extent of continued use of the same permanent beds, however, will largely likely depend on soil type and especially on cropping system (inclusion of sugar beets and potatoes, for example, will lead to extensive soil disturbance at harvest, perhaps requiring renewed tillage to establish a new cycle of permanent beds) and. However, experience has demonstrated that the potential to enhance and improve the soil properties associated with sustainability issues (soil chemical, physical and biological parameters) is slowed or even reversed whenever a renewed cycle of tillage is applied to form a new generation of permanent raised beds.
Therefore CIMMYT agronomists, together with scientists working in several countries are attempting to develop permanent raised bed technologies, including appropriate implements, that:

- Minimize/eliminate the need for tillage on top of the beds where the crops are seeded;
- Can manage full retention of all crop residues if no other suitable residue marketing opportunities exist leaving burning as an attractive option;
- Establish the appropriate threshold crop residue levels that must be retained on the soil surface to generate needed improvements in soil properties associated with production sustainability when there are other, alternative, economical uses for the crop residues;
- Encompass a wide gamut of potential crops (cereals, grain legumes, oil seeds, industrial crops and cover crops among others) in order to offer farmers a wide range of potential options for diversifying crop rotations.

Crucial to advancing the development of appropriate CA technologies, including permanent raised beds, has been the need to focus considerable efforts to develop suitable implements, especially for use by small and medium scale farmers. Commercially available CA implements are generally too large and expensive and almost none are available that are capable of seeding onto raised permanent beds (especially small grain crops like wheat and rice) without major modifications since almost all have been developed for large-scale farmers managing large areas of flat planted rainfed crops. CIMMYT agronomists have made considerable progress in developing small-scale, inexpensive implements that are suitable for small-scale farmers.

The concept of a multi-crop/multi-use implement has guided these efforts. This concept involves the development of a single implement which can simply be reconfigured to plant conventional or zero till on the flat, plant on tilled or permanent raised beds, band apply basal and top/side-dress fertilizers and reshape permanent beds for the various crops that may comprise a diversified cropping system.

**Results from CIMMYT Long Term Permanent Raised Bed Planting Trials for Irrigated Production Conditions**

Figure 7 presents the wheat yield results from the main, CIMMYT long term, raised bed planting trial at CIANO ongoing since 1992. This trial compares several tillage/crop residue management practices and superimposed on these practices are a series of N rate and application timing alternatives. The trial was set-up to include continuous wheat during the winter crop cycle with maize and soybean alternating during the summer crop cycle (an annual double crop system). The loss of soybean as a viable crop in the Yaqui Valley in 1994/1995 because of a new white fly biotype has required modifying the summer crop used and maize has been planted more frequently than originally planned. Soybean has been planted on occasion since 1995 (during the summer cycle of 2001, for example) but essentially as a cover crop. The 300 kg N/ha, 1st node treatment is presented in Figure 7 to illustrate wheat yield performance, purportedly without N limitation.

**Figure 7. Effect of tillage and residue management over several years on wheat grain yield (kg/ha at 12% H2O) when 300 kg/ha N are applied at the 1st node stage at CIANO/Cd. Obregon.**
Figure 12 illustrates several important factors associated with long term trials in general and raised bed planting systems in particular including:

- During the first five wheat crops (10 crops including the summer crops) there were only very minor yield differences for the management practices. This clearly indicates why such trials need a long-term commitment. If the trial had Permanent raised beds with full surface residue retention as well as permanent beds with partial residue retention (retaining approximately 30% of residues on the soil surface yielded as well or better than conventional tilled beds with full residue incorporation. The latter practice offers a good compromise if opportunities exist for producers to use or sell crop residues.

- For the 6th wheat crop, however, all hell broke loose, especially for permanent beds where all residues had been burned. After the 6th wheat crop, wheat yield levels for the other practices tended to stabilize at similar yield levels but permanent beds with residue burning continued to follow the road to perdition.

- Permanent raised beds with full surface residue retention as well as permanent beds with partial residue retention (retaining approximately 30% of residues on the soil surface yielded as well or better than conventional tilled beds with full residue incorporation. The latter practice offers a good compromise if opportunities exist for producers to use or sell crop residues.

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Permanent raised beds with full surface residue retention as well as permanent beds with partial residue retention (retaining approximately 30% of residues on the soil surface yielded as well or better than conventional tilled beds with full residue incorporation. The latter practice offers a good compromise if opportunities exist for producers to use or sell crop residues.

Figure 8 presents the average yield for these treatments at the same N level and timing for the 13-year duration of the trial. As can be observed, permanent beds with all residues burned, has a substantially lower yield compared to all other treatments. Conventional tilled beds with all residues incorporated yielded significantly lower than permanent raised beds with full residue retention of surface on the soil surface over the thirteen years with permanent beds with partial residue retention showing an intermediate yield level between these two practices.

Figure 9 compares N application timing for 150 kg N/ha, the intermediate N rate, to allow better resolution of N response. The 0 N treatment is also included for comparison. As can be observed, there are small, insignificant effects of the timing of applying 150 kg N/ha (all at basal versus all at 1st node) but permanent beds with full residue retention had higher yields, especially with the 1st node N application timing. It is also of interest to note the 0 N yield levels for the management practices. Again permanent beds with full surface residue retention had significantly higher yield indicating a more positive soil N status.

Table 4 provides some insights that help explain the yield differences between the tillage/residue management practices observed in Figures 7, 8 and 9. It presents information pertaining to the status of some chemical, physical and biological parameters that are believed to be related to soil quality/sustainable issues. Soil samples (0-7 or 0-10 cm on top of the beds) were taken in either 2002 or 2004 (10 or 12 years, respectively, after trial initiation). As can be observed in Table 4, there are minor, yet significant differences in soil organic matter with the lowest level for conventional tilled beds and the highest level for permanent beds with full residue retention. Na levels are highest for permanent beds with residues burned, followed by conventional till beds and then permanent beds with partial residue removal. Permanent beds with full residue retention have the lowest Na levels and indicate the potential benefit this system may have for use in to help ameliorate salinity in saline-prone areas.
Both soil dry and wet aggregates were lowest (low is bad) for permanent beds with burning all residues which probably explains the low yields for this management practice after 1997 when adequate soil degradation had occurred to negatively affect wheat yields (the straw that finally broke the camel’s back). Soil wet aggregates seem to be better related to yield expression being low for permanent beds with burning, increasing for tilled beds with residue incorporation and then with permanent beds with partial residue retention with highest levels for permanent beds with full residue retention, very similar to the yield ranking in Figure 8.

Finally the soil biological parameters in Table 4 (C and N levels measured in soil microbial biomass) clearly indicate that permanent beds (with undisturbed soil on the bed surface) combined with either partial or full residue retention on the soil surface have markedly higher levels of both biological parameters as compared to tilled beds and permanent beds with residues burned. These factors also tend to parallel yield levels for the different management practices.

The suite of soil parameters that are included in Table 4 and the nature of their importance/value quite clearly
support permanent raised beds with adequate retention of crop residues on the soil surface as very promising and sensible CA technology for irrigated crop production systems.

Figure 10 presents the wheat yield results from another CIMMYT long-term trial at CIANO that supports much of the above as well as providing additional information concerning bed planting. The trial was initiated in 1993 but only the results from 2001 to 2004 are presented.

Similar to the results presented above in Figure 9, permanent beds with residue retention yielded dramatically better than permanent beds with residues burned and somewhat better than conventional tilled beds with all residues incorporated by the tillage.

However, Figure 10 includes some additional management options. Many visitors show concerns that compaction from natural soil settling on top of the beds could be a limiting factor. To test this, small, winged sub-soil shanks, which can break potential compaction without destroying the permanent beds, were fabricated for use on top of the beds to a depth of 15-20 cm. For this trial, these miniature sub-soil shanks are used annually following wheat harvest when the soil is dry and subject to better shattering for breaking up possible compaction layers.

As can be seen in Figure 10, these shanks tended to reduce wheat yield for permanent beds with full residue retention but yield was significantly increased when the shanks were applied to permanent beds with residue burning. These results, together with those presented above as well as many other experiences from irrigated and rained conditions, confirm the thesis that trying to manage zero till systems with full residue removal just does not function. The many attempts by various entities in many locations (including in Mexio) to advise farmers to adopt zero till while failing to fully understand and/or explain to these farmers the full ramifications of zero till with residue removal, largely explains most of the “zero till does not work” complaints.

The contrasting results in Figure 10 for the sub-soil shanks (reduce yield for permanent beds with residue retention on the soil surface and increase yield when residue is burned) also support the premise that well managed CA technologies perform better with no soil disturbance beyond that caused by the seeding operation itself (and even this disturbance should be kept to the absolute minimum). However, the explicit positive effect of the shanks to increase wheat yield for permanent beds with residue burning is related to the remediation of the degradation in soil properties that most likely has occurred over time from “doing the wrong thing” as was observed in Table 4.

Finally, it is of interest that conventional till beds with residue burning out-yielded tilled beds with residue incorporation (very opposite to much conventional wisdom). Another long-term trial at CIANO with eight-year duration has produced similar results. Further soil monitoring is underway to try to explain this apparent dichotomy and differential soil N dynamics are suspected to be a likely explanation.

![Figure 10. Effect of Tillage and crop residue management on average bread wheat yield from 2001 to 2004 at CIANO, Cd. Obregon.*](image)

* Small scale sub-soil blade with side wings, used to about a 15-20 cm depth in the center of the bed to break possible compaction. Structure is maintained with no soil inversion.
Figure 11 provides a comparison of wheat yield, variable costs and economic returns above variable costs for conventional tilled beds with residue incorporation versus permanent raised beds with full surface retention of crop residues. In the trials described above, planting date for all management practices were within 1-3 days of each other. In the long term trial for Figure 16, large farm size plots are used and wheat planting after summer maize was done as soon as each management practice permitted (ranging from 7 to 14 days earlier over the years for permanent beds due to earlier field access opportunities).

![Figure 11. Comparison of average wheat grain yields variable production costs and returns over Variable costs for wheat produced on conventional tilled beds versus permanent beds at CIANO, Cd. Obregon for the 2000/01 to 2003/04 crop cycles.](image)

This explains a part of the markedly higher yield for the permanent beds in Figure 11. When this higher yield is combined with the 22% lower variable costs for permanent beds, then the economic returns over variable costs were dramatically higher for permanent beds (over 60% higher) averaged over the four years included in the analysis.

CONCLUSIONS

It would seem adamantly clear, based on the above results and discussion, that raised bed planting systems offer many positive features for farmers to both improve input use efficiency and reduce production costs for irrigated cropping systems. It is a technology that can be applied by all farmers, including small and medium scale farmers, when appropriate equipment are developed and made readily available and farmers are made aware of the technology (most efficiently by direct farmer participation in the testing and modifying the technology for their conditions).

Permanent raised beds provide a suitable technology to insure the application of CA to surface irrigated production systems while offering opportunities to reduce production costs and increase economic returns with the added benefit of assuring a more sustainable production base compared to the existing widely used conventionally tilled systems. And with the development of functional implements, suitable crop management practices and appropriate cultivars, the permanent raised bed planting system can for nearly all surface irrigated production situations.

One issue seems patently obvious. Farmers will always require superior and sustainable crop management practices irregardless of the cultivars they choose to grow. Similarly, all cultivars will be better able to achieve their genetic yield potential if farmers can apply superior and sustainable management practices. Given the widespread reductions in the allocation of resources to applied crop management (agronomy) efforts by most NARS and IARCS, it would appear that it is time to rethink priorities especially if the genetic yield potential “locomotive” truly is slowing down as appears to be the case for many crop production situations.

REFERENCES


Avenues to Increase Yield Potential of Short Season, High Latitude Wheat in Northern Kazakhstan and Siberia

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Summary

In the short-season, high-latitude areas of Northern Kazakhstan and Siberia, yield potential is limited by lack of moisture in the dry years and by leaf rust in years with sufficient precipitation. Three main approaches would be required to maximize yield in the region: improved agronomic practices, better adapted germplasm, and policy interventions, especially for the former. The authors conclude that application of zero and minimal tillage would provide a sustainable alternative to avoid the erosion caused by current management practices.

Introduction

Northern Kazakhstan and Western Siberia of the Russian Federation lie between 50°N and 56°N and 60°E-95°E and have a typical continental climate (Fig. 1). Moving from south to north, the desert of Central Kazakhstan changes to steppe, where wheat cultivation starts. Further north, the steppe transitions to forest-steppe and eventually into Siberian forests. These changes in soil and vegetation are related to precipitation and temperature. Moving further north and east precipitation increases, but temperature and the frost-free period decreases. The North Kazakhstan steppe at Astana has an average yearly precipitation of 320 mm. Barnaul and Novosibirsk situated to the northeast have at least 100 mm more precipitation. Average distribution of precipitation follows certain patterns, with most rainfall coming in June-August. However, there are normally drought conditions in May and early June, and high variation in moisture availability from year to year. Rains in June are of crucial importance in yield determination. Severe winters with heavy snow allow planting only in May. Every five years, there is frost at the end of August, which limits the frost-free period to 100 or even 90 days (Kaskarbayev, 1998). The region has fertile soils ranging from chestnut in the south to chernozem and grey forest soils in the north, with a humus content of 3-4%.

Figure 1. Wheat area in Siberia and Northern Kazakhstan.
The history of wheat cultivation in Russian Siberia and Northern Kazakhstan is an example of how settlers in harsh environments can successfully transform virgin land into productive agriculture. Millions of hectares of fertile soil were brought into cultivation in the area, which has an average winter temperature of \(-20^\circ C\). Because this region initially attracted settlers by its mineral resources, the development of industry and roads was a high priority. However, in the middle of the 20th century the region was transformed into a very important agricultural area supplying high quality grain for the local population and for the rest of the USSR. The wheat area at its maximum in the 1960s and 1970s reached 35 million ha (Morgounov et al., 2001). Recent data indicate substantial reductions, and in 2005 Kazakhstan grew close to 11 million ha of spring wheat, essentially half of the area in 1965-1975 (Table 1) (Gossen, 1998; FAO on-line database). As seen in the table, average yield does not exceed 1 t/ha, which is typical for a short-season, dry, low-input environment. Most wheat produced in Siberia and Northern Kazakhstan can be classified as a Hard Red Spring type according to the North American description. The continental climate, nutrient supply, and genotypes grown result in the production of grain with high protein (12-17%) and gluten (25-32%) content. The gluten is also characterized by good strength and elasticity, allowing it be used as component in flour mixtures with grain of medium or poor quality.

Table 1. Wheat area and yield in Kazakhstan in 1946-2005.

<table>
<thead>
<tr>
<th>Years</th>
<th>Area (million ha)</th>
<th>Yield (t/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1946-54</td>
<td>7.0</td>
<td>0.56</td>
</tr>
<tr>
<td>1955-64</td>
<td>24.6</td>
<td>0.70</td>
</tr>
<tr>
<td>1965-75</td>
<td>23.8</td>
<td>0.89</td>
</tr>
<tr>
<td>1976-85</td>
<td>25.3</td>
<td>0.96</td>
</tr>
<tr>
<td>1986-90</td>
<td>24.1</td>
<td>1.00</td>
</tr>
<tr>
<td>1991-95</td>
<td>14.9</td>
<td>0.80</td>
</tr>
<tr>
<td>1996-2000</td>
<td>10.7</td>
<td>0.85</td>
</tr>
<tr>
<td>2001-05</td>
<td>11.2</td>
<td>1.02</td>
</tr>
</tbody>
</table>

Sources: Gossen (1998) and FAO on-line database.

The disintegration of the USSR in 1991 resulted in an economic crisis and changes that affected the rural agricultural framework and wheat production enterprises. Privatization of the former collective and state farms in Kazakhstan by 2005 resulted in the establishment of relatively small private farms covering 1000-2000 ha; small cooperatives uniting several farmers and operating 5000-10,000 ha; big grain companies purchasing whole big farms and operating 100,000 ha or more. All these enterprises operate in a market environment driven by maximizing the profit per unit area. The 1990s economic crisis resulted in a sharp decrease of the wheat production area due to the abolishment of a command planned economy and the conversion to a market economy when the producers did not have the means for field operations, nor reliable wheat marketing channels. The current status of wheat production is characterized by a market environment with limited government support; conversion to modern field machinery and application of modern agronomy practices; search for better markets and wheat processing opportunities. This paper describes the possible directions for enhancement of wheat yield and production in the region through sustainable agronomy practices, new varieties, and new economic policies.

Enhancing Wheat Production through Sustainable Agronomic Practices

There are three main agronomic factors affecting the crop production system in Northern Kazakhstan and Siberia: tillage system, fallow, and choice of crops. When the virgin lands of Northern Kazakhstan and Siberia were first brought under cultivation in the mid-1950s and early 1960s, the production system was constrained by wind erosion. Plowed soils were very vulnerable to wind and resulted in tremendous dust storms. The research community developed and introduced soil conserving technology based on tillage without turning over the soil surface. However, 50 years of continuous tillage (even of the conservation type) reduced the amount of soil organic matter (Table 2) (Wall et al., in press). Water erosion remains a real threat especially on sloping fields. In some years, quick snow melt in spring causes substantial soil losses. More commonly it happens in fields with southern exposure to the sun. The current prices of diesel fuel in Kazakhstan (US$ 0.65-0.75 per liter) make tillage one of the main crop production costs. There is a need to improve the farming system through the application of more sustainable practices and, in particular, zero tillage.

Table 2. Reduction in soil organic matter content in virgin lands of Kazakhstan.

<table>
<thead>
<tr>
<th>Soil organic matter (%)</th>
<th>Virgin</th>
<th>Cultivated</th>
<th>% reduction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common</td>
<td>8.30</td>
<td>6.30</td>
<td>24</td>
</tr>
<tr>
<td>Chernozem</td>
<td>5.30</td>
<td>4.22</td>
<td>20</td>
</tr>
<tr>
<td>Southern</td>
<td>4.10</td>
<td>3.40</td>
<td>17</td>
</tr>
</tbody>
</table>

Source: Wall et al. (in press).

Due to dry climate in Northern Kazakhstan and Siberia, moisture availability is very important for crop production. There is a strong belief that summer fallow is needed to
preserve and accumulate moisture. It certainly contributes to nitrogen availability for wheat, which is important in a system where N fertilizer is hardly applied. The yield penalty of wheat following wheat is 15-20% for the second crop, 20-25% for the third crop, and more than 25% for the fourth crop, depending on the severity of moisture stress (Kaskarbayev, 1998). However, current fallow management is not only unsustainable but also destructive to the soil. Ideally, 3-4 shallow cultivations are practiced in black fallow during the summer to control weeds and prevent moisture evaporation from the upper soil layer. Nevertheless, at best 1-2 cultivations are normally practiced, leaving some soil covered by weeds. There are strong arguments to abolish fallow from the rotation entirely (Suleimenov et al., 2005). Long-term experiments at Kazakh Research Institute of Grain near Astana (Shortandy) suggest that although wheat yield after fallow is higher, the average wheat yield per year of rotation is lower (Table 3) (Kaskarbayev, 1998). Continuous wheat for more than 20 years produced higher annual yields than any rotation with fallow. Conservation agriculture principles also suggest that a bare field without a crop is not a sustainable option. This gives rise to a dilemma: whether to maximize yield in a single year or optimize average yield in a sustainable manner.

Table 3. Effect of fallow on spring wheat yield in Northern Kazakhstan: 27-year averages.

<table>
<thead>
<tr>
<th>Rotation</th>
<th>Average yield (t/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>F-W</td>
<td>1.00</td>
</tr>
<tr>
<td>F-W-W</td>
<td>1.05</td>
</tr>
<tr>
<td>F-W-W-W</td>
<td>1.10</td>
</tr>
<tr>
<td>F-W-W-W-W</td>
<td>1.15</td>
</tr>
<tr>
<td>F-W-W-W-W-W</td>
<td>1.20</td>
</tr>
<tr>
<td>W-W-W-W-W-W-W</td>
<td>1.25</td>
</tr>
</tbody>
</table>

* F = fallow; W = wheat.

Wheat remains the only economically viable crop for Northern Kazakhstan. However, if fallow is eliminated, other crops should be introduced into the production system. There is a choice of possible crops that were commonly used in the past, but they do not compete with spring wheat due to higher production costs and unreliable marketing. Canola recently emerged as a higher value crop processed locally and exported to Europe. Although it is more profitable than wheat, the market for it is still limited. The situation is different in Siberia, where more crops are grown and utilized due to more diverse demands by the processing industry and consumers. This diversifies the cropping system and allows producers to increase their income. Wheat yield potential in a diversified production system could increase or decrease, depending on the preceding crop.

Over the last 5-7 years, Kazakh research institutions, international organizations (FAO and CIMMYT), and private companies have made substantial cooperative and individual efforts to test and introduce zero tillage system into Northern Kazakhstan, as summarized by Wall et al. (in press). These efforts have combined both on-station research experiments and on-farm trials and production experience. They came to the conclusion that zero tillage is a viable option for spring wheat production in Northern Kazakhstan, for it produces high, stable yields and savings in fuel and machinery costs. Figure 2 shows relative yields of zero tillage plots compared to conventional tillage over a period of five years. Yields are the same or slightly higher, with substantial environmental benefits and savings in fuel and machinery. The adoption of zero tillage in Northern Kazakhstan is progressing, though important issues are still to be addressed, including zero tillage drills, weed control, residue, and nitrogen management.

Agronomic approaches to raise wheat yield potential in Northern Kazakhstan are available but may go against soil conservation. Greater tillage intensity and practicing fallow every other year or every third year, coupled with adequate disease and pest management would produce the highest yields. But even in this case, farmers’ return per unit area may not justify the yield increase, taking into consideration input and grain prices. On the other hand, aiming for the highest possible yield under dry conditions may not be the best option from an environmental viewpoint. Zero tillage with optimal residue and nitrogen management would maintain yields and protect the soil from water and wind erosion.

Figure 2. Average spring wheat yield over a five-year rotation period under no-till and conventional technologies, 2002-2006.

Increasing Yield through New Varieties

Gomez-Becerra et al. (2006) analyzed genotype x environment interactions of a set of 40 spring wheat varieties and breeding lines from Kazakhstan and Siberia.
grown across 11 locations in the region for two years. The AMMI analysis of variance for yield showed that environmental variation explained more than 70% of all variation, while varieties explained 7%, and variety x environment interaction, 15%. However, variation among sites was high, and the two years were quite different. In reality, for a particular farm or a smaller region, the role of variety is much greater. The study also identified a few varieties with wide adaptation across Northern Kazakhstan and Siberia. The study supports wide adaptation of varieties versus specific adaptation for the region. The production history shows that a few mega-varieties dominate, occupying a substantial area in the region. The landmark variety Saratov 29 at one time occupied 21 mln ha in the USSR, including Northern Kazakhstan and Siberia (Morgounov et al., 2001).

The study was based on data generated by the Kazakhstan-Siberia Network on Spring Wheat Improvement (KASIB), which includes 18 research and breeding institutions regionally and has conducted cooperative yield trials since 2000. The data demonstrated positive correlations between yield and number of days to heading. In general, the varieties grown in the region are of three maturity groups. Farmers are advised to grow varieties with different maturities to reduce risks due to unfavorable weather conditions such as early frost or drought during the crop’s early growth stages. Therefore, varieties with higher yield potential are usually later maturing.

The main biotic stress for spring wheat production is leaf rust. There is a belief that a dry climate serves as a natural barrier against diseases including leaf rust. This theory is quite common among the farmers, agronomists, and the research community, including wheat breeders. However, monitoring by the Kazakh Research Institute of Crop Protection (Koyshibayev, 2002) suggests that from 1970 until 2002, there were 14 local leaf rust epidemics. The total area affected reached 4-5 million ha in Kazakhstan in some years, causing yield losses of 15-35%. Interestingly, all the varieties sown in Kazakhstan are highly susceptible to leaf rust. Only recently have new, high yielding, leaf rust resistant varieties and breeding lines been identified through KASIB testing (Table 4) (Morgounov et al., 2007). However, they still need to be formally accepted for cultivation and promoted among producers. Improvement of leaf rust resistance of spring germplasm in Northern Kazakhstan and Siberia represents the single most effective step in increasing wheat yields, especially during years with adequate precipitation.

### Table 4. High yielding leaf rust resistant entries identified under natural infection through multilocational testing by KASIB Network.

<table>
<thead>
<tr>
<th>Variety</th>
<th>Country</th>
<th>Breeding program location</th>
<th>Test year</th>
<th>Number of locations</th>
<th>Average leaf rust infection (%)</th>
<th>Maximum leaf rust infection (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kazakhstanskaya 15</td>
<td>Kazakhstan</td>
<td>Almaty</td>
<td>2000-2001</td>
<td>5</td>
<td>13</td>
<td>20</td>
</tr>
<tr>
<td>E-736</td>
<td>Kazakhstan</td>
<td>Otar</td>
<td>2001</td>
<td>6</td>
<td>6</td>
<td>15</td>
</tr>
<tr>
<td>E-755</td>
<td>Kazakhstan</td>
<td>Otar</td>
<td>2001</td>
<td>6</td>
<td>7</td>
<td>25</td>
</tr>
<tr>
<td>Duet</td>
<td>Kazakhstan</td>
<td>Aktyube</td>
<td>2001</td>
<td>6</td>
<td>8</td>
<td>25</td>
</tr>
<tr>
<td>381-MC</td>
<td>Kazakhstan</td>
<td>Omsk</td>
<td>2001</td>
<td>6</td>
<td>10</td>
<td>20</td>
</tr>
<tr>
<td>Kvinta</td>
<td>Russia</td>
<td>Omsk</td>
<td>2001</td>
<td>6</td>
<td>10</td>
<td>25</td>
</tr>
<tr>
<td>Lutescens 71</td>
<td>Kazakhstan</td>
<td>Karabalik</td>
<td>2001</td>
<td>6</td>
<td>14</td>
<td>20</td>
</tr>
<tr>
<td>Aria</td>
<td>Russia</td>
<td>Kurgan</td>
<td>2003</td>
<td>11</td>
<td>0.7</td>
<td>5</td>
</tr>
<tr>
<td>Lyutescens 148-97-16</td>
<td>Russia</td>
<td>Omsk</td>
<td>2003</td>
<td>11</td>
<td>0.8</td>
<td>5</td>
</tr>
<tr>
<td>Udacha</td>
<td>Russia</td>
<td>Novosibirsk</td>
<td>2003</td>
<td>11</td>
<td>0.8</td>
<td>5</td>
</tr>
<tr>
<td>Fora</td>
<td>Russia</td>
<td>Kurgan</td>
<td>2003</td>
<td>11</td>
<td>3</td>
<td>15</td>
</tr>
<tr>
<td>Sonata</td>
<td>Russia</td>
<td>Omsk</td>
<td>2003</td>
<td>11</td>
<td>4</td>
<td>20</td>
</tr>
<tr>
<td>Lyutescens 30-94</td>
<td>Kazakhstan</td>
<td>Pavlodar</td>
<td>2003</td>
<td>11</td>
<td>4</td>
<td>30</td>
</tr>
<tr>
<td>Tertsia</td>
<td>Russia</td>
<td>Omsk</td>
<td>2003</td>
<td>11</td>
<td>5</td>
<td>40</td>
</tr>
<tr>
<td>L 210-99-10</td>
<td>Russia</td>
<td>Omsk</td>
<td>2005</td>
<td>7</td>
<td>15</td>
<td>40</td>
</tr>
</tbody>
</table>

Starting from the mid-1990s, CIMMYT initiated broad germplasm exchange and cooperative breeding efforts with the region to enhance leaf rust resistance while maintaining general adaptation and grain quality. Testing of CIMMYT germplasm showed that its rust resistance, effective in Mexico, was also effective in Northern Kazakhstan and Siberia. Spring wheat varieties from similar environments in Canada and USA also showed good resistance in Kazakhstan. A study undertaken in 2002-2004 compared the performance of high latitude spring wheat varieties from Northern Kazakhstan/Siberia, USA, Canada, China, and Mexico (Trethowan et al., 2006a) in each respective region. A total of 30 varieties were tested in a trial, six from each group. Averages for yield and leaf rust severity for each group are presented in Table 5.
Table 5. Average yield and leaf rust severity of high latitude spring wheat varieties from different countries grown in Petropavlovsk, Northern Kazakhstan, 2002-2004.

<table>
<thead>
<tr>
<th>Variety group</th>
<th>Yield (gr/m²)</th>
<th>Leaf rust infection (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2002</td>
<td>2003</td>
</tr>
<tr>
<td>N. Kazakhstan/Siberia</td>
<td>492</td>
<td>217</td>
</tr>
<tr>
<td>Mexico</td>
<td>466</td>
<td>223</td>
</tr>
<tr>
<td>Canada</td>
<td>461</td>
<td>185</td>
</tr>
<tr>
<td>USA</td>
<td>361</td>
<td>177</td>
</tr>
<tr>
<td>China</td>
<td>326</td>
<td>186</td>
</tr>
</tbody>
</table>

Despite the high incidence of leaf rust in the North Kazakhstan/Siberia group, yield was higher compared to varieties from other countries. Most foreign germplasm, including Mexican lines, were leaf rust resistant and produced relatively high yields. Another important observation from the study was that North Kazakhstan/Siberian germplasm was taller than Canadian and US varieties and was more sensitive to day-length. Interestingly, the varieties from the region competed in yield with Canadian varieties, even in Canada. The authors of the study concluded that a breeding program based on local varieties crossed with Mexican, USA, and Canadian rust resistant germplasm would be beneficial for combining adaptation and disease resistance.

Such a program was initiated within the framework of so called “shuttle breeding” (Trethowan et al., 2006b). Crosses between Kazakh and Mexican germplasm are made in Mexico and developed until F4-F5 generations under continuous leaf rust pressure. Frequently, top crosses or three-way crosses are made utilizing the best parents from USA and Canada. The resulting populations are sent to the region to be selected for adaptation, leaf rust resistance, and other traits. The best lines identified are advanced in the breeding program, utilized in crosses, and sent back to Mexico for the next cycle of crosses. The first crosses were made in 2000; by 2006 the program had produced lines combining leaf rust resistance with high yield. The lines originating from crosses AKMOLA 2/PASTOR, AKMOLA 3//3/TRAP#1/YACO//BAV 92, KAZACHSTANSKAYA 10 //PASTOR1/YACO//3//BAV 92, TSELINNAYA 24//HXL7573/2*BAU exceed the yield of the local check by 10-20% while demonstrating a high degree of resistance to leaf rust.

In summary, utilization of new varieties to increase yield potential in the region is possible through incorporation of leaf rust resistance in the first place. This will protect yields during years with sufficient precipitation. The general adaptation of Kazakh and Siberian varieties is adequate and competitive with germplasm from similar environments in Canada, USA, and China. It appears that tall stature and sensitivity to day length play a positive role in yield potential. New germplasm developed by regional breeding programs as well as lines coming from the shuttle breeding program with CIMMYT offer new alternative germplasm that combines high yield with leaf rust resistance.

Current Policies that Affect Wheat Production

Kazakhstan produces more wheat grain than it consumes. Average yearly exports vary between 2-3 mln t (Morgounov and Abugalieva, 2006). The country plays a role of regional food security insurance. The government strives to play a significant role as a wheat exporter. The policies and measures undertaken support both production and exports.

The wheat grain production system in Kazakhstan remains extensive with low input use and low costs. Production costs vary between US$ 60 and 90 per ha. With an average yield of 1 t/ha and the price of grain of US$100 per ton, the average producer generates a profit of US$10-40 per ha. The main subsidies for wheat production include free crop protection against diseases and pests by the semi-government services when there is danger of an epidemic. The purchase of certified seed is supported. The farm sector in Kazakhstan needs to replace old field machinery and tractors, which represents a major expense. A government service provides subsidized credit for the purchase of machinery. Recent support includes subsidies for herbicides to replace tilled fallow with chemical fallow and encourage producers to move towards zero and minimal tillage. These supports and subsidies do not reach all producers, but enough to encourage higher yields and more profitable farming. There is no program to support replacing some of the wheat area with alternative crops.

The competitiveness of Kazakh grain on regional and world markets is limited due to the lack of access to the open seas, and the high transportation and transit costs. Efforts to negotiate lower transit costs with Russia have so far been unsuccessful. The government realizes the need for branding and promoting Kazakh grain abroad, and some measures have been taken. However, big private grain-producing and trading companies are probably more efficient in finding efficient export channels and marketing the grain. There are some sales of flour abroad, and grain...
producers see some potential for exporting processed wheat products. However, this has not yet reached a significant level.

Current policies in Kazakhstan provide subsidies to wheat producers and encourage higher yields and more profitable and environmentally sustainable production. The subsidies are not excessive and play a positive role in wheat production. Maintaining a free market environment and not over-regulating production and export should be important components of Kazakhstan’s grain policy.

References


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Challenges to Wheat Production in Brazil


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Wheat production in Brazil is limited by several factors in the four different wheat breeding regions (Figure 1). The breeding regions are defined by latitude, altitude, and temperature. Acid soils, with aluminum and manganese content in excess for wheat production, are common in these breeding regions. Therefore, liming is a solution for the plow layer but sometimes insufficient due to the excess of aluminum and manganese in the subsoil. Pre-harvest sprouting, frost at flowering in the south and dry conditions in the Cerrado (Savanna) region as well as diseases caused by fungus, bacteria and virus are factors that limit the yield. The South region is the main wheat production area in Brazil (Figure 2). Over 90% of Brazilian wheat is produced in the three southermost states, Rio Grande do Sul, Santa Catarina, and Paraná (Figures 3, 4 and 5), being Paraná the main producer. Low wheat flour quality in the south, especially in the states of Rio Grande do Sul and Santa Catarina, is a constrain to increase wheat production. Yield, annual production per year, and cultivated area are indicated in Figures 3, 4, and 5, respectively.

Since its beginning in 1922, Brazilian breeding programs released 434 cultivars for different wheat production regions. During the last 30 years, Embrapa is working to select new genetic materials with better resistance to adverse environmental conditions and prevalent diseases. As a result, 115 cultivars were released by Embrapa since 1974 adapted to the different regions. Their characteristics include: dwarfing genes that confer better lodging resistance; genes for tolerance to diseases (fungus and virus) and abiotic stresses (pre-harvest sprouting and acid soils); genes that determine less responsiveness to vernalization and photoperiod duration, and better end use quality.

The research in crop rotation, no-tillage system and the use of new fungicides, associated with short and early varieties, with better harvest index and better resistance to biotic and abiotic stresses permitted to elevate the yield potential from 1,500 to 5,000 kg/ha in favorable environments. The four wheat breeding regions and the main characteristics and constrains are discussed below.

Region I – Cold, humid and high altitude

Region I has an altitude varying from 600 to 1,100 meters. The climate is subtropical to temperate and the latitude in general is higher than 24 degrees (south). Acid soils are predominant in this breeding region. In this region wheat is sown preferentially in June and July and is harvested in November and December. During the months of June, July and August, frost may occur every year. Sometimes frost also occurs in September and then it causes significant losses in yield. The region has high rainfall, frequently over 900 mm, during the growing season. In many years, most of the rain is concentrated in September, October and November, during which flowering and maturity occurs, causing pre-harvest sprouting. As a result, low gluten strength will be present in most of the years.

Figure 1. Wheat breeding regions in Brazil

- Region I – Cold/Humid/high altitude
- Region II – Moderately warm/Humid/Low altitude
- Region III – Warm/Moderately dry/Low altitude
- Region IV – Warm/Dry/High altitude -Cerrado
- Not recommended for wheat cultivation
Leaf rust (*Puccinia triticina*) and scab (*Fusarium graminearum*) are the main biotic constrains. Mildew (*Blumeria graminis*), glume blotch (*Stagonospora nodorum*), tan spot (*Drechslera tritici-repentis*) and the virus diseases, barley yellow dwarf virus (BYDV) and soil borne mosaic virus (SBMV) are also important in most of the years.

**Region II – Moderately warm, humid and low altitude**

In Region II the mean altitude is lower than 600 meters. The climate is also subtropical to temperate and wheat is sown in May and harvested in October and beginning of November. Frost in late July and August and excess of rain in October are important at the maturity stage and can cause severe pre-harvest sprouting damage and losses of yield.

The main constrains are: leaf rust (*Puccinia triticina*); scab (*Fusarium graminearum*); mildew (*Blumeria graminis*); glume blotch (*Stagonospora nodorum*); tan spot (*Drechslera tritici-repentis*); spot blotch (*Bipolares sorokiniana*) (*H. sativum*); wheat blast (*Magnaporthe grisea*); virus diseases (barley yellow dwarf virus and soil borne mosaic virus); pre-harvest sprouting and acid soils.

**Region III – Warm, low rainfall and low altitude**

The mean altitude of Region III is about 400 meters. The climate is subtropical and wheat is sown preferentially from the end of March to the beginning of May. Harvest occurs from the end of July to the beginning of September. Scarce rainfall and low humidity in the soil are a serious problem. The soils present two situations: with and without acidity and aluminum toxicity. In the north of Paraná, the most important wheat region in Brazil, the soils in general have no aluminum and acidity limitations. In this region, wheat quality (expressed by gluten strength) is high in most years and pre-harvest sprouting is rarely present.

The main biotic constrains are: leaf rust (*Puccinia triticina*); mildew (*Blumeria graminis*); tan spot (*Drechslera tritici-repentis*); spot blotch (*Bipolares sorokiniana*) (*H. sativum*); wheat blast (*Magnaporthe grisea*); and barley yellow dwarf virus (BYDV).
Figure 4. Wheat production in three states of the southern wheat region of Brazil, during the period of 1977 to 2005. RS (Rio Grande do Sul), SC (Santa Catarina), PR (Paraná).

Figure 5. Wheat area in three states of the southern wheat region of Brazil, during the period of 1977 to 2005. RS (Rio Grande do Sul), SC (Santa Catarina), PR (Paraná).
Region IV – Warm & dry or Warm & Irrigated (Brazilian Savanna/Cerrado Region)

In the Brazilian Savanna region (204 million ha, in which 54% are farmland), called locally “Cerrado”, soils are predominantly acid and with aluminum toxicity. It represents two environments, according to the CIMMYT mega-environments (MEs): Cerrado-ME1, where wheat is cultivated under irrigation and Cerrado-ME4 where wheat is cultivated under highly variable rainfall conditions and there is a drought period after the flowering stage. The Savanna area includes the states of Goiás, Distrito Federal, Minas Gerais and part of Mato Grosso, Mato Grosso do Sul, Bahia and São Paulo. The Cerrado wheat area is about 45,000 hectares considering both wheat (rainfed wheat sown in February to March and irrigated wheat sown in May. The production is about 180 thousand tons of grain. No-tillage predominates as a major planting process, except in some areas where wheat is cultivated after potato and other vegetable crops and farmers use conventional tillage. The major crops that compete with wheat under irrigation are common beans and corn. During the summer period the main crops under rainfed conditions are soybeans, corn, rice, and common beans.

Embrapa’s wheat breeding program main objective in the ME1 region is to increase wheat productivity, through breeding for reduced plant height and increased lodging tolerance by adding dwarf genes. Wheat blast (Magnaporthe grisea) and leaf blotsches (Bipolaris sorokiniana and Drechslera tritici-repentis) can affect negatively yield and quality, depending on environmental conditions. In the ME4 region, important initiatives were taken to implement a breeding program for tolerance to Magnaporthe grisea and drought. Heat and pre-anthesis moisture stress are also the important factors limiting wheat production in the ME4 region. Bread making quality is also a very important objective for wheat breeding in both environments. Gains in yield and bread making quality were recently obtained in the Cerrado-ME1 region by the release of two spring wheat varieties by Embrapa, BRS 254 and BRS 264. BRS 254 (Embrapa 22*3/Anahuac) is better in bread making quality than Embrapa 42 and Embrapa 22 (checks). BRS 264 (Buc/Chiropa/Tui) has the combination of earliness (seven days less than Embrapa 42) and higher yield potential (5,285 kg/ha), and represents an increase in yield of 17 %, compared to the widely grown check variety Embrapa 42 (4,404 kg/ha).

BR 18-Terena (CIMMYT origin) and Aliança (has BH 1146 in the pedigree) are the best varieties for the Cerrado-ME4 region. When blast infection occurs it can reduce yield up to 80 % when fungicides are not used. The average yield from 1988 to 2004 (Figure 6) in the wheat yield trials were 1,300 kg/ha under rainfed conditions, with highly variable yields (500 to 2,500 kg/ha), depending on biotic or abiotic stresses.

The most important biotic constrains in the Cerrado region are: wheat blast (Magnaporthe grisea); spot blotch (Bipolaris sorokiniana) (H. sativum); leaf rust (Puccinia triticina); mildew (Blumeria graminis); tan spot (Drechslera tritici-repentis); and barley yellow dwarf virus.

Figure 6. Grain yield (kg/ha) of the two most sown varieties across 16 years in the semiarid regional yield trial in the Brazilian Savannas, Planaltina, DF.
Improving or Preserving Bread Making Quality while Enhancing Grain Yield in Wheat

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Summary

Increasing grain production based on improved grain productivity is the main goal of wheat breeding. However, the world urban population and the demand for industrially processed foods are continuously increasing; thus a farmer would obtain a better income if his wheat crop is both highly productive and possesses the quality attributes demanded by the market. Breeders' interest in quality is greatly stimulated by the changing situation in many developing countries; in some, wheat production has become a significant component of the domestic economy, while in others farmers have started to sell their wheat grain on the export market, where quality is commonly one of the main factors determining the price of the wheat stock. To keep up with the demands of both domestic and international markets, farmers must produce high yields of wheat grain with acceptable quality. Not all wheat varieties possess the same type of quality attributes; therefore a wheat cultivar suitable for one wheat-based food type is not necessarily suitable for another food type. These quality differences result mainly from genetically-controlled grain traits such as endosperm hardness, grain protein, and gluten protein composition. These grain quality traits can be improved through breeding. However, there are non-grain factors (biotic and abiotic constraints) affecting the expression of quality. In addition, nitrogen availability during grain filling and maturation determines the amount of protein accumulated in the grain and, consequently, the expression of a genotype’s inherent quality traits. Wheat quality improvement by the CIMMYT Wheat Program is a team effort; breeders, agronomists, physiologists, and cereal chemists work together to achieve high yield and high quality. The problem is tackled by combining “good quality” genes/alleles and other previously identified quality-enhancing factors, by crossing the right wheat parents. At the end of every crop cycle, several quality tests are used to screen early and late advanced lines. There is an inherent problem in attempting to improve both grain yield and grain quality at the same time, since there is an inverse relationship between high yield and high protein content. Consequently, breeders must find ways to increase one without affecting the other. One additional strategy to increase grain protein content could be to introduce protein-enhancing genes from Triticum dicoccoides into improved wheat germplasm. These two aspects are being examined by an interdisciplinary team at CIMMYT.

Introduction

Recent social and economic events occurring at the global level are influencing both the consumption and supply of wheat in the world. The consumption of wheat has been increasing during the last decade by about 5.6 million tons/year (Carter, 2002), mainly influenced by the continuous increases in population growth and in the migration of people from rural to urban areas, particularly in developing countries of Asia. In addition, globalization has been promoting changes in dietary patterns mainly of urban populations; for example, wheat-based foods such as Asian noodles or flat breads are now commonly consumed in Western countries, while pan breads, hamburger buns, pizza, and pasta are now common in Asia and the Middle East. Consequently, the wheat processing industry around the world is increasing its demand for wheat with specific quality attributes necessary to satisfy the processing requirements of diverse traditional and non-traditional wheat-based foods. On the other hand, several wheat-producing developing countries (e.g., Kazakhstan, Ukraine, and Turkey) are making wheat production a significant component of their domestic economy. Therefore, these countries need to develop new wheat varieties combining high yield to satisfy farmers’ needs and high-quality to satisfy the demands of local consumers and the export market.

Increasing grain yield and quality at the same time is complicated by the fact that there is an inverse relationship between grain yield and grain protein content, an important grain quality trait. The grain yields achieved in exporting countries best known for high protein, high quality wheat (USA, Canada, and Australia) range between 1.8 t/ha and
2.9 t/ha. In these countries, wheat is mostly grown under rainfed conditions, sometimes under drought stress; therefore, yields are low and protein concentration tends to be high. In contrast, in countries where yield levels are much higher, such as China, Egypt, and Mexico (average yields are 3.8, 6.2, and 4.5 t/ha, respectively) (Ekboir, 2002), protein content is intermediate to low.

Given this negative relationship between grain yield and grain protein, the challenge is to develop wheat varieties with improved grain yield while improving or maintaining their grain quality. Hence, in breeding for increased yield and end-use quality, it is necessary to screen for yield-related agronomic characters as well as for end-use quality related traits more than for grain protein concentration in itself. Consequently, in the early 1990s CIMMYT began a concerted effort to increase grain yield while enhancing or maintaining grain protein and end-use quality. Fortunately, the main quality-related grain and non-grain factors influencing specific processing and end-product quality are becoming better understood (Peña et al., 2002), and therefore, breeding for yield while preserving quality is feasible.

**End-use and wheat quality traits**

Common wheat (*Triticum aestivum*) is used as flour (refined and whole meal) to manufacture diverse leavened and flat breads, biscuits (cookies), noodles, and other baked products. Durum wheat (*T. turgidum var. durum*) is milled into semolina (coarse grits) to manufacture alimentary pasta world-wide and to prepare couscous (cooked grits) in Arab countries. Some durum wheat flour is used in the production of medium-dense breads in Mediterranean and Middle Eastern countries (Quaglia, 1988; Qarooni, 1994).

Although consumption of traditional foods is still very important in the world, especially in rural areas of countries in Asia, West Asia-North Africa, and Latin America, today’s urban consumers look for more healthy, nutritious foods and/or convenience foods (frozen foods, instant noodles, etc.). Newly marketed wheat-based foods, such as noodles and flat breads in Europe, the Americas, and Australia, or leavened breads and wheat-based fast foods in Asia, are easily accepted by urban populations. The wheat quality requirements to prepare (at household or village level) acceptable traditional wheat-based foods (leavened and flat breads; flour noodles, regional dishes) in rural areas are different from those required to prepare the same products at the industrial level. Better dough properties and end-product quality uniformity are usually required in the latter case. Wheat end-use quality differences result mainly from genetically-controlled traits such as endosperm hardness and gluten protein composition. These grain quality traits can be improved through breeding.

**Grain hardness.** Grain hardness is a quality trait associated with the milling properties of wheat, the water absorption capacity of flour, and the baking quality of the resulting dough. Grain hardness is determined by the packing of grain components in the endosperm cells. Allelic variations of the puroindoline genes (*Pina; Pinb*) determine the presence of a 15KD protein attached to the surface of the membrane of the starch granule; starch from soft wheat tends to have more of this protein than starch from hard wheat (Greenwell and Schofield, 1986).

**Proteins.** The bread making quality of wheat is determined by the combined effect of grain protein (gluten) concentration and gluten protein quality-related factors such as the size of the aggregated protein polymer and the combination of specific gluten proteins, namely glutenins (high- and low-molecular weight) and gliadins (see Weegels et al., 1996, for a review). These characteristics confer differential visco-elasticity to gluten and are the main factors explaining differences in bread making quality among wheat cultivars. HMW-glutenin, LMW-glutenin, and gliadins, which are controlled by genes present in the complex Glu-1 (*Glu-A1; Glu-B1; Glu-D1*), Glu-3 (*Glu-A3; Glu-B3; Glu-D3*), and Gli-1 (*Gli-A1; Gli-B1; Gli-D1*), respectively (Branlard and Dardevet, 1985; Sozinov and Poperelya, 1980; see Weegels et al., 1996, for a review), can be identified electrophoretically or by the use of molecular markers; therefore, combinations of quality-desirable glutenin and gliadin subunits can be manipulated through breeding.

**Breeding for Yield and Quality in Wheat at CIMMYT**

A major change in CIMMYT’s crossing methodology began 10-12 years ago; it involved including at least one parent (mostly males) expressing medium-strong to strong and extensible gluten in roughly 90% of all crosses. This shift was possible because CIMMYT includes genotypic information associated with gluten quality in its conventional quality-trait (phenotypic) characterization of parental stocks. At the beginning, data on HMW-glutenin subunit composition and, later, on LMW-glutenin constitution, omega gliadins, and the presence of Sec-1-controlled secalins from rye (associated with the quality-undesirable 1B/1R translocation) were made available for use in new crosses (Peña et al., 2004). In the remaining 10% of crosses, high yielding parents are combined to keep pace with the need for ever-increasing yield. Little quality screening is carried out in segregating populations because applying early-generation quality testing is practically impossible at CIMMYT, where two crop cycles per year are the norm. Marker assisted selection for some traits under the control of a few genes (starch properties, grain hardness, specific HMW-glutenin subunits) may be applied in the very near future to screen at the segregating stages.
In comparing indirect quality tests such as protein content, sodium dodecyl sulfate (SDS)-sedimentation, and Sedimentation Index (SDS-Sedimentation/protein concentration) to screen for desirable dough mixing properties and gluten viscoelasticity (elasticity and extensibility), it was found that truncation using protein percentage alone results in a high reduction in the selection of high yielding lines (Trethowan et al., 2001); the best selection of lines possessing desirable dough mixing and viscoelastic properties (mixograph and alveograph parameters, respectively) and high grain yield potential was achieved using the Sedimentation Index (Trethowan et al., 2001). This ratio is weighted against those genotypes producing high SDS-sedimentation values primarily on the basis of their high protein content and favors those with higher SDS-sedimentation values at lower protein levels. As protein content is influenced more by environmental factors than SDS-sedimentation, this ratio improved the heritability of selection. Therefore, the SDS-sedimentation index is used to screen lines in the late-segregating (F5) and early-advanced (F6-F7) stages of breeding. Actual screening for dough-mixing (Mixograph), dough viscoelastic (Alveograph) properties, and bread making quality is performed on advanced (F8-F9) and elite high yielding lines.

The new advanced lines resulting from this screening strategy express increased dough mixing time and stability, improved dough strength and extensibility, and increased bread loaf volume. This improvement in quality is partly explained by the increased frequency of the Glu-D1 HMW glutenin subunit 5+10 and of several other quality-desirable LMW-glutenin alleles in newer materials. At the same time yield levels increased (up to 0.07%/year), grain protein content remained constant. Therefore, gluten protein quality, rather than its quantity, increased. The percentage of new lines expressing strong to very strong gluten type with medium to high yield rose to 20% (van Ginkel et al., 2003).

An additional strategy to increase grain protein in high yielding genotypes is the introgression of high protein genes from wheat-related species. At CIMMYT, efforts to manipulate the latter trait are already underway. To this end, crosses involving wheat possessing a major gene (located on chromosome 6B) for high protein from T. dicoccoides and high-yielding bread and durum wheat lines have been performed. The enhancement of grain protein concentration in high yielding levels (above 5.0 t/ha) has yet to be seen.

Environmental Effects on Protein Quantity and Quality

There are non-grain factors (biotic and abiotic) that affect the expression of inherent grain quality traits. However, important bread making quality traits such as grain hardness, glutenin and gliadin composition, and SDS-sedimentation, have high heritabilities and relatively small genotype x environment (GxE) effects (MacRitchie et al., 1990; Lukow and McVetty, 1991; Fenn et al., 1994; Peterson et al., 1998). Peterson et al. (1998) found that the variations in dough mixing properties and other baking parameters attributed to environment were greater than those associated with the genotype. In contrast, Lukow and McVetty (1991) found that genotypic variance was much greater than that of the environment for the same characters. Robert and Denis (1996) found that the Alveograph gave relatively small GxE effects for W (strength) and P (tenacity) but significantly larger effects for P/L (extensibility).

Although GxE interactions on quality traits are generally significant, they are less significant than those affecting grain yield. While location effects can be large, genotypes tend to rank similarly across locations. Therefore, screening for SDS-sedimentation, grain hardness, and grain protein can greatly assist breeders in identifying high-quality wheat lines. Even more, the SDS-sedimentation/flour protein ratio allows correction for variable protein levels associated with particular locations/fertilization regimes and correlates well with baking quality-related parameters while maintaining variability for yield potential (Trethowan et al., 2001). Therefore, while most breeding programs conduct yield evaluations over many locations, a subset of locations will provide an adequate representation of end-use quality requirements.

References


Innovation Systems and Impact Pathways for Wheat

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Summary

Wheat is produced in a wide range of agroecologies and farming systems. Bread wheat, which accounts for 90% of total wheat production, is grown on a substantial scale in 69 countries on five continents. As a result, wheat underpins food security in many developing countries, providing 40% of food crop energy to rural and urban consumers. Wheat improvement, therefore, has the potential to contribute substantially to the first Millennium Development Goal (MDG) of halving hunger and poverty by 2015, as well as to several other MDGs.

The complex web of partners who contribute to the process of wheat improvement, from the development of advanced wheat lines by international researchers to the adoption of improved cultivars by farmers, can be considered as an innovation system. Generally there is at least one dominant pathway through the innovation system that carries the major part of the improved germplasm from breeders to farm fields, often resulting in higher productivity of wheat and improved farm household livelihoods. This chain represents the first half of the impact pathway. The impact pathway continues, however, with secondary effects such as farming system diversification, which often follows the intensification of wheat. Further indirect impacts of adoption and intensification are generally evident in the local nonfarm economy as a result of production and consumption linkages.

The adoption of improved cultivars is influenced on the demand side by the characteristics of the farm household system and the wheat marketing or value-adding chains from the farm to the consumer; and on the supply side by the nature and performance of the germplasm/seed delivery pathway from the breeders to the farm. Together the three elements (germplasm delivery pathway, farm household system characteristics, and the wheat value chain) can be viewed as the “U” framework, which determines the rate and magnitude of adoption. In the early stages of agricultural development, germplasm delivery pathways and value chains are barely discernible. Where agriculture is dominated by the public sector, relatively well-defined single channel delivery pathways and value chains are often observed. In marked contrast, in middle income countries with commercializing agriculture and well developed institutions, the U-framework often takes the form of webs of interacting agencies and businesses.

Introduction: Evolving Production and Markets

Slow growth in wheat production

Wheat is produced in a wide range of agroecologies and farming systems and is grown on a substantial scale, i.e., more than 100,000 hectares in 69 countries on five continents, covering some 213 million hectares worldwide in 2005 (FAO, 2006). The food security of many developing countries depends heavily on wheat, which accounts for 99.6 million of the total 446 million hectares of cereals in the developing world (FAO, 2007). About one-fifth of the global wheat area is found in low-income countries with GNI per capita of US$ 825 or less in 2004.

This section of the paper describes how there has been a gradual slowing in the growth of wheat production after peaking in the 1980s against a backdrop of rapid transformation of wheat markets and value chains. In the second section, the drivers of adoption of modern wheat varieties are described, including factors such as agricultural input services, farm household characteristics, and market conditions. In the third section, the discussion of drivers of adoption is placed in the context of agricultural innovation systems that include users, transmitters, and producers of technology and information. In the fourth section, it is argued that a full appreciation of the adoption process requires an in-depth understanding of impact pathways that link gene banks, breeders, farmers, and other ultimate beneficiaries.

Wheat productivity increased significantly during the past 40 years (especially in developing countries) through, inter alia, the availability of better varieties, more effective pest and disease control, better production practices, and improved farm management. Annual yield growth rates peaked at 2.75% p.a. in the 1980s, after widespread adoption of semidwarf varieties; since then, yield growth has slowed in part because varietal replacement is now
more important than initial adoption and also because of environmental factors (Heisey, 2002). However, increased physical productivity has been offset, to varying degrees depending on location, by a substantial increase in input prices and a steady decline in grain prices. Nevertheless, genetic improvement of wheat continues to contribute to increased wheat yield and, in various ways, to the improvement of household livelihoods and the achievement of the Millennium Development Goals (MDGs), especially the first MDG of halving hunger and poverty by 2015. The contribution of wheat improvement to the MDGs is important given the slow progress toward meeting the Goals. Empirical evidence suggests that, for every 1% increase in wheat yield, poverty has been reduced by 0.5-1.0% (World Bank, 2005).

Investments in wheat improvement research in developing countries rose rapidly in real terms from the inception of the Green Revolution in the mid-1960s, but the pattern became mixed and uneven from the mid-1980s onwards (Heisey et al., 2002). One key challenge for wheat breeding in developing countries is to maintain the level of investment in the international system. Public sector research, of which the partnership between CIMMYT and the national agricultural research systems (NARSs) is an extremely significant component, has been particularly important for wheat improvement worldwide. In fact, NARSs in developing countries released about 3,000 wheat varieties between 1966 and 2005 (Lantican et al., 2005).

Several studies have shown that CIMMYT-related germplasm has made an important contribution to international wheat breeding efforts (Byerlee and Moya, 1993; Heisey et al., 2002; Evenson and Gollin, 2003; and Lantican et al., 2005) and continues to be used extensively by public wheat breeding programs throughout the developing world. The contribution of the private sector to wheat breeding efforts varies across type of wheat and regions. Beyond OECD countries, private sector releases were most significant in Eastern Europe and the former Soviet Union, East and Southern Africa, Latin America, and to a lesser extent in the Central and West Asia and North Africa (CWANA) region. Elsewhere, the private sector accounted for very few varietal releases (Lantican et al., 2005). Under these circumstances, continued support to national and international public sector wheat improvement programs and their partnerships with private sector is required (Heisey, 2002).

Changing access to markets
Food value chains are being transformed at an astonishingly rapid rate as a result of the fast growth and significant changes in the demand from expanding urban populations in developing countries (FAO, 2004). As a result of this demand, food systems can no longer be viewed simply as a way of moving basic staples from farm to local plates. Producers now often supply long and sophisticated market chains that deliver processed and branded products to mainly urban consumers (Barghouti et al., 2004). This is particularly the case with the growth and increasing concentration of supermarkets (Weatherspoon and Reardon, 2003).

As incomes rise in low and middle-income countries, consumers are shifting from traditional cereal-based diets, including wheat-based, to energy-dense diets with substantial amounts of meat, fish, and oil (Gulati et al., 2005). The demand for food quality, and for processed foodstuffs, is increasing. Meanwhile, the “supermarket tsunami” is rolling over developing regions in Latin America, Asia, and now Africa, setting private standards for quality, reliability, and timeliness (Reardon et al., 2003; Traill, 2006). The asymmetric economic relationships in such a globalizing world is aggravated by the aggressive global purchasing policies of many supermarkets, with the consequence of high levels of market risk for small producers because sources of supply can be quickly switched (Dixon et al., 2004).

Spread of Modern Varieties
Within the changing market context, the growth of wheat production has been driven to a large degree by the adoption of improved varieties. The adoption of wheat technologies and improved cultivars occurs in distinct waves or phases. Extending the framework of Gollin et al. (2005), four phases of the adoption of modern wheat cultivars can be visualized: (1) the initial adoption of input responsive modern varieties during the Green Revolution from 1965; (2) the so-called “first post-Green Revolution” input intensification phase, with increased allocative efficiency and strong yield gains; (3) the “second post-Green Revolution” input efficiency phase, as input/output prices ratios increased in many countries in the late 1980s and 1990s; and (4) the knowledge and management-intensive phase, in which knowledge and management complement and substitute for material inputs.

Building on the rapid adoption of modern wheat varieties in South Asia and Mexico in the 1960s and 1970s, successive generations of modern varieties spread and now dominate the wheat area of the world (see Figure 1). In developing countries, modern varieties were sown on 83% of irrigated and high rainfall wheat land by the late 1970s and on practically all high crop potential land worldwide by 1990.

The differing rates of adoption between regions can be explained by a variety of factors, including agricultural input services, farm household characteristics, and market conditions. Common farm-household system characteristics that determine adoption are resource base, including farm size and access to irrigation, and education levels. Empirical studies have shown that farm size is positively correlated with adoption rates of modern wheat. This may
also be attributed to the fact that large farmers are likely to have more opportunities to learn about modern varieties, and are more apt to handle the risk associated with the early adoption of these varieties. Studies demonstrate a positive correlation between the level of education of the farm household head and the probability of adopting modern seed varieties (Villaume, 1977; Gamba et al., 2002; Mussei et al., 2001). It should be noted that adoption rates are not solely correlated with formal education but with informal knowledge levels, which could stem from advice from neighboring farmers or radio programs (Mussei et al., 2001; Heisey et al., 1990; Kotu et al., 2000).

Many studies show that farmers with access to credit have a higher probability of adopting modern wheat varieties than those with no access. For example, Kotu et al. (2000) concluded that the extension of credit in Ethiopian rainfed farming systems increased the probability of adoption of modern wheat varieties by non-adopters by 84.3%.

On the output side, farmers need access to wheat markets to dispose of surplus production at a reasonable price. The function of the market chain from producer to consumer, also known as the value chain, often depended on the public sector in the Green Revolution areas. In recent decades, the role of the private sector has become dominant in the wheat value chains in a majority of wheat producing countries.

Overall, agricultural policies play an important role in creating effective input and market institutions that are essential for rapid adoption. As noted in the preceding paragraphs, the adoption of improved varieties is determined by complex characteristics of, and interrelationships among farmers, and input and market institutions, which can be viewed as an agricultural innovation system.

Agricultural Innovation Systems

It is the decisions of millions of farmers worldwide that ultimately will determine whether improved wheat varieties are adopted and adapted, leading to increased productivity, improved livelihoods, other primary and secondary impacts, and reduced poverty. Therefore, agriculture can be viewed as an integrated technical-social system in which farmers and service providers create solutions to production and livelihood problems, often taking advantage of new opportunities through the modification of new technologies and existing production systems (Hall et al., 2005).
Consequently, agricultural development is an immensely complex process characterized by, *inter alia*, a high degree of nonlinearity. To target germplasm improvement more effectively, CIMMYT and its partners need a better understanding of the innovation systems and impact pathways and networks that link research outputs (germplasm and information) to farm-level impacts, including improved household livelihoods. This approach implies a shift of focus from crops to people-centered livelihoods and from linear technology transfer to a nonlinear complex systems approach to understanding how farmers innovate and systems evolve.

The interactions of partners, from the development of advanced wheat lines by researchers to the adoption by farmers, can be considered as an innovation system, comprising a web of dynamic interactions among researchers, extension agents, equipment manufacturers, input suppliers, farmers, traders, and processors (Ekboir et al., 2003; Hall et al., 2005). A generally accepted definition of innovation systems would be: a set of interrelated agents, their interactions, and the institutions that condition their behavior with respect to the common objective of generating, diffusing, and utilizing knowledge and/or technology (Spielman and von Grebmer, 2004).

An innovation system can be described in terms of three elements (Watts et al., 2003): (1) the organizations and individuals involved in generating, diffusing, adapting, and using new knowledge; (2) the interactive learning that occurs when organizations are involved in the generation, diffusion, adaptation, and use of new knowledge (and how this leads to innovation); and (3) the institutions that govern how these interactions and processes occur (since the innovation process is influenced by institutional arrangement, research on institutional development is needed as well as research on technological issues such as the generation of improved wheat germplasm).

One good example of innovation systems at work in agricultural R&D is conservation agriculture, for which public agricultural research is but one source of technology (see Seth et al., 2003). In such cases, participatory methods can be very effective in facilitating interactions among multiple stakeholders for germplasm and technology generation and adoption. One common aspect of successful development is an effective enabling environment for public-private-farmer partnerships for technology adaptation, knowledge exchange, and entrepreneurship.

One useful feature of the innovation systems concept is the emphasis on the nature of the linkages within and between researchers, extension agents, service providers, traders, farmers, and other actors. The concept also pays attention to the flow and exchange of products (e.g., germplasm) and information throughout the system. The stress on the different agendas, preferences, and demands of various actors sets the concept apart from traditional disciplinary views of research. Not all actors in an innovation system are equal in motivation or power; a dominant entity may lead the innovation network.

Useful lessons can also be drawn from the related concept and approach of agricultural knowledge and information system (AKIS), which Röling (1990) defined as “a set of agricultural organizations and/or persons, and the links and interactions between them, engaged in such processes as the generation, transformation, transmission, storage, retrieval, integration, diffusion and utilization of knowledge and information, with the purpose of working synergetically to support decision-making, problem solving and innovation in a given country’s agriculture or domain thereof.”

Applying this concept, extension has been conceptualized as one of the three pillars of an “Agricultural Knowledge and Information System for Rural Development” (AKIS/RD), together with agricultural research and agricultural education and training. The concept of AKIS/RD emphasizes the need to foster the feedback linkages between agricultural extension, research, and education. It has been adopted by the World Bank and FAO to guide policy planning and investment in these three areas (FAO/World Bank, 2000; see Rivera et al., 2005, for a review).

Agricultural innovation systems, therefore, include both users and producers of information, and must link them in a dynamic process that needs to be supported by appropriate framework conditions—not just policies, but also financial, business, and educational systems. Furthermore, because innovation typically involves a range of organizations, research organizations need to collaborate with partner organizations in order to facilitate greater innovation (Watts et al., 2003).

**Wheat Impact Pathways**

Often one can trace a dominant pathway through the innovation systems that carry the improved germplasm to farmers: seed is multiplied, complementary inputs *attached* and the improved germplasm reaches farmers’ fields via the germplasm delivery pathway (Douthwaite et al., 2003). This also corresponds to the first part of the impact pathway, which continues with the on-farm effects of adoption, notably the increase in yield and profit, the improvement of household food security and livelihoods, the changes in crop and livestock production patterns, such as diversification, practices, often better management, and greater use of inputs.

Further indirect impacts of the adoption of improved crop germplasm are generally evident in the local nonfarm economy as a result of production linkages, such as increased business activity and employment, growth of
input supply and service providers, and expansion of traders and processors. Hence, beyond the farmgate, the intensification of wheat production on small and large farms generates additional indirect benefits in that extra farm income stimulates the local nonfarm economy, creates new jobs, and reduces poverty, especially among the landless, those often referred to as the “poorest of the poor” (Dixon, 2007). Furthermore, the transformation and transportation of wheat products from the producer to the consumer can be envisaged as a value chain, often characterized by competitive cooperation among actors along the chain (Kaplinsky and Morris, 2000). Additional indirect effects occur in the nonagricultural sectors as a consequence of consumption linkages, again taking the form of increased commercial activity, employment, and economies growth.

Potential direct and indirect impacts, therefore, need to be taken into account when prioritizing crop improvement research. There is a need to note not only the food security benefits, but also the distribution of benefits among farmers and consumers, the indirect benefits to farmers from diversification, and the benefits to other rural poor through the jobs created in the local nonfarm economy. Thus, the adoption of improved cultivars is influenced by two important sets of nonfarm factors—the germplasm delivery pathways to the farm and the product-related value chains from the farm to the consumer—which can be visualized as the U-framework. In the early stages of development, impact pathways and value chains can be relatively well-defined single channels. However, they often take the form of webs of interacting agencies and businesses in modernizing economies.

The mapping of impact pathways also allows for the identification of attribution. This is closely linked to the functioning of the innovation network (see above). Generally, impact pathway analysis provides plausible specification of the dominant links and critical roles of the key actors leading to the adoption and better management of improved germplasm and knowledge on farmers’ fields. An understanding of these links and roles allows for feedback, and for different actors in the innovation systems (researchers, NGOs, farmers, etc.) to adapt their work to bring about more and better impacts.

Conclusions

Wheat underpins global food security and, therefore, its improvement is critical and has the potential to contribute substantially to the first Millennium Development Goal (MDG) of halving hunger and poverty by 2015, as well as to several other MDGs.

The complex web of partners, who contribute to the process of wheat improvement, from the development of advanced wheat lines by international researchers to the adoption of improved cultivars by farmers, can be considered to be an innovation system.

Generally, there is at least one dominant pathway through the innovation system that carries the major part of the improved germplasm from breeders to farm fields, usually resulting in higher productivity of wheat and improved farm-household livelihoods. This chain represents the first half of the U impact pathway. The impact pathway continues, however, with the secondary effects such as farming system diversification that often follows the intensification of wheat. Further indirect impacts of adoption and intensification are generally evident in the local nonfarm economy as a result of production and consumption linkages.

The adoption of improved cultivars is influenced on the demand side by the characteristics of the farm-household system and the wheat marketing or value-adding chains from the farm to the consumer; and on the supply side by the nature and performance of the germplasm/seed delivery pathway from the breeders to the farm. Together the three elements (germplasm delivery pathway, farm-household system characteristics, and the wheat value chain) can be viewed as the U-framework, which determines the rate and magnitude of adoption. In the early stages of agricultural development, germplasm delivery pathways and value chains are barely discernible. Where agriculture is dominated by the public sector, relatively well-defined single channel delivery pathways and value chains are often observed. In marked contrast, in middle-income countries with commercialized agriculture and well-developed institutions, the U-framework often takes the form of webs of interacting agencies and businesses.

References


Agricultural R&D Spending at a Critical Crossroads*

Since 1980 many countries have changed the ways they invest in and organise public agricultural research and development (R&D). Support for public R&D has diminished, especially for near-market, applied, productivity-enhancing research, with funds being diverted to new agendas with environmental and food quality and safety objectives. These changes have important implications for sustaining productivity in developing countries, which in the past have relied on agricultural R&D spillovers from other countries. Some developing countries are becoming more self-reliant and developing their own R&D programs. However, the more disadvantaged countries will struggle to maintain productivity growth in the face of declining applicable spillovers.

Throughout the 20th century, improvements in agricultural productivity have alleviated poverty and starvation and fuelled economic progress. These productivity improvements have been closely linked to investments in agricultural research and development (R&D). However, in the past 25 years many countries have made major changes to the ways they fund and organise public agricultural R&D, and the incentives affecting private R&D. These changes raise questions about the prospects for sustaining productivity growth over the next 25 years and beyond. Early indicators suggest that a global slowdown in farm productivity may have already begun.

Agricultural R&D Trends

In the past, both developing and developed countries have been dependent on technology spillovers from a few of the world’s affluent countries, both directly and through the system of International Agricultural Research Centres (IARCs) including the Consultative Group on International Agricultural Research (CGIAR). However, this trend changed towards the end of the 20th century in many countries, with public and private roles shifting. Support for public agricultural R&D slowed, especially for near-market, applied, productivity-enhancing research. In the world’s most affluent countries, which traditionally provided the majority of the world’s agricultural R&D investments, a slower growing, stagnant, or shrinking pool of public agricultural R&D funding is increasingly being diverted away from the traditional agenda towards environmental objectives, food quality and safety, and other objectives. These changes mean that many countries (and especially developing countries) may have to become more self-reliant in the development of applicable agricultural technologies. Complete self-reliance will be beyond many countries, especially given recent and ongoing structural changes in science and scientific institutions, in particular the rise of modern biotechnologies and other high-tech agriculture, and the associated role of intellectual property (IP). The largest developing countries (Brazil, China and India) are making the transition; nevertheless, they have

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yet to overcome the problem of chronic underinvestment in agricultural R&D, and they have many problems to overcome with respect to the effective management and efficient use of their available resources.

The most disadvantaged countries will continue to rely on the supply of spillovers from other countries and from multinational efforts. However, current international investments in productivity-enhancing agricultural R&D seem too small to fill the vacuum being created by the changes in developed country research agendas.

Who, then, will do the R&D required to generate sustenance for a growing world population when, at least for another century, virtually all the population growth will occur in the poorer parts of the world?

Diverging Research Agendas

During the 1900s, the world’s agricultural economy was transformed remarkably, fuelled by agricultural productivity growth, primarily generated by agricultural R&D that was financed and conducted by a small group of developed countries, especially the United States (US), but also France, Germany and Japan.

In an increasingly interdependent world, both developed and developing countries have been dependent on agricultural R&D conducted in the private and public laboratories of these few countries, even though they have not contributed to financing the activity.

However, dietary patterns and other priorities change as incomes increase. As a result, developed country research agendas are shifting. In particular, the past emphasis on simple productivity enhancement and enhancing the production of staple foods is declining in favour of interest in enhancing certain attributes of food (such as increasing demand for processed and so-called functional foods) and food production systems (such as organic farming, humane livestock production systems, localised food sources and ‘fair trade’ coffee). In contrast, food security concerns are still pervasive among less affluent communities, predominantly in developing countries.

In addition, to growing differences in consumer demand for innovation between developed and developing countries, agricultural R&D agendas may diverge because of differences in producer and processor demands. Farmers in developed countries are demanding high technology inputs that are often not as relevant for subsistence agriculture (such as precision farming technology or other capital-intensive methods).

Agribusiness in developed countries is demanding value-adding processes designed to meet consumer demands, and farm production technologies designed to satisfy evolving demands for farm products with specific attributes such as particular food, feed, energy, medical, or industrial applications.

As developed country agricultural R&D programs respond to these changing patterns of demand for innovations, the emphasis of the science is being skewed in ways that could undermine the international spillovers that have traditionally contributed significantly to gains in food production throughout developing countries of the world. These spillovers are not generally well understood and their importance is under-appreciated.

Other aspects of agricultural science policy, and the context in which it is conducted, are changing as well. In particular, the rise of modern biotechnology and enhanced intellectual property rights (IPRs) regimes mean that the types of technologies that were once freely available will be more difficult to access in the future.

Moreover, the new technologies may not be as portable as in the past. Biotech companies are mostly located in developed countries, particularly in the US, and tend to emphasise technologies that are locally applicable.
These and other factors limit incentives for companies to develop technologies for less-developed countries. Hence, some fear less-developed countries may become technological orphans, abandoned by their former private- and public-sector benefactors in developed countries.

**New Pressures for Self-Reliance**

International spillovers of public agricultural R&D results are extremely important as they have profound implications for the distribution of R&D benefits between consumers and producers, and thus among countries (Alston 2002). They have also contributed to a global underinvestment in agricultural R&D, which the existing public policies have only partly succeeded in correcting. The stakes are high because the benefits from agricultural technology spillovers are worth many times more than the investments that give rise to them.

The world’s least affluent countries have depended on spillovers of technologies from industrialised countries (especially from the US, but also the United Kingdom, France and others) both individually and through their collective action via the CGIAR.

Until recently, much of the successful innovative effort in most developing countries was applied at the very last stage of the process, selecting and adapting varieties for local conditions using breeding lines and other materials developed elsewhere. Only a few larger countries, such as Brazil, China and India, were able to achieve much by themselves at the more upstream stages of the research and innovation process, even for improved crop technologies for which conventional breeding methods are widely applied.

Until recently, that strategy of conducting adaptive research and relying on spillovers for basic material was reasonable, given an abundant and freely accessible supply of suitable materials; at least for the main temperate-zone food crops.

Changes in the emphasis of developed country agricultural R&D, combined with new IP rules and practices in conjunction with an increased use of modern biotechnology methods, have already begun to spell a decline in the public pool of new varieties. In addition, the other main source of varietal materials, the CGIAR, has changed its emphasis and is scaling back its role of providing finished material or advanced breeding lines.

The reduction in spillovers from these traditional sources will mean that less-developed countries will have to find new ways of meeting their demands for new varieties.

**Pervasive Underinvestment**

Although investment in agricultural R&D has high returns and has played a major role in helping to provide food for large and expanding populations, support for this form of R&D is declining. Underfunding of agricultural R&D is pervasive, especially in developing counties. This trend is alarming given:

- the continuing and substantive growth of populations, especially in developing countries
- an increasingly scarce and deteriorating natural resource base
- the pervasive pockets of hunger and poverty that persist in developing countries, in many cases despite impressive national average productivity increases
- the growing divergence between developed country research agendas and the priorities of developing countries.

The problem of underfunding may worsen, especially for agricultural R&D that is related to the production of food staples in less-developed countries, as evidenced by the recent funding trends.
Public Research Investments

Worldwide public investment in agricultural R&D increased by 51% in inflation-adjusted terms between 1981 and 2000 from an estimated $15.2 billion to $23 billion in 2000 international dollars. During the 1990s, for the first time, developing countries as a group provided more of the world's public agricultural R&D than developed countries did (Figure 1).

Figure 1: Global public investment in agricultural R&D: 2000. *

Data is reported in international dollars based on purchasing power parity conversions of local currency units in 2000 prices.

Source: Pardey et al. 2006a

The Asia and Pacific region has continued to gain ground, accounting for an ever-larger share of the developing country total since 1981. In 2000, just two countries from this region, China and India, accounted for 39.1% of developing country expenditure on agricultural R&D; a substantial increase from their 22.9% combined share in 1981. In stark contrast, sub-Saharan Africa continued to lose market share, falling from a 17.3 to 11.4% share of the developing country R&D investment total between 1981 and 2000 (Pardey et al. 2006a).

Paralleling spending patterns for all the sciences, agricultural R&D has become increasingly concentrated in a handful of countries. Just four countries (the US, Japan, France and Germany) accounted for 66% of the public R&D conducted by developed countries in 2000; about the same as two decades before. Similarly, just five developing countries (China, India, Brazil, Thailand and South Africa) undertook 53.3% of the developing countries’ public agricultural R&D in 2000, up from 40% in 1981.

Meanwhile, in 2000, a total of 80 countries with a combined population of approximately 625 million people conducted only 6.3% of total agricultural R&D (Pardey et al. 2006a).

The patterns of spending growth are uneven. Certainly, the more recent rates of increase in inflation-adjusted spending for all developing regions of the world failed to match the rapid ramping up of public agricultural R&D spending that Pardey and Beintema (2001) reported for the 1970s.

The growth in spending for the Asia and Pacific region as a whole rebounded in the late 1990s from the slower growth rates observed for the 1980s. This was especially so in China and India during the 1996 to 2000 period, in both instances reflecting government policies to revitalise public R&D and improve its commercialisation prospects, including linkages with the private sector.

Spending growth throughout the Latin American region as a whole was more robust during the 1990s than the 1980s; although the recovery was more fragile and less certain for some countries in the region (such as Brazil, where spending contracted at the close of the 1990s).

Overall investments in agricultural R&D in sub-Saharan Africa failed to grow by more than 1% per annum during the 1990s; the continuation of a longer-term slowdown (Beintema & Stads 2004). Even more concerning is the fact that approximately 50% of the 27 African countries for which national total estimates are available, spent less on agricultural R&D in 2000 than in 1991 (Beintema & Stads 2004).

A notable feature of the trends was the contraction in support for public agricultural R&D among developed countries. While spending in the US increased in the latter half of the 1990s, public R&D was massively reduced in Japan (and also, to a lesser degree, in several European countries) towards the end of the 1990s, leading to a decline in developed country spending as a whole for the decade.

The more recent data reinforce the longer-term trends observed earlier. Namely a fairly widespread scaling back, or at best a slowing down of support for publicly performed agricultural R&D among developed countries is occurring. In part, this points to a shifting emphasis from public to privately performed agricultural R&D, but also to a shift in government spending priorities.
Inevitably, this will affect productivity prospects in agriculture for the countries in question. Pardey et al. (2006b) suggest a more subtle and arguably more important consequence is that a slowdown or cutback in developed country spending will curtail the future spillover of ideas and new technologies from developed and developing countries.

Developed-developing country linkages will be even more attenuated as the funding trends proceed in parallel with other policy and market developments. These include strengthening IPRs and biosafety regulations, and a reorientation of developed country R&D agendas away from productivity gains in food staples towards concerns for the environmental effects of agriculture and food quality, as well as the medical, energy, and industrial applications of agricultural commodities.

With developed countries as a group still accounting for 44% of public agricultural R&D worldwide (and nearly 80% of all science spending) the consequences of a continuation of these funding, policy, and market trends is likely to be particularly pronounced in terms of the productivity-enhancing effects on food staples.

In addition to these broad trends, other aspects of agricultural R&D funding that have important practical consequences are also of concern. For example, undue variability in R&D funding continues to be problematic for many developing country research agencies. This is especially troubling for agricultural R&D given the long gestation period for new crop varieties and livestock breeds, and the desirability of long-term employment assurances for scientists and other staff (Pardey et al. 2006b).

Variability encourages an over-emphasis on short-term projects or on projects with short lags between investment and outcomes, and adoption. It also discourages specialisation of scientists and other resources in areas of work where sustained funding may be uncertain, even when these areas have high pay-off potentials.

Public Agricultural R&D Intensities

Turning now from absolute to relative measures of R&D investments, developed countries as a group spent $2.36 on public agricultural R&D for every $100 of agricultural output in 2000; a sizable increase over the $1.41 spent per $100 of output two decades earlier, but slightly down from the 1991 estimate of $2.38 (Figure 2). This longer-term rise in R&D intensity in developed countries starkly contrasts with the group of developing countries where there was no measurable growth in the intensity of agricultural R&D (i.e. agricultural R&D spending expressed as a percentage of agricultural gross domestic product). In 2000, developing countries spent just $0.53 on agricultural R&D for every $100 of agricultural output.

At first glance the rise in developed country intensity ratios and the stagnating R&D intensities for developing countries appears to misrepresent the trends in spending, which showed that the growth in investments in agricultural R&D in developing countries significantly outpaced the corresponding growth in investments in agricultural R&D in developed countries (i.e. 3.13 versus 2.11% per annum from 1981–2000). Delving deeper, agricultural output grew much faster in aggregate for developing versus developed countries over the previous several decades, so that the faster growth in aggregate
agricultural R&D spending among developing countries had, nonetheless, barely kept pace with the corresponding growth in output. In addition, more than half of the developed countries, for which data were available, had higher R&D intensity ratios in 2000 than 1981. The majority spent in excess of $2.50 on public agricultural R&D for every $100 of agricultural gross domestic product. Only 10 of the 26 countries in sub-Saharan Africa in the sample had higher intensity ratios in 2000 than in 1981, while most countries in the Asian and Latin American sample increased their intensity ratios from 1981 to 2000 (9 out 11 Asian countries and 8 out of 11 Latin American countries).

Other research intensity ratios are also revealing. Developed countries spent $692 per agricultural worker in 2000; more than double the corresponding 1981 ratio while developing countries spent just $10 per agricultural worker in 2000, an increase of less than 50% over the 1981 figure. These developed-developing country differences are, perhaps, not too surprising. A much smaller share of the developed country workforce was employed in agriculture, and the absolute number of agricultural workers declined more rapidly in developed countries than it did in the developing ones.

While only some segments of society are directly involved in agriculture as producers, everyone consumes agricultural outputs, therefore agricultural R&D spending per capita is instructive. These new data signalled a break with earlier trends. For developed countries, spending per capita rose substantially from 1981 to 1991 (a continuation of earlier trends documented by Pardey & Beintema 2001), but declined thereafter so that spending per capita in 2000 had slipped well below 1991 levels. This developed country reversal was driven mainly by developments in Japan, although only half the developed countries continued to increase their per capita spending on agricultural R&D throughout the 1990s.

Per capita spending rates were much lower among developing compared with developed countries; typically less than $3 per capita for developing countries (especially those in Africa) whereas 59% of the developed countries invested more than $10 per capita in 2000. Nonetheless, and in contrast to the group of developed countries, spending per capita for the group of developing countries continued to rise from $2.09 per capita in 1981 to $2.72 in 2000. The outliers to this general trend are sub-Saharan Africa, where agricultural R&D spending per capita has continued to decline since 1981, and Latin America, where spending per capita declined from $5.43 in 1981 to $4.94 in 1991 and $4.96 in 2000.

Private Agricultural R&D Investment

In agriculture, in particular, it is difficult for individuals to fully appropriate the returns from their R&D investments, and it is widely held that some government action is warranted to ensure an adequate investment in R&D (Pardey et al. 2006b). The private sector has continued to emphasise inventions that are amenable to various IP protection options such as patents, and more recently, plant breeders’ rights and other forms of IP protection.

Private investments in agricultural R&D, similar to investments in all forms of R&D, are motivated and sustained by the returns to innovation reaped from the investment.

IP policies and practices are but one dimension of the incentive to innovate. Potential market size and the cost of servicing the market, which in turn are dependent on the state of communication and transportation infrastructure, farm structure and size, and farm income, are important dimensions as well. So too is the pattern of food consumption. As incomes rise, a larger share of food expenditure goes to food processing, convenience and other attributes of food, areas where significant shares of private agricultural R&D effort are directed.
The private sector has a large presence in agricultural R&D, but with dramatic differences between developed and developing countries and among countries. In 2000, the global total spending on agricultural R&D (including pre-, on- and post-farm oriented R&D) was $36.5 billion. Approximately 37% was conducted by private firms and the remaining 63% by public agencies. Notably, nearly 94% of that private R&D was performed in developed counties, where some 55% of the agricultural R&D was private (Table 1).

In developing countries, only 6% of the agricultural R&D was private, and there were large disparities in the private share among regions of the developing world. In the Asia and Pacific region, around 8% of the agricultural R&D was private, compared with only 2% of the R&D throughout sub-Saharan Africa.

The majority of private R&D in sub-Saharan Africa was oriented to crop-improvement research, often (but not always) dealing with export crops such as cotton in Zambia and Madagascar and sugarcane in Sudan and Uganda. Almost two thirds of the private R&D performed throughout the whole region was carried out in South Africa.

The private share of agricultural R&D spending in Organisation for Economic Co-operation and Development (OECD) countries grew steadily from nearly 44% in 1981 to over 55% in 2000 (Table 1). These increasing private shares reflected increasing industry R&D by the farm-input supply and, especially, the food processing sectors.

### Table 1: Private sector share of total agricultural R&D: 1981–2000.

<table>
<thead>
<tr>
<th>Region</th>
<th>1981 (%)</th>
<th>1991 (%)</th>
<th>2000 (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Australia</td>
<td>5.9</td>
<td>20.2</td>
<td>23.5</td>
</tr>
<tr>
<td>Japan</td>
<td>36.6</td>
<td>48.4</td>
<td>58.6</td>
</tr>
<tr>
<td>United States</td>
<td>50.1</td>
<td>54.3</td>
<td>54.6</td>
</tr>
<tr>
<td>Other (19)</td>
<td>45.7</td>
<td>48.5</td>
<td>56.9</td>
</tr>
<tr>
<td>Total</td>
<td>43.9</td>
<td>49.6</td>
<td>55.2</td>
</tr>
</tbody>
</table>

Source: Compiled by authors from data reported at www.asti.cgiar.org

Around the general trend was much country-specific variation. In the US the private share inched up from 50.1% (compared with an OECD average of 43.9%) in 1981 to 54.3% by 1991, and changed little thereafter. According to these data, Japan conducted slightly more of its agricultural R&D in the private sector than the US. The private share of Australian agricultural R&D has also grown from a small base of 5.9% in 1981 to 20.2% in 1991, then more slowly during the next decade to 23.5% of the total in 2000.

### Policy Implications

Agricultural R&D is at a crossroads. The close of the 20th century marked changes in policy contexts, fundamental shifts in the scientific basis for agricultural R&D, and shifting funding patterns for agricultural R&D in developed countries. These changes imply a requirement for both rethinking of national policies and reconsidering multinational approaches to determine the types of activities to conduct through the CGIAR and similar institutions and how these activities should be organised and financed.

Even though there is no evidence to suggest that the world can afford to reduce its rate of investment in agricultural R&D and there is every indication that more should be invested, it cannot be assumed that developed countries will play the same role as in the past.

In particular, countries that in the past relied on technological spillovers may no longer have that luxury available to them in the same ways or to the same extent. This change can be seen as involving three elements:

1. The types of technologies being developed in the developed countries may no longer be as readily applicable to less-developed countries as they were in the past.
2. Those technologies that are applicable may not be as readily accessible because of IP protection of privately owned technologies.

3. Those technologies that are applicable and available are likely to require more substantial local development and adaptation, calling for more sophisticated and more extensive forms of scientific R&D than in the past.

In short, different approaches may have to be devised to make it possible for countries to achieve equivalent access and tap into technological potential generated by other countries, and in many instances countries may have to extend their own agricultural R&D efforts farther upstream, to more fundamental areas of the science.

Conclusion

The balance of global agricultural R&D investments is shifting in ways that will have important long-term consequences, especially for the world’s least affluent countries. The primary reason is changes in supply and demand for agricultural technologies in developed countries, which have been the main producers of agricultural technologies.

These countries seem unlikely to provide the quantities of productivity-enhancing technologies, suitable for adaptation and adoption in food deficit countries, that they did in the past. This trend has been compounded by a scaling back of developed country support for the international agricultural R&D system, which has already diverted its own attention away from finished productivity-enhancing technologies, especially for staple food crops.

A shift in R&D agendas is forcing a rethinking of some national and multinational policies. National Governments can take some initiatives in national agricultural R&D policy, such as: enhancing IP and tailoring the institutional and policy details of IPRs to best fit local circumstances; increasing the total amount of government funding for their national agricultural R&D systems; introducing institutional arrangements and incentives for private and joint public-private funding; and improving the processes by which agricultural R&D resources are administered and allocated.

References


Note

This paper draws heavily on material presented in Pardey, Alston and Piggott (2006b) and Pardey, Beintema, Dehmer and Wood (2006a). The support the authors received in preparing this paper from the University of Minnesota, the University of California, Davis, and the International Food Policy Research Institute (IFPRI) through its Agricultural Science and Technology Indicators (ASTI) project is greatly appreciated.

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Summary of evaluation questionnaire for the International Symposium on Increasing Wheat Yield Potential

(Petr Kosina, Impacts Targets and Assessments Unit, CIMMYT)

63 questionnaires received (total number of participants = 148)

Information about respondents (of 63 received questionnaires):

- 27 senior scientists
- 14 scientists
- 9 Managers/directors
- 7 students
- 4 postdocs
- 2 other

- 34 from developed countries
- 26 from developing countries
- 3 unidentified

- 24 were participating for the first time in CIMMYT event
- 39 had already participated in some other CIMMYT event

Worthiness of symposium:

- Respondents were very satisfied with overall symposium (4.5 on 5 point scale).
- Respondents were satisfied with presented topics and their relevance (4.27 on 5 point scale).
- Respondents were satisfied with usefulness of the information to their research (4.26 on 5 point scale).
- Respondents were satisfied with the amount of time to network and share ideas with other participants (4.11 on 5 point scale).
- Respondents expressed their satisfaction with motivational experience from the symposium (4.29 on 5 point scale).

Effectiveness and length:

- Majority of respondents agreed that such a symposium should be repeated regularly in similar form as it was organized. (4.4 on 5 point scale).
- Vast majority (45 out of 63) recommended that symposium should be repeated every 3-5 years.
- Vast majority (58 out of 63) considered time allocated to the symposium (5 days) as appropriate.

Summary of written comments:

What was the most beneficial aspect of the symposium to you?

Clearly the most often mentioned beneficial aspect of the Wheat Yield Potential Symposium was networking—interactions with participants from other countries (especially interaction between scientists from NARS and ARIs)—to discuss the challenges and new trends, information exchange and knowledge sharing.

Somewhat contradictory comments were received in relation to the spectrum of topics that were covered in presentations during symposium. Although some participants appreciated the relevancy of the variety of topics that were presented, others asked for a narrower focus for the symposium.

Another often mentioned beneficial aspect of the symposium was learning about CIMMYT’s research and role in global context, however, a few respondents would have preferred more non-CIMMYT speakers.

Other valued aspects of symposium included mainly the topics of physiology, molecular biology, future strategies of increasing yield potential, the field day at CIMMYT’s research station, and brainstorming.

What other topics or themes are of interest to you for the next similar symposium?

Most often mentioned themes to be added or to have more time dedicated for the next or similar symposia were breeding methodologies and strategies; molecular techniques (especially MAS, QTL for traits of interest) and their practical implication (phenotyping), and pathological aspects (durable resistance)

Several respondents also asked for more active participation from NARS, and better representation of the some regions since certain countries were not represented. Also missing were representatives of universities. “There should be one day oral presentations solely from NARS scientists. …”

In relation to the field day at the CIMMYT experimental station, respondents asked that more time be given in field to follow up on special interests, and that less time be spent on presentations. More time should be allotted for ‘interactions’ related to particular plots.

Other topics that were mentioned several times (to be included or expanded in the future symposiums) included statistics and bioinformatics, quality (why domestic markets get the inferior quality product?), and abiotic stresses other than drought.

The following are topics mentioned by individual respondents: (i) the role of future researchers, where are
we heading?; (ii) nutrient physiology; (iii) seed multiplication and trade diversification of wheat products; (iv) wheat quality relative to physiological aspects and genetics.

Additional comments
Many respondents expressed their appreciation for a job well done by the symposium organizers (friendly and helpful support staff).

The symposium was characterized as very stimulating.

Several respondents mentioned, that ‘the day program seemed to be overfilled.’ While they considered afternoon brainstorming very interesting (although could be better structuralized), they said that it might be more efficient if participants were not fatigued by the large number of presentations earlier in the day.

Overlap and redundancy in some presentations was sometimes observed.

Some thought that some of invited speakers should come with new ideas and challenges rather than reviewing other scientists’ work

Prior to the meeting, the program for the final day was not clear about participants’ objectives for those sessions.

Logistics:
• The poster session could have been somewhat more organized.
• The afternoon of the field day could have been better organized.
• Would be useful to have names of organizations on name tags.
• Hard copy proceedings will be needed for NARS. Ensure that there are papers/pieces in the proceedings for the NARS posters.
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