Enhancing genetic grain yield potential and yield stability in durum wheat

W.H. Pfeiffer, K.D. Sayre and M.P. Reynolds
Wheat Program, International Maize and Wheat Improvement Center (CIMMYT),
Apdo. Postal 6-641, 06600 Mexico, D.F., Mexico

SUMMARY – By 2020, wheat production must increase by 40% to meet the global demand – mainly from elevating yield. “Increasing the intensity of production in those ecosystems that lend themselves to sustainable intensification, while decreasing intensity of production in the more fragile ecosystems” may be the only way for agriculture to keep pace with population (Borlaug and Dowswell, 1997). Hence, future crop improvement has to emphasize grain yield potential (GYP), yield stability, and user preferences in concerted, interdisciplinary approaches. Issues of environmental sustainability must be an integral part of the research agenda. To achieve these goals, crop breeding at CIMMYT aims to protect high genetic yield potential as a prerequisite of broad adaptation through incorporating resistance to abiotic and biotic stresses. This strategy capitalizes on newer empirical methods, advances in information technology, morphological and physiological markers, and emerging biotechnology procedures. This approach has resulted in high rates of progress for GYP in spring durum wheat, with grain biomass production rates from crop emergence to maturity of up to 89 kg/ha/day. For this study, data from maximum yield trials from 1991 to 1999 have been analyzed to investigate GYP and associated traits. The analysis revealed that improvements in GYP in modern durum wheat resulted from higher biomass, primarily through an increased number of grains/m^2 via an augmented number of spikes/m^2 and/or grains/spike. Straw yield, culm weight, spike weight, vegetative growth rate, and grain biomass production rate per day increased, while 1000-grain weight decreased. Results from the 1991-93, 1994-96, and 1997-99 time periods display higher rates of genetic progress for grain yield, biomass, and associated agronomic components in recent years, as well as changes in yield architecture in elite durums over time. In contrast to previous studies, this study showed that harvest index in CIMMYT durum germplasm declined since the early to mid-1970s, and advances in biomass production were largely partitioned into straw, particularly in the 1991-94 period. A comparison of the three top-yielding durums with the three highest yielding bread wheat genotypes over nine years reflected a trend towards a more uniform balance of yield components. Data covering a range of abiotic and biotic stress environments suggest that advances in GYP have been combined with improved stress tolerance and input efficiency. Implications and strategies are developed from recent research data in the context of linking to and extending upon “state-of-the-art” breeding. Dry matter partitioning, biomass enhancement, empirical and analytical approaches, expansion of the genetic base, stabilizing GYP, and hybrids are considered.

Key words: Wheat breeding, durum wheat, yield potential, yield components, genetic gains.

RESUME – *“Amélioration du potentiel génétique de rendement en grains et de la stabilité du rendement chez le blé dur”. En 2020, la production de blé devrait avoir augmenté de 40% pour faire face à la demande mondiale, principalement par une augmentation des rendements. “Augmenter l’intensité de la production dans les écosystèmes qui sont voués à une intensification durable, tout en diminuant l’intensité de la production dans les écosystèmes plus fragiles” serait probablement la seule manière pour l’agriculture de se maintenir au pas avec la croissance de la population (Borlaug et Dowswell, 1997). Ainsi, les améliorations futures des cultures, après une concertation pluridisciplinaire, devraient mettre l’accent sur le potentiel de rendement en grain (GYP), la stabilité des rendements, et les préférences des consommateurs. Les questions de durabilité environnementale doivent faire partie à part entière des perspectives de recherche. Pour cette étude, les données d’un maximum d’essais de rendements réalisés de 1991 à 1999 ont été analysées pour étudier le GYP et les caractères associés. Les analyses ont montré que l’amélioration du GYP chez les blés durs modernes provenait d’une biomasse plus élevée, principalement due à une augmentation du nombre de grains au m^2, conséquence d’un accroissement du nombre d’épis au m^2 et/ou du nombre de grains par épis, alors que le poids de 1000 grains diminuait. Les résultats des périodes 1991-93, 1994-96 et 1997-99 montrent que durant ces dernières années, il y a eu un taux plus élevé de progrès génétique pour le rendement en grains, la biomasse et les autres composantes agronomiques associées, ainsi que des changements dans l’architecture des blés durs à travers le temps. Contrairement aux précédentes études, ce travail montre que l’indice de récolte du germoplasme de blé dur du CIMMYT a baissé du début des années 70 à la mi-70, et que les augmentations de production de biomasse étaient en grande partie dues à la paille. Des implications et des stratégies sont développées à partir des données des recherches récentes avec l’idée de les associer et de les appliquer à la sélection d’excellence. La production de matière sèche, l’augmentation de la biomasse, les approches empiriques et analytiques, l’expansion de la base génétique, la stabilisation du GYP et les hybrides ont été considérés.*

Mots-Clés : *Sélection du blé, blé dur, potentiel de rendement, composantes du rendement, gain génétique.*

Introduction

As Borlaug and Dowswell (1997) observed, "The only way for agriculture to keep pace with population and alleviate world hunger is to increase the intensity of production in those ecosystems that lend themselves to sustainable intensification, while decreasing intensity of production in the more fragile ecosystems." By 2020, "The world's farmers will have to produce 40% more grain... most of which will have to come from yield increases" (Pinstrup-Andersen *et al.*, 1999). Projecting diminishing per capita land and water resources during the coming century, recent studies predict production must increase by 1.6% per annum over the next 20 years to meet the increasing demand for wheat on the global level. About half of the requisite production increases are expected to come from crop management research (CMR); which means that crop improvement must contribute close to 1% per annum. This poses an immense challenge to wheat improvement research, given that in recent years genetic gains of such magnitude have been realized infrequently (Byerlee and Traxler, 1999; Calderini *et al.*, 1999). An assessment of the impact of durum wheat germplasm developed at CIMMYT revealed that 77% of the varieties released by national agricultural research systems (NARSs) in developing countries in 1991-97 were CIMMYT crosses, 19% were NARS crosses with at least one CIMMYT parent, and 2% were NARS crosses with known CIMMYT ancestry. CIMMYT's role as a partner and major source of improved durum germplasm for national programs implies an enormous responsibility and concern for maintaining and increasing genetic gains and enhancing production.

Production increases can originate from various sources: (i) genetic gains in GYP; (ii) genetic gains in tolerance to abiotic and biotic stresses; (iii) gains through improved and novel CMR production techniques and technological gains related to optimizing permanent and variable factors of the environment; and (iv) synergistic effects among these factors. Of these, GYP and GYP improvement occupy center stage in research.

Hypothesis

Yield *per se* is relevant for all agro-ecological target zones, and hence it is a priority trait. Crop improvement efforts aim to protect high GYP as a prerequisite of adaptation through incorporating resistance to abiotic and biotic stresses (Fig. 1). Incorporation of buffering mechanisms will simultaneously increase environmental production potentials, yield stability (spatial, temporal, and system-dependent), and adaptation range. The combination of yield *per se* associated input-responsiveness and input-efficiency at low production levels allows shifting crossover points between low input and modern high GYP genotypes in marginal environments. Circumstantial evidence indicates that high GYP has a residual or buffering effect when environmental stress increases.

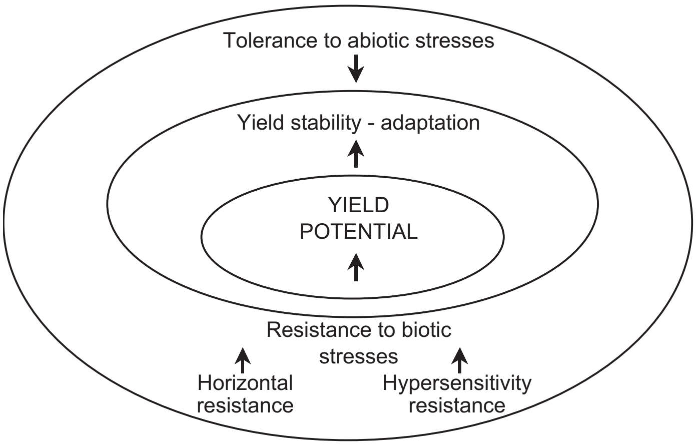

Fig. 1. Crop improvement efforts aim to protect high GYP.

Integrating and differentiating factors related to progress in GYP

Genetic progress for any of these factors will, directly or indirectly, enhance yield *per se*. Direct effects may result from improved efficiencies for nutrient uptake and utilization, or stabilization of biochemical processes over a wider temperature and moisture range. Better resistance to biotic stresses can result, through a healthier canopy and root system, in overall increased vigor and hence yield.

Such spillovers result from the fact that crop improvement cannot concentrate on GYP alone. Plant breeders do have to develop germplasm products carrying the required trait constellation, which includes stress resistance and end-use quality characteristics. When multiple traits and a widely defined target area are considered, rates of genetic progress automatically are affected negatively. The evolution of new virulent pathogen races, changing market and end-user demands, and economics of scale with larger target areas force breeders to consider a wider range of production constraints and make heavy investments in maintenance breeding necessary. To preserve past achievements via breeding requires about 60% of breeding program resources. After investing in breeding for value-added traits other than GYP and widening the genetic base through introducing new genetic variation, less than 10% of program resources will generally remain to enhance GYP. For this reason, resistance of durum to the prevalent rust races in Mexico has accelerated genetic progress in GYP since fewer traits had to be considered and breeding could concentrate on yield *per se*. Current breeding methodologies and procedures are designed to improve several traits at the same time and frequently not for direct improvement of GYP. This permits one to take an optimistic view of the possibilities for enhancing GYP, since existing options may have not been exploited and latent genetic variation for increased GYP may have been discarded due to selection pressure for other traits.

Furthermore, breeders have often been unable to forecast future cropping scenarios and the economics of production. Varieties were often grown under management situations for which they were not developed and as a result showed a lack of adaptation. CMR has to develop a sustainable agronomic platform for crop improvement research, and future gains in GYP and production increases will depend on the precision with which predictions of the agronomic environment are made.

Given the substantial number of publications on GYP improvement via crop physiological routes, to avoid duplication this paper will concentrate on avenues suggested by applied wheat breeding.

Origins of durum breeding at CIMMYT

Systematic durum wheat enhancement at CIMMYT in Mexico started in 1965 under the leadership of Nobel laureate Dr. Norman E. Borlaug. Early breeding ventures focused on the introgression of dwarfing genes and alleles for photoperiod insensitivity, improvement of floral fertility, and enhanced biotic stress resistance. Interestingly recent publications suggest re-visiting these options (e.g., photoperiod insensitivity). Breeding in Mexico concentrated on agronomic components associated with high genetic yield potential and wide adaptation in combination with quality attributes. The target areas were irrigated, subtropical environments, the initial zones of the Green Revolution.

The CIMMYT durum project became international in the late 1960s, once the agronomic problems of the first semidwarfs (e.g., sterility) were solved. Varieties such as Jori 69 (released in Mexico in 1969 – the last two numbers indicate the year of release) and other germplasm products were developed for a wider range of agro-ecological conditions and were adopted in a number of countries. After spillovers to other agroecological zones became evident in the 1980s – germplasm from traditional durum growing areas was heavily used as progenitors – breeding objectives were expanded to include high rainfall and moisture-stressed environments, with less attention given to GYP improvement.

The international reach of the durum breeding program is reflected in the adoption of its hallmark cultivars such as Cocorit 71, Mexicali 75, and Yavaros 79, which are still widely grown in many countries. Yavaros 79, for example, has been released in more than 30 countries under more than 40 names. The next generation of durum varieties, released in the 1980s (e.g., Altar 84 and Aconchi 89), trace back to breeding based on the ideotype concept. Common features are upright leaf characteristics, derived from the genetic stock Shearwater, and significantly improved end-use quality for yellow pigment and gluten characteristics.

Genetic advances in durum wheat

The five hallmark durums listed above are used as checks in Maximum Yield Potential Trials. These trials are conducted by CIMMYT's CMR group (for the last 10 years led by Dr. Ken D. Sayre) at Cd. Obregon, a semi-arid, irrigated desert site in northwestern Mexico. Breeders submit their 8-10 highest yielding elite wheat and triticale lines for evaluation of GYP under near-optimal conditions. The trials are planted in irrigation basins and, from 1995-96 onwards, also on raised beds. Crop management is optimized and consists of optimal irrigation, high doses of mineral and organic fertilizer (chicken manure), and chemical control of weeds, diseases, and insects. Netting protects the crop against lodging. Data for irrigation basins for nine crop cycles, 1990-91 to 1998-99 (designated by year of harvest 91 to 99), were analyzed to investigate progress and trends in GYP and related agronomic components.

Genetic progress in hallmark durums from the 1970s and 1980s

Comparing agronomic components of durum varieties of the 1980s (Altar 84, Aconchi 89) with those released in the early 1970s (Cocorit 71, Mexicali 75) and late 1970s (Yavaros 79) reveals on average substantial increases for grain yield and particularly biomass for the period 1991-1999 (Fig. 2). Straw yield increased partially because of a moderate decline in harvest index. Grains/m^2 increased over the two decades via a higher number of grains/spike. Similarly, grain biomass production rate measured from anthesis to maturity increased. Varieties of the 1980s headed and matured later and had improved test weights.

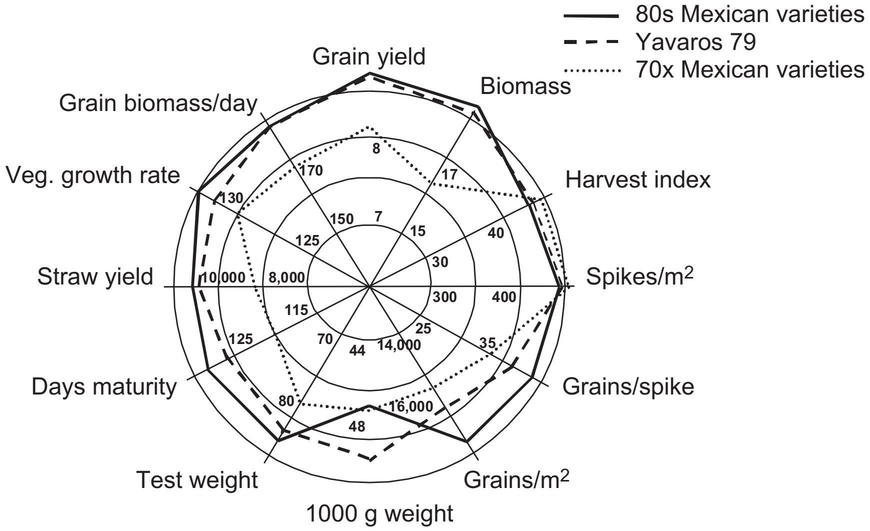

Fig. 2. Comparison of agronomic components of the highest yielding early 1970s (Cocorit 71, Mexicali 75), Yavaros 79 and 1980s (Altar 84, Aconchi 89) durum wheat varietes evaluated in maximum yield potential trials at Cd. Obregon 1991-1999.

A separate comparison of early 1970s (Cocorit 71 and Mexicali 75) and late 1970s germplasm, however, indicated that progress in grain yield and biomass and changes in related agronomic components occurred principally with the development of Yavaros 79. Compared to the two other cultivars, Yavaros 79 displayed substantial increases in grain yield (+7.7%), biomass (+11.3%), straw yield (+14.3%), grains/spike (+6.6%), and grain biomass production rate (+10.9%). Increases in grains/m^2 (+3.7%), 1000-grain weight (+4.2%), and test weight (+3.9%) were moderate while harvest index (-3.3%) and spikes/m^2 (-1.5%) decreased somewhat. There was a significant increase in days to heading (+11.2%) and maturity (+5.2%).

Compared with Yavaros 79, the durum cultivars from the 1980s exhibited increases in grains/spike (+5.5%) and grains/m^2 (+5.2%) and a concomitant decrease in 1000-grain weight (-4.4%). Grain yield and biomass remained basically unchanged.

Genetic progress in “state of the art” durum genotypes

Genetic progress of “modern-day” germplasm can be investigated via the average of the three highest yielding durum genotypes from each experiment. The mean of all five standard checks was used as a basis for comparison with the three highest yielding durum genotypes to minimize the effect of individual genotype x environment interactions. Comparison of the three highest yielding durums with the check varieties showed changes in agronomic components over time, which suggest differences in the underlying perceptions and strategies of yield *per se* enhancement.

For the 1991-99 period, elite germplasm exhibited genetic advances for nearly all the agronomic components displayed in Fig. 3, with drastic improvements in grain yield, biomass, and grains/m^2. Figure 4 shows higher genetic gains for grain yield and biomass in more recent time periods. Grain yield, for the individual years for the 1991-93 period averaged +2.5%, +5.5% for 1994-96, and +13.5% for the 1997-99 term. Increases in biomass (1991-93 +8.2%; 1994-96 +4.7%; 1997-99 +13.3%) and straw yield were of a similar magnitude. Smaller differences in grain yield during 1991-93 were due to a -5.1% reduction in harvest index and caused a corresponding over-proportional (+12.2%) increase in straw yield. Grains/m^2 consistently increased in the advanced breeding materials, averaging +6.6% in 1994-96 and reached +16.6% in 1997-99. In 1991-93 grains/m^2 did not improve: the increase in spikes/m^2 of +6.7% was compensated by the concomitant decrease in grains/spike (-5.9%). In this same period, 1000-grain weight increased by +3.8% and resulted in a higher vegetative growth rate (+7.9%). Breeders in the following period obviously stressed selecting for grains/spike. Increases during 1994-96 were substantial (+11.9%), and with a minor negative effect on spikes/m^2, resulted in a +6.6% gain for grains/m^2. Since 1000-grain weight could be maintained, this strategy proved to be successful in raising yield potential. Increases in spike weight (+9.6%) and grain biomass production rate from crop emergence to physiological maturity (+9.5%) and anthesis to physiological maturity were high. For the 1997-99 period, high increase in both spikes/m^2 (+8.9%) and grains/spike (+7.2%) produced a dramatic rise of +16.9% in grains/m^2. Grain biomass production rate (+16.6%), spike weight (+4.8%), and vegetative growth rate (+4.5%) all increased while the downward trend in 1000-grain weight (-2.8%) continued. Modern genotypes are later in heading (1991-93 +4.2%; 1994-96 +10.5%; 1997-99 +8.5%) and maturity (1991-93 +2.5%; 1994-96 +4.8%; 1997-99 +4.2%), with shorter grain fill duration. More recently developed high yielding durums exhibit shorter plant height and higher test weight.

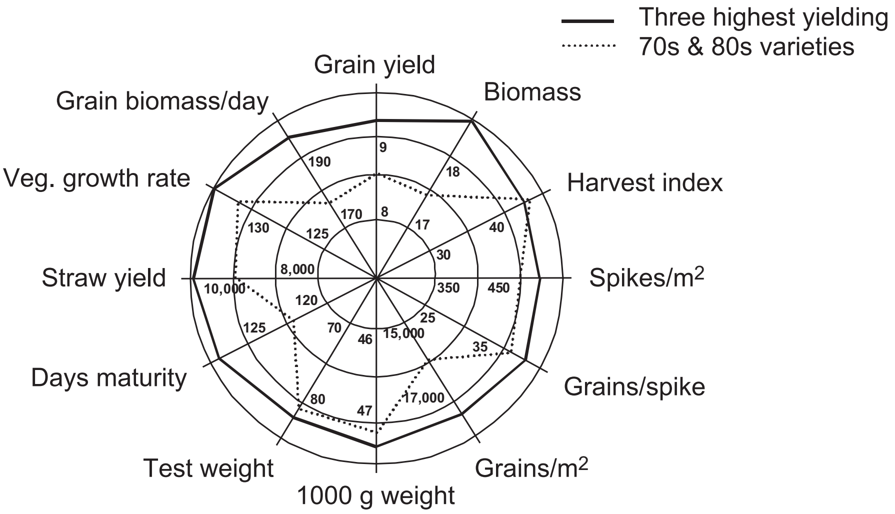

Fig. 3. Comparison of agronomic components of the three respective highest yielding durums compared with check varieties (Cocorit 71, Mexicali 75, Yavaros 79, Altar 84, Aconchi 89) evaluated in maximum yield potential trials at Cd. Obregon 1991-99.

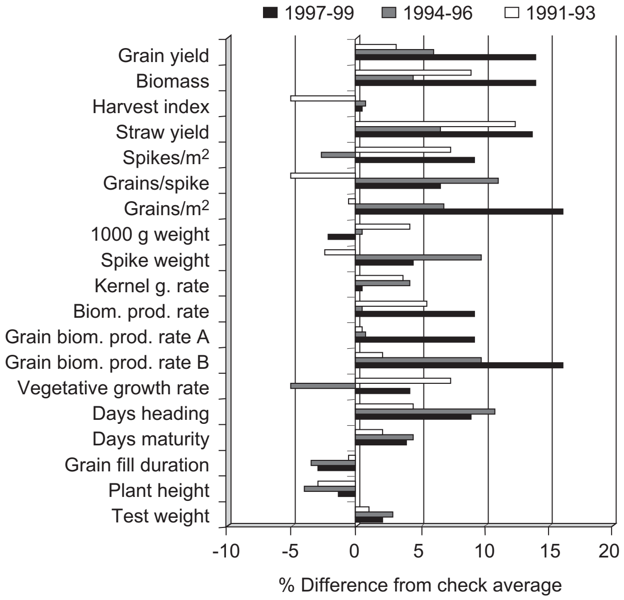

Fig. 4. Changes in agronomic components in durum in three time periods: comparison between the respective 3 highest yielding lines and 5 historical checks. Data source: Agronomy yield trials, 1991-99.

Identifying avenues for raising GYP: Crop comparisons

Comparisons of the three top yielding durums with the three highest yielding bread wheat genotypes may identify agronomic components with potential to raise GYP in durum. Further, crop comparisons can be used to investigate if the results obtained for durum wheat are artifacts or reflect real changes. Earlier comparative studies with yield component data suggested that the lower number of spikes/m^2 and associated number of grains/m^2 in durum compared with bread wheat should receive special attention in future crop improvement (Pfeiffer *et al.*, 1996). Past experience indicated superior bread wheat grain yields in years favorable for number of spikes/m^2.

Fig. 5 discloses the gradual correction of this deficiency in selecting for a more optimal balance in yield components. Between the 1991-93 period and the 1997-99 period, differences between durum wheat and bread wheat decreased by 17.2% for spikes/m^2, 14.2% for grains/m^2, +17.0% for grain biomass production rate, and 8.6% for kernel growth rate. With positive changes in harvest index, the effect on differences in grain yield was substantial. On the other hand, 1000-grain weight (10.7%), spike weight (17.2%), and number of grains/spike (6.4%) decreased in durum predominantly due to improvements in hexaploid wheat. Furthermore, there has been a significant shortening of grain fill duration in durum. These trends have been confirmed in comparisons of durum wheat, bread wheat, and triticale in maximum yield trials conducted in furrow irrigated bed planting systems. The results show a trend of converging yield architecture in durum and bread wheat.

Implications and strategies

Manipulation of dry matter partitioning

In contrast to other studies, results of this study have shown that harvest index in durum germplasm developed at CIMMYT declined since the early to mid-1970s. Over the 1991-94 period, advances in biomass production were largely partitioned into straw. The magnitude of actual harvest index values may imply scope for future gains in GYP, since values of 60% have been proposed (Austin *et al.*, 1980). On average, 42-44% of the biomass is partitioned into grain, with highest values (50%) observed in maximum yield trials in the 1998-99 crop cycle in durum (Mexicali 75) and in bread wheat checks from the early 1970s. It thus appears that the variation for harvest index in elite germplasm had been largely exploited in early semidwarfs, causing dramatic progress in yield *per se* through modifications in dry matter partitioning and associated changes in yield architecture.

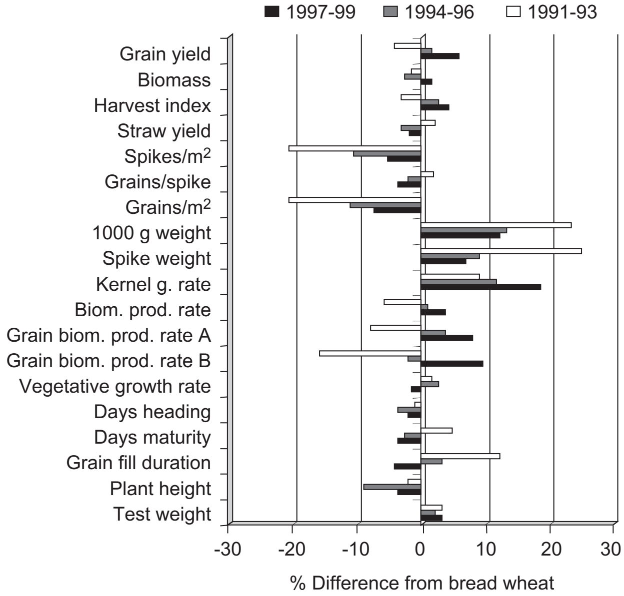

Fig. 5. Changes in agronomic components in durum in three time periods: comparison between the respective 3 highest yielding durum and bread wheats. Data source: Agronomy maximum yield trials, 1991-99.

Gene-effects (e.g., of *Rht* genes) are more profound in tetraploid genetic backgrounds than in hexaploid wheat. In durum, the lack of variation for dwarfing gene modifiers is reflected in a bimodal distribution with distinct height classes separating *Rht/rht*. These classes have largely been conserved, as confirmed by a recent study with *Rht1* near-isogenic lines (R.P. Singh, pers. comm.). This complicated the introduction of the *Rht* genes, and biomass initially decreased before genetic variation for above-ground dry matter could be developed in second-generation semidwarfs.

Pleiotropic effects had a significant effect on changes in agronomic components over time. Positive associations of a crop unspecific general nature between early maturity, grain size, and harvest index imply a higher number of grains/m^2 and negative effects on 1000-grain weight and harvest index for later maturing modern genotypes. Since the late 1970s, plant breeders have targeted increased biomass by accepting an extended growing cycle to raise yield *per se*. In addition, related changes and parallel improvements in tolerance to abiotic (e.g. heat) and biotic stresses enhanced spatial, temporal, and systems yield stability. Further, test weight increased and 1000-grain weight declined due to greater uniformity in grain size. Given the extent of pleiotropic effects and unlikely changes in crop cycle duration, harvest index improvements in the future may occur in incremental steps. Plant height in recent wheat varieties targeted for highly productive conditions has increased because of higher yield stability and superior adaptation. Very short varieties have been replaced.

Yield *per se* enhancement via biomass

Earlier efforts to increase biomass focussed on manipulating spikes/m^2 and later by augmenting the number of grains/spike, both of which are suitable traits in phenotypic selection. The avenue of selecting for grains/m^2 via a higher number of grains/spike proved superior in raising GYP. Negative effects on spikes/m^2 were minor and 1000-grain weight could be maintained. Over 1997-99, the simultaneous increase in both spikes/m^2 and grains/spike produced the highest increase in grains/m^2, GYP, and biomass. The balance in yield components may have approached a near optimal constellation, as results from crop comparison suggest. With limited scope for increasing the partitioning of assimilates to the grain, future progress has to be based on increased biomass.

Physiological strategies to accelerate the rate of breeding progress for biomass consider improving radiation use efficiency (e.g., via leaf photosynthetic rate and/or prolonged green-leaf area duration) and various strategies for manipulating the source-sink balance as one opportunity to further improve grain number (Reynolds *et al.*, 2000; Reynolds and Pfeiffer, this volume). These strategies have to be incorporated in analytical and empirical selection approaches.

Physiological strategies, which can be applied empirically to accelerate the rate of breeding progress, consider three broad approaches:

(i) Increase radiation use efficiency (RUE) and therefore total plant biomass. This strategy will be effective only if sufficient sink demand (i.e., grain number and potential kernel size) is already present. RUE could be improved at the biochemical level or by increasing light interception either early in the cycle (via more rapid canopy closure) or at the end of the cycle (via delaying of senescence processes). It may also be achieved by increasing sink demand through approaches 2 and 3.

(ii) Increase grain number. This strategy accounts for most yield progress achieved to date (Calderini *et al.*, 1999) and is associated with increased harvest index. Theoretically, a higher grain number could improve RUE by increasing the demand for assimilates during grain filling.

(iii) To date, increased grain weight potential has not been associated with increased yield potential. Nonetheless, much evidence suggests the potential for higher kernel weight, perhaps as a means to further push harvest index. Higher kernel weight is potentially another way in which sink demand could be increased and create a demand for higher assimilation rates during grain filling.

These three strategies do not address the issue of how to provide extra assimilates during the spike growth period (i.e., booting) so that higher potential grain number and grain weight potential can be achieved. Such strategies are discussed in more detail elsewhere (Reynolds *et al.*, 2000; Reynolds and Pfeiffer, this volume). These strategies should be incorporated into analytical and empirical selection approaches.

Parallel enhancement of yield components, which determine grains/m^2, may be recommended to minimize competition among yield factors with overlapping developmental stages. A further expansion of the duration of the reproductive phase or higher growth rates during the different phenological stages should result in higher biomass during this presumably source limited period.

Determination of individual grain weight is essentially independent of yield components associated with grains/m^2. Nevertheless, grains/m^2 and 1000-grain weight are negatively associated, as the decline in grain weight over time has been over-compensated by an increase in grain number. Several assumptions regarding this relationship have been discussed in the context of sink-source relationship to enhance GYP (Richards, 1996; Slafer *et al.*, 1996). Given high trait heritability and immense genetic variation for 1000-grain weight with maximum values above 75 mg/grain, improvement of grain size, *ceteris paribus*, is a promising strategy from a breeding perspective to raise yield *per se*. Heterosis for grain size in wheat and triticale hybrids, the primary trait affected, indicates enormous potential supporting a hypothesis that gains can be achieved without sacrificing grains/m^2.

Avenues and methods

Empirical approach

The empirical approach has contributed primarily to past achievements in elevating GYP and has driven improvements in computerization, experimental designs, analytical procedures, data processing, machinery, and higher breeding efficiency. This is manifested by larger numbers of field plots, a reduction in plot size and number of replications, and in extended multi-location testing. Testing efficiency (in plots/ha) at CIMMYT has doubled over the last decade due to improved crop management techniques and the adoption of higher precision spatial/augmented designs. These gains in efficiency made it possible to modify breeding methodologies and capitalize on genetic gains from direct yield estimations in early testing since the mid-1990s. Selection of progenitors has been facilitated by databases such as the International Wheat Information System (IWIS) and computer-assisted design of crosses.

Developed at CIMMYT, IWIS opens an information highway for wheat research by providing a public-domain core database/information system and information link to national programs. Major components are a pedigree management system, germplasm bank system, and a data management system, which make it possible to keep track of (and expand on) crosses and pedigrees, origins of cytoplasm and cytoplasmic diversity, synonyms for varieties, and other information. IWIS also serves as an active research tool, providing coefficients of parentage, genetic information (e.g., *Lr*-genes), data on international performance, and links to genome maps, which for example can assist in directing and monitoring parent building

Future improvements in such systems can be expected to have high payoffs. To achieve the required rates of progress in GYP, empirical methods must be combined with physiological and molecular selection procedures, particularly in light of limited resources.

Analytical approach

Recognition of physiological traits that determine GYP will facilitate analytical trait-based selection approaches, tailored breeding procedures, and the integration of biotechnological methods such as marker assisted selection. In durums, physiological traits such as chlorophyll content discriminate among and within cross progenies and have great potential in early generation screening for GYP. By integrating knowledge on the physiological basis of yield with new physiological selection tools such as canopy temperature depression, stomatal conductance, and spectral reflectance, we should be able to increase the rate of genetic progress through plant breeding significantly. Genetic transformation (allowing modification of biochemical pathways) or the application of genomics (allowing a better understanding of the genetic control of photosynthetic regulation) are expected to complement empirical and physiological approaches (Reynolds *et al.,* 2000).

Expansion of the genetic base: Probing gene pools

Progress in GYP and associated traits depends on existing genetic variation. Genetic variation in elite germplasm for these traits suggests that rates of progress in genetic GYP can be maintained in the future. Sources of genetic variation involve the entire spectrum of genetic diversity, including major tetraploid varieties, advanced lines, and unimproved/landrace germplasm from the spring and winter gene pools, interspecific and intergeneric sources (primarily major hexaploid wheat), as well as AAB and ABB genome hexaploid synthetics.

Alien substitutions and translocations are a promising option for increasing yield potential and GYP stability in durum. Observations in bread wheat suggest that the 1Rs.1Bl translocation could be exploited in durum wheat. More recently, a translocated segment from *Agropyron* sp. carrying the leaf rust resistance gene *Lr19* was linked with a 5-10% increase in yield in adapted bread wheat backgrounds. The effect of 1Rs.1Bl and *Lr19* in durum is currently under study. Similar effects from other substitutions and/or translocations may emerge.

Expansion of the genetic base and breeding for value-added traits is addressed by monitoring population parameters and capitalizing on actual trait expression to maximize selection efficiency. Resource allocation and the development of special trait populations for GYP associated components (e.g., increased sink capacity) are guided by the evaluation of projected genetic gains. For grains/spike, grains/spikelet, and spike length, genotypes with extreme expression of these characters have been developed from *T. polonicum* and other alien donors. Utilization of alien introgressions and unadapted sources requires progenitor building through pre-breeding and investigating traits and trait combinations in different genetic backgrounds. These endeavors would largely be facilitated by using physiological and molecular markers and polyhaploid production to increase the pace of breeding operations. A molecular characterization of genetic sources and adapted progenitors to determine the genetic diversity is essential to design tactical and strategic crop improvement concepts.

Stabilizing GYP

Achievements in GYP can be traced to raising yield *per se* and stabilizing GYP. Data from maximum yield trials reveal that in below average years, more recently developed genotypes exhibit a more stable performance compared with standard checks. This is manifested in relatively larger yield differences. Since genetic progress is measured across years, past achievements in GYP can be traced to stabilizing rather than raising yield *per se* (Pfeiffer *et al*., 1996). Current GYP stabilization efforts emphasize individual buffering of homozygous genotypes but should consider population buffering effects in heterozygous populations and different population structures in future breeding. CIMMYT’s breeding and testing methodology combining shuttle breeding and international screening and testing in close collaboration with partners in national programs was designed to prioritize spatial, temporal, and systems yield stability and associated traits in crop enhancement. These efforts will continue. Figure 6 indicates that superior spatial, temporal, and systems stability can be combined with maximum yield *per se*.

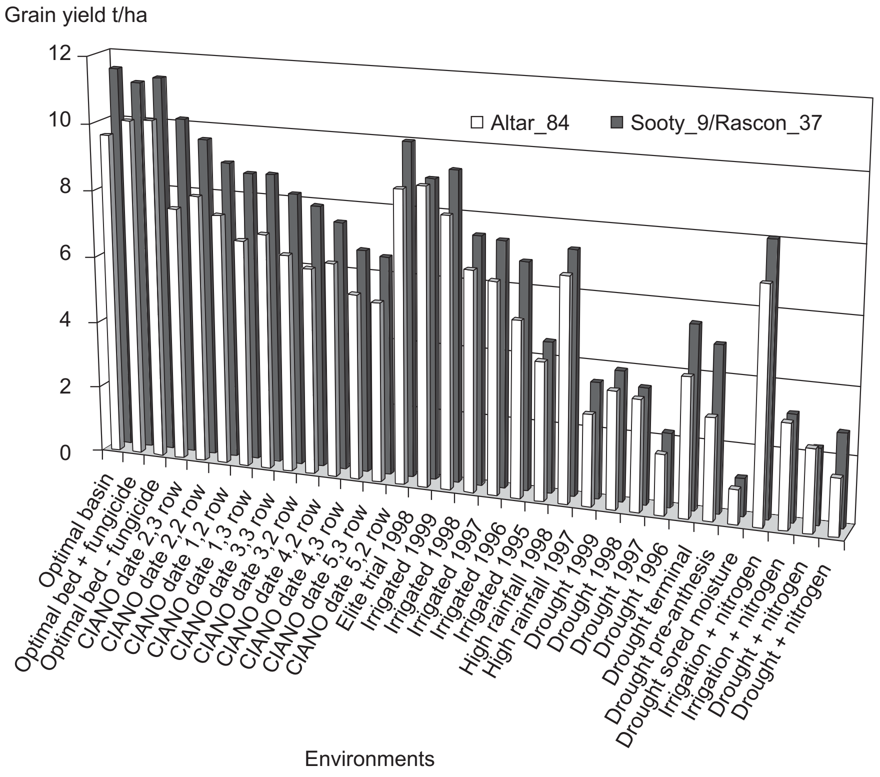

Fig. 6. Grain yield performance of Sooty9/Rascon37 compared to Altar 84 in 32 different environments (1995-1999).

A new arsenal of statistical tools and advances in the identification of relevant traits and their underlying biotic and abiotic determinants will assist in crop improvement ventures directed to GYP and yield stability improvement. This can be achieved by merging genotype, environment, and molecular data in a model to investigate the underlying factors of germplasm performance and genotype x environment interaction. New approaches, for example defining long-term similarities among transnational or even transcontinental international test sites, can help overcome the problem of sampling seasonal climatic variation. Experience indicates that over a large range of international locations, climatic extremes within a year tended to cancel each other to a degree that does not occur within countries or even continents. Data from similar highly productive international test sites can provide additional or complementary performance data and higher precision/type environment data in particular years. This may be of critical importance where genotype x year and genotype x location x year interactions dominate and breeders frequently opt to substitute temporal variation by spatial variation to ensure a parallel degree of temporal buffering capacity in their germplasm. National, regional, and international trials can be networked through common reference genotypes and a centralized public-domain database/information system such as IWIS.

Hybrids

High heterosis for value-added traits suggests the possible exploration of durum hybrids to raise GYP within the existing genetic variation. Hybrids can be successfully designed to capitalize on contrasting heterotic groups present in less adapted parents carrying alien substitutions and translocations, for example, or in genotypes with a more extreme expression of yield components. As with most commercial hybrid crops, an increase in heterosis can be anticipated along with the identification of heterotic gene pools and directed breeding efforts for hybrid progenitors. The high cost of hybrid seed due to low seed production yields is currently one of the major factors limiting the commercialization of hybrid wheat, and the economic feasibility of hybrids has in general yet to be established. Independent of different pollination control mechanisms and their effects on seed production costs (chemical hybridizing agents, CMA, cytoplasmic male sterility, CMS, and nuclear-encoded male sterility, NMS, hybrid systems), outcrossing floral characteristics (e.g., anther extrusion) in durum need to be basically improved or introgressed before commercial hybrids can be produced.

Conclusion: Critical elements of success

GYP growth rates must match future demands for food. To achieve projected production levels, breeding for realized GYP should emphasize enhancement of yield *per se* and GYP stabilization through integrated, interdisciplinary approaches that take into account environmental sustainability. This challenge requires concerted, complementary efforts to gather a critical mass of scientists and achieve essential operational sizes; sound hypotheses and strategies, translated into breeding objectives; free exchange of germplasm and information; and dynamic cooperation among the global community of scientists. Each one of these requirements must be met if we are to accomplish our common mission: the alleviation of poverty in developing countries.

References

Austin, R.B., Bingham, J., Blackwell, R.D., Evans, L.T., Ford, M.A., Morgan, C.L. and Taylor, M. (1980). Genetic improvement in winter wheat yields since 1900 and associated physiological changes. *J. Agric. Sci.*, 94: 675-689.

Borlaug, N.E. and Dowswell, C.R. (1997). The acid lands: One of agriculture's last frontiers. In: *Plant-Soil Interactions at Low pH*, Moniz, A.C. *et al.* (eds). Brazilian Soil Science Society, Brazil, pp. 5-15.

Byerlee, D. and Traxler, G. (1999). Estimation of actual spillovers of national and international wheat improvement research. In: *The Global Wheat Improvement System: Prospects for Enhancing Efficiency in the Presence of Spillovers*, Maredia, M.K. and Byerlee, D. (eds). CIMMYT Research Report No. 5. CIMMYT, Mexico, pp. 46-59.

Calderini, D.F., Reynolds, M.P. and Slafer, G.A. (1999). Genetic gains in wheat yield and main physiological changes associated with them during the 20th century. In: *Wheat: Ecology and Physiology of Yield Determination*, Satorre, E.H. and Slafer, G.A. (eds). Food Products Press, New York.

Pfeiffer, W.H., Sayre, K.D. and Mergoum, M. (1996). Enhancing genetic grain yield potential in durum wheat and triticale. In: *Increasing Yield Potential in Wheat: Breaking the Barriers*, Reynolds, M.P., Rajaram, S. and McNab, A. (eds). CIMMYT, Mexico, pp. 208-213.

Pinstrup-Andersen, P., Pandya-Lorch, R. and Rosegrant, M.W. (1999). World food prospects: Critical issues for the early twenty-first century. *2020 Vision Food Policy Report.* IFPRI, Washington, D.C., 32 p.

Reynolds, M.P., van Ginkel, M. and Ribaut, J.-M. (2000). Avenues for genetic modification of radiation use efficiency in wheat. *J. Exp. Botany* (in press).

Richards, R.A. (1996). Increasing the yield potential of wheat: Manipulating sources and sinks. In: *Increasing Yield Potential in Wheat: Breaking the Barriers*, Reynolds, M.P., Rajaram, S. and McNab, A. (eds). CIMMYT, Mexico, pp. 134-149.

Slafer, G.A., Calderini, D.F. and Miralles, D.J. (1996). Yield components and compensation in wheat: Opportunities for further increasing yield potential. In: *Increasing Yield Potential in Wheat: Breaking the Barriers*, Reynolds, M.P., Rajaram, S. and McNab, A. (eds). CIMMYT, Mexico, pp. 101-133.