Increasing Yield Potential in Wheat: Breaking the Barriers

M.P. Reynolds, S. Rajaram, and A. McNab, editors
Increasing Yield Potential in Wheat: Breaking the Barriers

Proceedings of a Workshop Held in Ciudad Obregón, Sonora, Mexico

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CIMMYT's focus on developing wheat varieties that produce higher and more stable yields has made a tremendous difference in the lives of millions of people in the developing world. In the mid 1960s, the dramatic increases in world wheat production achieved by the improved semidwarf varieties of the Green Revolution staved off impending widespread hunger and starvation in Asia. In more recent times, the modern wheats that have gradually replaced those early varieties in farmers' fields have generated a 1% average increase in wheat production each year. Today, however, yield increases in some of the most productive environments in the developing world have begun to level off.

Productivity in those favorable environments must improve, but without straining the natural resource base that underpins agriculture today and in the future. Expanding the land under cultivation to fulfill the demands for more food is no longer possible. We need new, resource-efficient varieties that produce higher and more stable yields to make up for the food deficit. Nonetheless, increases in wheat's genetic yield potential are becoming harder to achieve, and we have to find new approaches to break through the barriers before us.

Success in raising wheat's yield potential will hinge on creatively combining strategies arising from different disciplines. To generate new thinking on ways to improve the wheat plant's ability to yield more, in March 1996 the CIMMYT Wheat Program organized a workshop in Ciudad Obregón, Sonora, Mexico, with the invited participation of 12 internationally recognized experts in the fields of plant breeding, physiology, and biotechnology. The three-day workshop gave CIMMYT staff a unique opportunity to consider and explore novel approaches to the yield barrier problem. The ideas put forth by the specialists provided fertile ground for discussion, and the outcomes will no doubt influence the strategies the Wheat Program will adopt in facing this challenge.

We are extremely grateful to the 12 experts who generously gave of their time to preparing and participating in an extraordinarily fruitful workshop. Their willingness to put before their colleagues new hypotheses, as well as their openness to questions and suggestions, set the tone for this event, which will be memorable as an exceptional example of thought-provoking, collegial debate.

Timothy G. Reeves
Director General
CIMMYT
Breaking the Yield Barriers in Wheat: A Brief Summary of the Outcomes of an International Consultation

M.P. Reynolds, J. van Beem, M. van Ginkel, and D. Hoisington

Introduction

Since the beginning of the Green Revolution, production increases generated by modern semidwarf wheats have averted potentially disastrous shortfalls in world food stocks. Today, however, the global demand for wheat is increasing as a consequence of rapid population growth, principally in developing countries. Although for the moment global wheat production is keeping up with the pace of population growth, the rate of production increases must be stepped up if we are to feed the estimated one billion additional inhabitants that will swell the ranks of global population in 10 to 15 years. Another cause for concern is that the annual rate of increase in farmers’ wheat yields in key regions of the developing world, while still positive, has declined steadily since semidwarf wheats made their initial impact. To revert this trend and ensure that production increases stay abreast of population growth, CIMMYT’s Wheat Program emphasizes research aimed at raising wheat’s genetic yield potential; high yield potential, measured experimentally in well managed variety trials, is known to be strongly correlated with superior performance in farmers’ fields.

Searching for novel ways of further raising wheat’s genetic yield potential, in March 1996 CIMMYT organized a workshop in Ciudad Obregon, in northwestern Mexico, to solicit ideas from acknowledged international experts in crop science. By bringing together specialists in the areas of breeding, crop physiology, and biotechnology, CIMMYT hoped to generate a synergy of ideas that would help shape our future research agenda. The specialists were J.L. Araus, University of Barcelona, Spain; A. Blum, Volcani Center, Bet Dagan, Israel; G. Hollamby, University of Adelaide, Roseworthy, South Australia; J.P. Jordaan, SENSAKO, Bethlehem, South Africa; S. Peng, International Rice Research Institute, Los Baños, Philippines; W.E. Kronstad, University of Oregon, Corvallis, OR, USA; R.S. Loomis, University of California, Davis, CA, USA; D.C. Rasmussen, University of Minnesota, St. Paul, MN, USA; R.A. Richards, CSIRO, Canberra, Australia; G.A. Slafer, Universidad de Buenos Aires, Argentina; J.W. Snape, John Innes Center, Norwich, UK; and M.E. Sorrells, Cornell University, Ithaca, NY, USA. A brief synthesis of their main ideas is presented in the first section of this document.

Over the course of the meeting, six main research thrusts emerged as the ones most
likely to contribute to breaking the yield barriers in the context of CIMMYT's ongoing breeding efforts: 1) utilization of genetic diversity, 2) development of morphological and physiological ideotypes, 3) improvement of early generation selection criteria, 4) exploitation of heterosis, 5) insights into genotype x environment x management interactions, and 6) improved understanding of wheat phenology and development. The second section of this manuscript summarizes the conclusions of six working groups formed during the workshop to focus on these pivotal research areas.

**Summary of Presentations**

**Physiology**
The fundamental physical and biochemical constraints to total crop productivity are described by Loomis in "Limits to Yield Revisited," while Slafer's contribution, "Generation of Yield Components and Compensation in Wheat: Opportunities for Further Increase in Yield Potential," examines the critical aspects of yield determination and partitioning, and gives insights on how genetic aspects of wheat breeding may be further exploited to optimize partitioning of assimilates to yield. Richard's paper, "Increasing Yield Potential in Wheat: Source and Sink Limitations," is written from a strong breeding perspective and speculates on specific traits that might improve our conceptual ideotype of a high yielding plant. All three authors highlight the need to simultaneously optimize the sink (potential grain sites) and source (photosynthetic potential) capacity of germplasm. Greater sink strength may come from better understanding and manipulation of the processes determining growth and development of yield components (grain number and size), an idea endorsed by speakers from both breeding and biotechnology. Increasing radiation use efficiency (RUE) may improve yield directly by increasing total productivity, as well as indirectly by generating higher potential kernel number and weight. We may need to consider genetic variability in canopy architecture, and the efficiency of plant nutrition and transport processes to improve RUE.

In "Potential Yield and Drought Resistance: Are They Mutually Exclusive?," Blum discusses how an improved understanding of the physiological basis of specific versus broad adaptation may allow us to gain insights on yield potential itself. Most germplasm still carries adaptive traits, the legacy of millions of years of natural selection pressure in variable environments, that are of negligible value in a well managed crop canopy environment. Traits such as osmotic adjustment, high investment in roots, and chemical root signals that slow down leaf growth (even before water deficits are measurable) may be costly to yield.

Likewise, Richards mentions the 'conservative nature' of the wheat plant, which apparently exhibits excess photosynthetic capacity in spite of (or perhaps as a result of) empirical selection pressures. Such observations suggest interesting questions. What might the tradeoffs in broad adaptation be as we push forward the yield barriers? Might there be
other risks associated with breeding for such 'highly tuned' ideotypes—risks to plant health, for example?

In the meantime, selection for quantitative traits, in a time frame compatible with the scale of large breeding programs such as CIMMYT’s, is fast becoming a reality with technologies described by Araus and his colleagues in “Integrative Physiological Criteria Associated with Yield Potential.”

Breeding

In “Genetic Diversity and the Free Exchange of Germplasm in Breaking Yield Barriers,” Kronstad states that yield in the past 50 years has increased 136%, partly due to advanced germplasm. However, global growth rates in wheat area, yield, and total production are decreasing, for several reasons: 1) current yield gains seem small compared to the initial impact of varieties released during the Green Revolution, 2) the greater amount of resources presently diverted to maintenance breeding, and 3) the decrease in genetic diversity. It was suggested that progenitors of wheat be evaluated for possible genetic contribution to breeding programs even though enough biodiversity still exists within wheat and its related species.

Kronstad discusses a few of the limitations to free germplasm exchange and availability such as political instability, germplasm over-protection, plant variety rights, and lack of funds, and urges wheat scientists to take a stand against unrealistic quarantine laws.

Lastly, the author cautions against maintaining germplasm banks as “seed morgues” and stresses the importance of supplying enhanced trait materials for crossing, rather than ready-made products.

In “Germplasm Is Paramount” Rasmusson proposes that the highest priority be given to traditional breeding methods and examines the importance of parental choice over selection methods, and of goal setting, germplasm sharing, and staff continuity. The author also compares the relative benefits of using hallmark germplasm (global elite varieties) versus more distant parents. The importance of parental choice is evident in Rasmusson’s four most recently released barley varieties, which show modest levels of genetic diversity but express sizable yield gains. Progress in these varieties may have been due to the accumulation of favorable additive genes, or to mutations. The author cautions against the excessive search for genetic diversity and suggests that elite gene pools be further exploited. With regards to releasing breeding material to national agricultural research programs (NARSs), Rasmusson suggests sending elite parental stocks rather than early segregating materials.

Hollamby’s “Breeding Objectives, Philosophies and Methods in South Australia” describes how successful programs continuously re-examine the relevance, effectiveness, and representativeness of breeding choices and activities. He offers ideas on the importance of maintaining yield as the primary objective, of testing new varieties under farmers’ practices, and of maintaining a flexible breeding strategy. An effective breeding strategy is one in which data collection is streamlined and minimized in order to make discard/retain decisions more efficiently. The author views collaboration as an efficient means to investigate promising
Theories and pursue new cultivar development. From a breeding perspective, Hollamby describes three distinct types of crosses: 1) backcrosses towards the improvement of elite cultivars, 2) crosses to improve yield and genetic variability, and 3) crosses for parent building. Many segregants need to be examined in order to find the transgressive plant; probe genotypes, preferably isogenic lines, may be used as a selection tool.

The contribution of Peng, "Breaking the Yield Frontier of Rice", recounts the history behind the development of what IRRI scientists have come to call the 'new plant type' (NPT). Older IR8 types currently cover 60% of the world area and give 80% of total production. Because yield improvements have become marginal, the plant type was modified. The new rice ideotype has the following characteristics: low tillering (3-4 tillers), low unproductive tiller number, 200-250 grains per panicle, 90-100 cm in height, sturdy stems, dark green erect leaves, vigorous root system, 100-130 days crop cycle, multiple resistances, increased harvest index (HI), and acceptable grain quality. Although simulation modeling indicated that such a genotype would produce a 25% increase in yield, recent evaluations have indicated poor yields because of poor spikelet filling. Suggestions for increasing yield of the NPT include raising tiller number and improving synchrony. The authors also examine the probability of increasing yield potential through the use of hybrid rice technology, an issue of special importance in China, where half of the area is planted to hybrid rice. Constraints and advantages of various seed production methods are discussed, including thermosensitive genetic male sterility, photoperiod sensitive genetic male sterility, and more complex and cumbersome systems such as cytoplasmic male sterility. Apomixis was also discussed as a way heterosis may be fixed.

In "Hybrid Wheat: Advances and Challenges" Jordaan states that while recent reviews on hybrid wheat technologies are not optimistic, his experience indicates that hybrid wheats should be reconsidered in light of recently emerging knowledge. In Free State, South Africa, farmers traditionally plant wheat at very low seed rates (25 kg/ha) under low rainfall conditions. At low seeding rates and narrow row spacing, heterosis appeared high, with winter hybrids yielding 11.5-14.8% more than non-hybrids. Top hybrids yielded 18.5-23.2% more than conventional cultivars. In further GxE analysis, it was shown that hybrids have a greater advantage in lower yielding, water-stressed sites. The South African experience is convincing evidence that research on hybrid wheats, particularly for marginal environments, should be pursued.

**Biotechnology**

Biotechnology aids in the improvement of wheat yields by increasing genetic diversity through genetic engineering and by assisting selection of improved genotypes through the use of molecular markers. In "The Contribution of the New Biotechnologies to Wheat Breeding," Snape states that selection is normally carried out at the phenotypic level and is thus very dependent on chance. The process is time-
consuming, so genetic advances are not maximized and through-put is slow. To date, only a few genes, such as the photoperiod insensitivity (Ppd) and height reduction (Rht) genes, and the 1B/1R translocation have provided yield advances. Some of these also have pleitropic effects on yield.

Snape suggests that the use of doubled haploids could save a minimum of two years in the development of new varieties. In addition to the increased speed, selection efficiency is improved because additive variation is maximally expressed allowing for better discrimination. However, only a limited number of crosses can be handled and the method is expensive. Currently, the best method appears to be wheat x maize crosses, but Snape believes that microspore culture may allow larger scale production of doubled haploids. Genetic engineering will introduce novel genes for yield limiting traits such as abiotic and biotic stress resistance and the ability to suppress weed competition. In the future, biotechnology may make contributions by successfully inserting genes for quality into the wheat genome, by generating novel products, and by assisting in the development of hybrid wheats. While wheat transformation is feasible, limitations such as positional effects, gene silencing, intellectual property rights, safety concerns, and public acceptance must be dealt with when utilizing transgenics in any plant species.

Perhaps the most important result of molecular mapping of cereal genomes is the amount of conserved linearity between the genomes of all cereals. Examples presented by both Snape and Sorrells demonstrated that major genes exist which may be common to different species (e.g., vivipary in maize and preharvest sprouting in wheat). This mean that in the future, geneticists, breeders, and scientists in all other related disciplines need to be aware of ongoing research in related genome species.

In his paper, “Applications of Molecular Markers to Wheat Improvement,” Sorrells stresses that field testing is still of primary importance, but that proper combination with molecular data can lead to more efficient use of limited resources. Identification of transgressive segregants from single gene pools, crosses based on measures of coefficient of parentage (COP) or molecular diversity, introgression of exotic alleles from alien species, or synthetics could all contribute to improving yield in wheat. Sorrells presents an oat study that attempted to map QTLs for several traits without much success due to GxE effects and the presence of multiple alleles. Further efforts are needed to understand the underlying genetics of these complex traits, and to develop efficient statistical and lab technologies for handling the required number of plant samples. New marker systems based on microsatellites or AFLPs may provide increased efficiency. Current limitations of QTL mapping are the number of molecular loci available, genotypic and phenotypic resolution, and the presence of multiple alleles. Finally, Sorrells mentions that his own program is focusing on marker-assisted selection (MAS). He feels that genetic engineering will complement MAS and may aid conventional breeding methods in developing new and useful varieties.
Suggested Research for Raising Yield Potential: Conclusions of Six Working Groups

Strategies for exploiting genetic diversity

Hallmark germplasm. The group recommended continued emphasis on exploiting germplasm such as winter x spring crosses, and suggested that CIMMYT place greater emphasis on obtaining hallmark germplasm from leading wheat programs including NARSs.

Unexploited germplasm. It was suggested that more use be made of unimproved materials, including landraces and wheat progenitors (A, B, D genomes), interspecific crosses (e.g. synthetics), and intergeneric crosses. It was stated that CIMMYT can play a unique role in exploiting its collection, and that there should be more collaboration and distribution of information.

Traits. With respect to traits that help define elite germplasm, it was suggested that genetic studies of yield components be made. Also, a catalogue containing lists of stocks and describing important traits (e.g., phenological traits) should be prepared.

Parent building. In this area, it was suggested that we need to evaluate methodologies for gene introgression and manipulation through increased collaboration.

Testing. Transfer of traits must be systematically validated through estimating trait expression and varietal stability. The traits must be verified in materials having acceptable agronomic performance.

Developing morphological and physiological ideotypes

Morphological ideotype. Several years ago, CIMMYT’s Wheat Program developed an ideotype with the following distinctive traits: very large spikes, few tillers, wide leaf-blades, solid stem, high number of grains m\(^{-2}\). The ideotype was not promoted because it suffered from incomplete grain filling. The group suggested that the following be investigated with respect to the ideotype: 1) the physiological basis for poor grain filling, 2) the genetic basis of ideotype using QTL analysis, and 3) interaction of ideotype performance with management.

Physiological ideotype. It was also suggested that new ideotypes be developed, combining a number of physiological traits shown to be associated with higher yield potential. These may include traits such as large kernels and high kernel number, high stomatal conductance and canopy cooling, lodging tolerance, heat tolerance during grain filling, adaptation to canopy environment (communalism), and erect flag leaves (with adequate leaf area). Other traits that may also warrant consideration include reduced partitioning to peduncle and leaves, fast early leaf area development, efficient transport systems for nutrient and water uptake.

Complementary approaches. In addition, it was argued that there are many areas of research that would complement the above ideotype approaches and could be undertaken by CIMMYT or collaborating institutions. These include: 1) understanding the physiological basis for determination of grain size, 2) characterizing the effects of...
major genes on yield (e.g., Rht, Ppd, Vrn, Tin), 3) establishing the constraints to yield determined by transport functions and their regulation, 4) documenting basic differences in plant morphology among wheat lines (this may have important implications in, for example, the areas of transport and lodging tolerance), and 5) optimization of canopy photosynthesis.

Phenology and yield potential

Three main developmental phases.
Manipulation of phenological development was suggested as a tool for increasing yield potential in wheat. The importance of three main developmental phases was stressed, namely: 1) sowing to terminal spikelet (vegetative phase), 2) terminal spikelet to anthesis (spike phase), and 3) anthesis to maturity (grain-filling phase). The purpose would be to confirm whether lengthening the spike and grain-filling phases (while maintaining the overall growth period constant) contributes to raising yield potential.

Research needs. Initially, the variation of the three developmental phases would be assessed. The effect of photoperiod (Ppd), vernalization (Vrn), and temperature (Eps) genes on phenology was suggested as a way to manipulate the relative amount of time allocated to spike formation and grain-filling. Once the effect of phasic lengths on yield is confirmed, the optimum length of each phase would be determined.

Techniques for phase measurement.
Measurement of the early phases would rely mostly on dissection of stems to reveal terminal spikelet initiation. In addition, phyllochron, flag leaf emergence, and the use of growth scales such as Haun's would be employed to measure spike formation. Grain filling is delineated by flowering and physiological maturity, with intermediate phases being estimated by direct measurement of the grain growth/physiological stage.

Wheat germplasm. It was recommended that the following types of existing germplasm be used to study genetic variation: isogenics, double haploids, 1B/1R and 1A/1R translocations, and recombinant inbred lines. New and exotic sources of phasic variation, such as accessions stored in CIMMYT's Germplasm Bank, the Japanese line 'Kato', and developmental mutants should also be explored.

Validation experiments. Since identifying genetic variability of growth stages is time consuming, only a limited number of lines can be studied. In preliminary work, approximately 100 entries planted as short row-plots can be measured. In subsequent yield trials, a smaller subset of entries (perhaps 30-50) would be effectively characterized for phenology.
Characterization options are direct measurement of phasic development or molecular approaches in which the presence of genes can be established independently of expression. This type of work will require collaboration among breeders, physiologists, and geneticists. Field work will be conducted in several ME1 sites, while prebreeding and molecular approaches will be carried out mainly at CIMMYT.
Early generation selection criteria

Objectives. Objectives can be divided into several groups that partly overlap: yield, disease resistance, abiotic stress tolerance, quality traits, morphology, physiology.

Strategies. Strategies will depend on the objective and may include parent evaluation and selection; combining genes into parents through backcrossing or three-way crossing; assessing the optimum generation(s) for applying selection; developing double haploids and recombinant inbred lines (RIL); establishing correlations and relationships; and doing QTL analysis to identify genes.

Traits. The morphological traits mentioned included coleoptile length as related to stand establishment; evaluation of non-seed producing tillers; duration of developmental stages; embryo size; leaf thickness; biomass/competition among yield components; spike morphology; kernel number and/or kernel weight. Some of the physiological traits recommended as suitable for early generation selection for MEl conditions included CJ (in kernels, non-destructive, seedlings); ash analysis (kernels, non-destructive, seedlings); N15 for N use efficiency, and infrared temperature measurements.

Yield potential. For the mapping of genes for yield potential, the following issues are important: concentrate on optimum yield conditions, parent/population selection, identify the best cross strategy, handling, data on multiple traits, strategy to identify the best alleles, and new statistics for QTL analysis.

Plan of action. The plan of action entails: the study of phenotypic yield expression under optimum yield conditions involving several countries, coordination of data analysis, centralized interpretation of data/analyses at CIMMYT carried out by the participants through exchange scholars, post docs, or sabbaticals, frequent communications with all participants (Email, IWIS, Database), appropriate resource allocation to participants, integration of data with other groups.

Genotype by environment (G x E) by management interactions

Identifying G x E. It was recognized that G x E interaction is one of the most difficult problems in plant breeding, especially for centralized breeding programs. One way to address G x E is to develop databases such as IWIS to define problem environments and identify potentially suitable germ plasm. This process can be facilitated by utilizing probe genotypes of known sensitivities to stress, and perhaps by incorporating growers' empirical observations into the database.

G x E for high yield germplasm. The group tried to define environments where G x E for yield is likely. Environments where it was considered less likely to be a factor included ones affected by drought, heat, macronutrient stresses, waterlogging, and moderate salinity. On the other hand, stresses such as mineral toxicity, micronutrient deficiency, nematodes, soil borne pathogens such as root rots, and weeds were identified as likely to induce G x E.
Targeting for G x E. The occurrence of significant G x E interaction requires the development of discrete programs for specific stress conditions. Specific adaptive genes may be required for specific adaptation, and the potential cost to yield potential should be evaluated.

Role of breeding for specific management systems. The area of G x E by management interactions was touched on, and it was recognized that the three-way interaction must be studied to improve yield potential in the context of evolving crop management strategies and to evaluate ideotypes that may be adapted to specific cropping systems.

Exploiting heterosis

Background. The challenge of wheat scientists is to achieve a 2.5% increase in annual production. To reach this goal, hybrid wheat could be considered as a tool. The demand for hybrid wheat research at CIMMYT is client driven, particularly from advanced NARSs. It was recognized that to develop expertise, a long term commitment must be made by CIMMYT, recognizing that CIMMYT already has access to hybrid technology, and that hybrids allow faster genetic gains. However, it is important that there be balance between hybrid and pure line development. Hybrids may open new areas of research, e.g. in physiology. CIMMYT is in a unique situation to act as a mediator for outside groups for the transfer of hybrid technology. For example, a hybrid technology package for NARSs needs to be developed. The package must include germplasm, technology and methodology, and training (including seed production).

Identifying target MEs. To identify target megaenvironments for hybrids, the advantages of heterosis must be considered: grain yield, yield stability and adaptation, agronomic components, e.g. root characteristics, disease resistance, pyramiding genes (disease, quality). The environments likely to benefit from heterosis include highly productive environments with the highest payoffs, stress prone environments, and environments where there is co-development of appropriate management technology.

Identification of heterotic groups.

Emphasize the identification of distinct gene pools and/or germplasm products and the development of test hybrids among those genepools (e.g. winter, spring, Chinese, alien species derivatives). Use this information to develop parallel male and female genepools (e.g. use Chinese only in the spring female genepool). The use of molecular markers was recommended (e.g. fingerprinting to evaluate diversity). Effective restorer genes need to be identified (use molecular markers where available) and transferred to elite parents. Define traits in distinct male and female pools (e.g. nonsynchronized tillering with male parents to have long pollination period). Select for heterosis. Testing at CIMMYT should be followed by international testing. Exploitation of the power of IWIS during all phases (e.g. for heterotic groups use coefficient of parentage, information management).

Pollination control mechanism. A strategy must be chosen from among the following: 1) chemical hybridizing agent (CHA): availability will depend on agreements with
CHA producers, and their policies (CIMMYT, CIMMYT as mediator, NARSs, joint ventures including private sector; 2) cytoplasmic male sterility (CMS): evaluate available CMS donors, screen new CMS donors (germplasm bank, IWIS) (this system is a proven success and is relatively cheap); and 3) nuclear-encoded male sterility (NMS): a genetic engineering option; monitor progress, seek relationships, develop expertise. Financial, legal, and agronomic risk involved (e.g. in seed production) must be assessed for each system and could be a criterion to decide on the system used.

Other research areas. These include heterosis recovery in F2, feasibility studies involving socioeconomic components on the use of hybrid technology by small farmers (subsistence).

Collaboration. It was recommended that CIMMYT establish active linkages with centers of excellence in the public and private sectors, and with NARSs in basic and applied research.
On March 26-28, 1996, the CIMMYT Wheat Program organized a consultation-type symposium in Cd. Obregón, Mexico, to address the issue of yield potential in wheat. The presentations and recommendations of the invited experts—breeders, physiologists, and biotechnologists—are reported in this publication. Their recommendations will hopefully help us devise a future strategy for breeding for yield potential in wheat.

There has been continuous active involvement of CIMMYT breeders in the evolution of plant types for different agroclimatic conditions. It is critical that we state here our perspectives on how wheat germplasm has been modified to obtain continuously higher yields over the past 42 years. Since the mid 1950s, there has been a continuous rise in wheat yields in Mexico, as presented in Table 1. The most modern cultivars of the 1990s yield 3,000 kg/ha more than the original dwarf wheats released in Mexico in the late 1950s.

While there is general agreement among wheat scientists worldwide that bread wheat germplasm originating from CIMMYT has continuously increased in yield potential, the debate continues as to its physiological basis. CIMMYT plant physiologists have identified a number of characteristics associated with higher yield potential (Rees et al. 1993; Reynolds et al. 1994; Sayre et al. 1995; Waddington et al. 1986).

Table 1. Absolute yields of historical cultivars bred by CIMMYT over a 50-year period, as measured in Cd. Obregón, Mexico, and the Rht gene and Vrn gene status. Yield gain: 95 kg/year.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Yields (kg/ha)</th>
<th>Rht gene(^1)</th>
<th>Vrn gene(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yaqui 50</td>
<td>6000</td>
<td>None</td>
<td>n.a.</td>
</tr>
<tr>
<td>Pitic 62</td>
<td>6500</td>
<td>Rht, or Rht(_2)</td>
<td>Vrn(_1) + Vrn(_2)</td>
</tr>
<tr>
<td>Siete Cerros</td>
<td>6500</td>
<td>Rht, or Rht(_2)</td>
<td>Vrn(_1) + Vrn(_2)</td>
</tr>
<tr>
<td>Yecora 70</td>
<td>7000</td>
<td>Rht, or Rht(_2)</td>
<td>Vrn(_1) + Vrn(_3)</td>
</tr>
<tr>
<td>Nacozeri 76</td>
<td>7500</td>
<td>Rht, or Rht(_2)</td>
<td>Vrn(_2) + Vrn(_3)</td>
</tr>
<tr>
<td>Ciano 79</td>
<td>7500</td>
<td>Rht(_2)</td>
<td>Vrn(_1)</td>
</tr>
<tr>
<td>Seri 82</td>
<td>8000</td>
<td>Rht(_1)</td>
<td>Vrn(_3) (?)</td>
</tr>
<tr>
<td>Opata 85</td>
<td>8000</td>
<td>Rht(_1)</td>
<td>n.a.</td>
</tr>
<tr>
<td>Oasi 88</td>
<td>8500</td>
<td>Rht(_1) + Rht(_2)</td>
<td>n.a.</td>
</tr>
<tr>
<td>Bacanora 88</td>
<td>8800</td>
<td>Rht(_1)</td>
<td>n.a.</td>
</tr>
<tr>
<td>Weaver</td>
<td>8800</td>
<td>Rht, or Rht(_2)</td>
<td>n.a.</td>
</tr>
<tr>
<td>Baviacora 92</td>
<td>9000</td>
<td>Rht(_1)</td>
<td>n.a.</td>
</tr>
</tbody>
</table>

\(^1\) Rht status according to Singh et al. (1989).  
\(^2\) Vrn status according to Stelmakh (1987).
We wish to establish here a philosophy that supports Rasmusson's view (see Rasmusson, these proceedings) that germplasm is paramount to increasing yield potential. However, our approach differs from his in the utilization of genetic variability. Circumstantial evidence gathered from practical breeding supports the idea that breakthroughs in yield potential have been largely due to wider genetic resource utilization, as emphasized by Kronstad (see Kronstad, these proceedings).

The question remains, what pivotal advice to give to plant breeders who must continue to make advances in improving yield. Based on experiments conducted at CIMMYT and the experience of its breeders, we will outline the genetic basis of improved yield in CIMMYT bread wheat germplasm and address a number of specific issues.

Dwarfing Genes ($Rht_1$, $Rht_2$), and Photoperiod Insensitivity Genes ($Ppd_1$, $Ppd_2$)

The genetic stock Norin10/Brevor, of Japanese/USA origin, first utilized by N.E. Borlaug in 1954, was primarily employed for correcting lodging sensitivity by genetically reducing plant height. The dwarfing genes not only provided lodging tolerance but perhaps also through pleiotropic effects contributed to high yield by allowing more tillers to survive, thus increasing biomass. Using isogenic lines based on the varieties Maringa and Nainari 60, Hoogendoorn et al. (1988) were able to show that yield had increased by at least 15% by comparing $Rht_1$, $Rht_2$ or $Rht_1 + Rht_2$ carrying lines to tall varieties (Table 2).

Table 2. Yield and yield components, days to anthesis and plant height of tall and dwarf near-isogenic lines, averaged over seven experiments in Mexico and Brazil.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Days to anthesis</th>
<th>Plant height (cm)</th>
<th>Heads/m²</th>
<th>No.grains/ head</th>
<th>Mean grain weight (mg)</th>
<th>Index (%)</th>
<th>Harvest grain yield (t/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maringa</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$Rht_1$</td>
<td>82</td>
<td>93</td>
<td>395</td>
<td>31</td>
<td>35.4</td>
<td>36</td>
<td>4.8</td>
</tr>
<tr>
<td>$Rht_2$</td>
<td>81</td>
<td>93</td>
<td>406</td>
<td>31</td>
<td>34.5</td>
<td>37</td>
<td>5.0</td>
</tr>
<tr>
<td>$Rht_1$ $Rht_2$</td>
<td>83</td>
<td>59</td>
<td>454</td>
<td>31</td>
<td>30.6</td>
<td>39</td>
<td>5.2</td>
</tr>
<tr>
<td>(Mar2)</td>
<td>82</td>
<td>111</td>
<td>356</td>
<td>32</td>
<td>33.9</td>
<td>30</td>
<td>4.1</td>
</tr>
<tr>
<td>rht</td>
<td>82</td>
<td>119</td>
<td>359</td>
<td>29</td>
<td>38.6</td>
<td>31</td>
<td>4.1</td>
</tr>
<tr>
<td>Nainari 60</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$Rht_2$</td>
<td>84</td>
<td>83</td>
<td>349</td>
<td>36</td>
<td>36.5</td>
<td>36</td>
<td>5.6</td>
</tr>
<tr>
<td>$Rht_3$</td>
<td>87</td>
<td>42</td>
<td>382</td>
<td>40</td>
<td>29.7</td>
<td>38</td>
<td>4.9</td>
</tr>
<tr>
<td>rht</td>
<td>84</td>
<td>104</td>
<td>332</td>
<td>34</td>
<td>38.1</td>
<td>32</td>
<td>5.0</td>
</tr>
<tr>
<td>Maringa</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$Rht_1$</td>
<td>82</td>
<td>119</td>
<td>342</td>
<td>28</td>
<td>39.0</td>
<td>31</td>
<td>3.9</td>
</tr>
<tr>
<td>Nainari 60</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Seri 82</td>
<td>83</td>
<td>79</td>
<td>320</td>
<td>45</td>
<td>36.6</td>
<td>43</td>
<td>6.2</td>
</tr>
<tr>
<td>Thornbird</td>
<td>89</td>
<td>112</td>
<td>426</td>
<td>31</td>
<td>30.4</td>
<td>28</td>
<td>3.9</td>
</tr>
<tr>
<td>sed</td>
<td>1.01</td>
<td>2.61</td>
<td>25.6</td>
<td>3.2</td>
<td>1.42</td>
<td>2.3</td>
<td>0.41</td>
</tr>
</tbody>
</table>

Data from Hoogendoorn et al. (1988).
A physiologically determinable effect of these genes is an increase in harvest index (HI) (Waddington et al. 1986). Nonetheless, we should consider increased HI as a side effect of the \( Rht \) genes rather than their main effect. Not all combinations of \( Rht \) genes will produce high yields and not all varieties with high HI are high yielding. This indicates that other factors are necessary to achieve high yield. The direct application of increased HI as a selection criteria has been recommended as the most appropriate way to select for high yield. It is, however, much easier to breed directly for \( Rht \)-carrying plant-types based on reduced height. A large number of \( Rht \) genes have been identified, genetically catalogued, and otherwise studied. Not all of them have effects on yield. Only \( Rht_1 \) and \( Rht_2 \) significantly raise yield (Hoogendoorn et al. 1988). \( Rht_3 \) does not have a positive effect on yield, nor does \( Rht_5 \). Nonetheless, both \( Rht_3 \) and \( Rht_8 \) may provide a reasonable degree of lodging tolerance.

Incidentally, photoperiod insensitivity genes (\( Ppd_1, Ppd_2 \)) were introgressed into the CIMMYT breeding program at the same time as the two dwarfing genes (\( Rht_1, Rht_2 \)) were first utilized. Currently no isogenic lines are available to study the interaction of these four genes. Nonetheless, circumstantial evidence indicates that the best combinations are either \( Rht_1 + Ppd_1, Rht_1 + Ppd_2, Rht_2 + Ppd_1, \) or \( Rht_2 + Ppd_2 \). When both dominant alleles of photoperiod insensitivity are combined, yields are generally low. Most current high yielding lines have only one \( Ppd \) gene and either \( Rht_1 \) or \( Rht_2 \).

The \( Ppd \) gene establishes a proper balance between the vegetative phase and the reproductive phase, including the grain filling period. Without this optimum balance, the source/sink relationship is somehow biased and the plant's resources are not apportioned in such a way as to increase yield.

**Spring x Winter Gene Pool Exploitation**

Following the introduction of dwarfing and photoperiod insensitivity genes, the next group of high yielding lines at CIMMYT were the product of large-scale spring x winter wheat crossing. The first set of semidwarf wheats were hybridized with winter wheats in the late 1960s. Many combinations were very successful, but one spring x winter wheat combination is particularly noteworthy: Veery and Veery progenies, as represented by Kauz, Attila, Pastor, Baviacora, etc. These lines all carry the \( 1B/1R \) translocated segment from rye, but otherwise differ markedly in plant height, leaf size, maturity, head size, grain size, grain color, etc. There are studies at CIMMYT and elsewhere that suggest that the \( 1B/1R \) translocation markedly increases yield (Villareal et al. 1991, 1994a, 1995). However, other CIMMYT studies indicate that background effects may also be large, and that isogenic lines carrying \( 1B/1R \) are not always higher yielding than their counterparts (Singh, pers. comm.; van Ginkel, unpublished).

Besides the \( 1B/1R \) translocation, other agronomic characters, such as many grains/m² and, in some cases, many heads/m², contribute to the high yielding lines derived from spring x winter crosses. The spring x winter gene pool recombination has transmitted a higher number of grains.
through either a higher number of heads/m² or through bigger heads (Table 3; Villareal 1991, 1994a, 1995; van Ginkel, unpublished; Singh, pers. comm.). Rees et al. (1993) found that the resulting lines keep their canopies cooler than the surrounding environment, show higher stomatal conductance, and are photosynthetically more efficient.

In our experience, spring x winter wheat populations produce vigorous progenies, tiller profusely, have more surviving spikes, are robust in appearance, and keep their leaves healthy for a longer period. This phenomenon is also very common in segregating populations emanating from crosses involving Veery. Thus one would recommend that breeders select for vigorous populations, robust plants, healthy leaves, many heads/m² and/or bigger heads, to produce a plant type that we could call the Veery ideotype.

### Additional Contributions by Veery and Its Derivatives?

The Veery varieties and their progenies (such as the Kauz, Attila, Pastor, and Baviacora groups of lines) have demonstrated a superior level of tolerance to a number of abiotic stresses (drought, heat, etc.) and improved nutrient efficiencies (N-efficiency, P-efficiency). These characters have not been traced to any major qualitative genes, but such an exercise could well provide further opportunities to increase yield. These wheats are not only responsive to good conditions, but invariably have demonstrated superior performance under low input conditions. Hence they are also input efficient (Figure 1).

### Table 3. Means for the 1B/ and 1BL/1RS F₂ derived F₆ lines from the cross ‘Nacozari’/‘Seri 82’, under two irrigation practices during the 1991-92 and 1992-93 crop cycles.

<table>
<thead>
<tr>
<th>Plant characteristic</th>
<th>1BL/1RS</th>
<th>1B</th>
<th>F-test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grain yield (kg/ha)</td>
<td>5605</td>
<td>54374</td>
<td>*</td>
</tr>
<tr>
<td>Above-ground biomass (t/ha)</td>
<td>13.9</td>
<td>13.4</td>
<td>*</td>
</tr>
<tr>
<td>Harvest index (%)</td>
<td>40.2</td>
<td>39.8</td>
<td>ns¹</td>
</tr>
<tr>
<td>Spikes/m²</td>
<td>351</td>
<td>354</td>
<td>ns</td>
</tr>
<tr>
<td>Grains/m²</td>
<td>14990</td>
<td>14778</td>
<td>ns</td>
</tr>
<tr>
<td>Grains/spike</td>
<td>43.9</td>
<td>41.6</td>
<td>**</td>
</tr>
<tr>
<td>1000-grain weight (g)</td>
<td>38.62</td>
<td>38.20</td>
<td>**</td>
</tr>
<tr>
<td>Test weight (kg/hi)</td>
<td>79.0</td>
<td>78.3</td>
<td>**</td>
</tr>
<tr>
<td>Plant height (cm)</td>
<td>90.2</td>
<td>93.2</td>
<td>**</td>
</tr>
<tr>
<td>Spike length (cm)</td>
<td>10.5</td>
<td>10.5</td>
<td>ns</td>
</tr>
<tr>
<td>Days to flowering</td>
<td>80.0</td>
<td>79.0</td>
<td>**</td>
</tr>
<tr>
<td>Physiological maturity (day)</td>
<td>121.8</td>
<td>120.6</td>
<td>**</td>
</tr>
<tr>
<td>Grain-fill period (day)</td>
<td>41.8</td>
<td>41.6</td>
<td>ns</td>
</tr>
</tbody>
</table>

¹ ns = not significant.

*, ** Significant at the 0.05 and 0.01 levels of probability, respectively.

![Figure 1. Response of 10 historical Mexican cultivars to 300 or 0 units of N fertilization over the past 40 years (I. Ortiz-Monasterio, pers. comm.).](image-url)
We need to determine what kind of genetic control is involved in this multiple stress tolerance. It is clear that yield potential per se does not completely explain performance under stressed conditions (He and Rajaram 1993; van Ginkel et al., in press) (Figure 2).

**Erect vs. Droopy Leaf and Closed vs. Open Canopy**

After the rice variety IR8 was created (Evans, 1993), physiologists working with a number of different crops have debated the role of erect vs. droopy leaves in yield potential. Our attempt to produce near isogenic lines for this trait with CIMMYT wheat germplasm has not been successful, but we did compare random populations with erect and droopy leaves at the F6 level (Apichard 1990). In general, the erect leaf types were slightly higher yielding than their droopy counterparts. In current bread wheat lines, there is a great deal of variability in leaf blade width, leaf area, and leaf angle.

It seems likely that the canopy type represented by the line Kauz would be advantageous for the overall efficiency of its canopy. Rather than completely droopy or completely erect leaves, Kauz has an intermediate and dynamic habit; most pre-flag leaves are erect, but the flag leaf is only erect initially and then becomes droopy. This situation provides better light penetration into the canopy early on, and hence higher tiller survival, resulting in a large number of heads/m², and consequently more grains/m². Later, as the lower leaves start to senesce, the flag leaf becomes droopy and intercepts most of the incoming light, so it is not lost on the dying lower leaves. Grains are then able to fill properly. The support of such a plant type is proposed elsewhere.

**Grain Size and Grain Yield**

After having achieved a large number of grains/m², the grain size in Veery automatically adjusted to a somewhat smaller size (38-40 g/1000 grains), compared to 45-50 g/1000 grains in such traditional varieties as Sonalika. This regulatory balance cannot be broken without the introduction of a simply inherited large grain size characteristic of extreme value (> 60 g/1000 grain). Perhaps a new balance could be achieved at 50 g/1000 while maintaining the desired number of grains/m² and, hence, higher yield. The recently produced synthetic wheats (Villereal 1994b) offer such a possibility.

Recently van Ginkel (unpublished) selected larger grained lines that maintain a large number of grains/m², from a Kauz (many grains/m²) x Star (large grain) cross that realized a 5% yield advantage over Kauz. In
the above examples, we introduced new, non-conventional genetic stocks to change the grain size while raising the yield component balance to a new level. Again, germplasm proved paramount.

**Ideotype Approach at CIMMYT**

Many have argued that an ideotype approach should be taken at CIMMYT. However, this has not been possible, perhaps due to our complex crossing program, plus the inherent fear of genetic uniformity/homogeneity and the associated phenotypic similarity. On the other hand, if one analyzes improved CIMMYT germplasm, there are so-called CIMMYT ideotypes. There is a certain consistency in characters across the spectrum (such as reduced height, photoperiod insensitivity, rust resistance and an acceptable level of industrial quality), which is superimposed on two classes of maturity, two gradations in the semidwarfing character, two grain colors and two canopy structures. If multiplied, these latter four characters in all permutations would yield 16 wheat ideotypes within the broad CIMMYT ideotype for irrigated spring wheat production areas, also called mega-environment 1 (ME1). The 16 ideotypes would be composed of the following phenotypic expressions:

- **Height variation due to Rht1 and Rht2 genes and their combination.** Rht1 and Rht2 alone give a 90-95 cm short semidwarf wheat. The combination of both dwarfing genes would give a 70-80 cm short double-dwarf wheat. There are many additional height differences due to other minor gene effects. However, for practicality’s sake, let us define two classes for height: 90-95 cm and 70-80 cm.

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

- **Grain color.** Both amber and red-grained varieties are needed for irrigated ME1. The genetics of grain color is largely qualitative, although some minor genes are also operating. We consider only amber-grained and red-grained types.

- **Closed vs. open canopy architecture.** There would be two canopy categories based on erect and droopy leaves. Kauz, however, does represent an intermediate, dynamic canopy type that may even be preferable.

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

**Exploitation of Buitre-Based Long Spike Morphology**

After 20 years of genetic manipulation and countless recombinations, Ricardo Rodríguez, working on enhancing wheat
germplasm, under the guidance of Borlaug and Rajaram, was successful in combining the various yield components together into one plant type. This unique ideotype has a robust stem, a long spike (>30 cm, derived from the cultivar Buitre), multiple spikelets and florets, large leaf area, and broad leaves. However, due to some unknown physiological imbalance or disorder, the spikes remain largely sterile and resulting grains are mostly shriveled. In addition, the plants are generally highly susceptible to rust, especially leaf rust and stripe rust.

In the future, there are plans to exploit this genetic resource through further hybridization with the most recent advanced lines from our normal breeding program. The aim is to achieve a balance by slightly reducing spike size and completely restoring spike fertility. Plans to exploit these ideotypes in a hybrid wheat program are also being considered. If successful, these genetic stocks offer a possibility of increasing yield 10-15% above that of Veery’s descendants.

**Efficient Methods**

In the last 20 years, mechanized planting and harvesting, computerized field books and data analyses, adopting less costly but still biologically effective methods of field plot technique, handling segregating populations using new modified bulk/pedigree methodologies, and applying advanced staff management techniques have permitted the successful exploitation of large numbers of crosses and a high number of derived populations per cross.

Very recently, we confirmed our conviction since the early 1980s that one backcross to the adapted parent produces superior segregating populations that are more manageable, but still introduces sufficient new variability for higher yielding lines to be isolated in adapted backgrounds.

CIMMYT’s modified bulk/pedigree methodology for handling segregating populations, most probably creates selection pressure in the F3-F6 generations for increased lodging tolerance, as well as for adaptation to growing in a community environment, because the seed rate is kept at a commercial level. The method also identifies lines that are robust, vigorous, with dense head types, closed canopy architecture, and consequently with higher biomass. These traits are correlated with high yield in many of our studies.

**Conclusions**

In summary, we recommend the well-considered use of genetic variability, with an enterprising attitude towards testing the utility of new, even alien, sources. The exploitation of winter wheat, Chinese germplasm, Buitre type heads, wild relatives of wheat, and related grasses will be expanded. At the same time, flexibility in the use of methodologies is crucial to increasing the effectiveness and efficiency of the breeding process without excessive demands on land, labor, time or funds. Breeding, genetics, plant pathology, industrial quality, physiology, biotechnology, crop modeling, advanced trial design, and other new sciences will need to be integrated at a much more
intimate level than in the past, if the potential of these disciplines is to contribute significantly to improving breeding efficiency. What is presently a multidisciplinary approach will need to be molded into a synergistic interdisciplinary undertaking.

References

Apichard, V. 1990. Canopy architecture and its association with yield in spring wheat (Triticum aestivum L. em. Thell), Oregon State University, Corvallis, OR.


Genetic Diversity and the Free Exchange of Germplasm in Breaking Yield Barriers

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Abstract
In order to enhance wheat production, it is important to identify realistic yield expectations and realistic yield barriers. It has been estimated that wheat yields of 21 t ha\(^{-1}\) are possible under optimum conditions. The record yield has been reported to be approximately 14 t ha\(^{-1}\); however, the world average is less than 2 t ha\(^{-1}\). This latter situation reflects the need for improved cultivars and management practices, as well as the realization that most cereals are grown in marginal environmental conditions and subjected to a wide array of biotic and abiotic stresses. In a recent CIMMYT Publication, a comparison was made for the periods 1951-92 and 1983-92 suggesting that in the latter period a decrease in the percentage change has occurred in the growth rate of the area devoted to wheat, and in yields and total production. The question is: have we exhausted the genetic diversity necessary for achieving further breakthroughs in yield? It is apparent that any constraints placed on collecting, preserving, evaluating, and freely sharing germplasm must be avoided. Political uncertainty and protectionism of genetic materials within and between countries, unrealistic quarantine laws, restrictive plant variety protection laws, and retention and stagnation of funds for agricultural research will have a serious negative impact on overcoming yield barriers. Programs such as the CIMMYT/ICARDA and Oregon State University/CIMMYT/USAID international winter x spring wheat germplasm enhancement activity, which involves public and private breeding programs in over 100 countries, help maintain the free exchange of improved genetic materials. The systematic hybridizing of winter and spring gene pools has also proven to be an effective strategy for creating additional genetic variability for many desired traits.

Introduction
To enhance wheat production it is important to identify realistic yield expectations and realistic yield barriers. Cook and Veseth (1991) in their publication Wheat Health Management describe yield in four ways. Absolute yield is where the only limiting factor is the genetic potential of the crop. Attainable yield is the possible yield for a given environment, location and year; it is limited by factors that cannot be controlled, i.e. climate, depth of soil, etc. Actual yield is the yield from any given field and is the product of a crop's response to various biotic and abiotic stresses. Affordable yield considers the economic costs of inputs in relation to the net income or return to the grower.

It has been suggested that under ideal growing conditions the absolute yield of a crop is 20 t ha\(^{-1}\) (Hanson et al. 1982). To date, the highest commercial attainable yields reported are close to 14 t ha\(^{-1}\) (Cook and Veseth 1991). Unfortunately, the world’s average yield is much less, approximately
2 t ha\(^{-1}\). In many countries, and especially those noted as developing, the discrepancy between actual yields achieved on experiment stations and by the best farmers and the average yields of the majority of farmers in the surrounding area is great. For the wheat breeder concerned with enhancing grain yields, the focus must be on actual and affordable yields and reducing the ratio between actual and attainable yield while maintaining profitability and environmental sustainability.

It must also be recognized that genetically superior cultivars will not reach their attainable yield levels without the appropriate management systems. The importance of the cultivar management interaction to enhance grain yield was clearly demonstrated by the Turkish wheat program in the 1970s. High yielding spring wheat cultivars developed in Mexico were introduced into the annual cropping areas found along the Mediterranean and Aegean coasts. These areas are characterized by high winter rainfall, mild winters and hot summer temperatures. Under these conditions, spring type wheat can be planted in the fall with the only major constraints being diseases. Subsequently, a program was developed for the Anatolian Plateau, where the majority of the wheat is grown in Turkey. Due to limited winter rainfall, a summer fallow management system is employed where the moisture collected over a two-year period is required to produce one crop of wheat. Since winter temperatures are low, winter type wheats are necessary. While cultivars were largely responsible for the yield increases in the coastal areas, timeliness of the tillage practices and weed control on the Anatolian Plateau, both of which conserve moisture, were the major factors in increasing Turkey’s national wheat production from 7 to 17 million tons per year.

**Yield Plateaus**

The question is frequently asked, "Have attainable yield levels been reached for wheat and other major food crops?" As noted by Evans (1986) in his paper ‘Opportunities for Increasing the Yield Potential of Wheat,’ people at various periods in history have raised the same question even though wheat yields have increased 136% over the past 50 years. However, in the 1992/93 CIMMYT publication *World Wheat Facts and Trends* (CIMMYT 1993), when the period 1983-92 was compared to the 1951-92 period, there was a decrease in the percentage change in the growth rate of the area devoted to wheat, wheat yields, and total wheat production. This trend was true for both developing and developed countries with only a few exceptions being noted. The difference in the percentage growth rate between these periods may reflect the impact the Green Revolution had in the mid 1960s and 1970s. It might also suggest that wheat breeders are spending more of the limited resources on breeding for resistance and tolerance to various biotic and abiotic stresses. There is also the possibility that the genetic diversity necessary for achieving major breakthroughs in yield may no longer exist, and only smaller increases in yield will be possible in the future. It must be remembered, however, that small increments in increased yield in extensive areas like the Anatolian Plateau of Turkey translates into large increases in production.
Constraints

The major steps in all plant breeding programs are 1) identifying the limiting factors, 2) determining whether genetic variability exists, 3) selecting the most promising parents and subsequent progeny, 4) applying appropriate selection pressures, and 5) evaluating, multiplying, and disseminating germplasm and cultivars. Potentially, of the steps noted, the greatest barrier to enhancing all desired traits, including yield, is the availability of usable genetic diversity. This paper will focus on concerns regarding genetic variability and the free exchange of genetic materials and on describing one program that addresses some of the issues.

Genetic variability is the foundation of all plant improvement programs; thus concerns expressed as to the fate of such biodiversity must be taken seriously. The problem of genetic erosion is the result of: 1) old heterogeneous landrace varieties being replaced by higher yielding cultivars, 2) breeders’ reluctance to use older varieties in their crossing strategies, 3) more exacting management practices dictating more genetically uniform crops, and 4) valuable genetic stocks being discarded due to changes in the leadership of the breeding programs. Thus, it is critical even with the newer approaches to enhancing genetic variability (i.e. interspecific hybridization, somaclonal variation, somatic hybridization, plant transformation, etc.) that progenitors that are close relatives of wheat, including landrace varieties, be collected, preserved, evaluated, and freely disseminated.

Currently there are 28 major wheat germplasm collection centers in the world. Concerns have been raised regarding the genetic integrity of these collections. Factors such as outcrossing, unsuitable growing conditions resulting in natural selection, human error, and inadequate facilities may all contribute to this potential problem. Perhaps one of the most outspoken critics of germplasm centers is Mr. Paul Raeburn, a scientific editor for Associated Press. In his recent book, The Last Harvest, he notes that while there have been extensive arguments over spotted owls and property rights, the importance of conservation to agriculture is never mentioned. He takes special issue with the lack of support for the National Seed Laboratory located at Fort Collins, Colorado, pointing out that the variability of many accessions has been lost and that the present staff cannot keep up with the growing number of new accessions. The subtitle of the book is The Genetic Gamble that Threatens to Destroy American Agriculture. He refers to seedbanks as seed morgues and points out the consequences of the loss in biological diversity for future plant breeders. As evidence for his concern, he blames the most recent epidemic of gray leaf spot, a disease that reduced the U.S. corn crop by an estimated 27% this past year, on the genetic uniformity of crop species. Since he is a science editor for Associated Press, perhaps Mr. Raeburn’s comment will help raise the public awareness of this issue.

On a more positive note, there is a relatively new approach for managing biodiversity; an in situ area for germplasm conservation has been established in Turkey (Diversity 1995). The project emphasizes non-woody species
(wheat, chickpeas, lentils, and barley) and fruit and nut species (pear, apple, walnut, chestnut, and pistachio). In contrast to *ex-situ* collections held in genebanks, the approach avoids the loss of vital evolutionary processes by maintaining the desired biodiversity in its natural state, rather than maintaining genes and genotypes in the present state of evolution.

**The Free Exchange of Germplasm**

Along with concerns regarding the status of biodiversity, the question arises, "Will such genetic variability be freely available or are there situations that will prevent such exchanges?" These are factors that impact the free exchange of germplasm: 1) political uncertainties and protectionism within and between countries, 2) unrealistic plant quarantine laws, 3) Plant Variety Protection Laws which reduce the exchange of germplasm and new protocols or make them too expensive for most programs to obtain, and 4) reduction or stagnation of funds for agricultural research for national programs and international research centers. In 1986 Oregon State University conducted a survey of cooperators involved in the international winter x spring wheat germplasm program, and the most important constraint mentioned was the lack of funds.

The need to evaluate and freely distribute wheat germplasm has long been recognized as a critical activity for all breeding programs. Historically, several international nurseries have been developed, most often for the identification of new sources of disease resistance. Budget reductions and changes in priorities, however, have canceled many, including: 1) the International Winter Wheat Performance Nursery coordinated by the University of Nebraska (1969 to 1991), 2) the International Septoria Nursery (1971 to 1992), 3) the International Powdery Mildew Nursery (1960 to 1984), and the oldest, 4) the International Winter Wheat Rust Nursery (1932 to 1996). Currently active international wheat nurseries are provided by CIMMYT's spring wheat program headquartered in Mexico, the CIMMYT-ICARDA facultative and winter wheat program based in Turkey and the international spring x winter program conducted by Oregon State University. The latter program is funded by the U.S. Agency for International Development.

Concern over seed health issues has caused modifications in how seed is distributed in such nurseries. Because of Karnal bunt, some countries have placed restrictions on seed received from México. With Turkey identified as a flag smut country by U.S. quarantine officials, it is necessary to grow the candidates for the CIMMYT-ICARDA screening nursery under isolation in Oregon prior to distributing the material to cooperators in the U.S., Canada, and some South American countries.

**The International Winter x Spring Program**

This collaborative wheat germplasm enhancement program has evolved as the result of the complementary activities and expertise of a U.S. university (Oregon State), two international centers (CIMMYT and
ICARDA), and 200 national programs in the public and private sectors. The underlying approach is the systematic hybridization of winter and spring genepools. These genepools have tended to become somewhat isolated due to different ecological requirements and the reluctance of breeders to make such crosses. In the past, breeders have only turned to such crosses out of necessity to seek specific genes for resistance to diseases and other desired traits. Such famous cultivars as Ridit, Reliance, Thatcher and Federation 41 resulted from this type of cross. Even the wheats of the Green Revolution trace their short stature to the Rht1 and Rht2 genes obtained from the winter source Norin 10-Brevor 14 and the photoperiod insensitivity to spring germplasm from Australia and India.

It was the late Dr. Joseph Rupert, a Rockefeller Foundation scientist working with CIMMYT, who saw the potential for systematically probing these gene pools to enhance genetic variability for the improvement of both winter and spring wheat. Initiated in Chile, the program was first moved to the University of California at Davis in the late 1960s and then transferred to Oregon State in 1970. Unfortunately, Dr. Rupert died before he could see the full impact this approach had in enhancing genetic diversity in wheat.

The winter x spring single crosses are made at Toluca, Mexico, where because of the high elevation, it is possible to satisfy the vernalization requirement of the winter parents. The resulting F₁ populations are divided with a portion staying in Mexico for top and backcrossing to spring material. Other F₁s are distributed to Oregon State and the CIMMYT-ICARDA program in Turkey, where a similar crossing strategy is followed, except the material is crossed to winter germplasm. Following selection, the superior lines are sent to cooperators throughout the world with CIMMYT Mexico focusing on the spring wheat growing areas, CIMMYT-ICARDA on regions requiring short cycle facultative and winter wheat and Oregon emphasizing long cycle winter and facultative wheat germplasm.

A unique feature of the programs has been the development of an international shuttle breeding approach. Promising F₁ populations selected at the Pendleton, Oregon, site are sent to both the CIMMYT program in Mexico and the CIMMYT-ICARDA sites in Turkey. In Mexico, in addition to the disease complexes, it is possible to identify populations with different levels of photoperiod responses. In Turkey, different selection pressures can be employed, with a key factor being the selection of genotypes with a rapid grain filling period. Following two or three selection cycles, the material is returned to Oregon State, from where the most promising lines are sent to cooperators participating in the winter x spring screening nursery. Similarly, desired germplasm, meeting the objectives of the two CIMMYT-ICARDA programs, is also disseminated through their respective international nurseries.

In addition to being an effective vehicle for distributing enhanced germplasm, the international nurseries have provided an opportunity for national programs to share...
their genetic materials. Of particular interest are countries such as the People’s Republic of China and some Eastern block countries, which were previously reluctant to share their germplasm, but now have become very much a part of the international wheat network. A further role these nurseries have filled is the monitoring of new diseases and insect problems or detecting changes in biotypes of existing pests. As cooperators return their local observations on the performance of lines within the nurseries, the data are summarized and a complete set of information is sent to all participants.

Probing the winter and spring genepools has provided enhanced genetic variability for nearly all the desired agronomic traits. Such abiotic factors as aluminum tolerance, winter hardiness, frost and sprouting tolerance, etc., have been achieved. Also, more durable and multisource resistance to diseases and to insects has been realized. It has also been possible to change the architecture of winter and especially spring wheats. For spring wheats, the winter germplasm has contributed to larger and more fertile spikes, stiffer straw, shorter plant stature, etc.

The most significant feature has been the opportunity to adjust the life cycle of the wheat plant by modifying the vernalization and photoperiod responses. It has been possible to select genotypes that fit desired windows for planting, flowering, and harvesting for different environments and crop management systems. The current work of Dr. Edgar Haro at CIMMYT in Mexico, where he has developed near isogenic lines for different vernalization and photoperiod responses will be particularly interesting in this regard.

The winter x spring crossing approach may prove interesting for breeders developing hybrid wheat. In limited studies where comparisons were made with winter x spring F1s and those resulting from winter x winter or spring x spring crosses, the former gave a greater expression of hybrid vigor, perhaps reflecting a greater degree of diversity between these two genepools.

In terms of improving spring wheats through the winter x spring crossing approach, one of the best known examples are the Veery lines. This material resulted from the cross (Kawkaz/Buho’s' / Kalyansona/Blue Bird, with Kawkaz contributing among other factors the 1B/IR translocation. Despite some concerns regarding their milling and baking properties, the Veery lines are being grown on an estimated five million hectares under a number of different cultivar names. Currently, it has been estimated that 80% of the advanced spring wheat lines at CIMMYT carry some degree of winter parentage.

Based on the pattern of expansion and an increase of 8% yield attributed to the use of winter wheat from winter x spring crosses, a return in excess of 10 million U.S. dollars each year in the 1980s has been realized (Mitchell et al. 1988). Other evaluations of such an impact have reported similar monetary returns. Methods of estimating impacts are crude and subject to extreme caution, but the weight of evidence is that both winter wheats and spring wheats have
substantially benefited from the additional genetic diversity that results from systematically crossing winter and spring genepools. It should be emphasized, however, that the intent of these international screening nurseries is to provide enhanced germplasm for specific traits for the cooperators' crossing programs, and not necessarily as new cultivars per se.

A complementary aspect of the CIMMYT-ICARDA/Oregon State international germplasm enhancement program has been the opportunity to train young scientists. A large number of breeders, pathologists, agronomists, extension specialists, etc. have received research experience as part of the CIMMYT applied training program, and Oregon State has provided the opportunity for graduate education in similar disciplines.

**A Holistic Approach to Wheat Improvement**

Wheat breeders today and in the future will benefit from the technologies emerging from other disciplines. These tools will: 1) enhance genetic diversity, 2) provide for more effective selection of parents and progeny for both qualitatively and quantitatively inherited traits, 3) provide a better understanding of factors responsible for plant growth and development, 4) and give considerable insight on the nature of plants response to stress. Also, it will be possible to gain a better understanding of cultivar x environment x management system interactions. As noted by the late Dr. Orville Vogel, "Future levels of economic production of wheat will continue to depend on how successfully the various private and public interests and involvements function in the development and production of new varieties and systems of management to meet the changing natural, economic, and political constraints on production." Much is said today regarding low input agriculture that relies on minimum or no tillage management systems, and reduced use of pesticide and fertilizer. Thus, wheat breeders can anticipate that the requirements of a successful wheat cultivar in the future will be far greater than they are today.

Following a more holistic approach, it will be more important to develop economically sustainable systems that optimize production while taking advantage of nature's own contribution to plant health and protect soil and water resources. This requires the integration of pest and crop management. However, the overriding factor remains that population growth must be brought under control. Relying on AIDS and other diseases, or other inhumane methods to control population is unacceptable.

It took 10,000 years until 1975 to produce 3.27 million metric tons of food a year, and even considering a conservative rate of population growth, in the next 60 years, 6.60 million metric tons of food will be required just to maintain the current per capita food levels. It is apparent that breeders and all scientists working toward increasing food production have a major challenge and responsibility. It is equally true that all segments of society share in the responsibility of ensuring that everyone has an acceptable standard of living. As Nobel Laureate Lord John Boyd Orr noted, "you can't build peace on empty stomachs."
References


Questions and answers

J. Dubin:
You spoke about the quarantine situation today. How do you think quarantine regulations can be rationalized to facilitate germplasm movement?

W.E. Kronstad:
Many plant quarantine laws, like human health regulations in years past that required many inoculations, have become outdated. Bureaucracy, rather than a realistic understanding of the pathogen and the necessary environment for disease expression, appears to have become the major activity of many quarantine agencies. More appropriate research needs to be carried out by such agencies in order to make sound judgments as to the real or imaginary threat a particular pathogen may present.

G. Ortiz-Ferrara:
I share your concern regarding the lack of sustainable research in most NARS in the developing world. Although CIMMYT and other IARCs in the CGIAR have been training young scientists for the last 30 years, the constant emigration of those trained scientists to administrative jobs or to private companies forces IARCs to continue this activity. The well documented decline in the budget for research in those NARS is an additional factor affecting the IARCs effort to make NARSs in developing countries sustainable in research. This issue needs to be addressed and further emphasized in this meeting since I believe it would play an important role in breaking wheat yield barriers in the future.

W.E. Kronstad:
It does not bother me that many former trainees are now administrators or in the private sector. I strongly believe that training should receive the highest priority at CIMMYT and other international centers. It is important that a critical mass of
knowledgeable people representing different segments of agriculture be established if an impact is to be made in developing countries.

M. Reynolds:
The idea of using novel sources of germplasm to improve yield potential is of great interest to physiologists and breeders. However, there is an overwhelming volume of potential material from which to choose, such as spring and winter wheats in other breeding programs, landraces, wild progenitors, and alien species. Could you make some suggestions on how we at CIMMYT might systematically exploit other sources of germplasm to improve yield potential?

W.E. Kronstad:
CIMMYT is exploiting new sources of germplasm, as evidenced by programs such as Dr. Kazi’s. However, until we have a better understanding of wheat physiology, such factors as dry matter partitioning and a way of measuring various functions associated with grain yield, I believe wide crosses and other sources of such germplasm will only provide valuable genes for resistance to biotic and perhaps abiotic stresses.
Germplasm Is Paramount

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Abstract
Relying on experience from my barley breeding program, my goal is to make suggestions to stimulate thinking about ways to strengthen the CIMMYT wheat program. The central theme of the presentation is that germplasm is paramount and that management of germplasm exceeds all other facets of breeding in affording opportunity for genetic gain. Three factors which influence gain in a breeding program are so fundamental that they are deserving of the title cornerstones of progress. Each of them can determine success or failure. They are goal setting, sharing germplasm and continuity in breeding. Goal setting deserves higher priority than it commonly receives and goals should be continually revised. Germplasm going out from CIMMYT has had an immense impact and germplasm from other programs has benefitted the CIMMYT wheat program. This sharing and building on genetic gains made worldwide should continue. Reflecting on the value of continuity in breeding programs serves to call attention to the CIMMYT gene pool and the favorable gene combinations that have been accumulated for a host of traits. These traits can serve to enhance breeding gains everywhere, especially in developing countries. Improved germplasm or core germplasm can be thought of as germplasm with a favorable combination of five trait groups: adaptation to soil and climate, resistance or tolerance to pests, favorable yield response, positive harvestability traits and market acceptability. Recognizing the five trait groups helps a breeder better visualize the worth of a core gene pool and the opportunities for improvement. The CIMMYT wheat team should nurture and build its superior core germplasm by pursuing even more vigorously than in the past its parent building effort, which encompasses traits such as pest resistance, drought tolerance, and grain quality.

Introduction
The goal of this paper is to offer ideas pertaining to the main-line breeding effort and the germplasm strategy of the wheat program. To set the stage for offering a range of things to ponder, I will review experiences I have had as a malting barley breeder concerned with developing varieties for the upper midwestern six-row malting barley market. While not large in wheat terms, it is the principal malting barley growing area in the United States. My philosophy of breeding has been shaped by my barley breeding experience and understanding a bit about that program should be helpful in setting the stage for the discussion that follows.

Barley Improvement in Minnesota

Six-row barley breeding in the midwestern U.S. began early in the twentieth century and was characterized by introduction and evaluation of Manchuria-type barley
Early cultivars commonly grown for malting and brewing and used as parents in breeding programs for malting quality were: Manchuria (CI 2947) introduced from Manchuria; Odessa, O.A.C. 21 and Lion from Russia; Oderbrucker from Germany; Trebi from Turkey; and Peatland from Switzerland. This diversity in geographic origin implies that early germplasm was genetically diverse; however, coefficients of parentage showed that five ancestors contributed 52% and 44% of the germplasm pool in six-rowed cultivars in North America for two respective time periods (Martin et al. 1991).

In recent decades, cultivars have been developed to match malting and brewing industry specifications (Peterson and Foster 1973). According to Martin et al. (1991), 'industry quality guidelines' encourage development of cultivars that closely match a quality profile consisting of as many as 22 quality traits. These guidelines, the strong preference for a consistent barley product, and the premium paid to growers for preferred malting cultivars dictate that new cultivars be like older ones.

Two premier programs of the 1960s and 1970s in barley improvement in North America were located in North Dakota and Brandon, Manitoba. In the 1960s, North Dakota barley breeders utilized Traill and improved germplasm from Canada in developing 'Larker', which dominated malting barley acreage in the Upper Midwest from 1964 to 1979. The two programs, which emphasized six-row malting barley and utilized Manchuria-type germplasm, can be viewed as sharing a common gene pool. In the tri-state area of Minnesota and North and South Dakota, the major production area for malting barley in the U.S., closely related cultivars have dominated the acreage over the last 50 years (Horsley et al. 1995; Martin et al. 1991; Wych and Rasmusson 1983).

While the University of Minnesota barley breeding effort dates back to the early years of this century, germplasm contributing to recent cultivars traces almost exclusively to post-1960 introductions from North Dakota and Brandon, Manitoba. As indicated above, these two centers, which emphasized six-row malting barley breeding, shared a common gene pool. The germplasm that was introduced to Minnesota shortly after 1960 ultimately led to the development and release of Manker in 1974 and Morex in 1978 (Figure 1).

The closely related cultivars, Manker and Morex, and a full sister of Morex (M28) provided the germplasm leading to Robust, Excel, and a large share of the germplasm leading to Stander (Figure 1). Two cycles of breeding initiated by crossing Robust with M72-146, which has the same pedigree as

![Figure 1. Pedigree of Minnesota malting barley cultivars (1972-1993).](image-url)
Robust, led to Excel. One quarter of Stander germplasm came from Bumper which is a North Dakota germplasm and outside the Morex x Manker lineage.

**Variety performance and evidence of genetic gain**

Multi-location data are presented to show improvement of four cultivars—Morex, Robust, Excel and Stander. Larker, a North Dakota cultivar which serves as a check against which to measure gain in extract, was the dominant cultivar in the tri-state area (MN, ND, SD) from 1964 through 1979. The four Minnesota cultivars were released in 1978, 1983, 1990 and 1993.

While Morex, Robust, Excel and Stander provided significant gains for several traits, three are of special note—malt extract, lodging resistance and grain yield. In 1978 Morex represented an industry-wide breakthrough in malt extract of 2.3% compared to Larker, the cultivar replaced by Morex (Figure 2). The gain in extract was unexpected since breeding experience had shown that gains of one-half percent were difficult to achieve. Another unexpected gain was in lodging reaction, a trait in need of significant improvement. Stander, the newest cultivar, surpassed Robust and Excel in resistance to lodging (Figure 3). Its lodging resistance is a significant step forward compared to all midwestern U.S. malting barley cultivars. Impressive gains were made in grain yield where the cultivars in turn represented a sizeable yield improvement. In trials conducted over several years, Robust, Excel, and Stander yielded 9.3%, 21.0%, and 21.0%, respectively, more than Morex (Figure 4).

The most recent release, Stander, provided an impressive gain compared to Robust in a trial designed to measure yield potential. Stander

![Figure 2. Malt extract of five cultivars.](image)

![Figure 3. Lodging reaction of three cultivars.](image)

![Figure 4. Yield comparison of four cultivars (1988-1995).](image)
produced 6.3 Mg/ha\(^1\) compared to 5.5 for Robust, a 14% gain (Table 1). This is significant since Robust has been popular with growers and has dominated the midwestern barley acreage for 11 years (1985 to 1995). Additional yield gains are likely to come from within the narrow pedigree tree since advanced experimental lines from the Morex x Manker lineage have ranked at the top of the cooperative regional nursery in recent years.

In reviewing the genetic gains for the three traits and the degree of genetic diversity in the parents, we conclude that modest levels of genetic diversity based on pedigree information can permit sizeable genetic gains. Excel is essentially a 'Robust progeny' based on the pedigree relationships (Figure 1) but, even so, sizeable gains were made for several traits (some not reported here). Making a number of assumptions, the coefficient of parentage between Robust and MN77-825 (the parents of Excel) was 0.87. Stander also is of special interest because its resistance to lodging is markedly superior to any of its parents.

**Enhancing Gains in the Wheat Program**

Relying on my experience in barley breeding, I would like to present ideas and suggestions that are intended to stimulate thinking about ways to strengthen the highly regarded CIMMYT wheat program. The themes that I will address are: cornerstones of progress, germplasm is paramount and germplasm strategy.

**Cornerstones of progress**

Many factors influence gains achieved in a breeding program. Three of these are so fundamental that they are deserving of the title cornerstones of progress. Each of them can determine the success or failure in a breeding program. They are goal setting, germplasm sharing and continuity in breeding.

**Goal setting**—It can be confidently stated that the degree of success or failure in a breeding program depends on goal setting. Traits differ greatly in their potential to enhance the value of a cultivar and in the ease with which they can be manipulated in a breeding program, but the challenge is even greater because pests are dynamic and grower and market preferences change. Thus it is necessary to project goals into the future for traits that are not wholly predictable. In the CIMMYT wheat program the magnitude of the challenge of goal setting can be seen by reflecting on the relative priority that should be given to yield potential, disease resistance, and quality breeding for the different mega-environments around the world.

It is likely that goal setting deserves higher priority than it receives in nearly all breeding programs. Final decisions should be made by teams of researchers and continually reviewed.
Germplasm sharing—Of all the things to applaud about plant breeding, the most noteworthy is the practice of sharing germplasm. Nearly everyone has benefited from shared germplasm and, for many, a gift of germplasm has led to significant progress. Germplasm from North Dakota and Brandon, Canada, contributed greatly to the Minnesota barley program. North Dakota shared germplasm having disease resistance, lodging resistance, and grain yield, while the Brandon Station in Canada contributed desirable agronomic traits and malting and brewing quality.

Perhaps it is appropriate to speculate that one-half of all breeding progress in a target area has come from sharing improved germplasm. Germplasm from other programs has benefited the CIMMYT wheat program and germplasm going out from CIMMYT has had immense impact. This sharing and building on the genetic gains made world-wide must continue. In this context CIMMYT researchers might make a commitment to introduce into the CIMMYT program the best germplasm from around the world.

Continuity in breeding—Though difficult to document, it appears that relatively few breeders achieve improved varieties with only a few breeding cycles, while the converse seems true, improved varieties can be commonplace in long-term breeding programs. From the theoretical standpoint, it follows that several cycles of stepwise breeding are essential to accumulate the complex polygenic systems that govern adaptation, quality, pest resistance, and agronomic traits (Lundin et al. 1970; Mac Key 1986). Reflection on this theme serves to emphasize the value of gene pools like that developed by the CIMMYT wheat breeding program over several decades. The repeated rounds of crossing and selection have made it possible to accumulate favorable gene combinations for a whole host of traits. Like classical recurrent selection programs in maize (Hallauer 1981), recurrent-like programs in wheat require continuity extending for several years and even decades to attain maximum benefits.

Germplasm is paramount

Over decades, breeders have learned that breeding methods and plot techniques contribute to breeding progress, but are not powerful enough to overcome inferior germplasm. What matters most in plant breeding is germplasm. Fortunately, elite gene pools appear to have the characteristic of being ‘eternally’ productive. Breeding experience, long-term selection experiments, and population improvement programs are consistent in demonstrating that genetic variability is rarely exhausted. Hallauer (1981), commenting on long-term selection experiments, said he knew of no evidence on any crop with materially reduced additive genetic variance after four or five cycles of recurrent selection. Mac Key (1986) indicated that with polygenic systems and recurring mutation, genetic variation is very complex and unlikely to be exhausted or fully utilized in short-term breeding efforts.

Especially interesting in relation to genetic variation is the University of Illinois long-term selection studies for modified oil and protein in maize (Dudley and Lambert 1992). Lines have been selected for over 90
generations with abundant variability still present—enough to achieve progress from selection. Reverse selection from high lines and from low lines resulted in progress, again indicating the absence of gene fixation.

The barley program in Minnesota serves to focus attention on the amount of genetic diversity within elite gene pools, i.e., there appears to be significant diversity even though phenotypic uniformity is approaching and pedigrees are narrow. One explanation for the continued gain in breeding populations can be found in classical theory, i.e., improved performance depends on accumulation of favorable genes acting in an additive or epistatic manner. Gradual breaking of close linkages and forming of new epistatic gene combinations presumably ensures gains over many breeding cycles. Another hypothesis concerning genetic gain is that the genome is dynamic and that variation arises more frequently than previously thought via mutation and mutation-like events.

**Hallmark germplasm**—In seeking larger gains and especially in choosing parental varieties, it is advantageous to be informed about genetic progress that is being made in plant breeding programs worldwide. Utilizing elite germplasm from compatible programs is a good idea, especially when information indicates that superior or hallmark germplasm has been found. As a beginning breeder, I didn’t recognize the degree of difference that exists among barley cultivars for traits of interest nor did I look for hallmark germplasm. The malting barley cultivars Triumph in Europe, Clipper in Australia, Bonanza in Canada, and Morex in the U.S. have made major contributions as parents and serve as examples of hallmark germplasm in barley. CIMMYT wheat should take advantage of hallmark germplasm wherever it occurs, whether for individual traits or outstanding cultivars.

**Germplasm strategy**

It is good to reflect on the decades of crossing, selection and genetic recombination that has culminated in an extremely valuable resource, i.e., the elite gene pool. The value of an elite gene pool where many traits are at an acceptable level and some at a superior level is hard to overestimate.

Two aspects of the elite gene pool seem to warrant attention. One is the elite gene pool itself, which might be called core germplasm. Of interest is how to build and strengthen core germplasm. This calls for a thorough understanding of the core germplasm as well as strategizing about ways to incorporate new traits into the core gene pool.

**Core germplasm**—Core germplasm can be concept germplasm as well as real germplasm. In a new breeding program, it is a concept to strive to achieve; in a mature program it is elite germplasm that deserves recognition and identification as special germplasm. Mature core germplasm can be thought of as germplasm with a favorable combination of five groups of traits: adaptation to soil and climate, resistance or tolerance to pests, favorable yield response, positive harvestability traits and market acceptability.

Recognizing the five trait groups helps a breeder better visualize the worth of a core gene pool as well as the opportunities for
improvement. CIMMYT breeders might benefit from itemizing and analyzing the traits that fall within the five categories. In the first place, it will probably lead to crossing programs that give priority to core germplasm in the breeding effort; second, it might call attention to traits or categories of traits that represent breeding opportunities.

**Parent building**—Numerous cycles of crossing and selection in many crop species have in effect created a genetic gap between improved and unimproved gene pools, i.e., a difference in gene frequencies for desired traits that essentially precludes recovering improved cultivars from crosses between improved and unimproved germplasm. In these wide crosses, there are simply too many traits and corresponding segregating genes to effectively select in a typical breeding effort.

Consequently, I visualize that parent building programs will grow to the point where parent building crosses will far exceed the number of crosses directed to obtaining a new cultivar within that breeding cycle. In the case of CIMMYT, a large parent building effort is needed, for example, in the wide-cross program, with emphasis on genes for pest resistance, as well as the program to identify and incorporate potentially useful morphological-physiological traits to enhance yield. Fortunately, parent building efforts in all breeding programs stand to benefit from molecular marker and gene transformation technology. This new technology provides altogether new ways to manipulate germplasm.

**Concluding Remarks**

The purpose of this presentation, which included breeding philosophy and ideas on strategy, was to encourage continuing analysis and improvement of CIMMYT wheat germplasm and the overall program. The general theme was that germplasm is paramount and that wise management of germplasm is central to continuing improvement.

**References**


Questions and answers

G. Ortiz-Ferrara:
There is value in sending early segregating populations to NARS in developing countries. The obvious advantage is that it allows selection of material under the stresses of importance in that particular area. The experience of CIMMYT-Mexico and CIMMYT-ICARDA programs in Syria is that most varieties released in those developing countries have been released from direct introduction of advanced material. In my opinion, this is due to the lack of trained scientists in those NARS to handle segregating populations and also due to the reduced budget for research in those NARS. Would you like to comment on what should be the future approach by CIMMYT in the distribution of advanced versus segregating generations?

D.C. Rasmusson:
As you suggest, there are advantages associated with providing early generation as well as advanced generation germplasm. The answer as to which type of germplasm is most valuable is not straightforward and depends on the individual situation. However, in general, I favor sending advanced material that can be used directly as new varieties or as parents by the local research team.

M. Kohli:
I agree with your analysis regarding building on selected elite germplasm to make progress rapidly. However, do you know of any limitation to such an approach after which introduction of diversity will become necessary?

D.C. Rasmusson:
The issue of the desirable amount of genetic diversity is a challenging one and it is appropriate to voice concern about too little diversity in narrow gene pools. Undoubtedly, there are circumstances that justify high priority for introgressing of genetic diversity. Even so, it is my belief that much more progress will be made in breeding by emphasizing elite germplasm in crossing than by emphasizing genetic diversity.

M. Reynolds:
Using the best germplasm in a breeding program implies knowing what traits in that germplasm will realize the breeding objectives. This is very difficult to be sure of when our objective is raising yield potential since we have to extrapolate from our current understanding. Nonetheless, can you make some suggestions on which traits we should consider in a new parent or how we might go about deciding?

D.C. Rasmusson:
I favor trying to match traits to specific target environments. In irrigated or high rainfall areas, for example, I suggest breeding to enhance the three grain components of yield as well as leaf area, i.e., expanding both sink and source. On the other hand, in dry growing areas, matching heading date and maturity to the seasonal moisture supply and breeding to enhance harvest index via modifying sink size and vegetative biomass may be advantageous.
Breaking the Yield Frontier of Rice

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Abstract
Over the next 30 years, Asia must increase its rice production by at least 70% to meet the needs of population growth. Yield potential of irrigated rice in the tropics has stagnated at 10 t ha⁻¹ since 1966 when the first semidwarf indica variety, IR8, was released. During the past 30 years, rice improvement efforts have been directed towards incorporation of disease and insect resistance, shortening of growth duration and improving grain quality. Since 75% of total rice production is from irrigated land, breaking the yield ceiling of irrigated rice becomes the top priority in rice research. For another quantum jump in rice yield potential, we must explore the possibility of further modifying the present high yielding plant type and the physiological processes governing yield potential. Another approach for increasing the yield potential of rice in the tropics is the exploitation of hybrid vigor or heterosis through hybrid rice breeding. Breeding for new plant type using tropical japonica germplasm has resulted in a phytotype with increased sink size due to large panicles, less unproductive tillers, sturdy stems, and erect leaves. The yield potential of this new plant type, however, is limited by poor grain filling, low biomass production, and susceptibility to pests and diseases. New crosses are being made and selection criteria have been modified to overcome these problems. Intervarietal hybrids between indica rices have demonstrated a yield potential of 10.8 t ha⁻¹ under tropical conditions. Intersubspecific hybrid between indica and japonica showed higher heterosis for yield than indica/indica hybrids. Hybrids between elite tropical indica varieties and the new plant type tropical japonicas are being developed to further increase rice yield potential.

Introduction
Major increases in rice production have occurred during the last 25 years due to large scale planting of high-yielding semidwarf rice varieties and improved production technology. World rice production doubled from 257 million tons in 1965 to 520 million tons in 1990. During this period, rice production increased at a slightly higher rate than the human population. However, the rate of increase in rice production has slowed down and is now lower than the rate of increase in the number of rice consumers. Severe food shortages will occur in 20-30 years if this trend is not reversed. To keep up with population growth, an additional 380 million tons of rice will have to be produced by 2020.

Major increases in the area planted to rice worldwide, which has remained stable since 1980, are unlikely. In fact the rice area is likely to decrease because of urbanization and industrialization pressures. The increased demand for rice will have to be met from less land, with less water, less labor and less pesticides. Therefore, we need rice varieties with higher yield potential and better management practices that will allow
them to express that potential. In its strategy for 2000 and beyond (IRRI 1989a), IRRI accorded the highest priority to increasing the yield potential of rice.

The ‘green revolution’ in Asia started in 1966 when IRRI released the first semidwarf indica inbred, IR8. Compared with traditional cultivars, the semidwarf was characterized by high tillering, stiff culms, erect leaves, photoperiod insensitivity, N responsiveness, and high harvest index (Chandler 1969). The yield potential of IR8 is about 10 t/ha during the dry season in the tropics. Today, more than 60% of the world’s rice area is planted to semidwarf plant types similar to IR8, and they account for more than 80% of total rice production (Khush 1990). During the 30 years after the development of the semidwarf plant type, however, only marginal improvements have occurred in the yield potential of rice. Rice improvement efforts have been directed towards incorporation of disease and insect resistance, shortening of growth duration and improving grain quality. For another quantum jump in rice yield potential, we must explore the possibility of further modifying the present high-yielding plant type and the physiological processes governing yield potential. Another approach for increasing the yield potential of rice in the tropics is the exploitation of hybrid vigor, or heterosis, through hybrid rice breeding.

**New Plant Type for Increasing Yield Potential**

Semidwarf rice produces large amounts of unproductive tillers and excessive leaf area; this causes mutual shading and reduces canopy photosynthesis and sink size, especially under direct-seeded conditions (Dingkuhn et al. 1991). To break through the yield potential barrier, IRRI scientists proposed further modifications of the present high-yielding plant type that would support a significant increase in rice yield potential, particularly for direct-seeded crop establishment. The emphasis on direct seeding was based on projections of increased labor costs and shortages as industrial development accelerates in the rice-growing countries of Asia. Although the proposed characteristics of the new ideotype came from several different perspectives (Vergara 1988; Janoria 1989; Dingkuhn et al. 1991), the major components were essentially the following:

- low tillering capacity (3-4 tillers when direct seeded)
- no unproductive tillers
- 200-250 grains per panicle
- 90-100 cm in height
- very sturdy stems
- dark green thick and erect leaves
- vigorous root system
- 100-130 days growth duration
- multiple disease and insect resistance
- increased harvest index
- acceptable grain quality

Simulation modeling indicated that a 25% increase in yield was possible if the following traits were modified in the present high-yielding plant type (Dingkuhn et al. 1991): 1) enhanced leaf growth in combination with reduced tillering during early vegetative growth, 2) reduced leaf growth along with sustained high foliar N concentration during late vegetative and reproductive growth, 3) a steeper slope of the vertical N concentration gradient in the leaf canopy, with more N
present in the top, 4) expanded storage capacity of stems, and (5) improved reproductive sink capacity along with an extended grain filling period.

This ideotype became the 'new plant type' (NPT), highlighted in IRRI's strategic plan (IRRI 1989a), and the breeding effort to develop this germplasm became a major core research project in the 1990-1994 work plan (IRRI 1989b) and the 1994-1998 medium-term plan (IRRI 1993). The goal was to develop within 8-10 years a new plant type with yield potential 20-25% higher than that of existing semidwarf varieties in tropical environments during the dry season.

**Germplasm for the new plant type**

When we started looking for donors for the various characteristics needed to breed the NPT, we first examined germ plasm classified as bulus or javanicas from Indonesia. Bulus are known for their low tillering, large panicles and sturdy stems. The javanica rices are genetically very close to the japonicas grown in temperate areas. On the basis of allelic constitution at 15 isozyme loci, Glaszmann (1987) showed that javanicas and japonicas belong to the same varietal group. We therefore now refer to the javanicas as tropical japonicas. Crosses between tropical and temperate japonicas are fully fertile and there are no barriers to recombination. On the other hand, crosses between indicas and japonicas have varying levels of sterility and give poor recombinant progenies as restrictions to recombination exist in such crosses.

We decided to limit the hybridization work for NPT to tropical japonica germplasm with selective introduction of genes from temperate japonicas and indicas. The reasons for this approach are threefold:

- Intercrosses within the japonica germplasm would not encounter problems of sterility and restriction to recombination.
- After the major breakthrough in raising the yield potential of indicas through the introduction of genes for short stature in the mid 1960s, significant increases in their yield potential have not occurred despite efforts by international and national rice improvement programs. We therefore decided to work with entirely different germplasm to explore the possibility of raising yield potential.
- F1 hybrids between indica and japonica rices are expected to have higher heterosis but the temperate japonicas are not adapted to tropical conditions and thus cannot be used for producing F1 hybrids. Improved tropical japonicas with genes for wide compatibility, short stature, disease and insect resistance, and long, slender grains would be most suitable for this purpose (Khush and Aquino 1994).

**Breeding for the new plant type**

Breeding work on the NPT was started in 1989, when about 2,000 entries from the IRRI germplasm bank were grown during the dry season (DS) and wet season (WS) to identify donors for various traits. Donors with low tillering, large panicles, thick stems, vigorous root systems and short stature were identified. Hybridization work was undertaken in 1990 DS and F1 progenies were grown for the first time in 1990 WS, F2 progenies in 1991 DS, and pedigree nursery in 1991 WS. Since then, over 1,800 crosses have been made, and 80,000 pedigree
nursery rows have been grown. Breeding lines with targeted traits of the proposed ideotype have been selected. They were grown in the observational trial for the first time in 1993 WS. Their morphophysiological traits and yield potential have been evaluated since 1994 DS in replicated field plots under various management practices.

**Field evaluation of NPT lines**

*Evaluation of NPT lines under different spacings—* Eleven NPT lines and IR72 were grown in 1994 DS at IRRI farm. Fourteen-day-old seedlings were transplanted at one seedling/hill and spacings of 25 x 25, 20 x 20, 15 x 15, and 10 x 10 cm with 4 replications. Plot size was 10 m². Total N was 200 kg/ha applied in five equal splits. All plots received 18 kg P/ha and 33 kg K/ha incorporated before transplanting. Growth analyses were done at 34 days after transplanting (DAT) and at flowering. Yield components were determined from 0.5 m² and grain yield from 5 m² harvest area at physiological maturity.

Tillering of NPT lines was 1/3 to 1/2 of IR72 across different spacings. At 34 DAT, IR72 had higher or same total dry weight compared with NPT lines. At flowering, NPT lines with longer growth duration than IR72 had greater biomass than IR72. Other NPT lines had the same or less biomass than IR72 at flowering. Single leaf photosynthesis per unit leaf area of some NPT lines was 10-15% higher than that of IR72 at vegetative and reproductive stages. The difference in photosynthetic rate was mainly due to the difference in leaf N concentration. There were no consistent differences in specific leaf weight (SLW) and leaf N concentration between IR72 and NPT lines. The number of panicles/m² of IR72 was 1.5-2 times higher than that of the NPT lines. Two out of the 11 NPT lines (IR65598-112-2 and IR64446-7-10-5) had ≥ 200 spikelets/panicle. The rest of the NPT lines had about 150 spikelets/panicle, 50% higher than that of IR72.

Because the NPT lines lack resistance to brown planthopper (BPH), hopper burn was severe during the late stage of ripening with more damage in the closer spacings. Only two lines that flowered at the same time as IR72, IR65598-112-2 and IR64446-7-10-5, partially escaped the sudden BPH buildup. These two lines also had large panicles and produced 15% more spikelets/m² than IR72 (Table 1). However, only about 55% were completely filled for the two NPT lines compared with 73-80% for IR72. The two NPT lines had 10-20% half-filled spikelets. Grain yield of the two NPT lines was not significantly different from IR72 despite 15% higher sink size (Table 2). Although yields were not significantly different, the trend indicates that the NPT had higher yield at narrow spacing (10 x 10 cm). It was not possible to evaluate the grain filling and yields of the other nine NPT lines because of BPH damage. We initially speculated that BPH damage might have partially caused poor grain filling of IR65598-112-2 and IR64446-7-10-5, although BPH damage was not visible.

Within the Japan-IRRI Shuttle Collaborative Project, S. Akita of the University of Tokyo studied two NPT lines (IR65598-112-2 and IR66740-AC1-3), IR36, IR72, and two Japanese cultivars under field conditions in 1994. IR65598-112-2 had 45-50% and IR66740-AC1-3 had 37% grain filling compared with 82% for IR36 and 67% for IR72. This resulted in significantly lower
yields for the NPT lines than the other varieties (Akita, unpublished). There was no BPH damage in this experiment. It is obvious that the NPT lines with large panicles have poor grain filling.

**Evaluation of NPT lines under wet season conditions**—Twelve NPT lines were compared with two indica checks (IR72 and IR59682-132-1-1-2) in 1994 WS at IRRI farm. Fourteen-day-old seedlings were transplanted at four seedlings/hill and spacing of 20 x 20 cm with 4 replications. Plot size was 30 m². Total N was 70 kg/ha applied in two splits.

The NPT lines produced less tillers, leaf area, and biomass than indicas at 27 DAT, panicle

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**Table 1.** Yield components and total dry weight of IR72 and two new plant type lines grown at different spacings, IRRI, dry season, 1994.

<table>
<thead>
<tr>
<th>Transplanting Genotype</th>
<th>Spikelets Panicles</th>
<th>Spikelets Filled</th>
<th>Half-filled</th>
<th>Seed</th>
<th>Total dry</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spacing (cm) per m² per m²</td>
<td>per panicle spikelets %</td>
<td>spikelets %</td>
<td>wt. (mg)</td>
<td>wt. (g/m²)</td>
<td></td>
</tr>
<tr>
<td>25 x 25</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>IR72</td>
<td>46400</td>
<td>420</td>
<td>111</td>
<td>79.5</td>
<td>4.9</td>
</tr>
<tr>
<td>IR65598-112-2</td>
<td>47500</td>
<td>170</td>
<td>280</td>
<td>54.2</td>
<td>18.8</td>
</tr>
<tr>
<td>IR64446-7-10-5</td>
<td>41800</td>
<td>210</td>
<td>200</td>
<td>61.1</td>
<td>11.1</td>
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<td>20 x 20</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>IR72</td>
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<td>107</td>
<td>78.9</td>
<td>5.3</td>
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<tr>
<td>IR65598-112-2</td>
<td>55500</td>
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<td>52.3</td>
<td>19.3</td>
</tr>
<tr>
<td>IR64446-7-10-5</td>
<td>43700</td>
<td>223</td>
<td>196</td>
<td>56.8</td>
<td>11.9</td>
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<td>15 x 15</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
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<td>44600</td>
<td>414</td>
<td>108</td>
<td>76.8</td>
<td>5.2</td>
</tr>
<tr>
<td>IR65598-112-2</td>
<td>52300</td>
<td>204</td>
<td>256</td>
<td>55.2</td>
<td>20.6</td>
</tr>
<tr>
<td>IR64446-7-10-5</td>
<td>51200</td>
<td>298</td>
<td>172</td>
<td>60.1</td>
<td>10.4</td>
</tr>
<tr>
<td>10 x 10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>IR72</td>
<td>40000</td>
<td>503</td>
<td>80</td>
<td>73.3</td>
<td>6.1</td>
</tr>
<tr>
<td>IR65598-112-2</td>
<td>52900</td>
<td>275</td>
<td>193</td>
<td>56.2</td>
<td>19.9</td>
</tr>
<tr>
<td>IR64446-7-10-5</td>
<td>51400</td>
<td>341</td>
<td>151</td>
<td>60.2</td>
<td>9.0</td>
</tr>
</tbody>
</table>

Transplanted with one seedlings per hill.

**Table 2.** Growth duration and grain yield (14% moisture content) of IR72 and seven new plant type lines grown at different spacings, IRRI, dry season, 1994.

<table>
<thead>
<tr>
<th>Transplanting Genotype</th>
<th>Growth duration (days)</th>
<th>25 x 25 Mean</th>
<th>25 x 25 SD</th>
<th>20 x 20 Mean</th>
<th>20 x 20 SD</th>
<th>15 x 15 Mean</th>
<th>15 x 15 SD</th>
<th>10 x 10 Mean</th>
<th>10 x 10 SD</th>
</tr>
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<tbody>
<tr>
<td>IR72</td>
<td>115</td>
<td>8.94</td>
<td>0.40</td>
<td>8.92</td>
<td>0.37</td>
<td>8.61</td>
<td>0.47</td>
<td>7.75</td>
<td>0.85</td>
</tr>
<tr>
<td>IR64446-7-10-5</td>
<td>114</td>
<td>7.78</td>
<td>0.52</td>
<td>8.45</td>
<td>0.47</td>
<td>8.63</td>
<td>0.33</td>
<td>8.67</td>
<td>0.93</td>
</tr>
<tr>
<td>IR65598-112-2</td>
<td>115</td>
<td>8.21</td>
<td>0.74</td>
<td>8.35</td>
<td>0.52</td>
<td>8.48</td>
<td>0.87</td>
<td>8.92</td>
<td>0.77</td>
</tr>
<tr>
<td>IR65600-42-5-2</td>
<td>120</td>
<td>8.37</td>
<td>0.63</td>
<td>8.47</td>
<td>0.89</td>
<td>8.56</td>
<td>0.56</td>
<td>8.81</td>
<td>0.38</td>
</tr>
<tr>
<td>IR65600-85-1-1</td>
<td>120</td>
<td>6.61</td>
<td>0.38</td>
<td>7.60</td>
<td>0.79</td>
<td>8.18</td>
<td>0.65</td>
<td>7.25</td>
<td>0.89</td>
</tr>
<tr>
<td>IR65600-129-1-1</td>
<td>120</td>
<td>7.13</td>
<td>0.63</td>
<td>6.85</td>
<td>0.57</td>
<td>7.03</td>
<td>0.44</td>
<td>5.22</td>
<td>0.61</td>
</tr>
<tr>
<td>IR66740-AC1-3</td>
<td>118</td>
<td>7.84</td>
<td>0.19</td>
<td>8.07</td>
<td>0.24</td>
<td>8.18</td>
<td>0.90</td>
<td>6.78</td>
<td>0.82</td>
</tr>
<tr>
<td>IR66740-AC1-6</td>
<td>119</td>
<td>7.72</td>
<td>0.19</td>
<td>8.31</td>
<td>0.51</td>
<td>8.45</td>
<td>0.33</td>
<td>7.40</td>
<td>0.67</td>
</tr>
</tbody>
</table>

* Final harvest was not done on the other four new plant type lines due to severe brown planthopper damage.
initiation, flowering and physiological maturity. Only one NPT line (IR65598-112-2) had about 200 spikelets per panicle (Table 3). The other NPT lines had panicles with 150 spikelets. None of the NPT lines produced more spikelets/m² than indica checks in this wet season study. Three NPT lines had 60-69% grain filling, but small sink size limited their yields. The grain filling of indica checks was 70%. The highest yield obtained from NPT lines was 5.7 t/ha compared to 7.1 t/ha from indica checks. BPH damage also occurred in the study.

Flag leaves of IR65598-112-2 and IR72 were sampled weekly to determine changes in leaf N concentration. These data suggested that the flag leaves of this NPT line may senesce faster than those of IR72.

**Evaluation of NPT lines under different establishment and N levels**—Two NPT lines (IR65598-112-2 and IR65600-42-5-2), IR8, and IR72 were grown under transplanted and direct-seeded conditions in 1995 DS at IRRI farm. Two N levels (130 and 195 kg N/ha) were applied with four replications. Fourteen-day-old seedlings were transplanted at four seedlings/hill and spacing of 20 x 10 cm. Higher plant density was used in this study than in the 1994 WS study because we observed low panicle number/m² for NPT lines in the 1994 WS study. Seeding rate was 120 kg/ha for direct-seeded establishment. Plot size was 30 m².

Because of the increased plant density, there was no difference between NPT lines and indicas in biomass production until panicle initiation. At flowering and physiological maturity, however, the total dry weight of indica checks was significantly higher than NPT lines. IR8 and IR65600-42-5-2 were severely damaged by BPH. Comparison can be made only between IR72 and IR65598-112-2. In the transplanted treatment,

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Growth duration (days)</th>
<th>Yield (t/ha)</th>
<th>Spikelets per m²</th>
<th>Panicles per m²</th>
<th>Spikelets per panicle</th>
<th>Filled spikelets %</th>
<th>Half-filled spikelet %</th>
<th>Seed wt. (mg)</th>
<th>Total dry wt. (g/m²)</th>
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</thead>
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<tr>
<td>IR72</td>
<td>115</td>
<td>6.94</td>
<td>38974</td>
<td>419</td>
<td>93.1</td>
<td>70.3</td>
<td>6.0</td>
<td>21.6</td>
<td>1407</td>
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<td>IR59682-132-1-1-2</td>
<td>115</td>
<td>7.21</td>
<td>45667</td>
<td>446</td>
<td>102.5</td>
<td>69.8</td>
<td>10.1</td>
<td>19.1</td>
<td>1390</td>
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<tr>
<td>IR64446-7-10-5</td>
<td>112</td>
<td>4.70</td>
<td>33659</td>
<td>234</td>
<td>144.9</td>
<td>42.2</td>
<td>15.3</td>
<td>24.5</td>
<td>1051</td>
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<td>IR65564-44-2-3</td>
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<td>5.70</td>
<td>27149</td>
<td>242</td>
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<td>58.4</td>
<td>16.8</td>
<td>26.9</td>
<td>1274</td>
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<tr>
<td>IR65598-112-2</td>
<td>112</td>
<td>4.84</td>
<td>34749</td>
<td>169</td>
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<td>22581</td>
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<td>22387</td>
<td>223</td>
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<td>11.1</td>
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<td>119</td>
<td>4.49</td>
<td>26445</td>
<td>213</td>
<td>124.1</td>
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<td>1145</td>
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<td>119</td>
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<td>22715</td>
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<td>29939</td>
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<td>61.7</td>
<td>18.4</td>
<td>27.2</td>
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</tr>
</tbody>
</table>

Transplanted at 20 x 20 cm with four seedling per hill.
IR65598-112-2 had 25% lower yield than IR72 at high N level and 40% lower at low N level despite its 15% more spikelets per m² than IR72 (Table 4). Poor grain filling (45%) was observed for this NPT line. Grain yield of direct-seeded plots was similar to that of the transplanted plots for the NPT line under both N levels. Biomass production, leaf area index, and canopy photosynthetic rate of IR65598-112-2 were significantly lower than IR72. Interestingly, IR65598-112-2 had about 15 days shorter growth duration than IR72 in 1995 DS, while the two genotypes had similar growth duration in 1994 DS and WS. Short growth duration might limit the biomass production and yield of IR65598-112-2. The reason for the variable growth duration of IR65598-112-2 from season to season is not clear.

**Evaluation of NPT lines under high solar radiation and low pest pressure**—Two NPT lines (IR65598-112-2 and IR65600-42-5-2), IR68284H (tropical indica F₁ hybrid), and IR72 were grown under transplanted and direct-seeded conditions in 1995 DS at the Philippines Rice Research Institute (PhilRice), which is 250 km north of IRRI. This site has higher solar radiation than IRRI site, especially in April during the grain filling period of the DS rice crop. Fourteen-day-old seedlings were transplanted at four seedlings/hill and spacing of 20 x 10 cm with four replications. Seeding rate was 120 kg/ha for direct-seeded establishment. Plot size was 30 m². All plots received 210 kg N/ha applied in four splits.

Differences in biomass production between NPT lines and indica checks was consistent with the 1995 DS experiment conducted at IRRI. Although BPH was found in this experiment at late stage, no obvious damage was observed due to small BPH population. Table 5 shows that IR65598-112-2 produced 12-18% lower yield than IR72 as a result of poor grain filling (50%). No difference in spikelets per m² was found between IR65598-112-2 and IR72 in this study. The grain filling of IR65600-42-5-2 (65-70%) was

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**Table 4. Growth duration, grain yield (14% moisture content), yield components, and total dry weight of IR72 and IR65598-112-2 (new plant type line) grown under transplanted and direct-seeded conditions at two N levels, IRRI, dry season, 1995.**

<table>
<thead>
<tr>
<th>Method</th>
<th>N rate</th>
<th>Genotype</th>
<th>Growth duration (days)</th>
<th>Yield (t/ha)</th>
<th>Spikelets per m²</th>
<th>Panicles per m²</th>
<th>Spikelets per panicle</th>
<th>Filled spikelets %</th>
<th>Half filled spikelets %</th>
<th>Seed wt. (mg)</th>
<th>Total dry wt. (g/m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TR²</td>
<td>130</td>
<td>IR72</td>
<td>118</td>
<td>8.34</td>
<td>35658</td>
<td>536</td>
<td>66.5</td>
<td>90.0</td>
<td>2.4</td>
<td>22.9</td>
<td>1633</td>
</tr>
<tr>
<td>TR</td>
<td>130</td>
<td>IR65598-112-2</td>
<td>103</td>
<td>5.99</td>
<td>41332</td>
<td>250</td>
<td>165.6</td>
<td>45.9</td>
<td>16.4</td>
<td>23.4</td>
<td>1295</td>
</tr>
<tr>
<td>TR</td>
<td>195</td>
<td>IR72</td>
<td>118</td>
<td>9.07</td>
<td>40711</td>
<td>569</td>
<td>71.7</td>
<td>86.4</td>
<td>2.9</td>
<td>21.9</td>
<td>1785</td>
</tr>
<tr>
<td>TR</td>
<td>195</td>
<td>IR65598-112-2</td>
<td>103</td>
<td>7.22</td>
<td>47505</td>
<td>281</td>
<td>169.3</td>
<td>45.0</td>
<td>14.5</td>
<td>23.8</td>
<td>1448</td>
</tr>
<tr>
<td>WS</td>
<td>130</td>
<td>IR72</td>
<td>110</td>
<td>7.83</td>
<td>44093</td>
<td>572</td>
<td>77.2</td>
<td>89.3</td>
<td>2.9</td>
<td>22.6</td>
<td>1769</td>
</tr>
<tr>
<td>WS</td>
<td>130</td>
<td>IR65598-112-2</td>
<td>93</td>
<td>6.01</td>
<td>36474</td>
<td>340</td>
<td>107.5</td>
<td>58.5</td>
<td>20.8</td>
<td>23.5</td>
<td>1304</td>
</tr>
<tr>
<td>WS</td>
<td>195</td>
<td>IR72</td>
<td>110</td>
<td>9.60</td>
<td>48534</td>
<td>644</td>
<td>75.5</td>
<td>88.8</td>
<td>3.2</td>
<td>22.8</td>
<td>2057</td>
</tr>
<tr>
<td>WS</td>
<td>195</td>
<td>IR65598-112-2</td>
<td>93</td>
<td>7.27</td>
<td>49544</td>
<td>358</td>
<td>139.1</td>
<td>63.3</td>
<td>15.5</td>
<td>23.6</td>
<td>1694</td>
</tr>
</tbody>
</table>

² TR=transplanted at 10 x 20 cm with four seedlings per hill, WS=direct seeded.
better than IR65598-112-2 but the yield was significantly lower than IR65598-112-2 due to smaller sink size. The panicle size of IR65600-42-5-2 was similar to that of IR72. The hybrid rice IR68284H produced 10.4 t/ha under transplanted conditions, about 5% higher than IR72. As observed in the 1995 DS experiment at IRRI, NPT lines did not yield differently under transplanted and direct-seeded establishments.

**Evaluation of NPT lines in a high yielding temperate environment**—Taoyuan Township, Yongsheng County, Yunnan Province, China, is known for its high rice yields. It is 1100 m above sea level with low humidity, low night temperature, and high solar radiation during the rice growing season. Consequently, disease and insect pressure is low for the rice crop. We grew two NPT lines (IR65598-112-2 and IR64446-7-10-5), IR72, IR59682-132-1-1-2 (elite IRRI indica), Guichao 2 (Chinese indica inbred) and Shanyou 63 (Chinese indica hybrid) in 1995 with four replications. Forty-five-day-old seedlings were transplanted at 16 x 10 cm spacing with two seedlings/hill for the two NPT lines and one seedling/hill for the other varieties. Plot size was 30 m². All plots received 205 kg N/ha applied in three splits.

Growth duration of all entries was on average 45 d longer than when grown in the tropical environments (Yin et al., unpublished). IR65598-112-2 had growth duration of 153 d, 10 d shorter than IR72. No disease and insect damage was found in this study. Before panicle initiation, the two NPT lines grew at almost same rate as the indicas. This was achieved by doubling plant density of NPT lines. The growth rate of NPT lines was significantly lower than indicas after panicle initiation (Figure 1). IR65598-112-2 produced 9.8 t/ha with an improved grain filling percent of 66% (Table 6). IR72 produced the same amount of spikelets per m² as IR65598-112-2 but yielded 12.7 t/ha with 78% grain filling. Harvest index of IR65598-112-2 was not significantly different from indicas. IR64446-7-10-5 did not perform as well as IR65598-112-2 due to smaller sink size and poor grain filling. Guichao 2

**Table 5. Growth duration, grain yield (14% moisture content), yield components, and total dry weight of IR72, IR68284H (indica hybrid), and two new plant type lines grown under transplanted and direct-seeded conditions at two N levels, PhilRice, dry season, 1995.**

<table>
<thead>
<tr>
<th>Method</th>
<th>Genotype</th>
<th>Growth duration (days)</th>
<th>Yield (t/ha)</th>
<th>Spikelets per m²</th>
<th>Panicles per m²</th>
<th>Spikelets per panicle</th>
<th>Filled spikelets %</th>
<th>Half filled spikelets %</th>
<th>Seed wt. (mg)</th>
<th>Total dry wt. (g/m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TR a</td>
<td>IR72</td>
<td>123</td>
<td>9.92</td>
<td>55186</td>
<td>743</td>
<td>74.2</td>
<td>79.7</td>
<td>3.1</td>
<td>21.5</td>
<td>2141</td>
</tr>
<tr>
<td>TR</td>
<td>IR68284H</td>
<td>134</td>
<td>10.40</td>
<td>51562</td>
<td>601</td>
<td>85.8</td>
<td>78.6</td>
<td>4.3</td>
<td>25.9</td>
<td>2357</td>
</tr>
<tr>
<td>TR</td>
<td>IR65600-42-5-2</td>
<td>136</td>
<td>7.43</td>
<td>42760</td>
<td>542</td>
<td>79.0</td>
<td>70.9</td>
<td>6.2</td>
<td>24.4</td>
<td>2061</td>
</tr>
<tr>
<td>TR</td>
<td>IR65598-112-2</td>
<td>106</td>
<td>8.42</td>
<td>57579</td>
<td>406</td>
<td>142.0</td>
<td>48.8</td>
<td>18.7</td>
<td>22.2</td>
<td>1775</td>
</tr>
<tr>
<td>WS</td>
<td>IR72</td>
<td>116</td>
<td>9.30</td>
<td>53003</td>
<td>870</td>
<td>61.1</td>
<td>75.3</td>
<td>3.6</td>
<td>21.6</td>
<td>2089</td>
</tr>
<tr>
<td>WS</td>
<td>IR68284H</td>
<td>127</td>
<td>9.04</td>
<td>45501</td>
<td>699</td>
<td>65.2</td>
<td>65.1</td>
<td>6.0</td>
<td>26.1</td>
<td>2203</td>
</tr>
<tr>
<td>WS</td>
<td>IR65600-42-5-2</td>
<td>130</td>
<td>6.74</td>
<td>34670</td>
<td>531</td>
<td>65.7</td>
<td>65.5</td>
<td>7.5</td>
<td>24.6</td>
<td>1767</td>
</tr>
<tr>
<td>WS</td>
<td>IR65598-112-2</td>
<td>101</td>
<td>8.34</td>
<td>50974</td>
<td>442</td>
<td>116.3</td>
<td>50.8</td>
<td>16.6</td>
<td>22.5</td>
<td>1653</td>
</tr>
</tbody>
</table>

a TR=transplanted at 10 x 20 cm with four seedlings per hill, WS=direct seeded.
produced the highest yield (13.6 t/ha) among all entries. No lodging was observed from any plots. It was also observed that the flag leaves of NPT lines senesced faster than IRRI indica inbreds based on changes in flag leaf N concentration.

**Studies on the causes of the poor grain filling of NPT lines**

In the 1995 DS experiment at PhilRice, panicles uniform in size and emergence date were tagged in each plot at heading and sampled at harvest for IR65598-112-2, IR68284H, and IR72. The panicles were divided into top, middle, and bottom segments and the number and weight of filled, half-filled, and empty spikelets were determined for each segment. Figure 2 shows the location of filled, unfilled and half-filled spikelets in the panicle. In the case

![Graph showing aboveground dry matter accumulation](image)

**Figure 1.** Aboveground dry matter accumulation of IR72 and IR65598-112-2 grown in Taoyuan, China in 1995.

**Table 6. Growth duration, grain yield (14% moisture content), yield components, total dry weight, and harvest index (HI) of IR72, IR59682-132-1-1-2 (indica inbred), IR64446-7-10-5 (new plant type line), IR65598-112-2 (new plant line), Guichao 2 (indica inbred), Shanyou 63 (indica hybrid), Taoyuan, Yunnan, China, 1995.**

<table>
<thead>
<tr>
<th></th>
<th>Growth duration (days)</th>
<th>Yield t/ha</th>
<th>Spikelets per m²</th>
<th>Panicles per m²</th>
<th>Spikelets per panicle</th>
<th>Filled spikelet %</th>
<th>Seed wt. (mg)</th>
<th>Total dry wt. (g/m²)</th>
<th>HI</th>
</tr>
</thead>
<tbody>
<tr>
<td>IR72</td>
<td>163</td>
<td>12.7</td>
<td>65177</td>
<td>583</td>
<td>111.8</td>
<td>77.7</td>
<td>22.7</td>
<td>2396</td>
<td>0.48</td>
</tr>
<tr>
<td>IR59682-132-1-1-2</td>
<td>160</td>
<td>11.3</td>
<td>70695</td>
<td>661</td>
<td>107.2</td>
<td>80.7</td>
<td>20.2</td>
<td>2632</td>
<td>0.44</td>
</tr>
<tr>
<td>IR64446-7-0-5a</td>
<td>162</td>
<td>6.9</td>
<td>52511</td>
<td>342</td>
<td>154.2</td>
<td>47.5</td>
<td>25.0</td>
<td>1846</td>
<td>0.34</td>
</tr>
<tr>
<td>IR65598-112-2a</td>
<td>153</td>
<td>9.8</td>
<td>64717</td>
<td>256</td>
<td>256.4</td>
<td>66.0</td>
<td>21.5</td>
<td>1972</td>
<td>0.46</td>
</tr>
<tr>
<td>Guichao 2</td>
<td>163</td>
<td>13.6</td>
<td>65686</td>
<td>464</td>
<td>141.7</td>
<td>78.8</td>
<td>23.9</td>
<td>2684</td>
<td>0.46</td>
</tr>
<tr>
<td>Shanyou 63</td>
<td>168</td>
<td>12.7</td>
<td>52071</td>
<td>371</td>
<td>140.8</td>
<td>87.9</td>
<td>26.5</td>
<td>2479</td>
<td>0.49</td>
</tr>
</tbody>
</table>

*New plant type lines were transplanted at 10 x 16 cm with two seedlings per hill, the others with one seedling per hill.*
of IR72 which has 98 spikelets per panicle, percentage of filled spikelets was around 80% while half filled percentage was 5% and unfilled spikelets was 15%, whether in the top, middle or bottom part of the panicle. In the case of the hybrid IR68284H, which has 110 spikelets per panicle, slightly more half-filled and unfilled spikelets were found in the middle and bottom part of the panicle compared to the top portion. IR65598-112-2 with 226 spikelets per panicle distinctly showed an increase in half-filled spikelets from the top to the bottom part of the panicle and a corresponding decrease in filled spikelets. This shows that as the number of spikelets per panicle increases, spikelets in the lower portion of the panicle are disadvantaged in terms of carbohydrate availability and grain filling. This also suggest that the poor grain filling of NPT was partially due to source limitation possibly caused by early leaf senescence.

In another experiment conducted in 1995 DS at IRRI, the grain filling and grain weight of IR65598-112-2, IR68284H, and IR72 were measured after removal of flag leaf and/or spikelets at 2 and 11 days after heading. About 50% spikelets were removed alternately on a panicle. Table 7 shows that flag leaf removal at start of grain filling was most detrimental to spikelet filling percentage. This treatment resulted in a 13% decrease in filled spikelet percentage for IR72 and 8% for IR68284H compared to a 44% decrease in IR65598-112-2. Removing half of the spikelets did not significantly affect the filled spikelet percentage and weight of each grain in IR72 and IR68284H. For IR65598-112-2, however, there was a 42% increase in filled spikelet percentage when half of the spikelets were removed at 2 days after heading. There was also an 8% increase in the weight of individual grains. The effect was less when the removal was done later during the ripening period. This result suggests that the high density of spikelets (i.e. spikelet number per unit panicle length) is one of the reasons for the poor grain filling in NPT.

Summary of NPT studies
After evaluating the NPT lines for three seasons at three locations, the following points can be summarized:

Table 7. Effect of flag leaf and spikelet removal on the percentage of filled spikelet and weight of single grain on IR72, IR68284H ( indica hybrid), and IR65598-112-2 (new plant type line). IRRI, 1995 DS.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>IR72</th>
<th>IR68284H</th>
<th>IR65598-112-2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Filled spikelet %</td>
<td>Seed wt. (mg)</td>
<td>Filled spikelet %</td>
</tr>
<tr>
<td>Intact plant</td>
<td>88.0 a</td>
<td>22.6 a</td>
<td>80.3 bc</td>
</tr>
<tr>
<td>Flag leaf cut (-FL) at 1 DAHb</td>
<td>76.8 b</td>
<td>22.7 a</td>
<td>74.1 c</td>
</tr>
<tr>
<td>1/2 spikelets at 2 DAHc</td>
<td>88.0 a</td>
<td>22.9 a</td>
<td>85.8 ab</td>
</tr>
<tr>
<td>1/2 spikelets, -FL at 2 DAH</td>
<td>89.4 a</td>
<td>23.2 a</td>
<td>88.2 a</td>
</tr>
<tr>
<td>1/2 spikelets at 11 DAH</td>
<td>91.2 a</td>
<td>23.0 a</td>
<td>84.3 ab</td>
</tr>
<tr>
<td>1/2 spikelets, -FL at 11 DAH</td>
<td>90.6 a</td>
<td>23.1 a</td>
<td>84.2 ab</td>
</tr>
</tbody>
</table>

a Means followed by the same letter within a column are not significantly different at 5% level by DMRT.
b Removal of flag leaf at 1 day after heading.
c Removal of about 50% spikelets alternately on a panicle at 2 days after heading.
Tropical japonicas have been improved into NPT lines within less than five years. The NPT lines tested did not yield well due to poor grain filling. However, we have evaluated only a few of the large number of NPT lines. New crosses are being made and more NPT lines will be available. Selection pressure for good grain filling will be applied in early generations. Research on NPT will continue with the goals of breaking the yield barrier and increasing germplasm diversification.

IR65598-112-2 consistently performed better than other NPT lines. It has large panicles and its morphological traits resembles the ideotype design proposed in 1989 by IRRI scientists. This partially proves that the major aspects of NPT design were correct.

Low biomass production, poor grain filling, and pest susceptibility are the major constraints to yield of NPT lines. The cause-effect relationship between low biomass production and poor grain filling needs to be determined. It is unlikely that only poor grain filling causes low biomass production since low growth rate was observed between panicle initiation and flowering as well as ripening phase.

Nitrogen concentration and photosynthetic rate on a single-leaf level of the NPT lines showed no disadvantage compared to indica rices. Lower canopy photosynthetic rate and biomass production might be largely attributed to less tillering. A slight increase in tillering capacity of the NPT should be considered.

Early flag leaf senescence can cause poor grain filling and large sink size can cause early leaf senescence as well. Early flag leaf senescence can be overcome by N application at flowering. Selection of long panicle while maintaining large sink size may partially improve the grain filling of NPT lines.

Tillering synchrony of NPT lines needs to be improved since late maturing tillers may contribute to poor grain filling.

Panicle size (i.e., spikelets/panicle) of NPT lines decreased more than that of the indicas when panicle number increased (Figure 3). This partially explains why the NPT lines did not perform better under direct-seeded than under transplanted conditions.

We should also compare the efficiency of C and N remobilization from storage to grain between NPT lines and indica rices. At this moment, we cannot rule out the possibility that assimilate transport is limiting in NPT lines.

Figure 3. Relationship between spikelet number per panicle and panicle number per m² for IR72 and IR65598-112-2. Field experiments were conducted at IRRI in 1994 DS, 1994 WS and 1995 DS, at PhilRice in 1995DS, and at Toayuan, Yunnan, China in 1995.
• Resistance to tungro and BPH must be incorporated into NPT lines. We also need to improve grain quality. Donors for these traits have been identified and are being used in the hybridization program.

• Hybridization between the NPT lines and indica inbreds is in progress. An intermediate cultivar between tropical japonicas and indicas could overcome some problems of the NPT lines. In the meantime, some NPT lines will be kept purely in a japonica background for the creation of indica/japonica F₁ hybrid rice.

• Another strategy is to cross the NPT lines with U.S. cultivars from Texas. Since these cultivars are intermediate between japonicas and indica, we will have no sterility problems or barriers to recombination. Hopefully, good traits from the Texas cultivars, such as grain filling, can be transferred into the NPT lines.

**Hybrid Rice for Increasing Yield Potential**

F₁ hybrid rice have been grown in China since 1976 and on average have a yield advantage of about 15% over the best inbred varieties. Approximately 50% of China’s rice area is now planted to rice hybrids (Yuan et al. 1992). These hybrids were evaluated in tropical countries and found to be unadapted. Hybrid rice research was initiated at IRRI in 1978. Selected hybrids showed a yield advantage of about 15% under tropical conditions in farmers’ fields. The increased yield of tropical rice hybrids is due to increased total biomass, higher spikelet number and, to some extent, higher 1000 grain weight.

Yield potential of elite tropical hybrid IR68284H was compared with IR72 at IRRI and PhilRice in 1995 DS. The hybrid produced 10.8 t/ha at IRRI and 10.4 t/ha at PhilRice, while IR72 yielded 7.7 t/ha at IRRI and 9.9 t/ha at PhilRice. The higher yield of the hybrid was attributed to more spikelets per m² at IRRI and higher 1000 grain weight at IRRI and PhilRice than IR72 (26.3 vs. 21.3 g). Total dry matter at harvest of the hybrid was 10-17% higher than IR72. At PhilRice, the hybrid produced 23.5 t dry matter/ha which was the highest biomass production reported for tropical rice. The most important trait of this hybrid is its stable and high grain filling percentage compared with earlier tropical hybrids. The grain filling percentage of this hybrid was 83% at IRRI and 79% at PhilRice, which was equivalent to IR72. High grain yield and grain filling percentage were also observed in 1994 DS from this hybrid.

Tropical hybrids did not show higher single-leaf photosynthetic rate than indica inbreds in the entire growing season. In fact, the hybrids had slightly lower single-leaf photosynthetic rate during rapid growing period and ripening phase due to lower leaf N concentration than inbreds. The physiological basis of heterosis is still unknown.

Rice hybrids in China are based on cytoplasmic genetic male sterility (CMS) and fertility restoration system. Hundreds of CMS lines have been bred in China for hybrid seed production. These CMS lines could not be used as such to develop rice hybrids for the tropics because of their susceptibility to diseases and insects, poor adaptability and poor grain quality.
Therefore, new CMS lines were bred at IRRI and by national programs using the WA cytoplasmic male sterility system from China. There is no dearth of restorers among the elite indica rice germplasm in the tropics and subtropics. New sources of CMS have also been identified at IRRI.

The thermosensitive genetic male sterility system (TGMS) and photoperiod sensitive genetic male sterility system (PGMS) simplify hybrid rice seed production. Several sources of TGMS and PGMS have been reported from China (Sun et al. 1989; Wu et al. 1991). A few mutants have been identified in Japan (Maruyama et al. 1991) and at IRRI (Virmani and Voc 1991). TGMS and PGMS systems do not require maintainer lines for multiplication and hybrids can be developed by using only two lines (instead of three in the case of the CMS system) e.g., TGMS and pollen parent. The latter does not have to be a restorer. Two line hybrids are likely to show higher heterosis because there are fewer restrictions on the choice of parents in comparison to the CMS system. It should be possible to use the TGMS system to develop tropical rice hybrids by utilizing the temperature differences at different altitudes or in different rice growing seasons. TGMS should be a good alternative to the complex and cumbersome CMS system.

Technology for producing hybrid rice seeds in the tropics has been outlined (Virmani and Sharma 1993). Using this technology, yields of 1-2 t/ha of hybrid seed and 1-2 t/ha of pollen parent have been obtained by IRRI and some national programs. Seed yields can be increased further by improving the outcrossing potential of the parental lines and fine-tuning of the technology by the prospective seed growers and the national programs.

The magnitude of heterosis depends upon the genetic diversity between the two parents of the hybrids. The greater the genetic difference between the parents, the higher the heterosis. During the past 30 years, the genetic diversity among the improved indica rices has narrowed down due to massive international exchange of germplasm (Khush and Aquino 1994). Indica and japonica germplasms have, however, remained distinct as there has been very little gene flow between these two varietal groups. As expected, hybrids from indica and japonica parents showed higher heterosis for yield (Yuan et al. 1989). As discussed in an earlier section, the new plant type development program was based on tropical japonica germplasm so that this improved germplasm would also be utilized for producing hybrids with higher heterosis. Our preliminary results show that the level of heterosis of the indica/tropical japonica hybrid is higher than that of an indica/indica hybrid.

Major constraints in utilizing hybrid rice for increasing rice production are: 1) the need to buy fresh hybrid seed for every planting season, 2) the high cost of hybrid seed and (3) the need to establish seed production infrastructure in developing countries. Farmers would be willing to buy fresh seed at a price higher than that of inbred rice provided there is a cost benefit ratio of 1:4. With this cost benefit ratio, national programs would also invest to strengthen or establish a seed industry in the public/private and/or cooperative sectors. These
constraints could also be overcome if true-breeding hybrids with permanently fixed heterosis were developed through apomixis. The search for apomixis in rice or inducing it through mutagenesis is being pursued at IRRI and in China.

References


Questions and answers

M. Mergoum:
In 1966, IR8 rice cultivar, which has a yield of 10 t/ha, was identified. Since then, yield has not gone beyond 10 t/ha (according to your data) even in the new type genotypes, yields of 10 t/ha were achieved under 1966 cultural and management practices (soil, nutrients, etc.) Since 1966 these practices would have evolved and improved to permit better expression of yield potential, as is the case in wheat here at Obregon (ref. K. Sayre, input management and yield potential trials). The question is: what are the most important management practices developed during the last 30 years that will allow better expression of yield potential? In other words, for example, what would IR8 yield under 1996 cultural and management practices?

S. Peng:
There has been no major improvements in cultural and management practices during the last 30 years that allow better expression of yield potential. Most improvement in cultural and management practices have resulted in increased efficiencies of inputs such as labor, nutrients, seeds, etc. IR8 would have the same yield potential of 10 t/ha under 1996 cultural and management practices.

R.A. Fischer:
What has been learnt from the lodging resistance work?

S. Peng:
IRRI’s major work on lodging resistance has been associated with breeding programs such as semidwarf breeding and selection of thick stems in breeding for a new plant type. Other morphological studies of lodging resistance include lowering panicle height to reduce the height of the shoot’s center of gravity. Ecophysiological, biophysical, and biochemical studies on the mechanism of lodging resistance are just underway.

M. Kohli:
What was the level of fertilization you used in getting the highest yields? I believe there is further room for increasing nitrogen fertilization, as in the case of wheat in southern Chile, in order to utilize the full potential of NPT rice.

S. Peng:
The potential yield of 10 t/ha was achieved with N input levels of 160-200 kg/ha. In the case of current high yielding cultivars, further increases in N fertilization would not enhance grain yield because they do not have resistance to lodging and sheath blight. After the improvement of grain filling and resistance to diseases and insects in the NPT, the N input level may need to be increased to fully express its yield potential.

K. Sayre:
Why has IRRI waited so long to exploit indica x japonica crosses given CIMMYT’s highly successful use of spring x winter crosses?

S. Peng:
The germplasm used for developing NPT and future intersubspecific hybrids are tropical japonicas. Before 1987, we did not understand the genetic background of these bulu materials, also called javanicas, from Indonesia. We thought they belonged to an
independent group. On the basis of allelic constitution at 15 isozyme loci, Glaszmann (1987) showed that javanicas and japonicas belong to the same varietal group. We therefore now refer to javanicas as tropical japonicas. The work on breeding for NPT began after the genetic background of bulu germplasm was very well understood.

V.S. Chanlan:
In the new rice plant, the number of grains, which is 225-250, seems to be much higher and this may be one of the reasons for more unfilled grains. What are your views on this?

S. Peng:
A negative relationship between grain number and grain filling percentage commonly exists across rice genotypes. Since the NPT has only 50-60% grain filling percentage, large panicle size should not be the only cause of poor grain filling. In addition, we observed large variation among large panicles in grain filling percentage within a genotype. It is possible to improve the grain filling percentage of the NPT without reducing panicle size.
Breeding Objectives, Philosophies and Methods in South Australia

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Abstract
For a breeding program to be successful, a good knowledge of farming practices, soils, climate and market requirements is needed to set relevant objectives, use effective screening procedures, and ensure that yield and quality evaluation is carried out in representative locations using appropriate management. Wheat in South Australia is grown under semiarid dryland conditions in hostile soils, often with trace element deficiencies, boron toxicity and fungal and nematode root diseases. Genotype x environment interactions are large from year to year as well as from location to location. Most of the harvest is exported, so quality is critical. Breeding objectives are based on stress tolerance and marketable quality. The philosophies and strategies of the Roseworthy wheat breeding program are described with special reference to recent and future improvements. Essentially the program is a modified pedigree method with a large number of lines yield tested at the F4 stage after selection for foliar disease resistance has occurred but before any testing for grain quality. Multilocation evaluation of F5 (about 3000 lines) is carried out on survivors from the single replicate F4 trial on the basis of yield and a NIR reading calibrated for grain hardness, milling yield and extensibility. High and low molecular weight glutenin composition is also used at this time for culling. Two dimensional spatial analyses are performed to take account of within location variability. Across location and year variability is described by site sampling and the use of probe genotypes.

Introduction
It is easy for breeders to describe their breeding programs in terms of strategies and methodologies. However, it is much more difficult to pinpoint reasons for success, which is the aim of this paper. There is no attempt, and it would be very audacious, to compare breeders’ abilities or the constraints imposed upon them by administrators. Enough controversy and debate should occur from considering our philosophies and strategies.

In considering this issue and making comparisons with other breeding programs, we found three aspects continually recurred, viz. relevance, effectiveness, and representativeness. If breeders queried everything they did along these lines, their programs might be more successful.

Target Area
The target area in the past has been the wheat growing belt of South Australia but recently this has been extended to include relevant areas throughout the southeastern region of Australia as defined by the Australian Grains Research and Development Corporation. South Australian varieties have shown broad adaptation and ready acceptance by farmers in this area and also in Western Australia.
The wheat growing environment over most of South Australia is quite stressful, with soil borne diseases, often low and irregular rainfall, widespread nutrient deficiencies, and boron toxicity. South Australia would be included in CIMMYT’s mega-environments MB4A and MB9. Foliar diseases are infrequent problems but still occur often enough that resistance to stem rust, stripe rust and *Septoria tritici* is high priority. Root diseases, encouraged by common cropping rotations, are far more debilitating to crop yields.

Mean rainfall varies from 250 mm to over 500 mm annually (about 80% falling during the crop growing season April to November) and is almost as variable on the one farm from year to year.

A range of soil types is cropped to wheat in South Australia; the largest expanse is ‘mallee soil’, light sandy topsoil prone to wind erosion overlying a solonised clay or limy, often stony, clay marl. Mallee soils are alkaline (pH = 7.5-8.5) on the surface and increasingly so with depth. They are low in organic matter and deficient in P and N. Trace elements, particularly Zn and Mn, are often ‘fixed’ and unavailable, and subsoils usually have toxic levels of boron. Red Brown Earth soils are another important soil type on which wheat is grown. These occur in climatically more favorable areas and have fewer problems, being heavier and having a good water holding capacity. They too are alkaline with free calcium carbonate starting deeper in the profile and can have nutrient deficiencies and boron toxicity. Sodicity and salinity can be problems in both these soils.

Farm management practices are also very variable. A typical ley system involves wheat followed by one or two years of annual legume-based pasture grazed with sheep, then back into a cereal. At the other extreme, many farmers now continuously crop alternating cereals with pulses at different frequencies, depending on considerations of sustainability and commodity prices. Fallowing is rare nowadays, and minimum tillage systems are becoming more widely practiced. These practices lead to problems that affect potential yields, especially with respect to soil fertility and soil borne diseases, both fungal and nematode.

Wheat, almost always spring wheat, is sown in the fall, mid-May to late June, as soon as possible after the seasonal ‘opening rains’, at 50 to 80 kg per hectare with up to 10 units of P and 10 units of N. Heading ideally occurs in late September, but if planting is late, can extend to early November. Harvest is from mid-November to late December under hot dry conditions. Moisture and heat stress are common after anthesis.

Generally we are breeding for stress tolerance rather than yield potential *per se*. Although physiological characteristics are carefully considered in choosing parents, the essential ingredient in selecting for yield is yield performance over a range of representative sites and seasons. How to screen for yield while maintaining adequate variability for yield improvement within populations and avoiding decimation by selection for other characters such as disease resistance, agronomic characters and quality are important strategic considerations in our methodology.
Breeding Philosophy

There are two wheat breeding programs in South Australia, both within the University of Adelaide. One is headed by A.J. Rathjen at the Waite Agricultural Research Institute and ours is at the Roseworthy Campus. Both are breeding for the same region and both have similar breeding objectives, but our philosophies and strategies are different, as is the germplasm base. Rathjen's program is based on an F2 progeny technique (Rathjen and Pederson 1986). In this paper, I will concentrate on the Roseworthy method.

The breeding procedure that has evolved is based on the following premises:

1. Yield is the prime objective. Despite a new cultivar's improvements, including quality capable of attracting premiums, farmers will not grow it unless they expect it to yield well on their farms.

2. Because of large unpredictable interactions between genotype, location and year, in South Australia selection must be carried out across several sites and seasons. These sites must be relevant and representative of the range of climatic and edaphic conditions, and farming practices in the target region. Experiment stations are often not representative of real farm situations. They tend to be located on better soils and usually their management in terms of nutrition, disease and weed control is not financially feasible for farmers. They are thus not very relevant as yield evaluation sites. Genotype x environment interaction (G x E) is a reflection of our lack of knowledge of operating environmental factors, and the safest way to account for such interactions is to sample them.

3. Yield is density dependent and thus can only be properly assessed in farm situations using row spacings, sowing rates and fertilizer levels that farmers will use. If we want to release new cultivars with a changed package of practices, we must select under such changed practices early in the selection cycle.

4. Yield is expensive to pursue, so other objectives should be attained before widescale yield evaluation. However, the program should have enough breadth (crosses) and depth (selections per cross) of germplasm after selecting for major genes that progress in selecting for yield increases can be sustained. We want to select for yield and adaptation, not just test what we have.

5. Maintenance of a large germplasm pool with depth and breadth is essential to give flexibility. Flexibility to change direction when farmer or consumer needs change, to adopt new technologies and/or to take on new objectives. Flexibility is important to the breeding strategy as well, so that the breeder is not locked into a certain infrastructure which prevents the adoption of new methods.

6. Resources are limiting, so book-keeping, data collection, and field and laboratory activities must be streamlined and kept to the minimum necessary to allow the discard/retain decision to be made.

7. New improved cultivars are the measure of success so we must steadfastly pursue this goal and not get sidetracked. Instead we should encourage others to use our germplasm to investigate promising theories.
Breeding Objectives

Our objectives, detailed in Figure 1, are under constant review. If we have appropriate germplasm and effective screening procedures (screening sites detailed in Table 1), then current objectives will be achieved in the near future and moved into the inner core area. Although some undesirable segregation will still occur, most germplasm will contain the desirable genes. Resources previously devoted to these objectives will no longer be as necessary and can thus be redeployed to other, newer objectives or techniques.

We include future objectives for different reasons. Some are less important than those currently being tackled (e.g., BYDV), others are important but the knowledge of how to breed for them is lacking (e.g., root rots), while still others are potential objectives if further research shows them to be important (e.g., embryo size).

Improved cultivars are released if they are improvements on what farmers are already growing. They

Figure 1. Wheat breeding objectives for the Roseworthy program 1996.
Table 1. Sites planned for 1996 Roseworthy Wheat Breeding Program.

<table>
<thead>
<tr>
<th>Location</th>
<th>Soil</th>
<th>Specific characteristics</th>
<th>Long term yield, t/ha</th>
<th>Plots 1996</th>
</tr>
</thead>
<tbody>
<tr>
<td>Roseworthy 'farm'</td>
<td>mallee soils of variable texture</td>
<td>good fertility, B toxic, stripe rust, leaf rust</td>
<td>2.4</td>
<td>25000</td>
</tr>
<tr>
<td>Palmer farm</td>
<td>sandy to sandy loam</td>
<td>B toxic, root disease, P and trace element def</td>
<td>1.8</td>
<td>4800</td>
</tr>
<tr>
<td>Minnipa Res stn</td>
<td>sandy loam</td>
<td>B toxic, Take all, short season</td>
<td>1.5</td>
<td>3900</td>
</tr>
<tr>
<td>Stow farm</td>
<td>sandy duplex</td>
<td>min.till., B toxic, <em>P. neglectus</em>, grass weeds</td>
<td>2.3</td>
<td>3800</td>
</tr>
<tr>
<td>Tuckey farm</td>
<td>siliceous sand over clay</td>
<td>B toxic, Mn &amp; Zn deficiencies</td>
<td>1.8</td>
<td>3400</td>
</tr>
<tr>
<td>Kapunda farm</td>
<td>heavy red brown earth</td>
<td>stripe rust, high herbicide use, long season, low protein</td>
<td>4.5</td>
<td>2400</td>
</tr>
<tr>
<td>Heggarton farm</td>
<td>deep siliceous sands</td>
<td>acid problems, new site</td>
<td>?</td>
<td>2100</td>
</tr>
<tr>
<td>Taldra farm</td>
<td>calcareous sand</td>
<td>short season, high protein</td>
<td>1.8</td>
<td>1900</td>
</tr>
<tr>
<td>Warnertown</td>
<td>Red brown earth</td>
<td>early sowing, stem rust prone</td>
<td>2.1</td>
<td>1800</td>
</tr>
<tr>
<td>Bordertown</td>
<td>sand over clay</td>
<td>stripe rust, waterlogging</td>
<td>3.0</td>
<td>2100</td>
</tr>
<tr>
<td>farm site 1</td>
<td>calcareous loam</td>
<td>stripe rust, high fertility</td>
<td>4.0</td>
<td>1500</td>
</tr>
<tr>
<td>farm site 2</td>
<td>shallow sand</td>
<td>Cu def, water logging, CCN, <em>Septoria tritici</em></td>
<td>2.0</td>
<td>900</td>
</tr>
<tr>
<td>Yeelanna farm</td>
<td>heavy clay</td>
<td>stripe rust, trace element deficiencies, CCN</td>
<td>2.0</td>
<td>900</td>
</tr>
<tr>
<td>Coonalpyn farm</td>
<td>siliceous sand over sodic clay</td>
<td></td>
<td>2.0</td>
<td>900</td>
</tr>
<tr>
<td>Buckleboo farm</td>
<td>sandy mallee</td>
<td>severe B toxicity, short season</td>
<td>0.8</td>
<td>800</td>
</tr>
</tbody>
</table>

Special single factor nurseries

<table>
<thead>
<tr>
<th>Location</th>
<th>Characteristics</th>
<th>Heads/ha</th>
<th>Rows</th>
<th>Plots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Roseworthy irrigated nursery + inoculum</td>
<td>three rusts</td>
<td>60000</td>
<td>3000</td>
<td>10000</td>
</tr>
<tr>
<td></td>
<td>irrigated, early sown + inoculum</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>single rows</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marion Bay</td>
<td>severe manganese deficiency ± Mn</td>
<td>Mn efficiency</td>
<td>400</td>
<td></td>
</tr>
<tr>
<td>Lameroo</td>
<td>severe zinc deficiency ± Zn</td>
<td>Zn efficiency</td>
<td>400</td>
<td></td>
</tr>
<tr>
<td>Mallala</td>
<td>natural CCN infestation</td>
<td>CCN</td>
<td>1600</td>
<td>1400</td>
</tr>
<tr>
<td>Palmer</td>
<td>natural CCN infestation ± nematicide</td>
<td>CCN tolerance</td>
<td>1400</td>
<td></td>
</tr>
</tbody>
</table>

Some of these sites are shared with the Waite Wheat Breeding Program.
do not have to meet the newer changed objectives, but have to achieve the objectives set in the early stages of the production and selection of that set of crosses.

Most South Australian wheat is exported and so end product quality is critical for cultivar improvement. Hard grained high protein cultivars suitable for pan bread (Aus Hard), hard grained medium protein for flat bread (Aus Premium White) and soft low protein cultivars for biscuits (Aus Soft) can be grown in different districts. Aside from white grain color, early generation quality testing has not been very useful for culling. Recent research into high molecular weight (HMW) and low molecular weight (LMW) glutenins, however, has indicated that certain alleles are not conducive to good quality in any class, so more effort is being put into purging undesirables in early generations (Payne et al. 1987; Cornish, 1994).

Drought resistance per se is not considered an objective. It has not been possible to define drought in southern Australia in a way that is useful to breeders. If the opening rains are late, sowing time is delayed and farmers try to avoid post anthesis stress by planting earlier maturing varieties or switching to barley. A single day of hot, dry, desiccating wind can occur any time from about boot stage but is more likely post anthesis. Whatever the season, it is rare to find the soil depleted of available moisture below 50 cm deep at harvest time. In such situations, it is probably wrong to declare drought as the limiting factor. We would get better water use efficiency and better yield gains by considering the ways in which we can achieve a large, strong and healthy root system in a stressful soil environment that is often waterlogged in mid-winter, has many fungal and nematode problems, and is deficient in some trace elements and toxic in others.

Routine Breeding Method

The routine breeding method is detailed in Figure 2. Shaded boxes indicate work carried out by others external to the Roseworthy staff, which consists of two scientists and four technicians. The Roseworthy method is essentially a pedigree method modified to overcome many criticisms of the classical method. Some of the techniques being used are those used by CIMMYT and Oregon State University, having been adopted following previous visits. For example, crossing (twirl method) is carried out in the field in organized crossing blocks of potential parents; this allows large numbers of crosses to be made.

Crossing

About 400 crosses are made annually and are of three main types:

Type 1. Those made to protect or improve elite cultivars. Mainly backcrossing to introgress one or two major genes such as a rust resistance, cereal cyst nematode resistance or a protein component.

Type 2. Crosses made to advance yield and quality potential, and to increase genetic variability and guard against genetic vulnerability.

Type 3. Parent building. Crosses aimed at combining some but not enough desirable attributes for selection of a new cultivar without further crossing.
Figure 2. Flowchart of Roseworthy routine breeding program 1996.
Each of these is critical to achieve short term improvements and also to establish a base for yield jumps and continued long term progress. Unfortunately, in today’s climate of short term funding and accountability, the last two types of crosses are in danger of being discontinued in many programs. Type 1 crosses are performed in part by collaboration with the National Rust Control Program at the Sydney University.

Parents for type 2 crosses are chosen on the basis of their performance in their own state or country of origin and data collected in South Australia. Usually at least one parent will be based on adapted material from within our own program. It is at this time that agronomic, physiological and phenological attributes are particularly observed. Crosses are made between lines of good performance but with contrasting characters in the hope that each will possess complimentary genes which, when recombined, will give transgressive segregation for yield improvement. A mild vernalization requirement is desirable so that the crop is kept vegetative long enough to produce a limited number of tillers and not run to head in dry, warm years. A height of about 80 cm is most desirable. Parents are laboratory tested for boron tolerance and protein alleles. Early crop vigor and leaf area duration are also taken into account.

**Early Generations**

One of the major criticisms of the pedigree method is that there are too few genotypes remaining by the yield evaluation stage to have much chance of finding transgressive segregants with higher yields. Such programs test what yields they possess but do not allow for selection for yield. Yield and quality evaluation is expensive, made even more expensive by the need to account for G x E effects. The Roseworthy strategy accounts for these two problems by yield testing only those lines that have already been adequately screened for simply inherited characters, while ensuring that there are enough such lines to contain some with improved yield and quality. With current resources and hard work, we can yield test about 10,000 entries in the first generation yield trial (F4), one site, unreplicated but with augmented checks (SPYT). This yield trial is carried out at Roseworthy in a farm field and close to our office headquarters, so observation from establishment through to harvest is almost daily. With such observations and two-dimensional spatial analyses of the underlying fertility trend surfaces, effective selection for yield can be practiced. Because it is only one site and one season, selection pressure is kept low. About 40 to 50% are retained. After grain conformation has been studied and a preliminary quality test performed, the number carried forward to replicated across-site evaluation is reduced to about 3,000 (30%). Fortunately, time and experience has shown that Roseworthy is an effective site, adequately representing the South Australian wheat belt for this preliminary screening on yield.

Counting backwards from this bottleneck to earlier generations leads to a total of about 60,000 F3 lines needing to be screened for foliar disease resistance, agronomic characters and grain conformation. To handle this number, single F2 heads are selected and planted unthreshed into an irrigated, inoculated, field rust nursery; unwanted hills are bent over whenever
identified, and survivors are sickled and threshed individually for grain conformation. About 10,000 remain.

About 10 years and more ago, the disease nursery needed to be about 180,000 hills, such was the culling rate when the frequency of stem and stripe rust resistance in our germplasm was low. The resources have been diverted into a septoria nursery. Pelschenke and sedimentation tests are no longer capable of discriminating quality differences among our lines. Thus for some years we have performed quality tests on only a few of the crosses and lines surviving this first generation yield trial, usually after they have been replanted in the next season. For the last three years, we have planted with this trial a replicated group of 100 lines selected from our program to represent the range of existing quality types, both good and bad (Burridge et al. 1994). These are harvested and subjected to a Buhler milling; the resultant white flour is put through the full range of quality tests, such as farinograph, extensograph, and baking.

As well, NIR readings are made on a wholemeal sample. These data are then used to calibrate the NIR apparatus for quality parameters. Good calibrations result for grain hardness, flour yield, protein content, extensibility, and water absorption. There is no correlation between NIR and dough strength. An NIR reading on a wholemeal sample from each of the SPYT survivors is then used to construct a quality selection index for further reducing the 50% retention down to 30%. HMW and LMW glutenin determinations on lines surviving from crosses likely to produce undesirable allelic combinations will give us a prediction of dough strength. The next step is to experiment with NIT on whole grain.

**Replicated Trials across Sites**

Yield and quality evaluations are carried out in multilocation trials as soon as seed supplies permit. Sites are chosen on representative farms in relevant locations. Plots are managed as closely as possible as fields of the farming community. Replication at a site is determined more by the quantity of grain that needs to be harvested for quality testing than by statistical considerations. Statistical procedures are kept relatively simple. The same randomization is used for the same experiment at each site. One field book suffices for all sites so observations from different sites are easily scanned. The first replicate is usually ordered so that highly heritable characters are easily compared between lines of greatest interest. The ordered first replicate simplifies subsequent seed and quality preparation.

TwoD spatial analysis software is used to analyze single experiments (Gilmour 1992), and across site analyses are graphically illustrated as scatter diagrams to display specific as well as wide adaptation. Quality data are simplified by the use of a selection index for initial culling (Burridge et al. 1990). Stepwise culling is often used to remove poor millers before proceeding with other tests.

In future, spatial analyses across sites and seasons that can handle the non-orthogonality resulting from annual culling will give a better estimate of variety performance in the later
generations (Basford and Phillips 1996; Cullis et al. 1996).

Accounting for G x E interactions: Use of probes
Some of the consequences of G x E interactions have been mentioned, particularly the uncertainty that such interactions introduce into the culling decisions, the need for representative sites and trial management to adequately sample the effects, low selection pressures to take account of the effects, and the increased costs that all this brings with it.

Thinking as a physiologist, unpredictable G x E effects and unpredictable environments, particularly the weather, upset ideotype descriptions and crop modeling.

Perhaps individual experiment results have been made worse by extraneous error brought on by poor experimental techniques. Two-dimensional spatial analyses can identify and extract some of this error—or at least highlight the problem—which can then be avoided in future experiments. Perhaps some of the conservative low selection pressure has been to take account of this problem, as well as real G x E.

Which data are relevant? What am I selecting for in a particular trial? These are questions that constantly concern breeders. Are there ways of getting better answers?

In the Roseworthy program, since 1981 a set of probe lines has been planted at each site as a bioassay. About 20 lines have been common to all sites and years; others are replaced by better probes or come and go for other reasons. This ‘indicator’ trial is used as a tool to improve selection amongst lines tested in other trials at the same site. Uses to which these probes can be put include:

1. Providing grain for trace element analysis to determine the importance of such problems at each site.
2. Determining the effects of foliar diseases as discriminating factors at a site by protecting some replicates with fungicide.
3. Providing grain of reference varieties for preliminary quality analysis to decide from which sites grain for quality assessment should come.
4. Providing grain of lines prone to late maturity α amylase for falling number tests to decide which sites could discriminate for this problem.
5. Keeping a biological record at distant sites infrequently visited by the breeder, e.g., height responses, vernalization.
6. Long and short term across-site and -season cluster analyses as a means of
   a. Determining the relevance/representativeness of a particular site-season.
   b. Determining the frequency of certain growing conditions in the future.
   c. Identifying specific G x E reactions to help in unraveling unknown stresses.
   d. Relative weighting (as contrasted to statistical weights) to apply to any one trial result.
   e. Giving a scientific basis on which to delete, move or add trial sites.
   f. A field repository for genotypes with ‘peculiar’ environmental responses.

Such probes are best sets of near isogenic lines varying for different combinations of certain known genes. This is difficult to achieve. Probes can include lines from other
cereals, e.g., barley to indicate boron toxicity and triticales for cereal cyst nematode. They could also be different agronomic treatments.

The best way to handle G x E effects is to understand and describe them in abiotic and/or biotic terms, discover the genetics of the response patterns and then breed and screen for desirable alleles, just as is done with stem rust resistance. After all, variation amongst lines in their response to stem rust infection would become part of the unpredictable G x E effect if the rust genotypes of the lines were not known and no one visited an infected site and took observations. Recent achievements using this approach are boron toxicity (Moody et al. 1993), zinc efficiency (Graham et al. 1992), LMW glutenin subunits and root lesion nematodes (Taheri et al. 1994 and Farsi et al. 1994). These are now understood and breeders can actively breed for them. Further research on root diseases is needed.

The Future

Advances in scientific knowledge and breeding technologies make the future of wheat improvement just as exciting as it has been in the past. Some future improvements to our routine breeding program have been mentioned in italics in previous paragraphs. There are many other areas which promise to speed the breeding and make it more effective. Examples are:

1. In Australia, using the Veery group of lines for their disease resistance and yield enhancing attributes without the problems of sticky dough. Langridge (pers. comm.) has succeeded in constructing an antisense secalin gene which he has transferred into wheat; he now has several plants growing from seeds that have disease resistance but where secalin production has been completely suppressed. Shepherd (pers. comm.), attacking the problem as a cytologist, has produced recombinants with smaller portions of the 1Rs arm; he has plants growing that have disease resistance but appear to have lost the secalin gene.
2. Use of marker genes for cereal cyst nematode resistance.
3. Setting up controlled and automated screening procedures for root lesion nematode.
4. Simultaneous selection of improved cultivars with an appropriate package of practices to give improved yields and quality.
5. A double haploid laboratory to speed up introgression of one or two genes into an otherwise elite variety.
6. Using IWIS and pedigree information to improve the choice of parents.
7. Making more use of animal and maize breeding principles and establishing male-sterile recurrent selection programs which should shorten the cycle time.

Acknowledgments

The breeding program described could not be successful without scientific and technical expertise provided by people too numerous to mention. Their efforts are indicated by the shaded boxes in Figure 2. Nor could the many trials be carried out without our farmer cooperators, whose locations are described in Table 1. The contributions of these people to the whole breeding effort is gratefully acknowledged. The technical
expertise of the core staff, viz. A. Macleod, D. Smith, J. Menzel, and G. White, is also acknowledged.

References


Gilmour, A.R. 1992. TwoD. A program to fit a mixed linear model with two dimensional spatial adjustment for local trend. New South Wales Biometric bull 1, 72pp.


Questions and answers

M. van Ginkel:
How do you locate suitable farm sites and how is the farmer compensated?

G. Hollamby:
Actual farms are pinpointed with the help of district agronomists for their relevance and for the cooperative nature of the farmer. I
have not had the fortune to visit the countries for which CIMMYT breeds but in Australia wheat farms are large and it is no problem to use up to five hectares of a farmer's land. The farmer is compensated in cash according to the income foregone by our presence. All grain harvested from trials is retained by the breeders.

J. Dubin:
Are lines that are tolerant to B excess sensitive to B deficiency?

G. Hollamby:
Good question, to my knowledge no one knows for sure. The physiology of the boron toxicity tolerance which we use is active exclusion of boron in the soil solution from entering the transpiration stream so that boron tolerant plants have less boron in their tissues. This begs the question as to whether, in boron deficient soil, these same genotypes would absorb enough boron to meet essential requirements.

J. Dubin:
Is Pratylenchus thornei tolerance good for P. neglectus?

G. Hollamby:
No, the genetics of tolerance and especially of resistance are different for both species. In South Australia Vanstone has identified the varieties Virest and Excalibur as having useful levels of resistance to P. neglectus. Because of our experiences with cereal cyst nematode we want to have both resistance and tolerance in a cultivar. Generally lines tolerant to a particular problem will tend to be selected if germplasm is evaluated for yield in locations with the as yet unidentified problem. Such lines though, if continually grown, may exacerbate the problem if the problem is due to a pathogen. Resistance can only be recognized after the problem has been characterized.

M. Mergoum:
Under stress (drought) conditions in Australia, in order to achieve high yields in wheat, you have ventured that you need plants with strong healthy systems. However, under such conditions root diseases are very important and might be one of the limiting factors. Are there any estimates of yield losses due to root rot? If so, what are the figures?

G. Hollamby:
Yield losses due to take-all (Gaeumannomyces) have been estimated at over 5% annually, but individual crops can be so badly damaged that they are not worth harvesting. Crown rot (Fusarium spp.) also causes severe losses in particular situations, especially in durum wheat crops. Root lesion nematodes (Pratylenchus spp.) can account for up to 20% yield loss in heavily infested crops. One of my students, Abdol Taheri, has demonstrated, in both controlled and field conditions, that there are interactions between many of these disease-causing organisms. With P. neglectus, for example, even minor pathogens such as Bipolaris and Microdochium can cause serious disease.

M. Mergoum:
Did you try to screen for root rot resistance using information and screening techniques developed particularly in Australia, for example, by Dr. G. Wildermuth?
G. Hollamby:
Yes, we certainly are trying to screen for root rot resistance. In fact, G. Wildermuth himself screens our most advanced lines as part of a national disease progress nursery. These techniques are not very suitable to screening large numbers from a breeding program. Pathologists are working to improve them. However, crown rot damage in South Australia is not always due to *Fusarium graminearum*, which is the species currently used in screening. Surveys indicate that *F. equisiti* and *F. acuminatum* are often present. Maybe there is a problem of properly identifying the true disease causing organisms and this, together with interactions between them, are hampering our attempts at breeding for resistance.

I. Ortiz-Monasterio:
Particularly for the micronutrients Zn and Mn, are you selecting for performance under low availability conditions or are you selecting for response to nutrient applications?

G. Hollamby:
For low availability. In the case of zinc the reasons for this are that it is our subsoils that are particularly deficient; because roots will not grow into zinc deficient soil, zinc fertilization will not get the wheat roots down into the moist subsoil. In the case of manganese, it is the highly calcareous nature of many of our soils that makes manganese unavailable to plants; even manganese fertilizer added to the soil quickly becomes unavailable to inefficient plants. VAM may be involved here too.

Let me make a point. Breeding programs have a pathologist as part of the team, some have a physiologist and an agronomist; maybe it is time we had a soil scientist also.

K.J. Young:
We have had more success with on-station yield testing than off-station testing where sites in farmer fields have been disappointingly variable. Would you comment on uniformity of test sites in farmer fields? Incidentally, I believe that difficulties in obtaining high quality yield trials is the most limiting factor in plant breeding efforts in many national programs.

G. Hollamby:
I agree that experiments on farms are more variable than those on station, but the unevenness that exists on farms are the conditions in which any new cultivar must perform. If the evenness of a station site is because some of the on-farm limiting factors have been removed, then the on-station site is not representative of the real world. We use a small blanket application of nitrogen to overcome one of the main sources of unevenness. Spatial analyses will take account of much of what remains. Your comment about problems of getting good yield trials in national programs coupled with my concern about representativeness has implications when countries are considering setting up new experiment stations. Even and representative stations using recommended farming practices are what is needed, not one sited for convenience, nor one sited and managed for maximum yields.

While on this subject of yield stability, I wonder whether those varieties which demonstrate stability over sites also contribute less to error variance within a site?
Hybrid Wheat: Advances and Challenges

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Abstract
Various researchers have indicated that hybrid breeding in wheat is not a viable option. There are, however, reports to the contrary. Our experience has been that hybrids outperform conventional varieties in environments where heat and moisture stresses are common. Hybrid breeding should benefit from the use of chemical hybridizing agents, and products from biotechnology might reverse decisions that were made on hybrid wheat in the past. Developing a hybrid program should center around identifying heterotic groupings of germplasm, developing male and female pools, and selecting within and between pools for characteristics that could make hybrids more competitive with conventional varieties.

The Hybrid Wheat Experience
It has been almost a hundred years since Shull suggested a method for producing hybrid maize (Shull 1909). Maize hybrids are used in all developed countries, and breeding hybrids has become a very profitable industry. Breeding methods to produce pure-bred inbred lines have been developed as well as technology to optimize hybrid vigor in agronomically important traits, techniques to identify superior hybrids in field trials and production techniques to commercialize hybrid seed production. Wheat breeding has also been highly successful, and substantial progress has been made in developing conventional cultivars during the past 40 years. Selection for resistance against diseases, higher yields, better quality and better adaptation has resulted in the crop being grown around the globe. Yet many breeders, while admitting the significance of the progress achieved, have been looking for a means to hybridize the crop for improved performance similar to that in hybrid maize. The discovery of a male sterile/fertility restorer system in wheat in the early 1960s motivated most breeders to embark on hybrid wheat development, and a large number of breeders were employed by private companies. It became a popular subject for research in the public sector, and large volumes of reports and papers have been published on the expression of heterosis, male sterility systems, male fertility restoration systems, and hybrid performance in wheat. Discussions on hybrid wheat development became an intellectual exercise arguing the benefits of hybridization.

The whole field has been thoroughly reviewed by different authors (Johnston 1985; Lucken 1985; Maan 1985; Virmani and Edwards 1983; Wilson 1984; Wilson and Driscall 1983; Lucken and Johnson 1988).
Most of these authors are positive on the prospects of hybrid wheat, but in a recent review (Pickett 1993) of research and development of F1 wheat hybrids during the past 40 years, Pickett did not share their views on:

The feasibility of hybrids—The causes of heterosis in wheat include genetic dominance and overdominance. Evidence suggests that improvements in yield arise from dominance, making it possible to select conventional cultivars that match or excel F1 hybrids. Hybrids derived from modern, highly bred cultivars appear to show less heterosis relative to the performance of the parental lines than hybrids of older, lower yielding parents. Hybrids do not offer an improvement in important characteristics such as disease resistance, performance stability, suitability of ideotype and breeding time scales. It also appears unlikely that high, uniform grain quality will be achieved more readily by hybrid varieties.

The three systems of male sterility—Cytoplasmic male sterility has had the longest period under investigation and use, but is seen to be slow and lacks versatility in methods of fertility restoration. Nuclear male sterility has enjoyed the least success due to the lack of cost-effective methods of maintenance. Chemical hybridizing agents allow speedy hybrid development, but problems arise from toxicity and inadequate selectivity. Pickett also discusses ways in which biotechnology could help develop male sterility.

Hybrid seed production—Hybrid seed production has been problematic because the self fertilizing reproductive system of wheat is poorly adapted to outcrossing. Causes of poor outcrossing are considered to be influenced by the morphology and biophysics of pollen and the effect of climate.

The success of hybrid wheat—The relationships between the additional costs of male sterilization and seed production are clearly unfavorable in both developed and developing countries. The amount of research and development, principally in the area of genetics, required to test the possibility of making hybrid wheat worthwhile appears to be prohibitive. It appears that yield advantages obtained through heterosis are fixable and therefore improvement of conventional cultivars remains the chosen strategy in wheat breeding.

Most people involved in hybrid wheat breeding share Pickett's views and, consequently, several companies abandoned their research and development on hybrid wheat. Those who continued rescheduled their strategy to include chemical hybridizing agents and biotechnology.

Hybrids As a Commercial Product

However, some institutions in the public as well as the private sector have continued their research on hybrid wheat. Hybrids based on cytoplasmic male sterility/restorer systems have been developed, produced and marketed successfully. In South Africa,
wheat hybrids developed by both Cargill and SENSAKO have been very successful. Since SENSAKO has been highly effective in breeding and releasing conventional cultivars, our involvement and experience in hybrid wheat development over the past 25 years can be objectively reported here.

Successful commercialization of a hybrid depends on the wheat growers’ acceptance of the product. This depends not only on the hybrid’s performance, but also on the cost of hybrid seed. We were fortunate to identify an environment where historically wheat has been grown at very low seeding rates or population densities. In the Free State, a province of South Africa, wheat is grown during winter on moisture that has been conserved from summer rains and normally without any further rain from planting up to post anthesis, often even up to maturity. In Figure 1 the overall long term rainfall distribution has been summarized with the rainfall of the past two seasons for the drier, western part of the production area, and in Figure 2 for the eastern part, which has higher and more reliable rainfall during spring. The adult wheat plants are mostly under moisture stress often associated with very hot spells in spring. Fortunately most farmers in this environment also plant maize and sunflower hybrids and are thus familiar with hybrids and with the higher cost of hybrid seed.

Cost efficiency of planting hybrid seed

The cost efficiency of planting hybrid seed depends on: 1) the price of the hybrid seed, 2) the seeding rate, 3) the yield level, and 4) the planter technology.

Seed price—The major factor effecting the seed price is the effect of seed set on the production cost of hybrid seed. This is clearly demonstrated in Figure 3. At 50% seed set, the production cost rises to double that of non-hybrid seed; lower seed set makes the price of hybrid seed production non-viable. Environmental factors influencing cross pollination and the management thereof should be such as to promote high seed set on the female. Females differ in the period that their flowers remain receptive while males differ

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**Figure 1. Rainfall Western Free State.**

**Figure 2. Rainfall Eastern Free State.**
in the amount and distribution of pollen shedding. Parental lines should be selected for floral characters promoting successful hybridization and care should be taken to nick female receptiveness and male pollen production. Peak pollen production after 60% of the females’ flowers have opened optimizes nicking. It has also been experienced that the higher the seed set on the female, the better the quality of the seed. Optimizing hybrid seed production and especially seed set on the female is a critical factor in the successful exploitation of hybrids.

**Seeding rate**—In the Free State, seeding rate is normally not higher than the 25 kg ha\(^{-1}\) used with conventional cultivars. Engelbrecht (1991) found the number of tillers m\(^2\) to have the highest correlation with yield. The highest heterosis for this character and also for yield was found at low seeding rates of 5-10 kg ha\(^{-1}\) and narrow row spacing (25 cm instead of 75 cm). This production management of lower seeding rates and narrower rows (although not always possible when topsoil moisture is deficient) promotes stable yield over locations and seasons. In Figure 4 the effect of seed price and seeding rates on the input cost to the farmer is given as a percentage of the income per ton of grain produced. This clearly illustrates that at the maximum seeding rate for winter wheat cultivars (25 kg ha\(^{-1}\)) the cost will be 23.5% of the yield of one ton of grain. Higher seeding rates, 100 kg ha\(^{-1}\) or higher, as in the case in spring wheat, demonstrate the high cost effect of hybrid seed in relation to the seed price of a conventional cultivar. Seed costs can be significantly reduced by lowering the seeding rate to 10 kg ha\(^{-1}\) at which level the effect of hybrid seed (which costs four times more than commercial seed) is less than twice the commercial seed price at 25 kg ha\(^{-1}\) and less than 18% of the yield of one ton of grain.

**Yield level**—The yield advantage of hybrids has to compensate for the additional cost of hybrid seed at different yield levels, at two and four times the price of commercial seed and at two different seeding rates, as

![Figure 3](image-url) **Figure 3.** The effect of seed set in the female plants on the production cost of hybrid seed.

![Figure 4](image-url) **Figure 4.** Input cost, as a percentage of the price of one ton of wheat grain, relative to seeding rate and seed price (seed price of conventional cultivars = c).
summarized in Figure 5. This shows that with a seeding rate up to 25 kg ha\(^{-1}\), a seed price twice that of non-hybrid seed, and at a yield level of 1.5 ton ha\(^{-1}\), the yield advantage needed for a hybrid to offset the higher seed price of the hybrid is less than 4%. To achieve the same result with seed costing four times as much as non-hybrid seed, the yield level should be higher than 1700 kg ha\(^{-1}\). The lower the yield level at which the hybrid has been produced the higher the yield advantage of the hybrid must be and the less attractive it is to grow hybrid seed. Yield should be optimized by creating an environment to enhance the expression of hybrid superiority and to maximize the benefits of water conservation, seeding rate, and row width on the tillering ability of hybrids.

**Planter technology**—To plant wheat successfully at a very low seeding rate and in variable conditions where the dry topsoil varies in depth up to 15 cm requires special planter technology. Commercial planters that have a tine pushing the dry topsoil away and a press wheel have been modified to space-plant, break up shallow compaction (from water conservation techniques during the rainy season), and place the fertilizer in a vertical band away from the seed. We are using this technology in our research plots to optimize root development and tillering ability.

**Hybrid Performance**

Data from SENSAKO performance trials for the past two seasons will be used to compare the performance of hybrids. The trial was replicated over 25 locations in the winter wheat production environment of the Free State. Since all new hybrids tested have Russian wheat aphid resistance (*Diuraphis noxia*) from at least one parent, they were compared only to resistant conventional cultivars. Yield means are summarized and compared in Table 1. All winter hybrids tested outyielded all non-hybrids by 14.8 and 11.5% in 1994 and 1995, respectively. If the means of the five highest yielding hybrids are used, they outyielded the conventinals by as much as 23.2 and 18.5%. If, however, they are compared to Tugela DN (a very high yielding cultivar), these values drop to 5.7 and 11.1%, respectively, for the two seasons. The trial with intermediate types included excellent new conventional lines that the hybrids outyielded by only 9.3%.
Comparisons of the consistency of yield performance can best be done by a superiority measure for cultivar x location data (Lin and Binns 1988) defined as the distances mean square between the cultivars’ response and the maximum response averaged over all locations, the lowest value being the best performance. This analysis was done for both winter and intermediate cultivars. The highest yielding new winter type hybrid was compared to Tugela DN for both the 1994 and 1995 seasons (Figure 6). The highest yielding intermediate type hybrid was also compared to SST 333 as a check cultivar (Figure 7).

The regression of the yield deviation of these two hybrids from the two check cultivars, calculated on the yield of the check at each location, could be used to predict the expected hybrid advantage at different yield levels of the check. The predicted advantage was expressed as a percentage and is given in Figure 8.

<table>
<thead>
<tr>
<th>Cultivar / Hybrid</th>
<th>Mean yields (kg ha⁻¹)</th>
<th>1994</th>
<th>1995</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Winter wheat</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All hybrids in test</td>
<td>1808</td>
<td>2001</td>
<td></td>
</tr>
<tr>
<td>All conventional cultivars</td>
<td>1575</td>
<td>1794</td>
<td></td>
</tr>
<tr>
<td>Highest 5 hybrids</td>
<td>1940</td>
<td>2126</td>
<td></td>
</tr>
<tr>
<td>Tugela DN</td>
<td>1835</td>
<td>1914</td>
<td></td>
</tr>
<tr>
<td><strong>Intermediate wheat</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All hybrids in test</td>
<td>1848</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All conventional cultivars</td>
<td>1692</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Highest 5 hybrids</td>
<td>1915</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SST 333</td>
<td>1551</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Although based on the data for only two years, it clearly shows that hybrids do yield better than conventional cultivars. This performance is consistent over locations and seasons, while the hybrid’s advantage over the highest yielding check is much higher at the lower yielding locations than at the higher yielding ones. Since in this specific environment yield reduction is a function of water stress, it can be concluded...
that hybrids have an advantage over conventional cultivars under conditions of water stress. Although planting dates for winter and intermediate types differ, it seems the advantage is comparable but lower in the case of the winter hybrid.

These experiences are convincing evidence for continuing wheat hybrid research and development. This might be of particular importance for environments where wheat is being produced under marginal conditions.

**Challenges**

The development of hybrid wheat should be reconsidered and new knowledge and technology used to stay abreast of conventional wheat development.

The biggest limitation so far has been the lack of knowledge of heterotic grouping of parental germplasm. Optimizing genetic diversity between female and male gene pools has been the major strategy in breeding hybrids. In following this basic requirement of breeding maize hybrids, breeders developing wheat hybrids have lagged behind in their pursuit of hybrid vigor. Conventionally and historically, adaptation to an environment required the repeated use of certain parents as donors for disease resistance and quality characteristics. The selection techniques used, although highly successful, resulted in the development of related cultivars. Relatedness among the world’s spring wheat germplasm will be a major restriction in developing spring wheat hybrids. This will most certainly apply to germplasm introduced from CIMMYT programs. In South Africa, almost all spring wheat cultivars, except for donor parents for disease resistance, originated from a very narrow gene pool involving Inia 66 (Jordaan 1995).

Pedigrees and kinship relationships may help to decide what should be crossed to what, but a technique is needed to access genomic diversity precisely. Restriction fragment length polymorphisms (RFLPs) have been successfully utilized in maize (Lee et al. 1989; Melchinger et al. 1990; Smith et al. 1990). The relation of hybrid performance to parental diversity was tested in wheat by Martin et al. (1995). In their study, a narrow range of heterosis limited the ability to detect a relationship between genetic diversity and hybrid performance, but the results nevertheless showed that sequence tagged site (STS) polymerase chain reaction (PCR) primer sets effectively differentiated genetically and phenotypically similar genotypes in wheat.
When hand-crossing wheat plants, the small number of seeds produced per cross obstructs intermating progeny and the evaluation of such progeny. This has limited the use of short-cycle, recurrent, selection methods. Intermating wheat populations has been proved effective (Chandler et al. 1993), while the Taigu genetic male sterile gene was used to promote complex crossing and facilitate recurrent selection (Huang and Deng 1988). Positive results from the use of recurrent selection were also obtained by Löffler et al. (1983), but undesirable correlated responses limit the technique in the absence of multiple selection practices.

Chemical hybridizing agents (CHA) have been developed that facilitate hybrid seed production and implementation of selection for combining ability. However, CHA products are privately owned and their use restricted. It is also tempting to use the best products of large, intensive breeding efforts directly as parents for hybrid seed production. The absence of sterile plants in the F2 population might promote the use of F2 seed for cultivation by farmers.

Remodeling selection techniques to optimize genetic gain for combining ability seems to be one of the major challenges for hybrid wheat development.

Genetic engineering systems for wheat are developing very fast; since there is no shortage of agronomically useful characteristics to be improved, expectations of modifying the wheat genome are realistic. Methods for transforming wheat are becoming available; introducing foreign genes into wheat is a challenge to the wheat breeder. Marker assisted selection will not only speed up the development of parental lines but will also allow pyramiding genes from different species that influence the same character. Quantitative loci affecting complex characters such as yield and combining ability might be tagged to simplify selection.

Haploid breeding is already being successfully implemented in most breeding programs. This tool shortens generation time significantly and enables the breeder to stop segregation at will.

The price of hybrid seed should be comparable to that of seed of conventional cultivars. There should be a definite advantage in the characteristics of the hybrid to give the wheat farmer a reason to grow it. Research on seed production techniques and floral characteristics should be undertaken to make marketing hybrid seed a viable option. Changes in production techniques to lower seeding rates, especially under conditions where very high seeding rates are the standard, poses a real challenge.

Incorporating multiple characteristics or complex resistance into a single genotype is difficult and time consuming, but much easier to achieve when complementary characters are combined in a hybrid.

The identification of heterosis for characters involved in adaptation to stress environments might enable the breeder to develop varieties with better performance under conditions of moisture and nutrient stresses.
References


Questions and answers

J. Dubin:
You have heard about ‘genetic vulnerability’. What are you doing to assure diversity of resistance to diseases and what are your key diseases?

J. P. Jordaan:
Disease resistance is still a key issue. Resistance to stem rust, leaf rust, septoria nodorum and eyespot diseases are very important, but the level of resistance in the dominant commercial varieties is so high that epidemics are seldom experienced. Since the expression of resistance by most of the major genes is dominant, hybrid breeding enables the breeder to widen resistance in hybrids by including major genes or different forms of resistance from both parents in the hybrid.

R. A. Fischer:
You mentioned the solid stem gene in the context of resistance to eyespot lodging. Does it assist in other types of lodging?

J. P. Jordaan:
We found that the solid stem genes have a structural expression in preventing lodging. In this respect, it was observed to be a source of resistance to lodging caused by the root pathogens but also by abiotic factors.

E. Duveiller:
Is the SENSAKO plant adopted by many farmers and how much does it cost?

J. P. Jordaan:
The planter that we use to plant wheat trials under dryland conditions is a modification of planters being used by farmers. On the other hand, many farmers have adopted the principle of placing the fertilizer away from the seed in a vertical band with starter given at the seed. The technology was developed to stimulate root growth in wide rows and low seeding rates. The new commercial planters has been adopted by some farmers and included the features of the trial planter. It cost approximately US$4,000 for a planter with four units.

J. Shoran:
Can temperature dependent (induced) male sterility behavior be used for obtaining hybrid seed in wheat?

J. P. Jordaan:
This would be a helpful tool to produce hybrid seed. The induced male sterility should be stable at a given temperature and the temperatures in the production environment should be stable and predictable. We do not have any experience of this sterility mechanism in our country, but I would guess that it would be very difficult to use temperature-induced male sterility to produce hybrid seed.

D. Hoban:
Could you comment on the role of apomixis in exploiting hybrid vigor in wheat?

J. P. Jordaan:
I do not think that hybrids would be needed if apomixis were available in wheat. I don’t know of anyone having an apomictic wheat plant, but that does not mean that it cannot be produced in future.
Limits to Yield Revisited

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Abstract
An early effort aimed at exploring limits to radiation-use efficiency of crops (Crop Sci 3:67-72, 1963) is reexamined in light of current knowledge of photosynthesis and respiration. Light-limited gross photosynthesis estimated with a quantum requirement (qr) of 10 to 16 photons per CO₂ reduced to CH₂O can be translated to wheat biomass with a growth yield near 0.7 g biomass g⁻¹ glucose (to account for respiration associated with growth). Using that approach, it seems that RUE might be considerably more than values observed for real wheat crops (near 3 g DM MJ⁻¹ solar radiation intercepted). With further allowances for maintenance respiration (Rm), down-regulation of photosynthesis when light is not limiting, and other matters, however, qr rises towards 24 and the ‘gap’ between observed and potential productivity largely disappears. Values between 3 and 3.8 g DM MJ⁻¹ seem to represent a practical limit for wheat RUE. Maximum RUE is found to vary strongly with size of crop, temperature, radiation level, and ambient [CO₂]. In contrast to variations in those factors, variations in specific Rm have relatively little influence on RUE. Increase in ambient [CO₂] towards 600 ppm dramatically lowers qr, however, and RUE rises towards 5 g DM MJ⁻¹ at 600 ppm CO₂.

Introduction
Agronomists worry about crop yields reaching a limit that their continued efforts cannot raise. Over three decades ago, Loomis and Williams (1963) argued that maximum crop yields could be significantly greater than those yet achieved. Now, after a generation of research by plant physiologists and breeders, and technological innovation by farmers, it is time to look again at limits to yield.

Yield Levels of Agriculture
As yield depends in part on management and local environment, three measures of regional yield find use. Average yield for a region reflects farmers’ success with the many certainties and uncertainties surrounding production, and their average employment of technology. Some farmers regularly obtain high yields. They stand out above the average as a measure of what is attainable by skilled people employing the best available technology. Record yields and maximum yields, as predicted by models, are important in defining not only progress in breeding and agronomy but also ‘gaps’ between what is achieved and what might be possible.

The reasons why average yields lag behind attainable yields are sometimes readily apparent in poor stands or lack of nutrients. Other times, yield is influenced by a complex of factors including weather, soil fertility, pressures due to disease, pests and weeds,
market prices for inputs and produce, farmer
skill, and luck. Given limitations of labor and
machinery, for example, it is almost
inevitable that some fields in a region will be
sown too early and some too late. The
optimum sowing date varies with the
weather, and thus over years, and is difficult
to predict.

Conditions necessary for reaching attainable
yields are generally known including
freedom from weeds and disease, and soil
with appropriate pH and drainage.
Identifying the factors contributing to the
gap between average and attainable yields
within a region, while difficult and, in some
cases, impossible, can serve as a basis for
improving farm practices. Economic and
environmental factors dictate that gaps
should always exist between actual and
attainable yields, on one hand, and potential
yield, on the other. Carrying inputs to the
necessary levels of diminishing returns
greatly lowers the efficiency in use of
expensive inputs and greatly increases the
potential for environmental damage.

To produce a record crop, weather,
technology, farmer skill and other matters
must all be favorable. Record yields serve as
one measure of ‘genetic potential’.
Knowledge of such values for wheat is
sparse, however, particularly on a regional
basis, although values near 11 t dry grain ha⁻¹
(1100 g m⁻²) are not uncommon. That is
much greater than the current average yield
for any region of the world. Assuming a
harvest index of 0.45 for modern wheat, 11 t
corresponds to production of 24.5 t of
aboveground biomass. Recent reports of 15 t
grain ha⁻¹ being obtained in Chile and the
UK translate to nearly 30 t biomass ha⁻¹ after
correction for moisture content.

Because technology, farmer skill, and weather
change with time, genetic advances cannot be
calculated directly from changes in real
yields. This was revealed nicely in studies by
M.A. Bell and colleagues for the Yaqui Valley
in northwestern Mexico. Since 1968, that
region has been sown almost exclusively
with a series of modern semidwarf cultivars
of wheat. A linear regression of average yield
over years indicated a yearly increase of
57(±13 SE) kg ha⁻¹, from 3860 kg grain ha⁻¹ in
1969 to 1991 (Bell and Fischer, 1994). Much of
the variability was due to weather. When
average yields were adjusted with a model
for weather variations (including a trend
towards less favorable weather in recent
years), the yearly increase was seen to be 103
(±15 SE) kg ha⁻¹. Through survey research,
Bell et al. (1995) were able to define and then
isolate several factors contributing to that
gain (Table 1). In line with other recent
studies, genetic gains were relatively small,
particularly in recent years.

The principal question before us now is
whether photosynthetic systems are capable
of much higher yields than observed records,
or whether only further small improvements
are possible.

Table 1. Summary of sources of gain in average
yield of wheat in the Yaqui Valley of Mexico, 1969-
1991 (adapted from Bell et al., 1995).

<table>
<thead>
<tr>
<th>Source of gain</th>
<th>Yield gain kg ha⁻¹</th>
<th>Yield gain kg ha⁻¹ y⁻¹</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>2370</td>
<td>103</td>
<td>100</td>
</tr>
<tr>
<td>Genetic</td>
<td>660</td>
<td>29</td>
<td>28</td>
</tr>
<tr>
<td>N fertilizer</td>
<td>1140</td>
<td>50</td>
<td>48</td>
</tr>
<tr>
<td>Other</td>
<td>570</td>
<td>25</td>
<td>24</td>
</tr>
</tbody>
</table>
The Basis of Yield

Crop growth and yield are derived from photosynthesis and therefore dependent on receipt and capture of solar radiation. Correlations between leaf photosynthetic rates measured at points in time and yield are, unfortunately, weak (Evans 1993). Leaf photosynthetic rates vary widely, depending on a developmental history in the past environment leading to differences in leaf thickness, stomatal frequency, chlorophyll and enzyme contents, and other parameters. Also, leaf photosynthetic rates change quickly as \( [CO_2] \), temperature, water status and irradianc change. The individual leaves perform according to their age and place in complex canopies that progress from sparse to complete cover and then senescence during the season. Additional complexity arises from the metabolism involved in the biosynthesis, partitioning, and maintenance of biomass. Therefore, about the only way to relate leaf rates with yield is through dynamic models that embrace the key elements of that complexity (Amthor and Loomis 1995).

Much can be learned, however, through consideration of net biomass production per unit solar radiation absorbed by the entire canopy, the so-called radiation-use efficiency (RUE). RUE can be presented in various units; g DM MJ\(^{-1}\) radiation are used here. DM production (crop growth rate) is obtained through periodic sampling of the crop and radiation absorption is measured with sensors placed above and below the canopy. In simple terms, final yield is the product of cumulative seasonal radiation absorption, RUE, and the portion of total biomass that appears as grain.

Potential Radiation-Use Efficiency

Potential RUE can be calculated from physiological principles relating to photosynthesis and respiration, as was done by Loomis and Williams (1963). Steps in the analysis (Table 2) involve: 1) receipt and capture of photosynthetic photon (quantum) flux, 2) gross assimilation of \( CO_2 \) per photon of such light, and 3) correction for carbon losses associated with respiratory metabolism and conversion of photosynthate to biomass.

The photon flux in solar radiation

The absorption spectrum of chloroplast pigments and the level of energy required for a single photochemical event—electron transport, the first step towards production of energy carriers, ATP and NADPH, that do the work of \( CO_2 \) reduction—result in photosynthesis being limited to only some of the wavelengths found in solar radiation. For rough purposes, 400 to 700 nm define photosynthetically active radiation (PAR). This band is essentially the same as that for human vision. On an energy basis, PAR amounts to about 0.5 J J\(^{-1}\) solar radiation.

Because light is captured as individual quanta, an estimate is needed of the number of photosynthetically active quanta per MJ of solar radiation. That number varies with atmospheric conditions and the path length through the atmosphere of direct rays (and thus with time of day and year, and latitude). Loomis and Williams (1963) calculated 2.06 mol quanta MJ\(^{-1}\) total radiation based on P. Moon’s spectrum for direct sunshine through air mass 2. That has been criticized
as not giving sufficient weight to the greater fraction of useful quanta present in diffuse radiation. Monteith and Unsworth (1990, p. 49), for example, give a value for 2.3 mol PAR MJ⁻¹ from England and a range of 2.1 to 2.9 mol PAR MJ⁻¹ from other locations.

In addition to natural variation in the photon content of solar radiation, it is important to remember that the instruments in common use for measuring solar radiation in energy or quantum terms are usually accurate to only about ±5%. The calculations in Table 2 are based on 2.2 mol quanta MJ⁻¹, which seems appropriate to intermediate and lower latitudes during spring.

**Table 2. Estimates of potential radiation-use efficiency (RUE) of a C₃ crop with various values of gr. Assumptions are for a wheat crop at midseason with a closed canopy (LAI=3 to 4) completely intercepting incident solar radiation.**

<table>
<thead>
<tr>
<th>Solar radiation intercepted</th>
<th>1 MJ</th>
</tr>
</thead>
<tbody>
<tr>
<td>PAR quanta intercepted by canopy</td>
<td>2.2 mol</td>
</tr>
<tr>
<td>Canopy reflection</td>
<td>-0.13</td>
</tr>
<tr>
<td>PAR quanta absorbed by canopy</td>
<td>2.07 mol</td>
</tr>
</tbody>
</table>

**Absorption of PAR**

Only a portion of the light intercepted by leaves is absorbed usefully in chloroplasts by chlorophylls a and b and accessory pigments such as carotenoids. Some light is lost to reflection or transmission and through absorption by structures other than green tissues and by cell components other than those contributing to photosynthesis. For closed canopies (generally LAI=4 or more), about 6% of the light is reflected to the sky (Goudriaan and van Laar 1994). By contrast, most transmitted light (principally in the green region) can be captured deeper within the canopy; that loss is therefore small and may be ignored for our purposes. Absorption by other structures and pigments is not so easily assessed. Allowances can be made for absorption by nongreen tissues, and by green tissues such as stems with less photosynthetic capability than leaves. Comparison of albino and green leaves (Seybold 1933), for example, indicate that inactive absorption may amount to 10% of intercepted quanta.

In Table 2, 6% of the intercepted visible quanta are indicated as lost to reflection while losses due to inactive absorption and...
less-effective absorption by stems are ignored. This bases the calculations on all light absorbed by the canopy, in line with experimental measurements, rather than on light actually absorbed by chlorophyll.

**Quantum yield/requirement in photosynthesis**

*C3 and C4 photosynthetic systems*—Given extreme variations in light flux, a dry aerial environment containing a small concentration of CO\(_2\) (near 350 vppm) and a large concentration of O\(_2\) (near 21%), higher plants encounter difficulty in maintaining efficient photosynthesis over time. A major problem is that rubisco, the carboxylating enzyme for CO\(_2\) fixation into the Benson-Calvin cycle, also acts as an oxygenase, releasing CO\(_2\) from previously fixed carbon. Ribulose bisphosphate (rubP) is the substrate in both reactions. The relative rates of carboxylation and oxygenation of rubP depends on the concentrations of CO\(_2\) and O\(_2\) at the enzyme’s active site.

Two distinct photosynthetic systems have evolved with partial solutions to this problem. The C4 photosynthetic system (e.g., maize) carries out CO\(_2\) fixation in two stages that serve to concentrate the scarce supply of CO\(_2\) into bundle sheath cells, where rubisco and the Benson-Calvin pathway are located in those leaves, sharply raising CO\(_2\)/O\(_2\). Although less efficient in dim light than the C3 photosynthetic system because of the extra stage in fixation, this improves RUE in bright light and with less loss of water than is the case for the C3 system. The C3 system found in wheat, although lacking CO\(_2\)-concentrating mechanisms, is able to recover some of the carbon released by rubisco oxygenase activity through a process termed photorespiration, and use it subsequently in rubP regeneration and rubisco carboxylase activity. On average, depending on other activities such as amino acid synthesis, about 3/4 of the carbon in glycolate formed from rubP by rubisco oxygenase activity is saved. Most of the remainder is released as CO\(_2\).

The effect of photorespiration in a C3 leaf is illustrated in Figure 1a, and its absence in a C4 leaf in Figure 1b, by comparing performance in normal air with that in air low in O\(_2\). Photorespiration is also suppressed by supplying CO\(_2\) at a saturating level because, just as O\(_2\) competitively inhibits photosynthesis, CO\(_2\) competitively inhibits oxygenase activity.

*Light-limiting conditions*—Assimilation of CO\(_2\) by leaves of wheat and other C3 plants well nourished for nitrogen increases as light flux increases from 0 towards 800 mmol PAR m\(^{-2}\) s\(^{-1}\) (about one-half of midday sunlight), beyond which the light-response curve flattens to a plateau. This effect is termed light saturation. C4 species, with their CO\(_2\)-concentrating step, saturate at higher light levels. Photosynthesis is therefore most efficient for both C3 and C4 plants, in terms of the most CO\(_2\) being fixed per mol quanta absorbed (quantum yield), in dim light when light supply limits the photosynthesis rate. Canopy photosynthesis flattens less with increasing light and seldom comes to a plateau, even in full sunlight. This occurs because most of the leaves are either displayed obliquely to the sun’s rays (less flux per unit area leaf) or shaded by other leaves. Canopy light-response curves are concave down, however, so canopies also use dim light most efficiently.
Differences in efficiency are grasped more easily from the inverse of the quantum yield, here termed quantum requirement, \( q_r \), in mol quanta mol\(^{-1} \) CO\(_2\) fixed. (Quantum 'use' is perhaps a better description.) The theoretical minimum value of \( q_r \) is near 9 quanta actually absorbed by photosynthetic pigments (Nobel 1991). Corrected for 10% inactive absorption, minimum \( q_r \) would be near 10 mol quanta absorbed by a leaf mol\(^{-1} \) CO\(_2\) fixed. In their study, Loomis and Williams (1963) used \( q_r = 10 \), based on measurements with green algae in bicarbonate solution (saturating CO\(_2\)). Values of \( q_r = 10 \) have since been observed for O\(_2\) production (a concomitant of CO\(_2\) fixation) for C\(_3\) higher plants by Björkman and Demmig (1987) when a saturating level of CO\(_2\) (5% v/v) was used to suppress photorespiration. Production of O\(_2\), while stoichiometrically close to CO\(_2\) uptake, may differ from it. At 25°C, the smallest values of \( q_r \) for CO\(_2\) uptake, obtained with photorespiration suppressed by saturating CO\(_2\) or by air with low O\(_2\), are near 11. The constancy of this value across all C\(_3\) species indicates that very little variation in rubisco has been introduced during millions of years of evolution.

Due to photorespiration, rather different values of \( q_r \) are obtained in normal air (325 vppm CO\(_2\) and 21% O\(_2\); Figure 1a). In C\(_4\) leaves (Figure 1b), \( q_r \) is unaffected by O\(_2\) concentration because photorespiration is inhibited by the high CO\(_2\) levels in the bundle sheath cells. Values of C\(_4\)-leaf \( q_r \) exceed those for nonphotorespiratory C\(_3\) leaves, however, because extra ATP is required for regeneration of phosphoenolpyruvate in first stage of the C\(_4\) cycle.

McCree (1971) found requirements for quanta absorbed by leaves of several C\(_3\) crop species in normal air were near \( q_r = 15 \) at

![Figure 1](image-url)
28°C. For oat, at least, qr improved to about 13.5 at 11°C. As depicted in Figure 1c, Ehleringer and Björkman (1977) found that qr for C3 Encelia californica in normal air increased exponentially from near 14.5 at 14°C to almost 24 at 38°C. But, with photorespiration suppressed (air with 2% O2), qr was 12.5 and unaffected by temperature. This positive response of C3-leaf qr to temperature in normal air (Figure 1c) results mainly from the temperature dependence of rubisco’s CO2/O2 specificity, and to some extent from differential effects of temperature on solubilities of O2 compared to CO2.

Light not limiting—Quantum use per CO2 increases when the photosynthesis of C3 leaves saturates in bright light. This occurs because the dark reactions of the Benson-Calvin (B-C) cycle fail to keep pace with the photosynthetic light reactions. ATP and NADPH go unused and electron transport is ‘closed’. This may occur because the B-C cycle is simply too slow, because inorganic phosphate (Pi), which must cycle between chloroplast and cytosol, becomes tied up in intermediates, or because the CO2 flux through stomata does not keep pace with fixation, causing the leaf’s internal CO2 concentration (Cj) to decline. The decline in Cj is especially strong when stomata close due to moisture stress.

Continued over-excitation of the light-harvesting system with electron transport shut down causes short- or long-term damage to the system (‘photoinhibition’; Long et al. 1994). The possibility for damage is reduced by ‘down-regulation’ (Weis and Berry 1989) in which excess energy is passed to carotenoids and dissipated through long-wave radiation, convection, and transpiration. Maintenance of the plant’s water status and open stomates is important not only for cooling but also for a high conductance for CO2, which keeps the dark reactions going and electron transport ‘open’. In C3 leaves, protection from damage is also provided through CO2-recycling by photorespiration; ATP and NADHP are used, transport remains open, and qr for CO2 increases.

Down-regulation and photorespiration protect C3 systems from oxidative damage but they sharply increase the apparent quantum requirement. In addition, daily losses due to photoinhibition may easily amount to a 10% increase in qr (Long et al. 1994). It is useful to note, however, that Farquhar’s biochemical model of photosynthesis (Farquhar and von Caemmerer 1982), which includes photorespiration but does not consider photoinhibition, generally provides good agreement with leaf rates of well-watered plants (Long 1991; Amthor and Loomis 1995). That model also demonstrates how effects of temperature in increasing photorespiration are offset by a similar stimulation of B-C dark reactions. As a result, light-saturated C3 photosynthesis rates usually have a broad temperature optimum.

An increase in chlorophyll fluorescence is seen when light harvesting exceeds the capacity of the dark reactions. The fluorescence is closely linked with the increase in qr and fluorescence measurements are now used widely for...
detection and analysis of stress effects on crops (Seaton and Walker 1990; Snel and van Kooten 1990).

It is clear that high RUE in strong light depends on several factors: adequate water to allow high stomatal conductance and transport of CO₂ into leaves; leaf arrangements that avoid excessive display normal to direct beam radiation; adequate leaf nutrition to support a large photosynthetic capacity and rapid processing of assimilated carbon; and canopy ventilation that permits supply of CO₂ and dissipation of heat by convection. It also is clear that qr=10 cannot be achieved by C₃ or C₄ crops except with limiting light and CO₂ saturation. With so many factors acting to increase $\xi_{II}$ under field conditions, values from 10 to 30 mol quanta mol⁻¹ CO₂ are employed for calculations presented in Table 2.

Maintenance respiration and growth yield

Dark respiration in plants—Respiration can be partitioned into two functional components, one related to maintenance of existing material ($R_m$), and one related to biosyntheses involved in growth ($R_g$). Allowance must be made for assimilate use in $R_m$ before attempting to estimate net production of biomass.

$R_m$ adjustment—Maintenance respiration occurs in all living tissues. It is presumed to relate to repair of existing structures and maintenance of ion balances against leakage and is proportional to the amount of existing biomass and protein content, rather than to radiation intercepted. $R_m$ increases exponentially with temperature with a $Q_{10}$ near 2 over the short term but can acclimate to long-term changes through a smaller $Q_{10}$. Estimating use of photosynthate in $R_m$ is problematic. Observed values of specific $R_m$ in crop species are affected by age and plant composition, and may vary over a factor of more than five (Amthor 1989).

For Table 2, 0.015 mmol CH₂O g⁻¹ biomass h⁻¹ is taken to represent a wheat crop in midseason with daily mean temperature of 15°C. This is close to the value calculated with coefficients developed by Mitchell et al. (1991; their Table 3). It is important to remember that crop $R_m$ is a function of crop biomass. RUE values are calculated for Table 2 with 1000 g m⁻² near anthesis, which is less than would be the case for truly high yields. Because RUE is expressed per MJ radiation in Table 2, the correction for $R_m$ also varies with radiation level. With less than 20 MJ radiation d⁻¹, as used for Table 2, the $R_m$ term would be larger.

A slowing of leaf respiration in the light is sometimes observed or inferred (Krömer 1995). The interpretation is that some features of metabolism that use products of 'dark' respiration, such as the step from NO₂⁻ to NH₄⁺ in nitrate reduction, or the active transport of ions across membranes, can be accomplished in the chloroplast or elsewhere with ATP and reductant generated by photosynthetic processes. Given the uncertainties in the occurrence and magnitude of such changes in respiration, it is ignored in Table 2. It might reduce the $R_m$ component and/or increase slightly the growth yield, $Y_g$ (see below).

$R_g$ evaluated through growth yield, $Y_g$—

Newly reduced CO₂, represented here as an equivalent amount of simple carbohydrate,
CH\textsubscript{2}O, can be translated to wheat biomass using a 'growth-yield' factor (\(Y_g\); g biomass formed g\textsuperscript{-1} CH\textsubscript{2}O consumed; Pirt 1965). \(Y_g\) (and corresponding respiratory exchanges of CO\textsubscript{2} and O\textsubscript{2}) can now be calculated accurately from either elemental (McDermitt and Loomis 1981; Laflitte and Loomis 1988) or proximal analyses (Penning de Vries et al. 1974).

Assuming that new wheat biomass being formed near anthesis consists of 75% carbohydrate, 12% protein, 5% lignin, 3% lipid and 5% minerals (Subcommittee on Feed Composition 1982), \(Y_g\) calculated by the least-cost method of Penning de Vries et al. is 0.72. Thus, \(\frac{1}{0.72} = 1.38\) g CH\textsubscript{2}O is consumed for carbon skeletons and growth respiration for each g biomass formed. \(R_g\) amounts to 0.22 g CH\textsubscript{2}O g\textsuperscript{-1} biomass formed, and 7.35 mmol CO\textsubscript{2} is released. Multiplication of gross photosynthesis, minus maintenance respiration, by 0.72, as is done in Table 2, accounts for the minimum possible amount of respiration (\(R_g\)) associated with heterotrophic synthesis of biomass with that composition.

During grain filling, protein-N (reduced N) is mobilized from vegetative tissues, lessening the cost of protein synthesis. \(Y_g\) can then increase towards 0.8. \(Y_g\) also would be greater than 0.72 if some nitrogen is taken up from soil as NH\textsubscript{4}\textsuperscript{+} or if respiration is reduced in the light through, for example, a smaller cost for nitrate reduction.

**Potential RUE of wheat**

The calculations given in Table 2 indicate that potential RUE may range from 4.1 g biomass MJ\textsuperscript{-1} solar radiation with \(qr=10\), to 1.1 with \(qr=30\). Per MJ PAR, the range is 8.2 to 2.2 g. The dependence of RUE on \(qr\) is depicted in Figure 2a. This is total biomass and therefore includes roots. For a rough estimate of RUE based on aboveground material in crops well supplied with nutrients and water, these values can be divided by 1.1.

![Figure 2](image-url)
Fischer (1983) compared crop growth rates (GR) observed in several field experiments with PAR absorbed by the canopies (Figure 2b). (Aboveground biomass was multiplied by 1.1 to account for roots.) The slope of the relation in Figure 2b is very near 3.0 g MJ⁻¹ PAR or 1.5 g MJ⁻¹ total radiation. Because wheat biomass has a heat of combustion near 17 kJ g⁻¹, the corresponding efficiencies are 5.1% of PAR absorbed and 2.6% of total solar absorbed. Interpolating in Figure 2a (with the assumptions given for Table 2), Fischer's value corresponds to a quantum requirement near 24 mol quanta mol⁻¹ CO₂. Several outliers on the high side of Fischer's graph are fit by RUE=3.8 g MJ⁻¹; from Figure 2a, this corresponds to qr=20.

**Assessment**

The earlier study (Loomis and Williams 1963) focused on limitations imposed in real canopies by light saturation, CO₂ supply, pattern of assimilate partitioning, and the amount, duration and manner of leaf display. All of those topics have received attention in wheat and continue to offer avenues for further small improvements in RUE.

**A practical potential RUE**

The estimate of RUE=8.2 g dry matter MJ⁻¹ PAR given in Table 2 with qr=10 is larger than the value of 6.8 g MJ⁻¹ PAR obtained in the earlier study (Loomis and Williams 1963). The difference comes in part from the greater number of quanta per MJ irradiance and inclusion of inactive absorption. In addition, the respiration allowance, now placed on a reasonably mechanistic basis, is smaller at qr=10 (26% of gross photosynthesis; R/P, Table 2) than the 33% used by Loomis and Williams based on measurements for alfalfa crops. In Table 2, R/P increases as qr increases, however, reaching 40% with qr=30. Amthor (1989) summarized observations for 'growth efficiency' (1-R/P) observed with wheat. Values of R/P calculated from his Table 6.1 range from 21 to 63% with a central tendency towards 33%, the same as in Table 2 with qr=20. Variations in photosynthesis rather than in respiration seem to be the main cause of the wide variation in R/P.

There is speculation that Rₘ might be reduced in crops through breeding, so the effect of a 20% reduction in Rₘ on RUE outlined in Table 2 was calculated. Reduction in the already small Rₘ used in this exercise did little to increase RUE: with qr=10, 20% smaller Rₘ increased RUE by only 1.9%; with qr=30, 20% reduction in Rₘ increased RUE by 6.8%.

R₉ seems a less likely source of variation in RUE as Y₉ is conservative. In a study with sorghum crops varying in age and nitrogen status, Y₉ calculated from elemental composition was 0.73 to 0.74 with adequate N and 0.77 to 0.78 with limited N (Lafitte and Loomis 1988). Arguably, protein content of wheat growth prior to anthesis may be nearer 18% (3% N) than 12% as used in Table 2, in which case, Y₉ would be near 0.69 (1.46 g CH₂O used per g biomass). Because variation in Y₉ has a direct effect on RUE, changes in Y₉ for Table 2 lead to similar changes in RUE.

If light saturation could be avoided, and with present atmospheres and temperatures near 20°C, wheat might be able to operate at qr=<20 and RUE=<4. Considerable light
saturation is unavoidable, however, and RUE=3.8 g DM MJ⁻¹ (qr=20) seems a practical estimate of maximum RUE of wheat under field conditions with long cool days and moderate radiation (20 MJ m⁻² d⁻¹).

Readers are referred to Austin (1993), Sinclair (1993) and Horton (1994), among others, for consideration of many other factors affecting photosynthesis as well as possibilities for improving production rate through altering system components, including rubisco. A principal conclusion from the present exercise is that RUE is a variable function of size of crop, temperature, radiation level, and ambient [CO₂]. Brief comments on several of these factors are presented in following sections.

[CO₂]

In the field, rapid photosynthesis can lower ambient [CO₂] to well below the current average of 350 vppm. Light saturation occurs at lower PAR, and RUE declines. These effects point up the importance of good ventilation (open canopy and turbulent air) and large canopy conductance (well-watered stand with open stomates).

The concentration of CO₂ in the atmosphere is expected to increase during the next century from about 350 vppm at present to between 500 to 600 vppm. To test the beneficial effect of increasing [CO₂] in lowering qr simulations were made using an analytical simulation model based on that of Farquhar and von Caemmerer (1982). The [CO₂] in wheat chloroplasts was assumed to be 50% that in ambient air (von Caemmerer and Evans 1991). At 25°C, predicted light-limited qr declined, and RUE increased, as follows:

<table>
<thead>
<tr>
<th>[CO₂] (vppm)</th>
<th>300</th>
<th>400</th>
<th>500</th>
<th>600</th>
</tr>
</thead>
<tbody>
<tr>
<td>qr (mol/mol)</td>
<td>19.2</td>
<td>16.2</td>
<td>14.6</td>
<td>13.6</td>
</tr>
<tr>
<td>RUE (g/MJ PAR)</td>
<td>3.1</td>
<td>4.0</td>
<td>4.6</td>
<td>5.0</td>
</tr>
</tbody>
</table>

**Temperature**

Wheat is a cool-season crop. Both fall- and spring-sown wheat crops generally encounter quite cool temperatures during the vegetative period, whereas grain filling occurs in much warmer weather. The analysis presented here indicates that maximum photosynthetic efficiency (light-limiting conditions) of C₃ plants is favored by cool temperatures (<20°C). On the other hand, the maximum rate of light-saturated photosynthesis occurs at 25 to 30°C because acceleration of the Benson-Calvin cycle partially offsets photorespiration. As Long (1991) showed, the optimum temperature for photosynthesis will increase in the future as photorespiration is repressed by increased [CO₂].

These effects of temperature on production processes interact with the effect of temperature on wheat’s developmental rate: rates of initiation of leaves (and thus canopy development) and spikelets (influencing potential kernel number) and the duration of grain filling. Temperature-response curves for developmental rate are similar to those for growth rate, perhaps because cell division and enlargement are integral to organ initiation.

The temperature response of development differs from that for photosynthesis leading to rather complex problems in defining ideotypes for crop improvement. Ideotypes that will raise yields beyond present levels may turn out to be more climate-specific (and thus regionally specific) than we have
supposed. Whereas effects of temperature on photosynthesis is well understood, we lack an equivalent understanding of mechanisms controlling development. This is an important area for basic research.

Radiation level
The frequency of light saturation of wheat crops is subject to several factors. The utility of erect leaves in moderating light saturation of crops has been a subject of considerable confusion. The question was analyzed theoretically by Duncan (1971) who made it clear that truly erect leaves offer great advantage only for dense canopies (LAI>5) and only with high solar elevation (e.g., summer and/or low latitude). Achievement of full interception is more important, however, and with less leaf area, that is accomplished best with leaves of moderate inclination. Given that wheat is most exposed to high solar elevation mainly during grain filling, when leaves are senescing and shaded by spikes, extremely erect leaves are not likely to offer the advantage to wheat that they lend to summer crops of maize and rice.

Conclusions
This analysis demonstrates that the upper limit of dry matter production by wheat crops is in the range of 3 to 4 g DM MJ\(^{-1}\) PAR (1.5 to 2 g DM MJ\(^{-1}\) solar radiation). This is considerably less than the 6.8 g MJ\(^{-1}\) PAR predicted by Loomis and Williams (1963) before photorespiration was known. Warm temperature, the small concentration of CO\(_2\) relative to O\(_2\), and light saturation limit attainment of greater RUE. Because present crops reach 3 to 4 g MJ\(^{-1}\) efficiency when conditions are favorable, further efforts at improving wheat yield need to focus on extending the duration of efficient photosynthesis and on improving the conversion to grain.

References


Questions and answers

R.A. Fischer:
Since I collected the RUE data of the 1970s and early 1980s to which you referred, I have been collecting whatever else has appeared on wheat RUE. The average number of 3 g Dm/MJ has not changed but there is clear evidence of a positive effect of canopy N concentration on RUE and a negative one of frost. With respect to cultivars there is no evidence that RUE has increased with yield progress over the last 30 years: the only evidence of a cultivar effect is a study showing higher RUE with more erect-leafed cultivars.

R.S. Loomis:
The positive effect with increased N generally relates to increased photosynthetic capacity as chlorophyll and enzyme content increase. Canopy reflectance declines, pointing to the importance of how radiation measurements are made. There are trade-offs, however. Less light may penetrate to shaded leaves, for example, and growth and maintenance respiration are increased.

Because wheat is relatively tolerant of direct freezing damage, the negative association with frost probably arises from increased photoinhibition at low temperatures. With low temperatures, the B-C enzymes fail to keep pace in bright light and photodamage occurs. Long et al. (1994) discuss this problem.

R.A. Fischer:
The N concentration effects were large, on the order of 15%, going from moderate to high concentration, and are unlikely to be compositional ones. Besides, the effects agree with those calculated by Tom Sinclair from individual leaf responses to leaf N concentration.
Yield Potential and Drought Resistance: Are They Mutually Exclusive?

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Abstract
Based on various sources of information, it can be concluded that in wheat there is a genotype x severe drought stress interaction for yield. High yielding varieties do not perform as well as drought adapted varieties when yield is depressed by drought stress to below the crossover point. For wheat and barley this crossover is expressed if yield is reduced to below 2-3 t/ha when annual (seasonal) precipitation is less than 300 mm. This interaction is perhaps the result of the way wheat cultivars have been bred, but it must also have a genetic/physiological basis. This presentation examines various factors that may explain the negative interaction between yield potential and resistance to severe drought in the hope of developing a more comprehensive approach to raising the yield barrier. Briefly examined in this paper are the non-competitive plant ideotype concept, plant phenology, source-sink relationships, and carbon assimilation and its utilization for growth, yield and adaptation.

Introduction
There is a continued interest among plant breeders in the extent of genetic gain in yield improvement in the historical perspective. Although there seems to have been progress under all growing conditions, it is generally recognized that genetic yield gains have been relatively higher in more favorable environments. For example, Cox et al. (1988) found 0.6% annual gain in hard red winter wheat yield in highly productive environments as compared with 0.4% in stress environments, between 1919 and 1987.

There is general consensus that in cereals the high yielding (and often short stature) varieties are more adapted to favorable growing conditions, while the lower yielding (often taller) varieties or landraces are more stable in their performance under stress conditions. This case has been well demonstrated by Ceccarelli et al. (1991) for high yielding varieties and landraces of barley.

Ceccarelli and Grando (1991) argued that progress in yield in stress environments is possible if selection for yield is performed in those environments. They concluded that the reason for slower progress in breeding for low yielding environments, as commonly claimed, is simply that most yield selection is performed under relatively favorable conditions. They thus set out to show that yield under stress can be effectively improved by selecting for yield under stress, while yield potential can be improved only if performed under non-stress conditions. Since selecting for yield under stress often results in reduced yield potential (e.g., Rosielle and Hamblin 1981; Cecarelli and
Grando 1991), it may therefore be suspected that stable yield under stress and high yield potential may be mutually exclusive.

In several studies where yield of appropriately different cultivars was evaluated under carefully varying water regimes, a clear genotype x water regime interaction for yield was observed. This interaction was graphically expressed in a crossover of genotype yields at a certain level of drought stress (e.g., Figure in Cecarrelli and Grando 1991; and Figure in Blum 1993). In the first example, for barley in Syria, the crossover occurred at a mean grain yield of about 2 t/ha, while in the second case, for wheat in Israel, it was 3 t/ha. This interaction seems to present a most convincing case for an apparent negative association between yield potential and yield under severe drought stress, provided stress is severe enough to reduce yields to below the indicated crossover levels.

However, at the same time, varieties with high yield potential are performing relatively better than all others not only under non-stress conditions but also under moderate stress conditions as depicted by the range of moisture (or mean yield) environments above the crossover point.

Therefore, a negative interaction between yield potential and drought resistance is expressed only when stress is sufficiently severe. Under moderate stress conditions, varieties with high yield potential still perform best. This conclusion has been reached also with respect to salinity stress. Kapulnik et al. (1990) found that vigorous alfalfa cultivars also yielded best under salinity stress. Richards (1983) proposed opting for high yielding varieties as a solution for salt affected environments, mainly because they are extremely variable, and most yield in such environments is produced in the less saline soil patches. Shannon and Noble (1995) demonstrated very limited genotype x salinity level interaction for clover shoot dry weight. Similarly, Kelman and Qualset (1991) did not find genotype x salinity level interaction among a large number of random wheat inbred lines derived from a salinity resistant x susceptible cross. The potentially higher yielding lines performed best irrespective of salinity levels, which, again, were relatively moderate.

Genotype x severe stress interaction for yield must be driven by distinct underlying physiological factors. Such interaction may raise the question of a possible penalty in yield potential when a genotype has superior adaptation to drought stress, and vice versa. In other words, raising the yield barrier of wheat most likely will not impact wheat productivity in environments that limit yields to below the crossover point, but may still do so where mean yield is above the crossover point. It may also change the crossover point. Recognizing the factors involved in the apparent negative association between yield potential and drought resistance is important for designing a more efficient approach to breeding for high yield and yield stability. A review of the literature indicates that our knowledge in this area is very limited. This discussion therefore depends on fragmented information as well as on conjecture.
Plant Phenology and Development

Undoubtedly, factors involved in plant phenology and development may constitute a conflict between yield potential and stress adaptation, largely because yield potential tends to increase with a longer growth cycle, up to a certain point. However, while early genotypes escape drought, high yielding late genotypes are not necessarily susceptible to it. In certain ways, late genotypes may be more drought tolerant than early ones. This has been well demonstrated by work with peanut (Nageswara Rao et al. 1989). When stress occurred during pod-filling, early and lower yielding genotypes sustained less yield reduction than later genotypes because of drought escape. However, when drought stress occurred mid-season, late flowering and high yielding genotypes sustained less yield reduction than earlier genotypes. Possibly, late flowering genotypes have a relatively better capacity for recovery from severe stress in terms of meristem availability and viability. This is prominent for the indeterminate growth pattern of certain soybean cultivars (e.g. Villalobos-Rodriguez and Shibles 1985), but also occurs in the cereals.

While late flowering genotypes have a relatively large leaf area and high water requirement, they also possess relatively larger roots. The distinct effect of maturity genes on sorghum root size has been demonstrated (Blum et al. 1977). Under certain stress profiles (such as available deep soil moisture), the large roots of late genotypes may constitute an advantage (e.g., Figure 1), while in other situations their large leaf area and long growth duration may be a disadvantage. Thus, depending on the timing and intensity of stress, late genotypes with high yield potential may have either an advantage or a disadvantage compared with the lower yielding early genotypes.

Beyond phenology, yield is derived from various factors operating at different levels of plant organization. Yield improvement has been approached by Donald (1968) through the ideotype concept. The concept was put forward based on the assumption that plant breeding should design the plant according to a pre-conceived ideotype. Donald proposed that a high yielding cereal crop must be composed of a population of non-competitive single plants, because competitive homozygous individual plants reduce the productivity of populations. The idea is conceptually very attractive, although outstanding exceptions can be

![Graph](image_url)
immediately recognized (see below). While indirect support of Donald’s concept had been published earlier (e.g., Hamblin and Donald 1974), it has also been supported more recently by controlled experiments in wheat (Reynolds et al. 1994).

**Non-Competitive Wheat Ideotype**

The idea that a non-competitive wheat ideotype is conducive to high yield potential conforms well with the actual progress made on modern high yielding cereal varieties (HYV) of short stature. The HYV plant is different from its taller predecessors in the greater partitioning of dry matter towards yield at the expense of shoots and roots. Such a modification, namely reduced root and shoot mass, should render the individual plant less competitive. The competitive (and perhaps the lower yielding) plant (which at the extreme is typical of natural vegetation) seems to be more capable of capturing resources. This capability would be at least partially linked to traits such as large roots and high tillering potential.

The competitive wheat genotype would seem to offer an advantage under drought prone conditions while the non-competitive one would not. Tillering is a distinct attribute of a competitive cereal plant. ‘Uniculm’ wheat, devoid of normal tillering, did not offer any advantage under low yielding conditions (Whan et al. 1988), while tillering was found to ascribe yield stability under limited moisture supply in both wheat (Hadjichristodoulou 1985) and pearl millet (Mahalakshmi and Bidinger 1986). A competitive plant with high seedling vigor is considered advantageous under dryland conditions (e.g., van Oosterom and Acevedo 1992) possibly for reducing soil surface evaporation and thus increasing the proportion of transpiration in total crop evapotranspiration (Lopezcastaneda et al. 1995). Fast and vigorous growth before flowering would also increase the potential for carbon storage in the plant, a reserve that later can be used for grain filling under stress (e.g., Schnyder 1993).

Pre-flowering storage of reserves has been considered a possible reason for reducing yield potential (Borrell et al. 1993) since storage at times can be regarded as a sink competing with yield. Additionally, excessive carbon storage in plant organs may constitute a feedback signal limiting the activity of the source (Krapp et al. 1991). Thus, carbon storage as a homeostatic mechanism for supporting growth during or after stress can perhaps be regarded as opposing high yield potential. However, there is some evidence against such an obligatory negative association (Blum et al. 1994).

It would be misguided to flatly equate high competitiveness with stress adaptation or low competitiveness with drought susceptibility. For example, at least in sorghum and maize, vigorous (and supposedly more competitive) hybrid plants produce more biomass and grain yield than their less vigorous parents or open-pollinated varieties. On the other hand, when sorghum was grown under limited stored soil moisture conditions, yield increased when plant growth was suppressed by increasing inter-plant competition (Blum and Naveh 1976), which
reduced leaf area and seasonal water-use. Our own preliminary studies have also shown that the smaller (less competitive) dwarf wheat genotypes suffered relatively less growth reduction by drought stress than the large (and more competitive) tall genotypes (Figure 2).

Thus, Donald’s idea regarding competitiveness and yield remains a challenge and an opportunity. To explore its applicability, the idea should be evaluated in the context of wider environmental conditions.

Sink

A large sink is an inherent characteristic of the high yielding genotype. The maintenance of a large sink poses a demand on the source. The capacity of the source to fill the potential sink is an essential component of yield potential. It is generally accepted that the actual rates of carbon partitioned to the yield sink (e.g., the wheat spike) at any given time also depends on competition for carbon by other sinks. Geiger and Servaites (1991) concluded from their review that part of the assimilated carbon is always allocated to (non-sink) reserves as a means of maintaining homeostasis in the face of unpredictable stress. This is how plants evolved. I propose that plant domestication and breeding may have intervened to reduce reserves at the expense of filling a larger sink.

The plant’s carbon balance may therefore be regarded as a pool. Materials are put into and are drawn from the pool into various sinks, including sinks such as reserves, root growth or osmotic adjustment. Planned genetic intervention to modify the partitioning of assimilates to various sinks has not been possible basically because of our ignorance of the control of assimilate partitioning and communication between source and sink. The only unplanned intervention that has been achieved thus far is the unbalanced increase of the grain sink size at the expense of shoot and root size, such as in cereal HYVs. The fact that selection directed only at grain yield so effectively reduced shoot and root size indicates that grains are most likely the primary and the preferred sink in the plant.

Because of their close interaction, a large sink related to grain number constitutes a load on the source, and hence the whole

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**Figure 2.** Percent reduction in juvenile (about 20 days old) plant growth rate under controlled drought stress in isogenic lines for height (rht-tallest; Rht₃-shortest) against the background of two wheat cultivars, Bersee and April Bearded. Stress was applied as polyethylene glycol in Hoagland’s nutrient solution giving -0.55 Mpa of solution water potential, as compared with a control nutrient solution, in the growth chamber. Bars = ± Standard Error. Seed of lines were supplied courtesy of Dr. M.D. Gale, John Innes Institute, Norwich, UK.
plant. A large number of kernels per ear promoted high leaf conductance, gas exchange, transpiration and consequently brought about a reduction in leaf water potential (Blum et al. 1988). A large inflorescence also accelerated drought induced leaf senescence in wheat and sorghum (Khanna-Chopra and Sinha 1988). Whole plant senescence under the demand of a large sink may well be related to the export of nitrogen from the leaves incited by the demand of the grain (e.g., Pell and Dann 1991). A large panicle in sorghum was found to be potentially associated with reduced capacity for leaf osmotic adjustment (Tangpremsri et al. 1995). Sorghum lines of relatively higher yield and osmotic adjustment under stress tended to be lower in yield under irrigation, compared with lines of lower osmotic adjustment (Santamaria et al. 1990). Sorghum hybrids were always lower in osmotic adjustment than their (lower yielding) parental lines (Basnayake et al. 1994).

It is therefore quite conceivable that a large grain sink is in opposition to drought resistance if stress occurs when the sink is filled. Again, however, this association is not obligatory for reasons that remain to be explored. For example, the association between a large sink and a lower capacity for osmotic adjustment is not obligatory (e.g., Tangpremsri et al. 1995). The relationship between osmotic adjustment and yield at the population level may not be as prominent as implied for the single plant level. Wheat lines showing high osmotic adjustment under stress were not necessarily low yielding under irrigation (Morgan 1983; Morgan and Condon 1986).

Source

The role of the source in the association between yield potential and drought resistance must be considered at the various levels of plant organization.

At the canopy level, reduced leaf area under limited soil moisture conditions is an advantage. It would allow more economical water-use and the avoidance of terminal severe water shortage (e.g., Blum and Naveh 1976; Richards and Townley-Smith 1987). However, the genetic design of smaller leaf area may limit potential productivity.

At the single leaf level, high nitrogen concentration, high chlorophyll concentration and high specific leaf weight would all support potential productivity, irrespective of the water regime. Despite the active debate on the subject, it seems that leaf photosynthetic capacity (Watanabe et al. 1994) and stomatal conductance (Shimshi and Ephrat 1975; Rees et al. 1993; Lu and Zeiger 1994) were generally improved by selecting for high yield in wheat. The volume of data recently accumulated on carbon isotope discrimination and yield appears to support a consistent positive relationship between crop yield and photosynthetic capacity across various genetic materials of wheat and other crops (Hall et al. 1994). If selection for high photosynthetic capacity or for higher crop productivity brings about an increase in stomatal conductance, then a concomitant increase in crop water-use is to be expected.

This is in agreement with long established linear relations between crop biomass production and transpiration (de Wit 1958).
Hence, the implications for water-limited environments can be projected. Where water-supply to the plant under drought stress can be provided, say by deep soil moisture extraction, the advantage of the high yielding genotype will be sustained, to a limit. This returns to the previous discussion of the possible advantage of late genotypes with large leaf area and large roots under midseason stress. Under such conditions, relatively low canopy temperatures (resulting from high stomatal conductance and high leaf water potential) are typical of the more dehydration avoidant genotypes (e.g., Blum et al. 1982; Garrity and O'Toole 1995). However, where soil moisture is very limited, the high yielding genotype, by virtue of its high stomatal conductance, may be at a disadvantage a priori. Thus, again, high yielding genotypes are expected to be relatively productive also under drought stress if stress occurs midseason and deep extractable soil moisture is available to provide for a yield level above that of the crossover.

Leaf Color

The productivity of the source depends on radiation interception and use. Plants under drought stress cannot benefit from high levels of irradiance, and at times these high levels may be the cause of photoinhibition. The possible involvement of photoinhibition in plant production under drought stress is still debatable. However, a recurrent observation by cereal plant breeders is that genotypes having light leaf color (light green) tend to be more stress resistant. This was recently documented for drought tolerant barley lines (van Oosterom and Acevedo 1992; Watanabe et al. 1995). These investigators proposed that light leaf color in barley was associated with higher chlorophyll a/b ratio. The high ratio was considered to be a marker for reduced total chlorophyll content and reduced chlorophyll antennae relative to core complex of photosystem II. This chlorophyll configuration is claimed to confer greater tolerance to stress induced photoinhibition. Therefore they concluded that light green leaves may confer adaptation to high levels of irradiance under drought conditions.

This rationale for the observed de facto advantage of light green leaves under drought stress is countered by Tyystjarvi et al. (1991), who cast a doubt on the role of chlorophyll antennae in the above context. Alternatively, the advantage of light green leaves under drought stress may be derived from their high reflectivity and albedo. Light green barley leaves were shown to result in lower leaf temperatures, as compared with dark leaves (Ferguson et al. 1973).

Whatever the underlying benefits of light green leaves under stress, they seem to constitute a specialized plant design for stress conditions. If high chlorophyll concentration is conducive to high yield potential, then it may not be compatible with the light green leaf ideotype for stress conditions, as seen in barley.

Conclusion

In conclusion, there is a range of drought stress conditions where high yield potential is an advantage or it is not a liability for attaining stable yield under stress. As stress
intensifies, high yield potential and drought resistance become mutually exclusive.
Understanding of these associations is very limited and extensive research is needed in this critical area of agronomy and breeding.
Such research is heavily dependent on whole plant and crop physiology and is an essential part of our attempt to achieve a wider impact on the improvement of yield potential.

References


**Questions and answers**

R.A. Fischer:
There are studies (e.g., Jim Welch, Colorado) which show that root length is no shorter in semidwarfs compared to their tall isolines.

I was glad to see the cotton work on increase is leaf cooling with genetic improvement juxtaposed with the wheat work here at CIANO in 1993. In fact, in 1994, the cotton workers Zeiger and Lu came down from UCLA to make measurements here on wheat with Ken Sayre. The results are summarized in the Abstracts booklet.

Your talk has forced me to reassess the conclusion I had been reaching after reading recent maize literature (Duvick, Tollenaar, Edmeades) suggesting that multi locational yield testing automatically built in a large degree of stress resistance, specially at the level of leaf photosynthesis, because even well managed crops in favorable environments see stress.

Also, is it not possible that some or many of the traits you referred to could be facultative and switched on only when they are needed, meaning only when they help performance? These two possibilities could eliminate crossovers as yield is improved?
A. Blum:
To the first point: I agree that multilocalational screening may result in improved environmental stress tolerance, but this is because certain (stress) locations create the appropriate selection pressure provided their mean yield level is below that of the point of crossover. I do not feel that selection in favorable environments should result in improved stress tolerance, as demonstrated already in selection experiments.

To the second point: By definition, a facultative trait is expressed irrespective of the environment. It is not stress-responsive in the sense that it does not require stress in order to 'switch on'. So in conclusion, my answer to your final question is that the points you raise do not allow to assume that crossovers will be eliminated with yield improvements.

M. Reynolds:
The data you present illustrate that natural selection has conserved many stress-adaptive traits in wheat which are in some cases detrimental to yield under more favorable conditions. Given that the relative performance of wheat genotypes over a range of conditions apparently show crossovers at yield levels of 2-4 t/ha, is it probable that increases in yield potential may also raise the yield level at which crossovers occur?

A. Blum:
Data on yield level at which crossovers occur in different countries and experiments show that the crossover reduces as the mean yield of the experiment is reduced. For example, crossovers with respect to a changing water regime in variety tests from developing countries (without fertilization, etc.) are lower than those where mean yield is high. However, whether the crossover would shift upward with the increase in yield potential is an intriguing question that we should explore. If the crossover is the result of a specific physiological interaction with stress, such as the expression of certain stress responsive genes, than the crossover should not be affected by the increase in potential yield. However, if the increase in yield potential involves change in certain constitutive traits which are detrimental to plant stress adaptation (say, later maturity when drought stress is terminal), than the crossover may shift upward.
Yield Components and Compensation in Wheat: Opportunities for Further Increasing Yield Potential

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Abstract

There are some indications that wheat yields may be leveling off. It may be necessary to analyze physiological processes to help identify opportunities for future breeding aimed at breaking the apparent barriers. There are various yield determining characteristics that can be considered, including those related to the crop's ability to intercept and use available radiation, to partition its dry matter into competing organs, and to absorb and use water and nutrients. We will concentrate on yield components and compensation, and discuss opportunities for manipulating phenological development as a tool for increasing yield potential in wheat. To analyze grain yield in terms of number of grains m\(^{-2}\) (and its components) and average individual grain weight has been traditional. However, this approach was lately recognized as ineffective because these components are negatively correlated to each other, and the magnitude of the parameters of these relationships are variable. Thus, only by understanding the basis of these negative relationships would it be possible to manipulate numerical components aiming to obtain a particular yield target. An initial step could be understanding phasic development, as there are relationships between the development of the apex and formation of yield components and stages that are most important in building yield potential. In this paper, we describe the initiation (and survival) of different yield components throughout wheat development, concluding that the formation of sub-components of number of grains m\(^{-2}\) overlaps somewhat and the negative relationships between these yield components could be attributed to some form of feedback processes, determining a sort of compensation between them. In contrast, the final weight of individual grains appears to be determined with only minimal overlapping with the determination of the number of grains m\(^{-2}\); thus negative relationships between major yield components may be different in nature. It is generally accepted that wheat yield is better related to grain number m\(^{-2}\) than to individual grain weight. Thus, a critical phase for yield potential, once the number of grains m\(^{-2}\) is established, has been recognized during the period of ca. 20-30 days immediately before anthesis, this indicates that only the narrow window of time coinciding with mortality of tillers and florets and with active growth of stems and spikes appears to be of critical importance for the determination of final number of grains m\(^{-2}\), regardless of the sub-components that could be responsible for this response. However, increases in number of grains will result in net increases in yield potential only if its negative association with individual grain weight is not due to mutually exclusive competition between grains for assimilates. The physiological basis of this relationship has to be analyzed. Most studies have shown that whenever yield potential was genetically improved, increased grain-setting ability was partially compensated for by decreases in average grain weight. In this paper, we discuss four hypotheses for explaining this negative relationship, including
non-competitive alternatives for the compensation between grain weight and grain number. The most widely accepted explanation is that increased number of grains m\(^{-2}\) reduces the assimilates available for each grain; however, we concluded that the negative relationship is mostly due to non-competitive reasons. The most important would be that increasing the number of grains m\(^{-2}\) will increase the proportion of grains with reduced weight potential. However, evidence from several sources indicates that in genotypes with a large number of grains there is small but significant source limitation. Thus, if breeders continue increasing the number of grains without changes in the availability of assimilates per grain, individual grain weight will decrease at a higher rate than in the past, since further reduction due to competition among grains will be added to the "natural" reduction expected from the increased proportion of grains with low weight potential. Breaking the barriers of yield potential in wheat will require simultaneous increases in both number of grains m\(^{-2}\) and availability of assimilates. In this paper, we also explore the idea that manipulating crop phenological development through responses to photoperiod and temperature during phases critical for determining number of grains and grain weight can be envisaged as a tool for increasing yield potential. We present evidence that sensitivities to photoperiod and temperature during stem elongation and to temperature during grain filling are strong, that there is genetic variation for these traits, and that the response in these phases appear to be independent of responses in other phases. This suggests that manipulating these responses could be an avenue to increased yield potential in wheat.

Introduction

Yield trends in the 20th century

During the 20th century, wheat production has increased substantially, from 90 to 600 million tons (Figure 1a). This is due to the increase in both harvested area and grain yield (Slafer et al. 1994a). The most important contribution of expansion of harvested area occurred during the first half of the present century. From 1903 to 1954, the increase in production could be explained almost entirely by the increase in harvested area (Figure 1b). During this period, wheat production increased from 90 to 200 million tons and the area under production rose from 90 to 190 million ha. From 1955 onwards, increased grain yield was the main cause of the continuous increase in wheat production (200 to 550-600 million tons) (Figure 1c). Grain yield in 1955 to 1994 rose from 1.0 to 2.5 t ha\(^{-1}\), while area increased by only 20%. Moreover, both production components have shown different behavior during the second half of the century: the increase in harvested area has not occurred in all regions of the world (with clear reductions in Europe, for example), while grain yield increases have been found in all continents (for details see Slafer et al. 1994a). However, a closer inspection of the records of average yields for the last years shows that wheat yields (which increased substantially from 1955 to the late 1980s) are commencing to level off (Figure 1d). This latest trend must be viewed cautiously due to the limited information on which it is based. But if the incipient leveling off is confirmed in the next few years and average yields are actually reaching a ceiling, new strategies for breaking the barriers of yield potential should be envisaged.

In the future, the contribution of new growing areas to increased wheat production is expected to be negligible (Slafer et al. 1994a). In fact, the area sown to wheat
worldwide has been consistently declining during the last 15 years (Figure 1d inset). Therefore, future production increases depend entirely on our ability to reach higher average yields. In this context, the apparent trend of negligible increases in average yields during the last five years or so (Figure 1d) is another reason for concern. If wheat breeding, mostly by selecting for yield per se, is not achieving the desired objectives vis-à-vis yield potential, it may be necessary (and rewarding) to analyze physiological processes to help identify opportunities for future breeding programs aimed at breaking the apparent barriers.

It was shown (Slafer et al. 1994a) that despite the great diversity of environments, cultures and economies, there has been a similar pattern of grain yield increases in different countries of the world (Slafer et al. 1994a, Figure 3). Past increases in grain yield could be attributed to: 1) genetic gains in yield potential, 2) other genetic gains (e.g., disease resistance, reduced lodging, tolerance to environmental stress), and 3) management or technological gains (e.g., better fertilizer and biocide use, better adjusted dates and sowing rates).

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Figure 1. Worldwide trend of wheat production during the present century (1903-1994, a); relationships between production and harvested area or grain yield as percentage of the values for 1903 (b) or 1955 (c) for the periods 1903-54 (b) and 1955-1994 (c); and worldwide trend of average yields (d) and area (d, inset) during the last 15 years (1980-1994). Data re-worked from Slafer et al. (1994a) and from FAO (Food and Agriculture Organisation of the United Nations, Rome) yearbooks (1980-1995).
Effect of genetic improvement on yield potential
The impact of wheat breeding on grain yield potential has been reported in several countries (Feil 1992; Loss and Siddique 1994; Slafer et al. 1994a). These increases ranged from 0.58 g m\(^{-2}\) year\(^{-1}\) in India (Sinha et al. 1981) to 5.84 g m\(^{-2}\) year\(^{-1}\) in Mexico (Waddington et al. 1986), but most studies reported values of \textit{ca.} 1.5 g m\(^{-2}\) year\(^{-1}\). These genetic gains in grain yield potential contributed \textit{ca.} 50\% of the total gain in grain yield during this century (Jensen 1978; Silvey 1978; Deckerd et al. 1985; Slafer and Andrade 1991). If the cost of major resources such as water and fertilizers increases and environmental constraints prevent high input agriculture from further expansion, the contribution of plant breeding to wheat yield increases in the future may be even more important than in the past. In other words, future yield and production increases would increasingly rely on genetic improvements.

However, genetic improvements in yield potential in the future will be harder to achieve than in the past. Breeders will have to further increase an already high yield potential and procedures that were successful in the past may not be as efficient in the future. Past successes in increasing yield potential have mainly been the result of an empirical selection approach of trial and error in selecting yield \textit{per se} (Loss and Siddique 1994). In the coming decades, using physiological attributes as selection criteria can be expected to accelerate genetic improvement (Shorter et al. 1991). This is particularly true for crops, such as wheat, that have already been subjected to intense selection pressure for yield \textit{per se}. Selection based on physiological traits may also be effective because it allows selection during early generations (and sometimes could be based on individual plant characteristics) and may reduce the number of plots and the size of the program, which might otherwise become progressively larger (Austin 1993).

Changes in grain yield components
There are different approaches for identifying the key physiological attributes that determine yield potential. Historical series of cultivars (i.e., those released in different eras have been largely used to determine which crop characteristics are modified when breeders successfully increase yield potential. The advantage of this approach is that any trait that has been consistently modified by breeders as they selected for yield \textit{per se} could be used as a selection criterion in further increasing yield potential. In attempting to find physiological traits that should be considered in breeding for further increases in yield potential, several authors have conducted experiments with historical series of cultivars from different countries (Loss and Siddique 1994; Slafer et al. 1994a). The aims of these studies were mostly to determine the magnitude of grain yield increases due to the release of newer cultivars, and to understand the changes produced in associated physiological traits.

For this purpose, grain yield can be divided into different physiological

\[ GY = BY \times HI \]

and numerical

\[ GY = NG \times JGWt \]
components, where GY, BY, HI, NG m$^{-2}$ and IGWt stand for grain yield, biomass yield, harvest index, number of grains per unit area and individual grain weight, respectively.

Most studies found that breeding during the last century or so has virtually not changed above-ground biomass, and the main determinant of grain yield increase has been the higher harvest index achieved by modern cultivars (Feil 1992; Loss and Siddique 1994; Siafer et al. 1994a). However, although these changes in dry matter partitioning have been very consistent, they cannot any longer be used in many cases. This is because in many wheat growing areas the harvest indexes of modern cultivars are already close to their maximum theoretical value (see Austin et al. 1980; and discussion in Siafer and Andrade 1991). Therefore, we must increase total biomass if we are to consistently increase yield potential in the future.

Alternatively, we should better understand the generation of numerical yield components and their interrelationships before attempting to break the barriers in yield potential. Evidence from historical series of cultivars indicated that number of grains m$^{-2}$ was the yield component that has mainly been modified by wheat breeding (Figure 2 and see also Siafer et al. 1994a). The other major yield component, individual grain weight, has experienced only small (or even negligible) change and, in some cases, has declined with increased yield (Siddique et al. 1989a,b; Slafer and Andrade 1989).

Objectives

Several yield-determining characteristics should be considered for future selection aimed at further increasing yield potential in wheat. They include traits related to the crop’s ability to intercept and use available radiation efficiently, to allocate different proportions of its growth into competing organs, to absorb and use water and nutrients. These characteristics have been considered in this workshop by others (but see also Slafer et al. 1994a). Our presentation will concentrate on grain yield components and their compensation. Based on better understanding of the causes for compensation between these components, we will attempt to find opportunities to manipulate phenological development as a tool for increasing yield potential in wheat.

First, the numerical components of yield are shown, analyzing their relative impact on yield and briefly discussing their generation

Figure 2. Relationship between grain yield and number of grains m$^{-2}$ for wheat cultivars released in 1920 (Klein Favorito, open squares), 1940 (Eureka F.C.S., open triangles) and 1980 (Buck Pucara, closed squares). Data from three experiments conducted by Slafer and Andrade (1989, 1990).
during plant development. Then the relationship between major yield components, viz. average individual grain weight and number of grains m$^{-2}$, is analyzed in more detail to determine its possible causes. Finally, possibilities for manipulating genotypic responses to photoperiod and temperature and differences in basic development rates as alternative (although not exclusive) tools for increasing yield potential in wheat are suggested.

**Grain Yield and Yield Components**

**Analysis of grain yield in numerical components**

It is traditional in physiological studies to analyze grain yield in terms of numerical components, so that final yield (per m$^2$) is considered as the product of

\[ (\text{Pl m}^{-2} \times \text{Sp Pl}^{-1} \times \text{sp Sp}^{-1} \times \text{Gr sp}^{-1}) \times \text{IGWt} \]

where Pl m$^{-2}$, Sp Pl$^{-1}$, sp Sp$^{-1}$, Gr sp$^{-1}$, and IGWt stand for plants m$^{-2}$, spikes plant$^{-1}$, spikelets spike$^{-1}$, grains spikelet$^{-1}$, and average individual grain weight, respectively. The components between brackets are sub-components of the number of grains m$^{-2}$, a major component together with the average weight of individual grains. A simple diagram showing grain yield composition through its numerical components is shown in Figure 3.

A few decades ago, this approach was thought to constitute “an effort to more carefully evaluate the several factors contributing to final yield” (Mitchell 1970). However, this approach to understanding yield determination was later recognized as ineffective (Fischer 1984), mainly because yield components are, almost invariably, negatively related to each other. These negative relationships indicate that as one component increases, others will decrease. Since the magnitude of the parameters of these relationships (intercept and slope) is variable, it appears unwise to suggest that increasing one of them will result in a net yield change of any particular magnitude. With this in mind, would it be sensible to try to select for a higher number of spikelets per spike if it brings about an associated reduction in number of grains per spikelet? The lack of answers to this kind of questions has probably determined that almost everywhere the main trait for which progenies are selected has been yield *per se*. Therefore, unless we understand the basis of these negative relationships, it would not be plausible to manipulate them (either by cultural management or breeding) aiming to obtain a particular yield target.

**Generation of yield components through plant development**

Although development is a continuum, for the sake of simplicity it is frequently defined as a sequence of discrete phenological events through plant development. Then the relationship between major yield components, viz. average individual grain weight and number of grains m$^{-2}$, is analyzed in more detail to determine its possible causes. Finally, possibilities for manipulating genotypic responses to photoperiod and temperature and differences in basic development rates as alternative (although not exclusive) tools for increasing yield potential in wheat are suggested.

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**Generation of yield components through plant development**

Although development is a continuum, for the sake of simplicity it is frequently defined as a sequence of discrete phenological events
controlled by external factors, each event making important changes in the morphology and/or function of some organs (Landsberg 1977). Descriptions of developmental stages can be found in Bonnett (1935), Waddington et al. (1983), Kirby and Appleyard (1984) and Gardner et al. (1985). Many different scales have been reported (Large 1954; Haun 1973; Zadoks et al. 1974; Nerson et al. 1980; Tottman and Broad 1987). We have summarized some of these stages and their relationships with morphological markers in Figure 4. This figure has an arbitrary time scale (as the actual length of each particular phase can be affected by genetic and environmental factors) and uses easily recognizable features of the apex as delimiters of phases (Slafer and Rawson 1994).

This approach is clearly a simplification but makes it easier to discuss the effects of environmental and genetic factors on rate of development, and allows for visual integration of the relationship between the length of a particular phase with particular yield components. A serious fault of this scheme is that the relationship between apical stages and the plant’s morphological appearance is weak (or even nonexistent beyond a limited range of genotypes and environments). For example, the double ridge stage, which has been used extensively

Figure 4. Schematic diagram of wheat growth and development adapted from Slafer and Rawson (1994), showing the stages of sowing (Sw), emergence (Em), floral initiation (Fl), first double ridge appearance (DR), terminal spikelet initiation (TS), heading (HD), anthesis (At), beginning of the grain filling period (BGF), physiological maturity (PM), and harvest (Hv). The periods of initiation or growth of specific organs and those of when different components of grain yield are produced are represented in the bottom boxes.
to vaguely mark the end of the vegetative phase (but see Delécolle et al. 1989; Kirby 1990), could occur at different morphological stages (Figure 4 shows only one example). On the other hand, the relationships of other markers are more stable and valid for a wide range of genotype x environment conditions. For example, the terminal spikelet initiation stage, when all spikelets have been initiated, coincides with the time when stems begin to clearly elongate in most agronomic situations (e.g., Kirby 1990; Stapper and Fischer 1990).

Figure 4 also shows the relationships between apex development and formation of yield components. During the initial stages (from seed imbibition to floral initiation), the plant remains in the vegetative phase, in which new leaves are initiated. During this initial phase, the number of plants m$^{-2}$ that are finally established is determined, as plant mortality is extremely unusual after this stage in healthy crops.

Tillering, the process determining potential number of spikes plant$^{-1}$, begins with the appearance of the fourth leaf (Masle 1985; Porter 1985). This is not related to any particular stage of apical development. It extends until intra-plant competition for resources is strong enough to limit the availability of resources for the growth of new tillers. The end of tillering and beginning of tiller death, under field conditions, frequently coincide with terminal spikelet initiation, when the stem begins to elongate, establishing a strong demand for assimilates and a profound shift in the pattern of dry matter partitioning (Fischer 1984). Tiller mortality normally ends around heading (under field conditions). By anthesis the number of spikes plant$^{-1}$ (and thus the number of spikes m$^{-2}$) has been established.

The number of spikelets spike$^{-1}$ is determined in the rather short period between initiation of the first and last (terminal) spikelets. Floral initiation occurs immediately after the initiation of the collar (Kirby 1984; Delécolle et al. 1989) and normally before double ridge (Kirby 1990; Delécolle et al. 1989), although the latter is the first clear morphological change visible in the apex indicating the plant is initiating spikelets. There is no strong association between the external appearance of the plant and the timing of floral initiation, when the plant becomes reproductive. This could occur before the beginning of tillering (e.g., some spring cultivars grown under long photoperiods; Slaper and Rawson, unpublished) or much later, when many tillers have been already produced (e.g., early sowings of winter wheats). Terminal spikelet initiation does not necessarily have to occur together with the beginning of stem elongation, but this is the case for most growing conditions in the field.

Determination of number of grains spikelet$^{-1}$ is more complex. Floret primordia initiate in the central spikelets well before terminal spikelet initiation, and by this time many florets are already initiated. Floret primordia initiation continues until a maximum number of primordia (ca. 7-11 florets spikelet$^{-1}$) is reached. During the period of fast spike growth and tiller mortality, a significant portion of florets degenerates and by anthesis only 3-4, or fewer, fertile florets spikelet$^{-1}$ can be found (Kirby 1988). Under
stress-free conditions, most (75-100%) fertile florets set grain after anthesis. Thus most determinants of final number of grains m⁻² (Figures 3, 4) overlap somewhat throughout plant development. The negative relationships between these yield components could be attributed to some form of feedback process that determines a sort of compensation between them.

The last yield component, final individual grain weight, appears to be determined with only minimal overlapping with determination of number of grains m⁻², the other major yield component (Figure 4).

**Determination of critical development phases**

The search for the most important stages in building yield potential is not recent. Hudson (1934) stated that the period between terminal spikelet initiation and anthesis was of paramount importance for yield determination. More recently, others have confirmed this association experimentally (Fischer 1984, 1985; Kirby 1988; Siddique et al. 1989a; Slafier et al. 1990; Savin and Slafier 1991; Slafier et al. 1994a).

A simple method for determining which development phases are most critical for yield potential consists of subjecting the crop to different radiation levels (e.g., through shading or thinning) at particular phases and determining the effects on yield and yield components (e.g., Fischer 1985; Thorne and Wood 1987; Savin and Slafier 1991).

Wheat yield has been found to be better related to grain number m⁻² than to individual grain weight (Slafier and Andrade 1989; Magrin et al. 1993; Slafier et al. 1994a). Thus, reducing the level of radiation before anthesis is frequently far more detrimental for yield than doing so after anthesis (Savin and Slafier 1991), indicating that grain growth is, in general, sink limited (Rawson and Evans 1971; Evans 1978; Börghi et al. 1986; Mac Maney et al. 1986; Savin and Slafier 1991; Slafier and Savin 1994a). In other words, the photosynthetic capacity of the crop during post anthesis would exceed what is required for filling the grains completely (Richards, 1996). Thus, the period around or before anthesis, when the number of grains m⁻² is established, has been largely recognized as being critical.

Fischer (1985), by re-analyzing data from several studies with shading imposed at different periods before anthesis, made a major contribution to understanding the physiology of grain number generation and identifying the critical developmental phase for yield potential in wheat. He stated that shading during the 20-30 days immediately before anthesis significantly reduced the number of grains m⁻² but was independent of the level of radiation at any other period of pre-anthesis growth (Figure 5). Therefore, even when numerical components of final number of grains m⁻² are produced during the whole seedling emergence-anthesis period (Figure 4), only the short period coinciding with death of tillers and florets and with active stem and spike growth appears to be critical for determining final number of grains m⁻². This approach was later followed in independent studies (e.g., Thorne and Wood 1987; Savin and Slafier 1991) with similar results, reinforcing the conclusions.
Fischer (1985) stated that accelerating development during active spike growth through increases in air temperature also reduced the final number of grains, despite the fact that high temperature increased the rate of spike growth.

There appears to be no single numerical component of number of grains that is most affected by stress during this period. Any of the two components being fixed at this time (number of spikes plant\(^{-1}\) and grains spikelet\(^{-1}\)) could be responsible for this response. The structure of the crop is thought to determine which of these two components is responsible for the reduction in number of grains m\(^{-2}\) (Slafer et al. 1994b). If we are thinking of taking advantage of this knowledge to further increase the number of grains m\(^{-2}\), it would be unwise to select for any of its numerical components in particular. Instead we should select for greater growth during the window of time in which grain number is determined.

There is, however, a potential flaw in simply assuming that increases in number of grains will directly result in net increases in yield potential. Number of grains m\(^{-2}\) is negatively related to individual grain weight. In order to establish whether or not this generalized negative relationship constitutes a counter-indicator to selection for higher number of grains m\(^{-2}\), the physiological bases of the relationship need to be discussed.

### Relationships between Grain Number and Grain Weight

Numerous results in the literature show that the negative relationship between number of grains and average individual grain weight is a common phenomenon. In the context of this paper, we will analyze these relationships when the components are affected by genotypes released at different periods of wheat breeding. We will also analyze the behavior of isogenic lines for semidwarfism, since the introduction of these genes was a major step in wheat breeding for yield potential (Slafer et al. 1994a).

**Evidence of decreases in grain weight as grain number genetically increased**

Most studies comparing major yield components of wheat cultivars released at different periods reported that modern cultivars have greater number of grains m\(^{-2}\) but lower average individual grain weight than their predecessors (Waddington et al. 1986; Perry and D'Antuono 1989; Siddique et al. 1989a; Slafer and Andrade 1989; and see Bulman et al. 1993 for similar results in barley). Although some exceptions can be found (Hucl and Baker 1987; Cox et al. 1988;
Calderini et al. 1995), most results indicate compensatory processes between grain number and grain weight (Slafer et al. 1994a). In other words, the success of wheat breeders in consistently increasing number of grains m\(^{-2}\) was somewhat counterbalanced by concomitant (but relatively smaller) reductions in the average weight of the grains.

This negative relationship between number of grains and their average weight has also been observed in studies analyzing the impact of semidwarfism on yield components. This is because the greater yields of semidwarf wheats compared with tall cultivars are associated with both greater number of grains per spike (Allan 1986, 1989; McClung et al. 1986; Slafer and Miralles 1993; Miralles and Slafer 1995a) and reduced average grain weight (Gale 1979; McClung et al. 1986; Borrel et al. 1991; Miralles and Slafer 1995a).

Figure 6 illustrates the relationship between these major components as yield potential was genetically improved. The increased grain setting ability of modern vs. old (Figure 6a) and semidwarf vs. tall cultivars (Figure 6b) was partially compensated by untoward decreases in average grain weight. These two components are generated in different phenological periods (see above and Figure 4) and, therefore, their negative relationship is not attributable to feedback regulation (as might be the case for negative relationships between components such as number of grains spike\(^{-1}\) and number of spikes m\(^{-2}\)). Thus, increases in grain number determine reductions in average grain weight.

Understanding the causes of this negative relationship is particularly necessary for future wheat breeding, due to its possible implications for efforts aimed at further increasing yield potential. That is, compensation between both yield components may (or may not) indicate that future attempts at increasing grain yield through increasing grain number would be unwise if they will be counterbalanced by reductions in individual grain weight.

![Figure 6](image_url)

Figure 6. Relationship between individual grain weight and number of grains m\(^{-2}\) for (a) Argentine wheats released in 1920 (Klein Favorito, open squares), 1940 (Eureka F.C.S., open triangles) and 1980 (Buck Pucara, closed squares) grown during three experimental years by Slafer and Andrade (1989, 1993); and (b) dwarf (circles), semidwarf (triangles) and standard height (squares) isogenic lines of spring wheat grown during two years by Miralles and Slafer (1995a). Lines represent curves of constant grain yield of 4 t ha\(^{-1}\).
Possible causes of the negative relationship between grain number and grain weight

The negative relationship between the two major yield components may reflect different facts. The most likely hypotheses for explaining this relationship can be grouped as follows:

1. When grain number is increased, the assimilates available during post-anthesis (i.e., those accumulated during pre-anthesis and those actually synthesized during grain filling) have to be distributed and shared by more grains. Reduced availability per grain would logically result in reduced individual grain weights.

Two alternatives are possible for this competitive-based explanation:

1. There is source limitation for grain growth during post-anthesis, that is, the demand for assimilates is greater than the availability, and a limited amount of dry matter is fully shared by an increased number of grains; or

2. There is simultaneous limitation for grain growth during post-anthesis imposed by the strengths of the source and sink (co-limitation). This occurs when the demand for assimilates is greater than the availability of assimilates per grain, but a higher number of grains is still needed to guarantee the complete use of available assimilates.

The simplest and perhaps most widely accepted explanation for the negative impact of increased number of grains on grain weight is that the greater the number of grains m⁻² produced by the cultivar, the lower the availability of photoassimilates for each grain, which leads to decreases in individual grain weight due to competition between them. However, more detailed analyses are required to confirm or reject this hypothesis.

Testing possible causes of the negative relationship between grain number and grain weight

The first alternative hypothesis, that the crop is source-limited during grain filling, can be easily discarded. The fact that the negative relationship between grain number and grain
weight has a slope greater (less negative) than that required for full compensation between these components (as illustrated in Figure 6) indicates that grain yield during post-anthesis is not completely source-limited. Therefore: 1) there could be a degree of co-limitation (i.e., individual grain weight is reduced as grain number is increased due to stronger competition, although this competition would not be mutually exclusive), or 2) the reduction in grain weight with increased grain number is independent of the level of competition (i.e., yield is limited by the strength of the sink during post-anthesis and assimilate availability would not change the nature and magnitude of the negative relationship between its components).

Not much information is available in the literature to directly test whether or not competition for assimilates during grain filling is responsible (partly or totally) for reductions in grain weight associated with increases in number of grains during past breeding. However, indirect evidence from studies applying different methods can be used. Evidence includes results from manipulation of sink-source ratios during post-anthesis. The most common treatments are shading the crop with shade cloths during all or part of the grain filling period, defoliating plants (or particular shoots) and/or degraining spikes (mostly through the removal of entire spikelets). These treatments can determine whether the negative correlation between the two major grain yield components is due to competition for assimilates between grains (Slafer and Savin 1994a).

Results of different studies modifying the source-sink ratios during post-anthesis have shown inconsistent responses (e.g., Fischer 1975; Fischer and HilleRisLambers 1978; Martinez-Carrasco and Thorne 1979; Caldiz and Sarandon 1988; Winzeler et al. 1989; Aggarwal et al. 1990; Grabau et al. 1990; Ma et al. 1990; Savin and Slafer 1991; Blade and Baker 1991; Slafer and Miralles 1992; Bonnett and Incoll 1993; Slafer and Savin 1994a). This lack of consistency in the effects of modified source-sink relationships on grain weight may reflect genotype and/or environment interactions with the availability of assimilates during post-anthesis for grain growth.

In various experiments Slafer and Savin (1994a) attempted a quantitative reanalysis of the effects on grain weight of manipulating the source-sink ratios after anthesis. Briefly (for details see Slafer and Savin 1994a) the procedure consisted of estimating the change in final grain weight in response to that in assimilate availability (Figure 7a), assuming that the treatments (e.g., trimming the spikes or shading) did not alter the pattern of senescence of the photosynthetic tissues (as stated by Aggarwal et al. 1990; Slafer and Miralles 1992; Slafer and Savin 1994b).
Defoliation experiments were not included since the reduction in the crop's radiation interception during grain filling could not be quantified. Clearly this is a simplification and some values could not be exactly placed on the abscissa. However, slight modifications in the x-values (reflecting effects of source-sink alterations on leaf and other green tissue assimilation capacity) would not affect the general trend. Despite the clear interaction between cultivars and environments (determining that at each level of change in availability of assimilates responses ranged from zero to positive or even negative response), the change in grain weight was well apart from the 1:1 ratio line. This suggests that wheat grain yield is either sink-limited (those points not significantly different from zero) or co-limited by both sources and sinks during grain filling.

The dotted line joins the points belonging to the most responsive cultivars in the most responsive environments (Figure 7a), emphasizing that even in these cases there was no source-limitation to grain growth but co-limitation by sink and source. This line for the interval from -100 to +100% change in availability of assimilates has a slope of approximately 0.4, indicating that even in the most responsive combinations of cultivars and environments there was only a moderate degree of source-limitation and a relatively higher degree of sink-limitation for grain growth. This slope suggests that under complete absence of production of assimilates during grain-filling the reduction in grain weight would be less than 50%. In other words, the contribution of assimilates accumulated in the stem and other tissues before the onset of grain growth would

![Figure 7](image-url)

**Figure 7.** Relative change in grain weight as a function of the relative changes in (a) potential availability of assimilates per grain, and (b) number of grains set per unit above ground biomass. Data re-worked from different experiments. For details of Figure 7a see Slafer and Savin (1994a). In Figure 7b both variables are expressed as a percentage of the mean for each experiment. Original data from Kim and Paulsen (1986, closed squares), Hoogendoorn et al. (1988, closed triangles), Nizam Uddin and Marshall (1989, open squares), Siddique et al. (1989a, open triangles), Slafer and Andrade (1989, open circles), Richards (1992, closed diamonds), and Miralles and Slafer (1995a, closed circles). Solid lines represent the 1:1 ratio. Dashed line was drawn by eye joining the most responsive cultivars in the most responsive environments.
potentially be up to 50% of final grain weight, which is in agreement with calculations based on changes in biomass yield between anthesis and maturity (e.g., Gallagher et al. 1976; Austin et al. 1980; Savin and Siafer 1991), and direct measurements made by Bremmer and Rawson (1978) and Bonnett and Incoll (1993).

In addition, data from several experiments reporting genetic improvements on final yield (mostly through the use of semidwarf genes) were reanalyzed to evaluate the magnitude of changes in grain weight in response to that in number of grains per unit biomass (Figure 7b). This figure shows that increases in the number of grains per unit of biomass (which provides an estimation of the balance between sink and source strengths) did not produce a proportional decrease in final grain weight. This is in agreement with the previous conclusions, from studies involving source-sink manipulations in high yielding cultivars, emphasizing that grain growth in modern cultivars might be co-limited by both source and sink during grain filling.

Analysis of grain weight at particular positions—Another indirect experimental approach to analyze the possible causes of the negative relationship between grain number and grain weight is the determination of changes in weight of particular grains as the number of grains is genetically increased. This analysis points to the possibility that increased number of grains determines whether a greater proportion of grains will be placed in positions of lower weight potential, reducing average individual grain weight. Several authors using Rht alleles in different genetic backgrounds reported that the positive effect of Rht alleles on grain number was negatively associated with those on final average grain weight (e.g., Gale 1979; McClung et al. 1986; Borrel et al. 1991; Miralles and Siafer 1995a).

A recent investigation (Miralles and Siafer 1995b) using near isogenic lines for Rht alleles found that the semidwarf line had greater number of grains and lower average individual grain weight; however, in this study grain weights were determined at specific floret positions within the spike. It was shown that the action of Rht alleles led to a larger number of grains placed in distal positions in the spikelets, characterized by lower weight potential than grains in floret positions more proximal to the rachis (Figure 8). Proximal grains, which are the heaviest, contributed less to total number of grains per spikelet (and than per spike) in lines carrying
Rht genes than in the standard-height lines. Obviously, the contrary was true for the contribution made in these lines by the lightest grains. Consequently, irrespective of source-sink ratio, the average weight is lowered by increasing the number of grains due to the increased contribution to total number of grains from those in distal positions of small size potential. The same reasoning would be true if increased number of grains is brought about by increases in the number of spikes m⁻², since grains from the 'extra' spikes would have lower weight potential.

Although the same analysis has been not done for cultivars released at different times, there is evidence that increased number of grains as a consequence of past breeding has brought about reduced average grain weight due to the increased proportion of grains with relatively smaller weight potential. For example, while modern Australian and Argentine wheats exhibited higher grain number and lower average individual grain weight than their predecessors (Siddique et al. 1989; Slafer and Andrade 1993), the basal grains of the central spikelets did not show a reduction in weight (Loss et al. 1989; Slafer and Miralles 1993).

Source-sink manipulations in modern and old cultivars—A better approach to determining whether the negative impact on average individual grain weight of a genetically increased number of grains m⁻² is due to stronger competition among grains consists of analyzing responses to source-sink manipulations in grains from different positions of cultivars released at different times or in isogenic lines for semidwarfism. Unfortunately, simultaneous analyses are not frequent in the literature, and any conclusions drawn from a limited number of cases have to be taken cautiously.

Miralles and Slafer (1995b) modified the source-sink ratios in isogenic lines of wheat for semidwarfism in three different environmental conditions. This was done by removing all the spikelets from one side of the spikes (effectively halving the number of grains per spike without changing the relative contributions of grains from different positions within the spike) a week after anthesis. Spikelet removal did not significantly modify the weight of the grains analyzed in any of the three environmental conditions (Figure 9a). However, grain weight of the dwarf line in most environmental conditions increased significantly as the source-sink ratio increased (Figure 9a). Averaging across all environments and grain positions and halving the number of grains in this line (i.e., increasing the source-sink ratio by about 100%) increased the final weight of its grains by about 20%. The conclusion is that the reduction in average grain weight produced by Rht alleles (at least in this genetic background) was not due to increased competition for assimilates, when the semidwarf and standard-height lines, which represent suitable agronomic types, are compared. However, further increasing the number of grains (as was the case with the additional dose of Rht genes) would result in final grain weight being co-limited by source and sink strengths.

A similar approach was followed by Kruk, Calderini and Slafer (unpublished) using wheat cultivars released in Argentina over the last 70 years. They completely defoliated
Yield Components and Compensation in Wheat

Figure 9. Relationships between individual grain weight in the control and in the treatment with manipulated source-sink ratio during post-anthesis for grains from specific positions within the spike of (a) isogenic spring wheats with halved spikes, and (b) wheats released at different eras in Argentina. In Figure 9a the treatment consisted of the removal of all spikelets from one side of the spikes 7 days after anthesis in dwarf (circles), semidwarf (triangles) and standard height (squares) isogenic lines used by Miralles and Siafer (1995b). In Figure 9b the treatment consisted of complete defoliation of specific shoots 10 days after anthesis of Argentine cultivars released in 1920 (Klein Favorito, open squares), 1940 (Eureka F.C.S., open triangles), 1980 (Buck Pucara, closed squares), and 1989 (ProINTA Pigiue, closed triangles). Grains were the proximal grains of near basal (G1B), central (G1C) apical spikelets (G1A) and grains 2 and 3 of central spikelets (G2C and G3C, respectively). Dashed lines represent the 1:1 ratios.
the shoots of these plants 10 days after anthesis in two growing seasons. The weights of individual grains were analyzed for different positions within the spikes. For simplicity, only results for the cultivars released in 1920, 1940, 1980 and 1989 on the main shoots are presented. There were small differences in individual grain weight between intact and defoliated shoots for cultivars released in 1920 and 1940 (Figure 9b), which were only exceptionally significant (one case in K. Favorito). Thus, it appears that in these cultivars grain weight was not restricted by the availability of assimilates during effective grain filling. The scenario was slightly different for the cultivar released in 1980; although the final weight of many of the grains was not significantly affected by defoliation, the general trend was for a stronger response. In the case of Prointa Pigie (a very high-yielding cultivar released in 1989), grains showing significant sensitivity were not an exception, and the reduction in grain weight was greater than that shown by the other cultivars (Figure 9b). This trend describing the responses of main-shoot grains of four cultivars represents the responses of the other cultivars and of the grains from tiller spikes (Kruk, Calderini and Slafer, unpublished). Results from Koshkin and Tararina (1989) also suggest that breeders have been systematically reducing the sink-limitation to grain yield; this may have resulted in modern, high-yielding cultivars whose yield is co-limited by source and sink strengths.

The future
The general conclusion that can be drawn by analyzing possible causes of the negative relationship between grain number and grain weight is that it is mostly due to non-competitive reasons and, in particular, that increasing the number of grains m\(^2\) will invariably increase the proportion of grains with reduced weight potential. However, it should be noted that direct and indirect evidence indicates that genotypes with a large number of grains have a small, but significant, source limitation. The degree of limitation to grain growth imposed by the strength of the source during post-anthesis appears to have been consistently increased from old to modern cultivars.

If breeders continue increasing grain number without changes in the availability of assimilates per grain, individual grain weight will decrease at a higher rate than in the past, since further reduction due to competition among grains will be added to the 'natural' reduction resulting from the increased proportion of grains with lower weight potential.

Thus breaking the barriers of yield potential in wheat will require simultaneous increases in both number of grains m\(^2\) and availability of assimilates to avoid developing competitive restrictions to grain growth. Different approaches are possible for attempting to increase grain number and the availability of assimilates for growing grains. Most of them deal with growth characters, such as changes in the crop's ability to intercept more radiation and in its radiation use efficiency. Araus (1996) has shown in this workshop how these physiological traits could be used as selection criteria in realistic breeding programs.

Alternatively, manipulating the crop's phenological development during phases that are critical for determining grain
number and grain weight has received much less attention but is certainly a possible avenue of exploration.

Since the possibilities of manipulating growth characteristics have been explored by others in this workshop (e.g., Araus 1996; Khush and Peng 1996; Loomis and Amthor 1996; Richards 1996), we will try to evaluate whether phenological development, through the manipulation of responses to photoperiod and temperature, could be an alternative, complementary tool for increasing yield potential in wheat.

Enhancing Phenological Development as a Way to Increase Yield Potential

Plant development and plant breeding

Phases of plant development that could be genetically manipulated include overall responses to environmental factors that determine the final length of the growing cycle. Plant breeders have been doing this for centuries. In particular, the duration of the sowing to anthesis period has been given flexibility so that, despite variation in sowing date, anthesis can be adjusted to occur at the optimum time for a particular location (Flood and Halloran 1986; Gomez-MacPherson 1993). It can be assumed that in most wheat growing areas, timing of anthesis is already close to the optimum, and there would be little room for further increasing yield potential through manipulation of the whole growing season to anthesis.

If, as suggested in many papers, there are associations between particular developmental stages and yield components (e.g., Rawson 1970, 1971; Rawson and Bagga 1979) and if there are associations between the duration of phases and absolute yield (e.g., Rawson 1988a, 1988b; Craufurd and Cartwright 1989), then it is important to be able to manipulate the duration of these phases in order to indirectly manipulate yield potential.

Therefore, in this paper we will concentrate on the possibilities of manipulating the duration of particular phases that are strongly associated with particular yield components.

Possible manipulation of development for increasing yield potential

The combinations of phasic development patterns in commercial wheat cultivars suggest that a growing season of a particular length could be achieved with different durations of component phases (Slafer and Rawson 1994). This leads to hypothesizing that manipulating development could bring about increases in yield potential with no modification of the total length of the growing period. For example, Halloran and Pennell (1982) reported that the lengths of phenophases in a number of wheat genotypes were independent of each other. They thus implied that the duration of any development phase could be modified independently of the duration of other phases. In the context of manipulating development to increase yield potential, it becomes relevant to explore the possibility of modifying the length of two phases defined as critical for increasing yield potential: stem elongation and grain filling. Extending the former phase would increase the amount of biomass accumulated during spike growth.
and the final number of grains to be formed by reducing the proportion of either floret abortion or tiller death (or both). This would result in an increased number of grains m\(^{-2}\) to be filled. Assuming that yield of modern cultivars is co-limited by source and sink sizes during post-anthesis (see above), extending the grain filling period would increase the availability of assimilates required for satisfying the increased demand.

To manipulate the duration of these phases, it is necessary to identify the factors affecting them. The main environmental factors affecting the rate of development are temperature and photoperiod. Cultivars are reported to differ in the duration of their phenophases independently of their responses to these factors due to the action of an ‘intrinsic’ genetic factor commonly termed ‘basic development rate’ or ‘intrinsic earliness’ (e.g., Flood and Halloran 1984; Masle et al. 1989).

It is frequently believed that differences in basic development rate apply only to the length of the vegetative period up to floral initiation (see review by Slafer 1996); that wheat is most sensitive to photoperiod during early phases and so responses to this factor are complete by the time stems begin to elongate (see review by Slafer and Rawson 1994); and that cultivars do not differ much in their sensitivity to temperature (this the basis for using thermal times with the same base temperature for any cultivar within a species; Slafer and Rawson 1994). If all these assumptions are true, there is no possibility of manipulating development to increase yield potential other than by selecting for ‘optimum’ flowering date.

The last sections of this paper will challenge these assumptions by reviewing differences among cultivars in response to photoperiod and/or temperature during stem elongation (from terminal spikelet initiation to anthesis) and grain filling (from anthesis to maturity). The existence of these differences is the first step required for using these characters in breeding for higher yield potential. Although basic development rate is frequently considered an additional factor controlling development, here it is considered part of the cultivar’s temperature response (for results supporting this see Slafer and Rawson 1995a; for a comprehensive discussion see Slafer 1996).

**Responses to photoperiod during stem elongation**

The assumption that wheat responses to photoperiod are complete by the beginning of stem elongation is possibly derived from studies in which development was compared between crops sown on different dates (e.g., Hay 1986; Porter et al. 1987; Masle et al. 1989; Martin et al. 1993). Generally, major changes in crop duration from sowing to anthesis are largely accounted for by changes in duration of the vegetative period, since duration of the sowing to anthesis phase is linearly associated with that of the sowing to double ridge phase, given the period from double ridge to anthesis is relatively constant (see example in Figure 1 of Slafer and Rawson 1994a). Based on this type of studies, it appears that the assumption that the phase to double ridge is more sensitive than later phases is well founded. However, in such studies, reproductive stages are forced into similar environmental conditions by virtue of the response in the duration of this early phase. So, any possible difference in
sensitivity cannot be revealed. On the other hand, when the floral stages of development are exposed to different photoperiods in the field, they appear to be quite responsive. For example, a field data set collected by Angus et al. (1981 for Gatton) showed a pattern that was at variance with the generalized pattern described above, i.e., changes in time to heading were more strongly associated with changes in duration of the reproductive phase than with changes in duration of the vegetative phase (see also Saini et al. 1986a).

In a recent study aimed at determining whether responses to photoperiod in wheat change with advancing phenology, Slafer and Rawson (1996) showed that photoperiod sensitivity could still be important during stem elongation (Figure 10). This study included a spring wheat (Condor), a semi-winter wheat (Rosella) and a winter wheat (Cappelle Desprez). In all of them, both the primordia (leaf and spikelet) initiation phase to terminal spikelet initiation and the stem elongation phase until heading were responsive to photoperiod. Remarkably, sensitivity of the initial phase was greater (Condor, Figure 10a), similar (Rosella, Figure 10b) or smaller (Cappelle Desprez, Figure 10c) than that of stem elongation. Two major conclusions may be drawn from this study: 1) that duration of the phase critical for determining number of grains m\(^{-2}\) can be altered in response to photoperiod, and 2) that responses during pre- and post-terminal spikelet initiation phases are independent. Obviously more data are needed before general conclusions can be drawn, but results from Allison and Daynard (1976) and Rahman and Wilson (1977) as re-examined by Slafer and Rawson (1994), as well as from Manupeerapan et al. (1992), and Slafer and

Figure 10. Relationships between time from the seedling stage to terminal spikelet initiation (circles), and from then to heading (triangles) and photoperiod for the wheat cultivars Condor (a), Rosella (b) and Cappelle Desprez (c) grown at 16/12 °C after plants were vernalized (4°C) for 60 d. Dashed arrow in c indicates that the response was qualitative. Re-worked from Slafer and Rawson (1996).
Rawson (1995b) strongly support the conclusion that the length of the stem elongation phase is responsive to photoperiod and that there is genetic variation in this response.

It could therefore be suggested that the number of grains $m^{-2}$ could be increased by manipulating photoperiod response during this phase. The only evidence we are aware of comes from an unpublished experiment that supports this hypothesis (see Table 7 in Fischer 1985).

**Do cultivars vary in their response to temperature?**

It has been demonstrated that development in all cultivars is sensitive to temperature, reaching heading earlier in higher than in lower temperatures (e.g., Halse and Weir 1970; Rawson 1970; Wall and Cartwright 1974; Rahman and Wilson 1978; Piratesh and Welsh 1980; Ford et al. 1981; Rawson and Richards 1993; Slafer and Rawson 1995c; 1996). This finding of universal sensitivity to temperature (Aitken 1974) could be the reason for the assumption that there is almost no variability in the response of different cultivars to temperature (e.g., Takahashi and Yasuda 1971). However, studies specifically designed to look for differences in temperature response among genotypes and, in particular, to search for different sensitivities in different phases are quite uncommon.

Reviewing data from the literature, Slafer and Rawson (1994) showed that genotypes could vary quite substantially in their degree of sensitivity to temperature (see their Figure 7). They also found that the degree of sensitivity to increased temperature (expressed as the reduction in days to heading) was independent of the time a genotype took to head. In other words, the fact that one genotype takes longer to head than another at low temperature does not imply that its sensitivity to temperature will be greater or less. Furthermore, there were some suggestions in the literature that cultivars could differ in their base temperature, in particular when winter and spring cultivars are compared (e.g., Slafer and Savin 1991). Therefore, there could be merit in searching for genetic differences in temperature response during stem elongation and grain filling.

**Temperature response during stem elongation**

Data from Rawson (1970) and Rahman and Wilson (1978) are useful for examining the effects of temperature in different phases, for determining whether sensitivity to this factor changes with ontogeny, and, if so, whether this change in sensitivity is common to all cultivars. As expected, all genotypes and all phases were sensitive to temperature, but genotypes differed in their response (Figure 11). In relative terms, sensitivity tended to be stronger during stem elongation than during primordia initiation (from sowing to terminal spikelet initiation; Figure 11). It can be concluded from Figure 11 that there is variation in the magnitude of temperature response during stem elongation but also that the degree of this sensitivity is not associated with that during previous phases. Saini et al. (1986b) confirmed this conclusion in an independent study. They found the greatest sensitivity to temperature and greatest variation between genotypes in the stem elongation phase.
To analyze genetic variation in temperature sensitivity in more detail, Slafer and Rawson (1995c) studied the responses of contrasting genotypes to a range of temperatures (10-25°C). Figure 12 summarizes the responses of two cultivars during stem elongation in terms of the rate of development from terminal spikelet initiation to anthesis (as re-worked by Slafer and Rawson 1995d). The different sensitivity is due to both changes in the slope of the response (reciprocal of the thermal time) and in the base temperature (Figure 12).

Thus, while Condor showed a slope of 0.0026 (°Cd)^{-1} (i.e., a requirement of ca. 390°Cd) and a base temperature of 4.64°C for stem elongation, corresponding figures for Cappelle Desprez were 0.0018 (°Cd)^{-1} (ca. 570°Cd) and 2.78°C. By virtue of the magnitude of these parameters, these cultivars exhibited a significant difference in time from terminal spikelet initiation to anthesis due to their differential sensitivity to temperature during this phase. In practice, it could mean that in cultivars similar to those in this example and growing at an average temperature of 20°C during stem elongation the length of this phase could range from 25 to 33 days. If both the slope of the relationship and the base temperature are under genetic control (which remains to be studied), any of these parameters could be manipulated with the aim of modifying the length of the phase, which could result in greater number of grains m^{-2}.

Figure 11. Relative magnitude of the response to temperature during stem elongation vs. that during the period sowing-terminal spikelet initiation estimated as [100 (Dht-Dlt) Dht^{-1}], where Dht and Dlt are durations under the highest and lowest temperature, respectively. Original data taken from experiments conducted at two constant thermal regimes throughout by Rahman and Wilson (1978; triangles) and Rawson (1970; circles). Straight line represents the 1:1 ratio. Figure re-worked from Slafer and Rawson (1994).

Figure 12. Relationships between rate of development from terminal spikelet initiation to anthesis and temperature for cultivars Condor (circles) and Cappelle Desprez (triangles). Solid lines were fitted by linear regression. The experiment was conducted with a long photoperiod (18 h) after the plants were vernalized (4°C) for 50 d. Re-worked from Slafer and Rawson (1995c).
Temperature response during grain filling

Since there is no clear evidence of response to photoperiod after anthesis, the only possibility for increasing duration of grain filling would be through manipulating temperature response. The principle is described above for the rate of development from terminal spikelet initiation to anthesis.

The fact that the length of the grain filling period is sensitive to temperature has been highlighted several times. In general there is agreement that the higher the temperature the shorter the grain filling period (see for example Table 2 in Wiegand and Cuellar 1981). Housley and Ohm (1992) clearly demonstrated the existence of genetic diversity for duration of grain filling period using 175 genotypes of winter wheat. However, their study could not be confidently used to determine genetic differences in temperature response because it included only a narrow range of temperatures during grain filling. Hunt et al. (1991) grew 10 wheat genotypes under the same conditions up to 1-2 days after anthesis and from then on exposed plants to thermal regimes ranging from 15/15 to 30/25°C. In this study, genotypes clearly differed in their sensitivity to temperature during grain filling. An example of these differences is illustrated in Figure 13. Assuming linear relationships between rate of development from anthesis to maturity and temperature, the slopes for the most sensitive genotypes (Neepawa and Glenlea, 0.0027 °Cd⁻¹) were approximately 50% greater than those for the least sensitive genotypes (Sun 27-B and Kechuang, 0.0017 °Cd⁻¹). Data from Marcellos and Single (1972) confirm the existence of large genetic variability in sensitivity to temperature during grain filling. In their work Festiguay was about 35% more sensitive than Gabo (see Slafer and Rawson 1994).

Concluding Remarks

To be successful in accelerating genetic improvement of wheat yield potential, empirical selection methods based on trial and error should be replaced by those based on physiological attributes determining yield. Among the different attributes that could be considered, we only discussed the use of phenological development as a tool for breaking the apparent barriers for further increasing yield potential in modern wheat.

It is known that increasing grain number m⁻² was effective for reaching higher grain yields in the past, and we accept that this strategy could be viable in the future as well.

Figure 13. Relationship between rate of development from anthesis to maturity and temperature for cultivars Neepawa (circles) and Kechuang (triangles) grown in controlled conditions of 16 h photoperiod. There was a single thermal regime up to anthesis and thereafter plants were separated into four thermal regimes (Hunt et al. 1991). Re-worked from Slafer and Rawson (1994).
However, there is a growing objection for this based on the negative relationship frequently found between number of grains m\(^{-2}\) and average individual grain weight. In other words, the concern is that increases in grain number could be counterbalanced by reductions in grain weight, and grain yield would not be increased. However, recent analyses considering data from different experiments manipulating source-sink relationships found that increases in grain number did not produce a proportional decrease in final grain weight, and that grain growth in modern cultivars might be co-limited by both source and sink strengths.

It appears that, in the future, simultaneous increases in both number of grains m\(^{-2}\) and availability of assimilates will be required for breaking the yield barriers in wheat—the former to increase sink strength and latter to avoid competitive restrictions to grain growth. Manipulating the crop's phenological development during phases critical for determining number of grains and grain weight could be an avenue to explore.

There is evidence in the literature that stem elongation, which is critical for determining number of grains m\(^{-2}\), can be altered in response to photoperiod and temperature, and that the magnitude of the responses during pre- and post-terminal spikelet initiation is independent. Regarding final grain weight, manipulation of temperature response is a possible strategy for lengthening the grain filling period. Genetic variation appears to be important for all these sensitivities.

Acknowledgments

We thank Prof. E.H. Satorre for critically reading an earlier version of this article. Drs. R. Savin and B. Kruk, members of our laboratory staff, collaborated in different ways on this review and are gratefully acknowledged.

References


Questions and answers

K.J. Young:

Plant breeders have experience with breeding for high kernel number. Apparently, most attempts have not
succeeded in achieving higher grain yield. Two explanations deserve mention. In many crosses, parent sources likely had extreme phenotypes, i.e., very high kernel numbers. Perhaps these were not optimum parents, they were too extreme. Another limiting factor is too small effort limited to a few crosses and a single cycle.

G.A. Slafer:
In addition to these comments, it is also possible that in most of these cases, the evaluation of very high numbers of grains had been made on a single (main) spike basis. Therefore, changing the level of organization to the crop level could result in different outputs (i.e., higher number of grains per spike does not necessarily mean high number of grains per m²). That is why our suggestion is to increase the pre-anthesis growth of the spikes (as number of grains appears to be closely related to spike dry weight at anthesis), through lengthening its growth duration, rather than selecting for large spikes.

G. Ortiz-Ferrara:
All the studies you described were done under optimum conditions in terms of moisture and fertility. Would you please speculate as to how these results and concepts would differ if the studies were done under reduced moisture (less than 300 mm)?

G.A. Slafer:
As you said, this can only be speculated upon due to the lack of many studies evaluating these aspects in stressful environments. My speculation is that most of the concepts would work in these environments as well. For example, the reduction in number of grains per m² when plants are grown under limited moisture is probably responding to reductions in spike dry weight at anthesis. For N fertilization, there is some evidence that this behavior is true (Field Crops Res. 33:57-80). Regarding final grain weight, it is well known that moisture stress reduces its value; however, it is possible to speculate that it is due to a direct effect which is independent of the availability of assimilates. For temperature stresses during grain filling, this has been shown by different authors (in our case, in a paper published in J. Agron. and Crop Sci. 168:191-200).

M. Reynolds:
You provided evidence that the negative relationship between grain number and weight may be a consequence of the grain weight potential, which is reduced with increasing number of grain sites per spike. When and how is grain weight potential determined?

G.A. Slafer:
We are not completely sure about when weight potential is actually determined. It is clear from the literature that the first 7-15 days after anthesis are crucial. This is because of the strong relationship between final weight and number of endosperm cells, and it is during this phase when endosperm cells are formed. In addition, we are now studying the possible impact on final weight potential of pre-anthesis factors.
Increasing the Yield Potential of Wheat: Manipulating Sources and Sinks

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Abstract
A genetic improvement in the yield potential of wheat will be achieved more quickly if we target and specifically select for factors that contribute to higher yields. This paper considers the numerous physiological processes that influence the yield of spring wheat grown under irrigation and discusses ways of genetically manipulating them. Discussion is divided into three phases of crop growth. The manipulation of early leaf area growth and phenology is discussed first and the impact that these may have on increasing grain yield in favorable and unfavorable conditions. The second phase discussed is the early reproductive period up to anthesis. Ways to increase the partitioning of carbon and nitrogen to the developing ear so as to increase grain number and thereby yield are suggested. Finally, the post-anthesis period of grain growth is discussed. It is noted that the rate of grain growth in wheat is substantially less than it is in barley and hence there should be opportunities to increase the grain growth of wheat. Factors that should contribute to increased grain growth are discussed and ways to genetically increase it are proposed.

Introduction
Wheat breeding at CIMMYT has been very successful in raising yield potential. At Ciudad Obregon, Mexico, where selection has been made, grain yields have increased by about 0.9% per year over the last 30 years (Waddington et al. 1986; Sayre et al. 1996). This increase may be substantially greater than in other breeding programs and is likely due to a number of reasons, for example, the size and quality of the breeding program. The single location used to select for yield potential and to evaluate progress has predictable weather, irrigation, good soils and nutrition, which also contributes to the excellent gains made for yield. Yield potential in these studies was assessed as the yield of adapted cultivars grown where water and nutrients were non-limiting, and weeds and diseases were controlled. This definition of yield potential will be used throughout this paper. The gains made at CIMMYT in these favorable environments have also resulted in yield increases in less favorable environments (e.g., Brennan 1986; Sayre et al. 1995). Thus, much of the following discussion on identifying ways to improve yield potential could have wider application.

It seems reasonable to assume that yield potential will continue to increase using current empirical methods provided new variation is incorporated into breeding programs. Why then should we seek
additional or different approaches to improve yield? A number of reasons can be advanced. First, selection efficiency using empirical methods has improved substantially over the last three decades due primarily to better machinery for handling small plots, new experimental designs to improve our ability to identify the best lines, and computers that have increased the speed of data handling and statistical analyses. However, it is possible that the rate of advance in these technologies applied to breeding may have slowed, thereby making future yield gains more difficult.

Second, lower gains are likely in many regions because less emphasis is being placed on improving yield potential. In these regions yield potential is only one factor that is important in varietal release. There is increased pressure on breeders to develop varieties with grain quality characteristics that are specifically suited to an end product. Also, as more is known about genes for resistance to shoot and root diseases, nutrient disorders, and other biotic and edaphic stresses, more emphasis is placed on incorporating these genes/characters into new varieties.

The third reason for seeking different approaches to increasing yields is that any increase in yield potential must have a physiological basis, e.g., photoperiod sensitivity, the presence or absence of dwarfing genes, greater photosynthesis, or a faster rate of grain filling. If we can target the factors contributing to greater yield, we should be able to select for them more easily and efficiently and be able to identify the most appropriate germplasm to use as parents.

Deficiency Breeding and Varietal Relay

In many wheat growing regions, breeding emphasis has moved away from increasing yield to overcoming disease, improving grain quality, or eliminating other defects that may constrain production and grain marketability. This can be referred to as 'deficiency' or 'maintenance' breeding. These factors are often more easily targeted than yield potential because of the better understanding of the diseases limiting crop yields and the grain quality attributes required by processors and consumers. Furthermore, the characteristics targeted usually have a high heritability and there is substantial genetic variation in them so that success is ensured.

This understanding of desirable quality traits and disease resistance has led breeders to construct varieties by combining known characteristics into a basic variety that is very acceptable to growers and the users of the grain. This approach is now very common and is successful if the number of cultivars released is the measure of success. To begin the construction process, a high yielding cultivar in the target region is required. This provides the basic structure. Additional building blocks are incorporated into the basic structure usually by backcrossing. These blocks often represent incremental but small changes in grain quality and disease resistance. Usually these small changes result in new varieties so that as new blocks are added the breeder becomes locked into what has been called a 'varietal relay race' (Plucknett and Smith 1986). It then becomes very difficult to alter the fundamental structure as it has taken a decade or two to
put the right combinations of desirable characteristics together and improved varieties are being released. A radical alteration to this basic structure would result in the building blocks collapsing and a new start would be required. This is the reason why many breeders are reluctant to stray too far from their current framework and make wider crosses. It is also the principal reason why future progress in improving yield potential is likely to decline if this approach continues.

One presumes that when we have a better knowledge of the underlying physiological processes to target in a breeding program, these can be incorporated into the very best germplasm by backcrossing. This will ensure that the desirable features for grain quality and disease resistance are maintained whilst yield potential is also increased. For this we will need to: 1) identify the yield determining processes, 2) identify suitable genetic variation for these yield determining processes, and 3) develop selection procedures so as to incorporate them efficiently into the appropriate wheat germplasm.

Targeting Desirable Physiological Characteristics

Breeding progress is achieved when specific characteristics are targeted. An understanding of the genetics of disease resistance and of grain quality parameters are good examples where an improved understanding of a varietal deficiency is targeted and has then led to substantial genetic improvement. The same level of understanding does not exist for yield potential; thus characteristics to improve grain yield cannot be targeted in the same way. The only exceptions to this would be selecting for genes (both major and minor) governing flowering time to improve adaptation to particular regions. Appropriate plant height can also be targeted because it is known to have large influence on yield potential. We need to better understand the underlying processes of physiological traits in order to select for them more precisely.

In the rest of this paper, I shall give my thoughts on the physiological processes that may be genetically modified to improve the yield of wheat. The main factors that have influenced my thinking come from field experiments comparing historical sets of varieties released in different eras. These studies have dissected yield into some of its components and then determined the changes in these components that are associated with yield increases. The simplest dissection of grain yield is into biomass and harvest index. Studies of historical sets of wheat varieties show that most, if not all, of the increase in wheat yield over the last 100 years has come from an increase in harvest index. It is very interesting to contrast this result with barley, where harvest index (HI) and biomass have contributed equally to improved yields (Gifford 1986). It would be a worthwhile endeavor to understand why these two cereal species differ in this respect.

A further interesting finding from historical data sets is that the increases in yield and HI in wheat and barley have been almost entirely due to an increase in grain number per unit area, rather than to an increase in grain weight (Austin et al. 1980; McCaig and
DePauw 1995; Cox et al. 1988; Sayre et al. 1996). Grain number is established in the period just before anthesis when the ear is growing rapidly. This would suggest that an increase in assimilate supply to the developing ear has been a significant factor for increasing grain number for the historical sets of varieties. The lack of increase in grain weight in the historical sets also suggests that assimilate supply is limiting after anthesis.

**Does the Supply of Carbon Limit Yield Potential?**

The obvious answer to this question is yes, as more growth and photosynthesis results in more biomass and more yield, provided the partitioning coefficient between grain and straw is maintained. However, the question is not as simple as it seems, since the obvious ways to increase carbon production per unit area, such as by increasing plant density, has not increased biomass and yield in well-managed experiments at Obregon (Fischer et al. 1976). Nor does CO\(_2\) fertilization at double ambient levels greatly increase total biomass under temperate conditions (Idso et al. 1989; Rawson 1995). Furthermore, the enormous selection pressure to increase grain yield by breeding has not resulted in an increase in peak rates of photosynthesis per unit leaf area or genetic gains in biomass in wheat (Evans 1993).

To examine whether the supply of carbon may limit yield, I have divided the crop growth period into three phases. This also makes it easier to identify the important processes in these periods that could be manipulated.

**Vegetative period**

Slower growth early in the crop’s life may not greatly limit grain yield in environments where nitrogen and water are freely available. This is certainly true in long-season environments where the crop overwinters and where leaf area and biomass prior to winter are small relative to final biomass. It is also true in favorable shorter-season environments. For example, Fischer (1983) has shown that limiting carbon supply by shading during the vegetative stage has little effect on the yield of irrigated spring wheats. Similar conclusions were reached in studies where it was shown that increasing planting density or decreasing row spacing had little effect on total biomass at maturity and on grain yield (Fischer et al. 1976). It seems that early deficiencies in growth are easily compensated for by later growth, provided there are no factors that limit later growth.

These conclusions may be true in well-managed crops where water, nutrients and light may be very favorable. However, if conditions become unfavorable either due to lack of water, salinity, nutrients, light, weeds or very short season environments, then slower growing crops may not be able to recover from the reduced vegetative growth and yields may decline. This may also be true in less ideal conditions of farmers’ fields compared with conditions on experiment stations. Increasing early vegetative growth may overcome some of the above limitations and enhance our opportunities to improve yields in well-managed crops by manipulating phenology. We have recently developed very different wheat germplasm with greater early vegetative growth that may be very important to provide these
opportunities for both sub-optimal as well as more favorable conditions. These will be described later.

**Reproductive period**

As crops approach anthesis, the environment progressively increases its impact on yield. For example, shading in the early reproductive period has less effect on crop yield than it does in the late reproductive period (Fischer 1983). The crop clearly has more time to compensate for any early check in its growth compared to a later check. During the late pre-anthesis period, a number of factors are expected to increase growth and thereby increase yield. For example, increases in photosynthesis, light interception and radiation-use efficiency should increase crop growth rate and, thereby, biomass and yield. However, there is little evidence that current germplasm has higher values of these variables than old varieties. This is rather curious considering that grain number, the yield component most closely associated with increased yield, is determined during the late reproductive period. This indicates that for our current wheats, it is the partitioning of carbon to reproductive structures, rather than increases in biomass, that has largely determined yield. Simplistically this suggests that the supply of carbon is not limiting yield, but rather the partitioning of carbon to the growing sinks.

Support for the idea that it is not the supply of C that is limiting, but rather its utilization, also comes from studies of large wheat fields. Measurements of carbon assimilation in well-fertilized crops with adequate water shows that assimilation increases to a peak at midday but is not sustained and declines thereafter (Dunin et al. 1989). This may be due to feedback inhibition of photosynthesis because of adequate or even excess carbon produced for both growth and storage (Azcon-Bieto 1983; Sage and Sharkey 1987), although factors other than C may also be limiting during this time. Uptake of water and nutrients by roots are the obvious candidates; further studies on root activity during this growth period are required.

**Post anthesis period**

The finding that there has been very little change in the grain size of wheat when historical sets of varieties are compared also suggests that the supply of carbon to the growing grains is limited. However, there is considerable evidence to the contrary. We have conducted several experiments both in pots and in field canopies where we have halved the leaf area several days after anthesis and, therefore, after the final grain number has been established. Despite the halved leaf area, grain weight and yield were not reduced (Table 1). Thus plants were able to achieve the same yield with about half the leaf area. This study is not unusual and other

<table>
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<tr>
<th>Relative leaf area</th>
<th>Seed number</th>
<th>Seed weight (mg)</th>
<th>$^{13}$C/$^{12}$C (grain)</th>
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<tr>
<td>100</td>
<td>125</td>
<td>49</td>
<td>15.8</td>
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<td>50$^2$</td>
<td>133</td>
<td>48</td>
<td>17.7</td>
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1 Plants were grown in large pots without nutrient or water limitations. The main stem and the first tiller were allowed to develop and additional tillers were removed as they appeared.

2 Leaf area halved at beginning of rapid grain growth.
defoliation experiments have given similar results (Davidson 1965; King et al. 1967; Rawson et al. 1976). This study indicates that photosynthesis of current high yielding wheats is in excess of that required for them to achieve their yield potential. Plants compensated for the reduced leaf area by increasing stomatal conductance which would result in an increase in photosynthesis. Carbon isotope discrimination also increased by 2% indicating that stomatal conductance increased substantially relative to assimilation capacity.

These results suggest that our current wheat plants are very conservative in carbon fixation. They have a photosynthetic system that is operating at a level considerably below its potential. It means that when required, crops can respond to an extra demand for photosynthate. For example, if leaf area is reduced due to foliar damage, this may not result in a yield penalty. It also indicates that if carbon requirements are increased (i.e., by an increase in the number of grains set), the crop should be able to fill the additional grains without significant reduction in weight per grain, and therefore result in a greater yield (see Siafer et al., these proceedings).

These results complement recent findings from CIMMYT where semidwarf cultivars released in northwest Mexico over the past 30 years were compared (Sayre et al. 1996; Fischer et al. 1997). In these studies it was found that increases in yield since 1962 were associated with increases in grain number per unit area (but no decrease in grain weight) and with increases in stomatal conductance. Furthermore, measurements that reflect variation in stomatal conductance, such as canopy temperature and carbon isotope discrimination, were also associated with yield. This is a very important finding as it has implications for how to select for future yield increases. One outcome of these results would be to begin selecting for higher stomatal conductance or reduced canopy temperature. However, whereas this may be useful in the short term, in the long term the rate of yield increase may be sacrificed.

The increased stomatal conductance and the corresponding increase in photosynthetic rate may be a direct response to the increased demand for assimilates driven by greater grain number i.e., greater sink strength. If the increases in conductance and in yield are both a result of increased grain number, the more successful approach in the long term would be to identify the underlying factors determining grain number, rather than to select for the consequences of increased grain number. This would target the principal factors governing increased yield rather than just the correlated response. It may well be that post-anthesis carbon supply is not limited at all. Photosynthesis appears to be well regulated by stomata according to the demand by the plant for carbon. If this is true, selection for stomatal conductance is doomed for slow gains, whereas if we could understand the underlying processes that control grain number, we may be able to greatly accelerate gains in yield.

In summary, it is suggested that grain yield for irrigated spring wheat may not be limited by the supply of carbon. In fact there is
ample evidence that crops may be more sink than source limited. However, considerable opportunities exist to increase both the total amount of carbon and the partitioning of this carbon to the growing ears and grains. These opportunities will now be examined in more detail.

**Increasing Carbon Supply**

**Early vegetative stage**

It has become evident that increasing carbon supply is far easier to achieve by increasing leaf area than by increasing photosynthesis. In our quest to improve the early growth of wheat for Mediterranean-type environments, we have been exploring the underlying factors that make barley much more vigorous than wheat, which in turn results in barley having a faster and greater development of leaf area and biomass by anthesis. Leaf area of barley just after seedling emergence is twice that of wheat, whereas dry weight is about 40% greater (López-Castañeda et al. 1995). The early growth advantage in barley arises for several reasons. Barley germinates marginally earlier than wheat, it has a higher leaf area:leaf weight ratio (greater specific leaf area, SLA) during early growth stages thereby spreading an equivalent leaf mass over a larger area, and for the same seed weight, the embryo size of barley is about double that of wheat (López-Castañeda et al. 1995; 1996). The larger embryo in barley results in more expanding cells after imbibition and faster early root and shoot growth. Additional factors that could contribute to increasing early vigor in wheat are the development of a coleoptile tiller (Liang and Richards 1994) and the absence of the major dwarfing genes (Richards 1992).

With our understanding of the factors responsible for early vigor we are now in a position to pyramid the above traits and incorporate them into commercially grown cultivars.

Very few wheats have just one of the above characteristics contributing to greater vigor and none have been found that combine several. Consequently we made a search of the world’s wheats for greater early vigor. We found two excellent donors for the SLA and embryo size characteristics. Because these traits should be genetically independent of each other, transgressive lines were identified that have a leaf area and biomass exceeding both donor parents (Figure 1). The canopy of these transgressive lines develops much faster and reaches full

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**Figure 1.** Leaf area at the four leaf stage of wheat lines grown outside during winter. Amery, Hartog and Janz are vigorous cultivars grown widely in southern Australia. Best parents are the two best lines identified after a global search of wheat germplasm for fast early vigor. One was found to be vigorous because of its thin leaves (high specific leaf area), whereas the other was vigorous because of its large embryo. The best progeny are data for F3 families derived from the cross of the two best parents.
light interception before that of any other wheat line we have tested. These lines are now being used as donors to incorporate early vigor into important commercial Australian wheats by backcrossing. Early results on the heritability of these traits and the genetic advance in several different populations are given by Rebetzke and Richards (1996).

Although these lines are being developed for rainfed Mediterranean-type conditions, they may also be important in short-season spring wheats grown under more favorable conditions. They may provide a number of opportunities to alter crop development. For example, earlier floral initiation may be possible in these lines; if so, it would enable a longer period of spike development or a longer grain filling period. Longer duration of spike or grain growth could increase grain number and grain weight, respectively. These lines may also be more robust in overcoming any early checks in growth in otherwise favorable environments.

**After canopy closure**

Spring bread wheats are generally different from other cereals bred under high input systems (such as maize, rice, and durum wheat) in that most cultivars have a more planophile (less erect) canopy. This is curious considering that the advantages of erect upper leaves for increased biomass would seem to be quite substantial once there is full light interception and provided water and nutrients are not limiting (Monteith 1965). In other, less favorable environments, an erect leaf canopy has contributed to increased yield and biomass in winter wheat (e.g., Innes and Blackwell 1983). Also, recent durum wheat cultivars from CIMMYT have a more erect canopy than older types, which may partly contribute to their greater grain and biomass yields (Waddington et al. 1987). In rice not only do erect upper leaves appear to provide a yield advantage but some lines containing both erect and rolled leaves have greater radiation use efficiency, greater crop growth rate and higher yields (Williams and Reineke, pers. com.). The reason for the different canopy structure of spring wheats compared to the other species is not known. It may be because there has been no conscious selection pressure for leaf erectness in spring wheats or that there is no advantage in having erect leaves at yield levels up to 6.5 t ha$^{-1}$, as was found by Araus et al. (1993), and that advantages only accrue at higher yield levels (Austin 1982).

Considering the arguments for the advantages of an erect canopy for increasing carbon supply at high yield levels, effort into breeding wheats with canopies composed of short, erect flag leaves seem warranted.

Improving the rate of photosynthesis should also translate into greater grain and biomass yields. However, there is little evidence to show that selecting for increased photosynthesis among genotypes results in increased yields (Evans 1993). Although in the study conducted at Obregon it was shown that, for CIMMYT bred material, genetic increases in grain yield in the last 30 years were associated with increases in stomatal conductance and in the maximum rate of photosynthesis (Fischer et al. 1997). However, as was discussed earlier, it is not clear whether the increases in conductance and mesophyll activity are true genetic differences or whether they reflect the
increased sink strength of the additional grains set. The gas exchange characteristics of cultivars in this historical set were very closely associated with grain yield but not related to crop biomass. If there were a relationship with crop biomass, this would provide good evidence that gas exchange characteristics are independent of sink strength.

**Increasing Grain Number**

Experimental evidence was presented earlier to indicate that increased grain number may be the driving force for sustained growth and greater yields. It would seem that plants have ample reserve capacity to meet any additional demand for carbon provided that water and nutrients are adequate. As a result, if grain number is increased, crops will be able to meet the extra requirement for carbon and nitrogen, and yield will be increased. In this section I will discuss a number of opportunities that may increase both grain number and yield.

There is good evidence that increasing carbon supply to the growing ear by reducing the size of the competing sinks results in increased grain number. This was part of the basis of the ‘green revolution’. It arose from the introduction of new dwarfing genes into spring wheats, which prevented crop lodging and enabled more inputs to be applied by farmers. These dwarfing genes also resulted in increased grain number per unit area. This increase occurred because in shorter wheats there is less competition between the developing ear and the growing stem for photosynthate in the pre-anthesis period. Thus more carbon is available for ear growth than it is in tall wheats. This results in an increased supply of carbon to developing florets and greater floret fertility, which in turn results in greater grain number and yield (Brooking and Kirby 1981; Fischer and Stockman 1986). Although further gains are unlikely to be made by further reducing plant height, because biomass is likely to decline if crops become shorter, there may be opportunities to maintain the height of the leaf canopy whilst reducing the height of the mature crop. This would be achieved by reducing the length of the peduncle, i.e., the internode between the uppermost leaf node and the ear. This is the most rapidly expanding organ immediately before anthesis, when the ear is also growing and kernel number is mainly determined.

Reducing the length of the peduncle may further diminish competition between the ear and the stem and result in more grains being set.

Reducing the size of the flag leaf may also increase grain number and yield. A smaller flag leaf may result in more assimilates going to the developing ear for the reasons described above, provided there is no allometric relationship between organ sizes. An additional benefit of a small flag leaf may be an increase in radiation-use efficiency, as more light would penetrate the canopy. However, this may be counterbalanced by a decline in canopy photosynthesis associated with more light reaching older leaves (Rawson et al. 1983).

Reducing the number of sterile tillers could also increase supply to the growing ear.

Wheat produces many more tillers than it can sustain and so many are aborted. Indeed,
A very interesting finding that may have large implications for improving grain number is how nitrogen content in the spike at anthesis is related to final grain number (Abbate et al. 1995; van Herwaarden 1996). In these studies the total nitrogen content of the spikes at anthesis was more closely related to grain number than was spike dry weight (Abbate et al. 1995) or water soluble carbohydrates in the spike at anthesis (van Herwaarden 1996). It seems that nitrogen in the spike may increase grain number by increasing floret survival. Several management opportunities to increase grain number follow from these findings as do several ways for genetic manipulation. For genetic manipulation, information is required on the amount of variation among genotypes for the allocation of nitrogen to the spike at anthesis. There is circumstantial evidence for differential partitioning of nitrogen among cultivars. Slafer et al. (1990) found little variation in nitrogen uptake among old and new varieties in Argentina but found differences in nitrogen distribution to the grain and straw at maturity. There is also substantial evidence for variation in nitrogen uptake during the vegetative stage (Cox et al. 1985; Dhugga and Waines 1989). This finding of nitrogen content influencing grain number also raises the question of whether it is both carbon and nitrogen allocation to the growing ear or some other substance that is important in the determination of grain number.

**Increasing Grain Weight**

Evidence from historical data sets indicates that increases in grain number rather than grain weight has consistently been associated with increases in wheat yields. In
fact a decline in average grain weight is usually observed as grain number increases (Slafer et al., these proceedings). There are two likely reasons for this. The reduction in average grain weight may be due to a shortage of assimilates or, more likely, may be a consequence of the fact that when more grains are produced in wheat they are from distal florets, which are always smaller. To further increase grain yield we need to better understand the relationship between grain number and grain weight and the determinants of grain weight.

Several avenues of research are suggested to improve our understanding of factors leading to variation in grain weight in cereals. An understanding of the differences between barley and wheat is likely to be a fruitful start. Barley typically produces a heavier kernel than wheat even when grain number per unit area is the same. This is surprising considering that the duration of grain filling in barley is shorter than it is in wheat; this means that the rate of grain filling is substantially greater in barley (López-Castañeda and Richards 1994). A comparison of the average growth of four barley and four wheat cultivars grown side by side in the field is given in Figure 2. The reasons for the substantially greater rate of grain growth both for individual grains and per unit area are not known, although a number can be proposed. Several of the reasons may be associated with the differences in structure between the barley and wheat spike.

There may be a vascular limitation in wheat that is not present in barley, which has to do with the differences in spike structure between the two species. For example, wheat may have up to 4 or 5 grains per spikelet, whereas barley has only 2 or 3 in the case of 2-row and 6-row barleys, respectively. Although this reason cannot be ruled out, evidence from several studies indicates that it is unlikely (Evans 1993). Other reasons associated with the differences in spike structure could be due to more synchronous fertilization of florets in barley than in wheat. Often there is a difference of seven days in anthesis time between the florets in the same spikelet of wheat, yet physiological maturity of all grains occurs at about the same time. This may result in longer duration of grain growth in wheat compared to barley, but it may be insufficient to make up for the difference in rate of grain growth. The early formed florets may inhibit the growth of later formed florets (Bremner and Rawson 1978); this is not a problem in barley because it has fewer florets. A possible way to overcome some of these factors in wheat would be to

![Figure 2. Increase in grain weight per unit area of barley and wheat between anthesis and maturity at Moombooldool, New South Wales. Lines are averaged over four cultivars each of barley and wheat sown in the same experiment. Data is expressed in thermal time units (TU - daily summation of averaged max + min temperature) as barley flowered earlier than wheat. Slope of the linear phase for wheat is 0.76 g m\(^{-2}\) TU\(^{-1}\) and 1.25 g m\(^{-2}\) TU\(^{-1}\) for barley.](image)
increase the number of spikelets, as this is likely to result in fewer florets per spikelet.

Differences in grain growth between wheat and barley may also be due to a number of factors that are not associated with spike structure. Grain growth in barley may occur at a lower base temperature than it does in wheat; this would result in more growth, particularly if temperatures fall below the base temperature (about 11°C in wheat). Wheats that have dwarfing genes Rht1 and Rht2 may have a smaller caryopsis, which limits grain growth. There is a direct relationship between the number of dwarfing genes and cell size (Keyes et al. 1989); if these genes limit the elongation of the caryopsis, as they do other organs, a smaller caryopsis may be the reason grains of semidwarf wheats are smaller. A further reason may be that assimilate supply to barley florets immediately after fertilization may be greater than it is in wheat.

Endosperm cell number is known to have a significant influence on rate of grain filling and final grain weight in wheat (Brocklehurst 1977) and barley (Cochrane and Duffus 1982). An understanding of the importance of endosperm cell number in determining grain weight and identifying ways to manipulate it is important if we are to discover how to improve the grain weight of wheat.

We do not yet understand what causes grains to mature and to cease filling. In some conditions it will be due to the lack of assimilates because of drought and the absence of current photosynthesis. However, in other conditions assimilates are not lacking because grains mature when there is still ample green tissues and stored carbohydrates. Better understanding of the causes of grain maturation would also be useful.

Molecular Biology and the Manipulation of Sources and Sinks

It should be possible to manipulate all of the factors discussed in this paper by conventional genetic means provided there is adequate genetic variation for the characteristics. It is unlikely that in the near future molecular biology will greatly enhance genetic variation for the characteristics discussed, although it is likely that molecular marker assisted selection will improve some selection processes. Nevertheless, although I cannot identify specific targets where molecular biology may directly improve grain yield, I would like to suggest two areas of research where it may substantially increase our understanding of crop processes that may influence yield: 1) regulating sucrose metabolism in the source tissues and its transport to sink tissues and the developing apices, and 2) using cell division cycle genes to better understand meristematic zones of organs, including the developing grains.

References


Questions and answers

M. Mergoum:
You mentioned in your talk that in order to obtain genotypes with high yield you need to increase spike size and reduce tiller number. However, in triticale, which fits your ideotype (few tillers and large spikes), the big hurdle is still tiller number under conditions that enhance high tiller capacity. Could you clarify this discrepancy?

R. Richards:
I agree that triticale does in many ways fit the ideotype I have proposed. However, I do not fully understand your point. The point I was trying to make is that wheat under optimal conditions, such as in Mexico, typically produces well over 1000 shoots/m² yet only about 450 of them are fertile. If later formed tillers were inhibited and assimilates were diverted to shoots that were fertile then this may be one route to greater grain numbers and greater yields.

M. Mergoum:
Previous speakers mentioned that sink is a load for plants (i.e., source is limiting) and you mentioned that sink is limiting. Is this controversy due to genetic material differences (genotype, for example) or to environmental factors?

R. Richards:
I believe there is overwhelming evidence for sink limitations and I have described the evidence for this more fully in my written paper.
J. Snape:
How do you reconcile pleiotropic effects of the Ppd1 gene in reducing spikelet number and increasing grain size (which results in an overall increase in yield) with a model that increasing grain number is the way of increasing sink capacity?

R. Richards:
There are large differences in environments that may account for your observation. For example, in the United Kingdom grain filling occurs under reducing day lengths and reducing temperatures, whereas in northwestern Mexico, which I have focused on, grain filling occurs under increasing daylengths and temperatures.

In northwestern Mexico there is very strong evidence that greater yields have been closely associated with increased grain number with very little, if any increase in grain weight. This is not to say that grain weight is not important. In my paper I have gone into a number of possible ways to increase grain weight. I believe we should be putting far more effort into understanding the control of both grain number and grain weight.

R.A. Fischer:
With respect to the apparent contradiction just posed by J. Snape, as arising in the recent Worland et al. study of a Ppd1 gene, it needs to be pointed out that spikelet number, reduced by the spring earliness gene, is only part of the kernel number story. There are two other components, spikes/m2 and kernels/spikelets, which could have been increased. Besides, the kernel weight increase with earliness is not surprising as it does not contradict the general pattern of a yield vs kernel number correlation—kernel weight increased because flowering was earlier, giving a more favorable grain-filling period in the warmer southerly sites in the reported study.

(No comment required.)

R.A. Fischer:
Just as you propose to increase efficiency by limiting wasteful tillering, what do you think of limiting wasteful floret production by limiting floret initiation to 2 or 3 florets per spikelet?

R. Richards:
This is an interesting point. This may be a disadvantage under very favorable conditions where crops are unable to compensate for the reduced floret number.

E. Duveiller:
If wheat is a conservatory crop and there is a possibility to increase the number of grain per spike, shouldn't we expect an increased level of senescence in relation to the sink effect to be associated with more disease susceptibility, particularly those which are stem related such as foliar blights and prevail in rice-wheat systems? Are we losing from the disease point of view what we may gain from the physiology side?

R. Richards:
If crops are adequately supplied with nitrogen, I would not expect to see increased senescence associated with a higher grain number.
Integrative Physiological Criteria
Associated with Yield Potential

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Abstract
The present study provides insights into physiological criteria that may be useful in breeding for yield potential in wheat and other cereals. Some of the most promising screening criteria currently emerging are 'integrative' in nature, that is, they can integrate the functioning of the crop in time (i.e., during the plant cycle) or level of organization (e.g. whole plant, canopy). They are based, for example, on the analysis, in different plant parts, of the stable carbon and nitrogen composition or the ash content. Also worth mentioning is the use of remote sensing approaches and, among them, indexes based on the spectral reflectance signature of the canopy or the utilization of NIRS technique as a surrogate for carbon isotope discrimination or ash content.

Introduction
Yield potential has been defined as the “yield of a cultivar grown in environments to which it is adapted, when nutrients and water are non-limiting, and when pests, diseases, weeds, lodging and other stresses are effectively controlled” (Evans 1987). There are several aspects of yield potential that merit attention: for example, how it might best be determined; the morphological and physiological characteristics that maximize its expression; the extent of genetic variability; and the efficient economical selection of genotypes with high yield potential.

While empirical (i.e., conventional) breeding programs aimed at improving yield in self-pollinating crops rely basically on direct selection, this actually limits breeding progress because of the particular nature of yield. Yield is a polygenic trait, strongly affected by the environment, and can only be applied as a selection criterion in the later generations of a breeding program. As the production of high yielding cultivars by empirical selection requires progressively larger and more costly breeding programs, the use of more analytical approaches is being postulated, in which a better understanding of physiological traits associated with yield and its responses to the environment might improve the effectiveness of selection (Austin 1993). In the analytical approach, a surrogate for yield (i.e., a set of criteria screening tests) would be used, particularly in the early stages of a breeding program (Austin 1993).

However, few, if any, alternatives to direct selection for yield have been adopted, though many have been suggested. The multiple selection criteria approach when breeding under Mediterranean conditions is an example of this (Acevedo and Fereres 1993).
Thus, whereas the theoretical framework of this approach would seem to be sound, its application to breeding programs has serious inconveniences. Frequently it implies a vast expenditure of working hours, which can only be met by the strongest breeding programs and, even then, not in all generations. But perhaps the most serious criticism is the strong empirical nature of the approach. Thus, even in the absence of pleiotropic negative effects, most characteristics will be of secondary importance (because they are neither additive nor independent), and the effort required is not compensated by the probable benefit.

Therefore, developing reliable screening techniques is necessary to make breeding more efficient. Provided there is enough inheritable variation for the trait, all screening tests must satisfy several other requisites (see Austin 1993; Acevedo and Fereres 1993) that can be condensed into two. The first requisite is physiological: there must be an appreciable genetic correlation between the trait being assessed and yield under field conditions. The second is more technical: screening for this trait must be simple, quick, and less expensive yet more convenient than screening for yield itself.

The following section introduces a conceptual framework that in principle allows identification of morphophysiological traits related to yield. In addition, some of the most promising screening techniques being developed to evaluate these traits are discussed.

Identifying Morphophysiological Traits Associated with Yield Potential

Several approaches have been developed, the most empirical of which is the 'ideotype' concept (Donald 1968), although reduction of the amount of empiricism in plant breeding was inherent within it (Sedgely 1991). Indeed plant breeders have selected and will continue to select for ideotype traits: maturity, height, kernel number and weight, head number, and leaf area, angle and duration (Rasmusson 1991). However, pleiotropy, trait compensations and inferior donor germplasm have all hindered progress in ideotype breeding. Thus, for example, Araus et al. (1993) concluded that the possibility of an allometric relationship between leaf erectness and smaller leaves, spikes and stems could modify the relative contribution of different yield components to final yield and complicate improvement of crop production via selecting for a more erect canopy. The challenge, therefore, is to identify traits that merit an ideotype breeding effort.

Retrospective analysis has also been widely used to identify morphophysiological traits. It is fully summarized in recent reviews (Slafer et al. 1993) and developed further elsewhere (see Slafer, these proceedings). This approach involves the use of a conceptual model for determining yield potential and may become a convenient way to extend the definition of integrative physiological criteria.

Processes determining yield potential
The transformation of solar energy into harvestable plant parts can be divided into
three major processes: first, interception of incident solar radiation by the canopy; second, conversion of intercepted radiant energy into chemical potential energy (i.e., plant dry matter); and third, partitioning dry matter between harvested parts and the rest of the plant. The yield or harvestable part ($Y$) of a crop over a given period of time can, therefore, be simply expressed by the following equation (Hay and Walker 1989):

$$Y = Q \times I \times E \times H$$

where $Q$ is the total incident solar radiation received by the crop over the growing period, $I$ is the fraction of $Q$ intercepted by the crop canopy, $E$ is the crop's overall photosynthetic efficiency (i.e., conversion efficiency of radiant to chemical potential energy: total dry matter produced per unit of intercepted radiant energy), and $H$ is the harvest index or fraction of the total dry matter harvested as yield. This is normally expressed in terms of above-ground production, excluding the root system.

It is widely accepted that total canopy photosynthesis during growth is closely related to yield (Zelitch 1982; Ashley and Boerma 1989). Indeed total biomass, the result of $Q \times I \times E$, can be physiologically understood as the consequence of crop photosynthesis over time. However, for wheat most retrospective studies have concluded that total above-ground biomass, either at anthesis or maturity, has not changed substantially as a result of breeding (see references in Slafer et al. 1993). Given the improvement in agronomic practices, most gains in wheat yield this century have paralleled changes in the harvest index.

From the above equation several ways can be postulated by which the crop photosynthesis might be increased. At canopy level there are at least two major ways. One is to increase interception ($I$) of photosynthetic active radiation (PAR) by the canopy throughout the growing season. This can be done by achieving faster soil coverage and longer-lasting photosynthetic organs. Another way is to increase the conversion efficiency of PAR into dry matter, either by improving PAR distribution through changes in canopy structure or by increasing photosynthetic capacity of photosynthetic organs, without concomitant decreases in their area or duration.

**Why Evaluate Integrative (Time and/or Canopy) Criteria?**

To be of any value in assessing yield potential in a population of plants, a screening test should evaluate one or more components of the above equation. However, many traits are measured with complex, expensive, time-consuming techniques unsuitable for routine screening of large numbers of progeny in breeding programs. Indeed, they are only useful for screening small numbers of genotypes to be used as parents. Moreover, quite often these tests are used to provide snapshots of a given plant process (e.g., photosynthesis, stomatal conductance, chlorophyll fluorescence) and/or they provide information at a level of organization that is too low (cellular or even lower) and in controlled environments. Although not always the case (Reynolds et al. 1994), information from these tests is generally poorly associated with yield.
Because of the very complex character of yield itself, particular emphasis should be given to (single) tests that integrate the function of the crop, either at highest level of organization (i.e., canopy) and/or during a part of the plant cycle (e.g., early development, grain filling). In fact, the most integrative test is yield itself. Some physiological techniques have been modified and, although not as accurate as more complex methods, may be useful for routine plant screening. In addition, some traits can be combined in a single measurement.

Below we discuss recent techniques for conducting single evaluations of integrative traits related to yield. These include remote sensing techniques based on spectral reflectance signature, composition of stable carbon and nitrogen isotopes, mineral content and other surrogates.

**Remote Sensing Techniques**

In principle, assessments of photosynthesis, plant biomass, total leaf area, water status, transpiration, etc., based on remote sensing have certain advantages. First, they may be less invasive and expensive. Second, they allow the study of upward scaling (canopy level) of physiological phenomena. Remote sensing products that are potentially useful for assessing photosynthesis and related processes fall into two categories (Field et al. 1994):

1) Photosynthetic capacity or CO₂ uptake potential. Spectral reflectance measurements in the visible, near-infrared and mid-infrared regions are promising new techniques for estimating above-ground biomass, leaf area index, absorbed radiation, total canopy chlorophyll, nitrogen and water status.

2) Instantaneous photosynthetic activity. Examples of these products include chlorophyll fluorescence (canopy-scale measurements by measuring laser-induced fluorescence), xanthophyll pigments (spectral reflectance techniques), and canopy temperature (by infrared thermometry).

Spectral reflectance measurements allow traits different from these two categories to be assessed.

**Spectral reflectance techniques**

Methods based on red/near infrared contrast of reflectances can yield estimates of leaf area index (LAI), green biomass, crop yield, and canopy photosynthetic capacity. In fact, green leaves are strong absorbers in the red, but highly reflective in the near infrared (Figure 1). The identity of the physical

![Figure 1. Spectral reflectance in the visible and near-infrared for three salinity levels (measured as ECa) in a barley genotype. Error bars are ±SE. This response is typical of barley's response to salinity (from Peñuelas et al. 1996).](image)
parameter or parameters measured by the red/near infrared contrast is not completely clear, but the dominant driver of the contrast is the fraction of photosynthetically active radiation (PAR) absorbed by green leaves. Because the contrast in reflectance between the near-infrared and red is large in green organs but small in soils and most other materials, the amount of contrast increases as the PAR fraction absorbed by the canopy increases.

Two single and widely used indexes are the ‘normalized difference vegetation index’ (NDVI) and the ‘simple ratio’ (SR) used as indicators of canopy structure, light absorption, and photosynthetic capacity.

a) NDVI *(normalized difference vegetation index)*

\[ \text{NDVI} = \frac{(R_{\text{NIR}} - R_{\text{RED}})}{(R_{\text{NIR}} + R_{\text{RED}})} \]

b) SR *(simple ratio)*

\[ \text{SR} = \frac{R_{\text{NIR}}}{R_{\text{RED}}} \]

where \( R_{\text{NIR}} \) and \( R_{\text{RED}} \) are the reflectance in the near infrared and red wave bands, respectively. These two indexes are readily convertible:

\[ \text{SR} = \frac{(1 + \text{NDVI})}{(1-\text{NDVI})} \]

The validity of these vegetation indexes as quantitative indicators of canopy structure or net primary production is largely based on empirical results with horizontally uniform (i.e., crop) canopies (Kumar and Montheith 1981; Bartlett et al. 1990), although they are also good indicators of PAR absorption, and thus potential photosynthetic activity, even in heterogeneous landscapes (Gamon et al. 1995). Indeed, NDVI is probably the most commonly used index for analyzing vegetation on a continental and global scale (see references in Gamon et al. 1995). In addition, these canopy reflectance-based indexes are attractive because they work well with broad-band radiances (Sellers 1987). They also provide inexpensive, large area estimates of N status since leaf chlorophyll \( a \) content is mainly determined by N availability. Therefore, photosynthetic capacity and leaf area duration can be evaluated at canopy level.

The NDVI seems the most powerful spectral combination with which to estimate total area of plant leaves and LAI and, in fact, is the most widely used index. With LAI between 0-2, NDVI is a sensitive indicator of canopy structure and chemical content (biomass, LAI, chlorophyll, and nitrogen contents). With LAI above 2, adding more canopy layers makes little difference to the relative interception or reflectance of red and near-infrared radiation, and thus little difference to NDVI (Sellers 1987). Therefore, NDVI is ideally suited for detecting subtle differences in cover in sparse canopies and makes a sensitive growth index in young crops and grasslands or crops growing under stress conditions (Tucker et al. 1979; Gallo et al. 1985; Fernández et al. 1994; Gamon et al. 1995; Peñuelas et al. 1996).

Indeed, the relationships between NDVI and these canopy parameters are clearly non-linear (Figure 2) and can be effectively described by semi-logarithmic relationships, expressing these canopy parameters on a (natural) logarithmic scale. The logic of this transformation lies in the negative
exponential extinction of PAR with canopy depth (Monsi and Saeki 1953; Sellers 1987). When SR is expressed on a logarithmic basis, this parameter is comparable to NDVI as indicator (Gamon et al. 1995).

On the other hand, and according to the theoretical basis of light extinction through the canopy (Sellers 1987, Bartlett et al. 1990), both indexes exhibit near-linear correlations with the fractional PAR intercepted or absorbed by green tissues over a wide range of canopy densities (Gamon et al. 1995). Therefore, NDVI and SR can be used as indicators of PAR absorption, and thus potential photosynthetic activity. In addition, where canopy development and photosynthetic activity are in synchrony (for example, during vegetative stages of cereal crops growing under non-limiting conditions), instantaneous maximum daily photosynthetic rates during vegetative stages of the crop can be evaluated with NDVI and SR (Gamon et al. 1995).

Effects of calibration changes, atmospheric transmission, solar elevation, and canopy architecture still present major challenges (Field et al. 1994). There are, however, other limitations. Some of the parameters assessed by spectral reflectance measurements of the canopy cannot be estimated independently of plant treatment, such as water regime or N-fertilization level. For bread wheat it seems that chlorophyll (Chl) content cannot be estimated by NDVI independently of plant treatment, despite the high linear correlation between the content of N and Chl (Fernández et al. 1994). However, total leaf area per plant, LAI and nitrogen content in wheat may be estimated from NDVI or from a linear combination of green and red reflectance independent of plant treatment (Fernández et al. 1994; Filella et al. 1995).

Reflectance in the visible wavelengths is sensitive to changes in the LAI of vegetation, particularly on light-toned substrates (Curran 1983) and with low biomass levels. On the other hand, reflectance in the near infrared is more sensitive to changes in the LAI of vegetation on dark-toned soils (either due to their composition or humidity), while in some instances soils can be so reflective that the near infrared wavelengths are insensitive to changing LAI (Curran 1983).

Figure 2. Relationship between NDVI and either yield (upper figure) or biomass. Data correspond to 10 barley genotypes and three salinity levels (0.8, 1.26, and 1.72 dS m\(^{-1}\) EC\(_s\)) (from Peñuelas et al. 1996).
Traditional vegetation indexes involving ratios of visible and near infrared reflectance, commonly used in early biomass estimations, may be inadequate under such circumstances (Elliott and Regan 1993). Nevertheless, Fernández et al. (1994) point out that NDVI seems to be a better estimator of LAI or total leaf area than other spectral indexes that attempt to incorporate soil reflectance.

Spectral reflectance should provide, in principle, a sensitive method for screening genotypes for early growth. Intraplot variability can be overcome by averaging several reflectance readings within a plot. However, the contribution of genotypic differences in canopy architecture (tiller density and growth habit) and plant height to spectral reflectance is poorly documented and further work is required (Elliot and Regan 1993). Accurate estimation of canopy structure and composition from NDVI may require individual calibration for distinct canopy architectures. Finally, the optimum method for collecting remotely sensed data needs to be determined, while the acceptable range of accuracy and error required to assess genotypic differences in biomass production confidently needs to be established (Elliot and Regan 1993).

Spectral reflectance techniques also allow the calculation of other indexes that are potentially useful indicators of crop response to abiotic stresses. Below we briefly discuss two of these indexes: the photochemical reflectance index and the water index.

c) *Photochemical reflectance index (PRI)*

\[
PRI = \frac{(R_{ref} - R_{531})}{(R_{ref} + R_{531})}
\]

Changes in the region of spectral reflectance from about 500 to 560 nm wavelength are the result of interconversion of xanthophyll pigments. The xanthophyll cycle is involved in processes of excess radiation dissipation (Demmig-Adams and Adams 1992), some of which have been associated with changes in leaf reflectance near 531 nm. The PRI index is used for quantifying the status of xanthophyll pigments without canopy-scale PAR manipulations.

In addition, PRI could be used to assess photosynthetic use efficiency at leaf or canopy level in a similar way to widely used fluorescence parameter indicators of PSII photochemical efficiency (Gamon et al. 1992; Filella et al. 1996).

d) *WI (water index)*

\[
WI = \frac{R_{970}}{R_{900}}
\]

Water status can be monitored at the canopy level using reflectance techniques. For example, the ratio between reflectance at 970 nm (a water absorption band) and 900 nm (reference wavelength), known as water index (WI), has been reported to closely follow changes in relative water content, leaf water potential, stomatal conductance, and canopy temperature when plant water stress is severe (Peñuelas et al. 1993). For cereals exposed to a soil salinity gradient, WI measured during grain filling has been seen to be well correlated with carbon isotope discrimination of mature kernels and canopy temperature (Peñuelas et al. 1996).

A simple-to-use, portable spectroradiometer of a size comparable to that of current infrared thermometers used to assess canopy
temperature should be developed soon (Peñuelas, personal communication). By combining the reading of several discrete wavelengths (e.g., 680, 900, 950 nm), simultaneous evaluation of NDVI, WI and total chlorophyll content should be possible.

**Stable Isotope Composition, Ash Content, and NIRS Analysis**

Selection based on remote sensing techniques requires that each genotype be cultivated in plots. Like yield itself, selection based on these traits is only possible in the more advanced generations of a breeding program because of the inherent limitations imposed by cultivation. Certain indirect selection criteria could be used in early generations to improve the genetic gains of any breeding program. These criteria should be easy to measure and applicable to a large number of plants in a relatively short time. The final part of this paper will discuss potentially useful traits as well as proposed surrogates that might substantially reduce the cost of applying such traits.

**Discrimination against $^{13}$C and growth**

It is widely accepted that for C$_3$ plants, such as small-grain cereals, carbon isotope discrimination ($\Delta$) provides an integrated measurement of water use efficiency (Farquhar and Richards 1984; Hubick and Farquhar 1989). As expected from the theory, the value of $\Delta$ correlates positively with the ratio between the atmospheric and the intercellular partial pressures of CO$_2$ ($p_i/p_a$), and, therefore, negatively with water use efficiency (WUE: measured either as net photosynthesis/transpiration or plant biomass produced/water transpired). In this regard, $\Delta$ is a potentially useful criteria to select for WUE in wheat (Farquhar and Richards 1984; Condon et al. 1990; Ehdaie et al. 1991), where considerable genotypic variation for $\Delta$ has been demonstrated.

Whereas selecting for WUE under limited water conditions has obvious interest, $\Delta$ may be a useful criteria to select for potential yield. Several studies have reported a positive correlation between grain yield and $\Delta$ for wheat (Condon et al. 1987; Araus et al. 1993; Sayre et al. 1995), barley (Romagosa and Araus 1991) and durum wheat (Araus and Nachit 1996), not only under drought but also in trials with no water stress (see Table 1 for durum wheat). Moreover, under adequate growing conditions, $\Delta$ is highly heritable and exhibits substantial genetic variation (Richards and Condon 1993), independent of phenological differences (Sayre et al. 1995; Araus and Nachit 1996).

The positive correlation between $\Delta$ and yield in the absence of water stress can be explained in several ways. Higher $\Delta$ is related to higher $p_i/p_a$ due to greater stomatal conductance (Farquhar and Richards 1984), which leads to higher photosynthetic rates and, hence, higher yield. In addition, when wheat is grown at supra-optimal temperatures, the observed positive correlation between stomatal conductance and yield may also be related to heat avoidance (Reynolds et al. 1994). On the other hand, a positive relationship between $\Delta$ and growth has been reported for seedlings grown under adequate water conditions (Febrero et al. 1992; López-Castañeda and Richards 1994). Indeed, increased early growth and leaf area development may be inherently linked with decreased water-use efficiency (Turner 1993).
and, hence, higher $\Delta$. One explanation might be that a higher photosynthetic rate (due to higher $p_i/p_a$) can supply substrate at a higher rate and favor faster growth. Alternatively, a lower $\Delta$ (and thus higher $p_i/p_a$) might be associated with lower specific leaf dry weight (SLDW: dry matter per unit leaf area, a rough indicator of photosynthetic machinery per unit leaf area), where SLDW is negatively correlated with leaf area (Wright et al. 1993; López-Castañeda and Richards 1994). The positive correlation between early vigor and $\Delta$ could be due to factors other than thinner leaves alone. Because $\Delta$ reflects the plant’s water status, higher $\Delta$ might be an indirect indicator of larger cell elongation due to better water status.

The use of $\Delta$ as a selection index for increased yield gives rise to several practical considerations. Whenever possible, two kinds of samples for $\Delta$ should be taken: leaf samples from early stages of the crop (Sayre et al. 1995) and mature kernel samples. Whereas the first sample would provide information about genetic variation in the population, the second sample would probably be more affected by genotype x environment interactions (even in the absence of severe stress) and therefore could provide information as to which genotype was less affected by mild stress. Indeed, even under ‘optimal’ agronomic conditions, plants are affected to some degree by abiotic stress: midday stomatal closure and transient photoinhibition are examples of this. In addition, $\Delta$ at seedling stage seems to be positively associated with early vigor.

**Ash content and NIRS analysis**

Due to the cost of carbon isotope analyses (> $10 per analysis), several surrogates for measuring $\Delta$ have emerged, including accumulation of minerals such as K or Si, or total ash content in vegetative tissues of cereals and forages (Walker and Lance 1991; Masle et al. 1992; Mayland et al. 1993; Araus and Nachit 1996). Several aspects still need to be clarified, particularly the mechanisms underlying the genetic association between mineral accumulation and WUE (Walker and Lance 1991; Masle et al. 1992). However, the amount of minerals accumulated by plants

<table>
<thead>
<tr>
<th>Environments</th>
<th>Number of genotypes</th>
<th>GY/AshL</th>
<th>GY/AshK</th>
<th>GY/KW</th>
<th>GY/$\Delta$K</th>
<th>GY/DH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Breda (rainted)</td>
<td>144</td>
<td>0.354***</td>
<td>-0.524**</td>
<td>0.429**</td>
<td>0.528***</td>
<td>-0.583***</td>
</tr>
<tr>
<td>Tel Hadya (rainted)</td>
<td>144</td>
<td>0.277***</td>
<td>-0.423**</td>
<td>0.307**</td>
<td>0.501***</td>
<td>-0.389***</td>
</tr>
<tr>
<td>Tel Hadya (irrigated)</td>
<td>124</td>
<td>0.525***</td>
<td>-0.465**</td>
<td>0.440**</td>
<td>0.511***</td>
<td>0.451***</td>
</tr>
</tbody>
</table>

* P<0.05; ** P<0.01; *** P<0.001
Source: Araus and Nachit 1996.
may be a useful indicator of WUE under field conditions (Masle et al. 1992; Mayland et al. 1993). Total ash (or mineral) content seems to be better (negatively) related to WUE than any one mineral. For this reason, as well as its low cost, ash content may become an alternative criteria to Δ, particularly during the early phases of a breeding program when large populations are usually involved. Later selections could be based on the more precise and accurate, yet costly, Δ analysis (Mayland et al. 1993). Ash content is positively correlated with Δ (Figure 3) and yield (Table 1) either under rainfed or well-watered field conditions (Mayland et al. 1993; Araus and Nachit 1996). Total ash content in mature kernels could be a complementary criterion in addition to Δ (or ash content in vegetative tissues) for assessing genotypic yield differences (Tables 2 and 3). The pattern of ash content in kernels behaves

![Figure 3](image-url)

**Figure 3.** Relationship across genotypes cultivated in three environments (see Table 1) between carbon isotope discrimination (Δ) in mature kernels and ash content (upper figure) of flag leaves or (lower figure) the same mature kernels. The coefficient of determination (r^2) refers to the correlation among all genotypes and environments considered together. The environments were: Breda (○), Tel Hadya rainfed (Δ), and Tel Hadya with supplementary irrigation (□) (from Araus and Nachit 1996).

**Table 2.** Percentage of grain yield (GY) variation among durum genotypes cultivated in three environments of northwestern Syria explained by the progressive combination of different integrative traits based on carbon isotope discrimination (ΔK) and total ash content of mature kernels (AshK) and of flag leaves (AshL) 2-3 weeks after anthesis.²

<table>
<thead>
<tr>
<th>Traits added</th>
<th>Breda (rainfed) n = 144b</th>
<th>Tel Hadya (rainfed) n = 144</th>
<th>Tel Hadya (irrigated) n = 124</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>% GY         CV (%)²</td>
<td>% GY         CV (%)</td>
<td>% GY          CV (%)</td>
</tr>
<tr>
<td>ΔK</td>
<td>27.9         18.3</td>
<td>26.1         14.6</td>
<td>35.3          19.8</td>
</tr>
<tr>
<td>AshL</td>
<td>30.0         18.1</td>
<td>29.8         14.5</td>
<td>44.4          18.5</td>
</tr>
</tbody>
</table>
| AshK          | 44.1         16.3           | 33.2         13.8           |                | ² Calculations were done by fitting grain yield to a multilinear equation where traits were sequentially added.

² n = number of genotypes assayed.
³ Coefficient of variation of estimated GY.
² Source: Araus and Nachit 1996.
differently to that in vegetative tissues, probably because, unlike mineral accumulation in vegetative tissues, grainfilling does not take place throughout the xylem. Although ash content in barley kernels seems to correlate (negatively) with yield only under rainfed, poor-yielding environments (Febbrero et al. 1994), current results with ICARDA’s Durum Core Collection (Araus and Nachit 1996) also indicate a significant correlation under irrigation (Table 1). This relationship cannot be explained based only on differences in kernel weight. Thus, ash content is better correlated with yield than with kernel weight in the three environments assayed (Table 1). Genotypic differences in Δ and ash content could be simply due to differences in phenology. To assess this possibility, Δ of kernels, AshK and AshL for durum wheat genotypes were analyzed using the number of days from planting to heading as a covariate. Even when the covariate was significant for all parameters evaluated (indicating that these traits were systematically associated with phenology), there were strong significant differences among genotypes for all these traits when corrected for heading time. Therefore, there is significant genotypic variability in Δ of kernels, as well as in AshK and AshL, which is not explained by differences in phenology.

A surrogate analysis of Δ (Clark et al. 1995) and total ash content (Windham et al. 1991) has been reported for grasses utilizing near infrared reflectance spectroscopy (NIRS). NIRS may be very useful in the routine screening of early generations. In laboratory settings, NIRS is currently the basis for quick, accurate, non-destructive and highly repeatable assays of many biological materials, including digestibility, nitrogen, energy content, moisture, ash, crude fats, total reducing sugars, alkaloids, and a number of other compounds and classes of compounds in plant matter (Clark 1989).

Preliminary analyses of barley kernels (Català et al., unpublished results) indicate reasonably good correlations between Δ,

### Table 3. Percentage of grain yield (GY) variation within genotypes in three different environments of northwestern Syria explained by the progressive combination of different integrative traits measured in the support irrigation trial and based on carbon isotope discrimination and total ash content of mature kernels and leaves. The traits assayed were: Carbon isotope discrimination (ΔK) and total ash (AshK) content of mature kernels, carbon isotope discrimination of the penultimate leaf (ΔL) and the total ash content of the flag leaf (AshL). Penultimate leaves were sampled around heading, flag leaves 2-3 weeks after anthesis and kernels at maturity.a

<table>
<thead>
<tr>
<th>Traits added</th>
<th>Breda (rainfed)</th>
<th>Tel Hadya (rainfed)</th>
<th>Tel Hadya (irrigated)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>% GY CV (%)</td>
<td>% GY CV (%)</td>
<td>% GY CV (%)</td>
</tr>
<tr>
<td>n = 125</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AshK</td>
<td>7.2 21.5</td>
<td>9.0 16.6</td>
<td>21.6 21.8</td>
</tr>
<tr>
<td>AshL</td>
<td>16.9 20.4</td>
<td>25.6 15.1</td>
<td>40.0 19.1</td>
</tr>
<tr>
<td>ΔK</td>
<td>30.4 18.7</td>
<td>31.9 14.5</td>
<td>44.4 18.5</td>
</tr>
<tr>
<td>ΔL</td>
<td>30.9 18.7</td>
<td>35.1 14.2</td>
<td>49.1 17.7</td>
</tr>
</tbody>
</table>

---

a Calculations were done by fitting grain yield to a multilinear equation where traits were sequentially added.

b n = number of genotypes assayed.

c Coefficient of variation of estimated GY.

Source: Araus and Nachit 1996.
measured by mass spectrometry, and the NIRS assessment (Figure 4).

**Stable nitrogen isotope composition and nitrogen uptake**

Nitrogen uptake by plants is performed without any particular discrimination between two stable isotopic forms ($^{14}$N and $^{15}$N). Under controlled conditions, the $^{15}$N composition ($\delta^{15}$N) in plants and nutritive solution is similar (Mariotti et al. 1982). The nitrogen in chemical fertilizers has significantly lower $\delta^{15}$N than the nitrogen from natural soil mineralization. By analyzing the $\delta^{15}$N of nitrogen accumulated by plants, the relative contribution in a crop of the two sources of nitrogen available in the soil can be estimated (Deleens et al. 1994). Therefore $\delta^{15}$N could become a simple integrative indicator of uptake efficiency and further assimilation of chemical nitrogen fertilizers by a given genotype (Amaro et al. 1995).

**Acknowledgment**

This work was supported by grant CICYT AGF95-1008-C05-03 from Spain.

**References**


Questions and answers

M. Mergoum:
What are the effects of foliar diseases on canopy reflectance (NDVI index)?

J.L. Araus:
The NDVI index will decrease as the foliar disease progresses. Because the occurrence of foliar diseases is related to a loss of chlorophyll, reflectance in the red will increase, whereas in the near-infrared, reflectance will remain unchanged and the NDVI index will decrease. At first, changes in reflectance in the near-infrared region would be detected only if disease severely damages the anatomy of the leaf. Also, the decrease in leaf biomass due to disease will result in a lower NDVI index.

MM:
Similarly, what would be the effects of soil management (e.g., zero or minimum tillage) on soil reflectance?

J.L. Araus:
If you use canopy reflectance techniques for rough evaluations such as relative differences among genotypes in early vigor, the problems should at first be minor. Because NDVI (among other indexes) is a normalized index designed to evaluate green area, straw should not affect this index. Of course, soil reflectance is taken into consideration to correct the canopy reflectance measurements from soil disturbances. Alternative empirical reflectance indexes in which correction for soil effects is included would imply among other approaches the use of derivatives of the reflectance spectra, the mixture model analysis, or the calculation of a weighted difference vegetation index.

R. A. Fischer:
The correlations between ash content, delta and yield look promising. Could you return to the Tel Hadya irrigated data, the most relevant to this workshop, and explain these more fully? What was the regression procedure to give the r² and CV? What was the yield range?

J.L. Araus:
Variables were added in a stepwise manner starting with ash (%) content of the leaf (positive correlation), then ash percentage of the grain (negative correlation), etc. The genotypes were from ICARDA’s durum core collection, with yield ranging from 2.5 t/ha to 7 t/ha.

RAF:
Can ash (%) and Δ be reliably assessed on spaced plants?
J.L. Araus:
Yes, if they are irrigated and your purpose is to use these traits to select for potential yield.

E. Duveiller:
In the effort to generate accurate data on disease resistance, tools like remote sensing based on assessment of photosynthesis can be promising to help breeders recognize the best genotypes regarding a particular disease. Since both control and diseased plots need to be evaluated in order to assess the effect of a disease, can techniques based on spectral reflectance be used for screening for disease resistance of early materials, and what would be the minimum plot size?

J.L. Araus:
There is no doubt radiometric indexes such as NDVI can be promising traits to evaluate disease (note the answer to the first question). However, the minimum plot size for such comparisons should be comparable to that required when evaluating yield. Therefore, I am skeptical of the evaluation of early materials based on any radiometric approach.

M. Reynolds:
Your data show that the spectral index NDVI shows a significant association with many canopy traits including ground cover, when LAI is 2 or less. To what extent does leaf waxiness confound this type of relationship, and can you compare the relative efficiency of the techniques with visual estimates?

J.L. Araus:
The effect of waxiness on NDVI is minor. For example, in a comparison between two near-isogenic barley lines differing in glaucousness, NDVI was about 4% lower in the glaucous compared with the non-glaucous genotype (unpublished data from our team). Of course visual estimates of some canopy traits are perhaps faster than spectral reflectance techniques. However, visual evaluations produce discrete narrow scores (e.g. from 1 to 5), which frequently are highly subjective and associated with the degree of experience of the people in charge of the evaluation. On the other hand, you can derive many canopy traits once you have recorded canopy reflectance data.

V.S. Chanlan:
In one of your slides, you indicated that under low nitrogen there is more fluctuation in chlorophyll content and more so in morning hours. What was the nitrogen level in your experiment and during which hours of the morning was it measured?

J.L. Araus:
If you are referring to the work of Filella et al. (1996) cited in my paper, nitrogen levels were 25 and 75 kg N ha\(^{-1}\), and chlorophyll content was measured in the morning between 7-9 h and midday between 11-13 h (solar time). Nevertheless, I suspect there is some confusion because I don't agree with your interpretation of this slide.
The Contribution of New Biotechnologies to Wheat Breeding

J.W. Snape

John Innes Centre, Norwich Research Park, Colney, Norwich, UK

Abstract
New biotechnologies presently emanating from developments in genetics, tissue culture and molecular biology can increase the efficiency of wheat breeding by providing new insights into the genetic control of key traits and markers for their manipulation; methods for introducing new and novel sources of genetic variation; and methodologies for speeding up the breeding cycle. This paper reviews the most significant technologies and their probable impact on wheat breeding into the next millennium. The power of genetic analysis in wheat has been revolutionized by the development of the first comprehensive genetic maps based on molecular markers. Now, loci controlling all agronomic traits, whether major genes or QTL, can be identified, located and ‘tagged’. Additionally, the property of DNA probes to cross hybridize to related species enables wheat breeders and geneticists to exploit the strengths of comparative mapping, which links the genetics of all the important cereals. The power of these methods is illustrated by recent discoveries on the genetics of adaptation in wheat, where most of the loci controlling flowering time have now been identified, so that their primary and pleiotropic effects on yield can be characterized. These methodologies are allowing new wheat phenotypes to be designed with a precision not previously possible. Doubled haploid systems are at last making a direct contribution to wheat breeding through the development of the maize pollination system. Modifications to post-pollination treatments and improvements in embryo culture techniques now make this a reliable system with a range of genotypes. Similarly, developments in tissue culture and biolistics are finally making it possible to reliably transform wheat. Targets, particularly with respect to disease and pest resistance, and end-use quality, are now being actively pursued, although problems relating to gene stability and expression remain to be resolved as well as issues relating to farmer and consumer acceptance.

Introduction
Continued genetic advance in a wheat breeding program depends on the identification and selection of individual plants or families containing new adapted gene complexes from within a population of recombinant products created from reassortment and recombination of parental genomes. This depends on new sources of genetic variation to create novel inter-varietal combinations and then the selection of new, adapted gene complexes in the resulting recombinant population. In the pedigree selection system normally practised in wheat, most selection is still carried out only at the phenotypic level. This restricts options for directed manipulation of the variation by, essentially, selecting desirable gene combinations only by chance. At the same
time, the long gestation period for these processes means that it takes wheat breeders many years to bring a new variety to the farmers. Thus, not only is genetic advance not generally maximised but through-put is slow. Methods for increasing generation through-put, combined with directed genetic manipulation, can bring particular advantages. Current advances in molecular biology and tissue culture can make an important contribution to these processes, as well as provide the basis for introducing novel traits through genetic engineering technologies.

**Potential Contribution of Genetic Analysis to Realizing Yield Potential**

Genetic analysis combined with character analysis plays a pivotal role in providing plant breeders with information about the characters and genes that they wish to manipulate to produce high yielding varieties with better adaptability to appropriate environments, better disease, pest and stress tolerance, and good quality. Current estimates are that wheat probably contains about 25,000-30,000 unique genes, but only a fraction of these have been mapped so that their primary and pleiotropic effect can be studied, understood and manipulated. There is an urgent need to use genetic analysis to identify, locate and then gene tag agronomically important loci. This would allow the available variation to be manipulated in a more directed manner than has hitherto been possible, enabling yield potential to be maximised in a given environment. There is evidence in the UK, for example, that dramatic increases in yields of varieties over the last 30 years can be traced, at least in part, to the introduction of a few major effects, such as the introduction of the Rht1 and Rht2 dwarfing genes and the 1B/1RS translocation (Angus, Nickerson Plant Breeders, pers. comm). The identification of other novel effects and their assembly into adapted backgrounds can lead to greater yields and yield stability.

Comprehensive genetic maps of the entire wheat genome developed through the use of molecular marker systems (Devos and Gale 1993) are now allowing detailed genetic analysis of all traits by associating allelic variation at marker loci with phenotypic variation for traits of interest. Precise methods of genetic analysis that enable the accurate location and manipulation of major genes and QTL controlling important agronomic traits are emerging. In wheat, this can be carried out, first, at the whole genome level, when partial or complete genome marker coverage can be achieved (Hyne et al. 1994), as is being practised in many other species, for example, in barley (Kleinhofs et al. 1993, Laurie et al. 1995). Second, and specifically for wheat, this can be done at the individual chromosome level, since it is possible to combine previously developed, sophisticated, chromosome assay procedures from cyto genetic approaches (Law et al. 1981, 1987), using the newly developed detailed genetic maps. By combining the current molecular-marker-derived maps with recombinant substitution lines, wheat geneticists have tools for genetic analysis that undoubtedly meet or surpass those available in other arable crop species (Snape et al. 1994).
In certain crosses, it is theoretically possible to dissect total phenotypic variation for any trait into components attributable to each individual gene. In practice, it is unlikely that all loci will be detected and located, since the effects of individual genes will probably vary in magnitude and only those reaching a threshold level greater than the experimental error will be detectable. Nevertheless, it should be possible to tie down a considerable proportion of the variation for any one trait, particularly if the variation is mediated, at least in part, by a few loci of relatively large effect. In wheat, this type of inheritance has been found for many traits of interest to plant breeders, such as flowering time, height, yield and yield components, stress responses, and quality characteristics (Table 1). Thus an efficient tagging strategy could be to target only a small number of major genes or QTL of large effect and to ignore other loci of small effect.

Genetic analysis using polymorphisms for different RFLP probes dispersed around the genome in a particular population can also establish whether variation for different characters is under the pleiotropic control of the same set of genes. Co-location of individual major genes or QTL for different characters implies either the pleiotropic action of the same genes or close linkage of different genes. Distinguishing between these possibilities is difficult. However, if QTL detected at different locations in the genome or in different segregating populations demonstrate the same relationships in terms of magnitude and direction of effect on two or more characters, then pleiotropy is the most likely explanation. There is now considerable evidence that many major genes (for example, dwarfing genes, photoperiodic genes, fertility genes, and others) and QTL in wheat have pleiotropic effects on yield and yield components, and these effects can interact with environment (see below).

Table 1. Current information on the genetic control of agronomic characters in wheat.

<table>
<thead>
<tr>
<th>Primary character</th>
<th>Major genes</th>
<th>Polygenic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biomass</td>
<td>Max. photosynthetic rate</td>
<td>Quantum efficiency</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Respiration rate</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Photo-respiration rate</td>
</tr>
<tr>
<td>Yield potential</td>
<td>Fertile tillers per m²</td>
<td>Grain number per spike</td>
</tr>
<tr>
<td></td>
<td>Grain size</td>
<td>Harvest Index</td>
</tr>
<tr>
<td></td>
<td>Plant height</td>
<td>Plant height</td>
</tr>
<tr>
<td>Adaptation</td>
<td>Vernalization response</td>
<td>Earlyness per se</td>
</tr>
<tr>
<td></td>
<td>Photoperiod response</td>
<td></td>
</tr>
<tr>
<td>Yield limiting</td>
<td>Disease resistance</td>
<td>Adult plant resistance</td>
</tr>
<tr>
<td></td>
<td>Pest resistance</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Herbicide tolerance</td>
<td>Drought tolerance</td>
</tr>
<tr>
<td></td>
<td>Cold tolerance</td>
<td>Cold tolerance</td>
</tr>
<tr>
<td></td>
<td>Chemical tolerance</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Salt, metal tolerance)</td>
<td></td>
</tr>
<tr>
<td>Quality</td>
<td>Protein quality</td>
<td>Protein quantity</td>
</tr>
<tr>
<td></td>
<td>Protein quantity</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Grain hardness</td>
<td>Sprouting resistance</td>
</tr>
<tr>
<td></td>
<td>Sprouting resistance</td>
<td></td>
</tr>
</tbody>
</table>
Comparative Mapping and Genetic Analysis in Wheat

The efficiency of marker mediated approaches to genetic analysis depends on the density of the genetic maps available. In wheat, there are several problems that are limiting map detail and hence the power of analysis, relative to the maps available in other cereal species such as maize and, to a lesser extent, barley. In particular, the levels of polymorphism obtained for DNA clones in wheat appear to be lower than in other species. However, the great advantage of molecular markers over conventional markers is that DNA probes hybridize across crosses within the same species, across genomes within polyploid species such as wheat, and frequently across independent genomes of taxonomically distant but related species.

An additional tool available to the wheat geneticist for gene location is comparative genetic analysis, which also provides new insights into gene action and gives breeders access to a wider spectrum of genes (Snape et al. 1995, 1996). The genetics of wheat can now be clearly linked to the genetics of other Triticeae species, particularly barley and rye, since extensive collinearity has been shown between the wheat, barley and rye genetic maps. Also, common markers are being used to combine the available information on important agronomic characters into a common framework (Devos et al. 1993). Since this synteny now extends much further (to maize, rice, sorghum, millet and forage grasses) (Moore et al. 1995), it should be possible to carry out comparative QTL analyses across all these species. This can be used to link known genes into homoeologous series or to search for previously undescribed genes. For example, we were able to exploit comparative mapping to locate Ppd-H1, a new major photoperiodic gene in barley, because we knew its chromosomal location in wheat (Laurie et al. 1994). Additionally, we have shown by RFLP mapping using cross-hybridizing probes that Vrn1, which controls vernalization response in wheat, is homoeologous to Sh2 in barley and Spl in rye (Galiba et al. 1995; Laurie et al. 1995).

A major discovery made during the initial development of wheat genetic maps was the extensive collinearity in gene order for molecular markers between the A, B and D genomes. Although there are major translocations between chromosomes (for example, a reciprocal translocation between the long arms of chromosomes 4A and 5A), most of the genome is still conserved in terms of gene order. This synteny can also be exploited to search for homoeologous variation for agronomic characters within wheat. Once major genes or QTL of interest are identified and mapped onto a particular chromosome, the known homoeologous regions in the other genomes can be searched for allelic variation. This can be done using the same probes if polymorphisms for them exist on the other genomes, or probes for closely linked loci if the detector loci are monomorphic. Many, if not most, traits currently mapped exhibit, as would be expected, synteny across the wheat genomes (for example, genes controlling plant height, grain storage proteins, grain protein amount, flowering time, stress tolerance and even disease resistance) (Worland et al. 1984).
Exploiting Genetic Variation for Adaptation in Wheat

The contributions of genetic analyses to directed wheat breeding can be illustrated by studies on wheat adaptation to specific eco-geographical environments through genetic control of flowering time. Indeed, genetic analysis is likely to make a major contribution to raising the yield plateau by helping us understand the specific interactions of specific flowering time genes in specific environments. Genetic control of flowering time is complex, and chromosome substitution line analysis has shown that chromosomes of nearly all homoeologous groups are involved (Table 2, after Law et al. 1991). The existence of extensive allelic variation for these genes make bread wheat \( (Triticum aestivum\) L.) the most widely adapted major cereal crop in the world.

Broadly speaking, three separate sets of genes are involved in the genetic control of flowering in wheat. The first set includes genes that control sensitivity to vernalization and determine the spring wheat/winter wheat difference, the \( Vrn \) genes. Because of these genes, autumn sown wheats need a period of growth at low temperatures before floral development can proceed. Spring sown wheats either have no vernalization requirement or have only a weak response; the lack of vernalization requirement is generally dominant. Five loci are known to control spring/winter differences. The chromosomal location of four of them, namely \( Vrn1(5A), Vrn3(5D), Vrn4(5B) \) and \( Vrn5(7B) \), has been established (Worland et al. 1984; Snape et al. 1985). However, wheat varieties in Europe and other major wheat growing areas of the world have alleles at the \( Vrn1 \) locus that appear to be predominant in reducing vernalization requirement (Pugsley 1971; Snape et al. 1976). For example, Snape et al. (1995) have shown that it is possible to convert a UK winter wheat into a spring wheat by transferring a vernalization insensitive allele at the \( Vrn1 \) locus, with no disadvantageous effects on other traits.

The second major group of genes control response to photoperiod and are located on the homoeologous group 2 chromosomes: \( Ppd1, Ppd2 \) and \( Ppd3 \) on chromosomes 2D, 2B and 2A, respectively (Welsh et al. 1973; Law et al. 1978; Scarth and Law 1983). In autumn sown wheats, these play an important part in accelerating or delaying flowering time in the spring, after vernalization requirement has been satisfied. Presently, most European varieties that are day length insensitive probably carry a \( Ppd1 \) allele derived from the Japanese variety Akakomugi (Worland and Sayers 1996). An alternative allele at this locus appears to be present in CIMMYT wheats such as Ciano 67. \( Ppd2 \) alleles for

<table>
<thead>
<tr>
<th>Homoeologous group</th>
<th>Genes located</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group 1</td>
<td>Genes for sensitivity to vernalization</td>
</tr>
<tr>
<td>Group 2</td>
<td>Genes for sensitivity to photoperiod</td>
</tr>
<tr>
<td>Group 3</td>
<td>Earliness ( per \ se ) genes</td>
</tr>
<tr>
<td>Group 4</td>
<td>Earliness ( per \ se ) genes</td>
</tr>
<tr>
<td>Group 5</td>
<td>Genes for sensitivity to vernalization</td>
</tr>
<tr>
<td>Group 6</td>
<td>Genes for sensitivity to vernalization</td>
</tr>
<tr>
<td>Group 7</td>
<td>Genes for sensitivity to vernalization</td>
</tr>
</tbody>
</table>
photoperiod insensitivity, such as those present in the variety Chinese Spring, appear to be less insensitive than corresponding \textit{Ppd1} alleles (Worland and Sayers 1996).

The third group of loci involved in flowering time are termed ‘earliness per se’ or ‘developmental rate’ genes. These genes do not respond differentially to different lengths of cold treatment or photoperiod, and seem to be distributed throughout the genome. In genetic analysis terms, these loci are generally located as QTL effects rather than as major genes. From a detailed genetic analysis in barley (Laurie et al. 1995), most chromosomes appear to carry such genes; by homoeology, these would be expected to be present in wheat, although detailed mapping in wheat is probably restricted to the \textit{eps.2} locus on chromosome 2B (Scarth and Law 1983). Genetic analysis with RFLP maps is currently being used to pinpoint these loci, and Table 3 illustrates the current status of the genetic analysis of flowering time loci in barley and wheat.

<table>
<thead>
<tr>
<th>Group 1</th>
<th>A Genome</th>
<th>B Genome</th>
<th>D Genome</th>
<th>H Genome</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group 2</td>
<td>\textit{Ppd3}</td>
<td>\textit{Ppd2}</td>
<td>\textit{Ppd1}</td>
<td>\textit{Ppd-H2}</td>
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<tr>
<td></td>
<td></td>
<td>\textit{Eps-2BS}</td>
<td>\textit{Eps-2DS}</td>
<td>\textit{Ppd-H1}</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>\textit{Eps-2HS}</td>
</tr>
<tr>
<td>Group 3</td>
<td></td>
<td></td>
<td></td>
<td>Denso</td>
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<td></td>
<td></td>
<td>\textit{Eps-3HL}</td>
</tr>
<tr>
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<td></td>
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<td>\textit{Sh}</td>
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<td>Group 6</td>
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<td>Group 7</td>
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Genetic analysis also indicates that the loci for these three genetic systems appear to have multiple alleles (Snape et al. 1976). This suggests an enormous potential to adjust and fine-tune the flowering time of wheat to particular geographical regions and specific environment within them. Studies also show that genes of all three systems have pleiotropic effects on other aspects of plant growth and development. This has important consequences for wheat breeding aimed at specific adaptation. For example, the influence of these genes on yield potential in different European environments is well illustrated by the work of Worland and Sayers (1996). They studied the primary and pleiotropic effects of \textit{Ppd1} using isogenic lines for the \textit{Ppd1/ppdl} allelic difference in a range of environments representative of the major wheat growing regions of Europe.

First, they showed that \textit{Ppd1} produces shorter plants and thus behaves as a major height reducing factor. It also produced fewer spikelets in the ear, but increased spikelet fertility. Overall, this more than compensated for the reductions in spikelet number in some but not all environmental conditions. When summer conditions are hot and dry, as is usual in southern and eastern Europe, genotypes with the photoperiod insensitivity allele flower earlier and produce larger grain than genotypes with the sensitive allele, and consequently have significantly higher yields. However, in the wetter, cooler summer areas of northern Europe, such as in the UK, effects are
more variable, and in a typical cool, damp summer, higher yields are usually found in genotypes with the sensitive allele, which allows a longer vegetative growth period. Recently, however, a run of warmer, drier summers (even in the UK) has led to early photoperiod insensitive genotypes producing the highest yields.

Typical percentage changes in yield associated with the Ppd1/ppd1 difference are shown in Table 4. They illustrate how large the effects of individual alleles on specific adaptation for yield performance in different countries and different years can be. In the UK environment, if warmer, drier summers (such as in 1992) become more frequent because of global warming, varieties carrying the Ppd1 insensitivity allele will be preferable to those presently grown, which overwhelmingly have the ppd1 allele.

A further requirement for the successful adaptation of winter wheats to many eco-geographic regions is they must be able to survive low winter temperatures. However, unlike vernalization requirement, frost tolerance in wheat appears to be a complex quantitative character, with its many component traits determined by an interaction between the plant genotype and the environment in which the plant is grown. Nevertheless, frost tolerance can be evaluated under controlled experimental conditions and genes influencing tolerance have been located on the homoeologous group 5 chromosomes and chromosomes 4B, 4D and 7A through the study of monosomic and substitution lines (Puchkov and Zhirov 1978; Sutka and Snape 1989; Sutka et al. 1995; Roberts 1986). Chromosomes 5A and 5D have been implicated most frequently and appear to carry major genes; we have mapped a major gene, Fr1, closely linked to Vrn1 on chromosome 5A (Galiba et al. 1995).

Interestingly, this region of 5A also appears to carry major QTL for other stress responses, such as abscisic acid production under drought stress, and osmotic stress tolerance. This implies that these effects may be pleiotropic of Fr1, or that there are a series of linked stress-response genes. Additionally, an effect of Vrn1 cannot be unambiguously ruled out. QTL controlling traits associated with winter hardiness in barley (field survival, LT<sub>50</sub>, growth habit [vernalization response], and crown fructan content) were also mapped to chromosome 7(SH) by Hayes et al. (1993). Comparative mapping by us suggests that an adapted gene complex analogous to Vrn1-Fr1 is associated with Sh2.

The genetic analyses described above are at last revealing detailed information about the genetic control of adaptation in wheat and the influence of specific genes on adaptation and yield performance in different environments. Similar information is

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**Table 4. Percentage change in yield associated with effects of the Ppd1/ppd1 allelic difference in different years in the UK, Serbia and Germany.**

<table>
<thead>
<tr>
<th>Year</th>
<th>Morley, UK</th>
<th>Novi Sad, Serbia</th>
<th>Gatersleben, Germany</th>
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<tbody>
<tr>
<td>1986</td>
<td>-6.1</td>
<td>+10.1</td>
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<tr>
<td>1987</td>
<td>-2.7</td>
<td>+31.7</td>
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<td>1988</td>
<td>-4.8</td>
<td>+59.6</td>
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<tr>
<td>1989</td>
<td>+6.4</td>
<td>+30.4</td>
<td>+25.1</td>
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<tr>
<td>1990</td>
<td>+4.9</td>
<td>-</td>
<td>-7.2</td>
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<tr>
<td>1991</td>
<td>+1.2</td>
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<td>+12.4</td>
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<tr>
<td>1992</td>
<td>+9.0</td>
<td>-</td>
<td>+28.5</td>
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emerging on the genetic control of pest and disease resistance, including adult and non-specific forms of resistance and many aspects of grain and end-use quality. The challenge now is to translate this genetic information into selection tools that can be used by wheat breeders on an efficient and low cost basis.

The Contribution of Doubled Haploid Systems to Wheat Breeding

Although directed genetic manipulation of the wheat genome is now becoming possible through marker-mediated selection following genetic analysis, the production of a new variety still requires many generations of self-pollination and selection to achieve the necessary levels of homozygosity and, hence, genotypic stability before a variety can be released. One of the major contributions of tissue culture techniques to wheat breeding has been the development of doubled haploid (DH) systems which can short-circuit this process. Generally, a minimum of two years can be saved in the release of a new cultivar by the development of recombinant DH populations from inter-varietal F₁s. An added and significant advantage is that these systems not only speed up the advance to homozygosity, but can also increase selection efficiency (Snape 1989). This is because of the greater proportion of additive genetic variation available for selection for quantitative traits and the absence of dominance effects for major genes. This allows better discrimination between genotypes within crosses, better discrimination between crosses, and greater selection response across generations (Snape 1982).

The widespread use of DH technology in wheat has been impeded by the lack of a technique that can satisfy all of the expected criteria for a successful system (Snape et al. 1986), namely, 1) easy, consistent production of large numbers of DHs of all genotypes in the breeding programme; 2) DHs should be genetically normal and phenotypically stable; and 3) recombinant DH populations should contain an adequate sample of the genetic variation in the parents. Until recently, the most widely used technique in wheat was anther culture. However, although useful in some breeding programmes (e.g., Hu and Yang 1986), it is restricted in general applicability by genotypic differences in response, low production frequencies, and high relative cost. An alternative system that exploited chromosome elimination in intergeneric crosses with wild tetraploid barley species (Hordeum bulbosum) was also attempted, but was restricted by genetically determined low crossability in many varieties (Snape et al. 1979).

The discovery by Laurie and Bennett (1988) that the same phenomenon could be exploited by using intergeneric crosses with maize pollen has at last led to a commercially exploitable system. This system is now enabling large populations of homozygous recombinant lines to be produced at reasonable cost. This has been possible by the modification of pollination techniques to allow large scale emasculation and high fertilization frequencies; the post-pollination application of plant hormones that allow high frequency embryo survival and germination; and efficient chromosome doubling techniques. Several commercial
wheat breeding companies are applying this technique and DH lines produced from this system are now entering national list trials in Europe.

Nevertheless, this technology is more expensive than conventional breeding techniques and only a limited number of crosses can usually be handled. There is a need to move the technologies on further. Current research in cereal microspore culture may provide the next breakthrough in DH technologies. If microspores (several thousand of which can be obtained from an individual spike) could be induced to undergo sporophytic development, the gate would be open for the large scale production of DH lines with low inputs. Studies in barley microspore culture suggest that this is possible (Harwood et al. 1994). Future developments in tissue culture should give further progress; if such successful microspore culture techniques could be transferred to wheat, the potential for producing large numbers of doubled haploids with low technical inputs would be greatly enhanced.

**Exploiting Transformation Technologies in Wheat**

Recent developments in tissue culture and transformation technologies are finally making the genetic engineering of wheat for agronomic traits a possibility (see Jahne et al. 1996). The most successful approach is via biolistic methods of gene delivery into proliferating scutellum tissue of immature embryos (Weeks et al. 1993). In addition to the introduction of marker genes to test and optimize the systems, there is now the opportunity to introduce agronomically useful genes. Primary candidates for introduction will be novel genes that alleviate pest, disease and stress problems or create new products from a range of biological sources. Table 5 lists targets currently being sought by different groups, particularly in commercial breeding companies.

The technology also provides the opportunity for modifying gene dosage and expression of endogenous genes. A particular target of several groups is to modify the expression of high-molecular-weight glutenin proteins to seek

<table>
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<th>Table 5. Some realistic targets presently available for the transformation of wheat crops.</th>
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<td><strong>Yield limiting factors</strong></td>
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<td><strong>Fungal resistance:</strong></td>
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<td><strong>Virus resistance:</strong></td>
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<td><strong>Quality characters</strong></td>
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<td><strong>Novel products</strong></td>
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<td><strong>Others</strong></td>
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improvements in bread-making quality. This can be achieved by introducing the x and y subunits of loci previously cloned, such as subunits 5 and 10. The success of these approaches will obviously depend on the availability of cloned genes of interest, and different sources of plant genes are becoming available for both crop and model plant species, particularly Arabidopsis. For example, sources of fungal resistance are now emerging from studies of resistance genes such as the Cf2 and Cf9 genes of tomato. The sequences of these genes have been determined and degenerate PCR primers can be designed to pull out homologues from other species, including wheat.

Transformation technologies are still in their infancy in wheat, and formidable challenges remain in terms of understanding gene expression, stability, and durability. Additionally, farmer acceptance and consumer concerns need to be taken into account, and these techniques are unlikely to be a panacea. At present, they should be regarded as complementary to conventional breeding technologies, and used in an integrated approach to crop improvement.

Discussion

Biotechnologies now available allow the wheat geneticist to elucidate and modify the genetic architecture of most characters in terms of the numbers of loci involved, their relative magnitudes, their dominance and epistatic relationship, and their primary and pleiotropic effects. Also, the commonality of genetic control that is emerging from studying widely different gene pools indicates that although different alleles may be present, the same loci appear to be responsible for variation. Information on economically important traits from a wide range of varieties can therefore be combined in a common framework. Through comparative genetic analysis, a common framework map is emerging for all major cereals (wheat, barley, rye, rice, oats, maize, sorghum, and millet), as well as sugarcane and forage grasses. Thus, wheat geneticists and breeders need to be aware of information emerging from genetic studies of other species since it may indicate where loci for agronomic traits are located in wheat.

Using the information on the genetic control of a particular character for directed genetic manipulation at the plant breeding level is still, however, problematic. To do so requires following each locus, and each ‘desirable’ allele, using a unique ‘gene handle’. With respect to RFLP markers, a unique band profile must be associated with each particular allele of the agronomic trait that is to be selected, the marker must be closely linked to the trait locus, and there needs to be linkage disequilibrium for both loci in different crosses of the gene pool being used. However, because of the low levels of RFLP in wheat, this is proving to be difficult and very few loci have been tagged to date. Additionally, RFLP analysis is expensive and unlikely to be usable routinely on the large populations that plant breeders handle. Thus, the technology needs to be developed considerably to make the process ‘breeder friendly’. This will probably involve using RFLP probes as entry points to clone regions of the genome as near as possible to the locus/allele being targeted, sequencing the region, and designing specific PCR primers
to target the allele in question. Such primers may be suitable for use in dot-blot or RAPD assays of breeding populations.

Genetic analysis is also the first requirement for cloning economically important genes at the molecular level, since in wheat, the probable generic method for gene isolation is via chromosome walking. Establishing detailed genetic maps containing defined RFLPs and agronomic genes is essential to form the entry point for walking. Once genes can be isolated, it will be possible to develop a much greater understanding of gene structure and function, and how they relate to plant phenotype. This, in turn, will lead to genetic manipulation at the molecular level to produce new alleles and allelic combinations. Eventually, it will also be possible to reintroduce these into wheat (using the transformation technologies now coming on stream), or they could be used for genetic manipulation of other cereal and non-cereal species. Clearly, the door is now open to conduct genetic analysis and genetic manipulation in wheat with a sophistication that previously had been possible only in model plant species.

References


Questions and answers

N. Bohorova:
Do you recommend using microspore culture for DH production?

J.W. Snape:
At the present time, there is no successful technique for microspore culture in wheat. Some success at regeneration has been obtained from some varieties, but there are large genotypic differences. However, the potential is enormous if the optimal tissue culture protocols can be developed, as is now becoming the case for barley.

N. Bohorova:
How many genotypes do you use for a transformation experiment?
J.W. Snape:
We have not had a major focus on wheat in our transformation work at JIC, but in the UK in general, several varieties have been transformed, including CIMMYT varieties such as Pavon.

N. Bohorova:
Do you have observations about the correlation between transient expression and stable gene insertion?

J.W. Snape:
Our observations do not indicate a clear relationship. However, unless shooting conditions are optimized to get high transient expression with a particular explant, stable transformation is not achieved with that explant.

R.A. Fischer:
You have watched the decline in crop physiology at the Norwich Institute over the last 25 years, and seen the dramatic progress of wheat molecular biology over the last 10. What has happened to physiology? What is its role now?

J.W. Snape:
Physiology is still at the Institute. It is now focused on the effects of manipulation of known major genes, and not on varieties. It remains an important component of the work, maybe more useful than before. Combining physiology with good genetic analysis provides a powerful tool for analyzing crop biology.

How solid is the information and what is its cause?

J.W. Snape:
The effect is well recognized in the UK, but it does depend on genetic background. It may be related to increased stay-green under our conditions.

M. Kohli:
You mentioned the problem of gene expression in transgenic materials. How wide is the problem? Are there genes or gene systems that do express better than others?

J.W. Snape:
Problems of gene expression depend on a number of factors: the source of the gene, the promoter, the locations of the transgene in the genome, copy number. Transgene expression varies widely even for transgenics developed at the same time using the same gene and conditions of shooting, selection and regeneration. All genes that we have used show up to 10x variation in gene expression between regenerants. There are not, to my knowledge, predictive criteria for stability of any known gene combination.

M. Kohli:
Are there any indications that genes, especially for disease resistance, transferred using molecular techniques, will be any more stable or durable than those done via conventional breeding methods?

J.W. Snape:
No. The durability of transgenes for disease resistance remains to be tested. It will, of course, depend on the mechanism of
resistance and the pathogen’s ability to evolve an altered response, but again, there are no predictive criteria as yet.

M. Reynolds:
Physiology is currently poorly funded in comparison to biotechnology in breeding institutes, though the disciplines share the common objective of providing information and techniques to improve breeding efficiency. Can you suggest some specific areas in which the two disciplines of physiology and biotechnology should work together to achieve this objective?

J.W. Snape:
I believe that one of the problems with past physiological studies is that they have been retrospective rather than prospective—they have told plant breeders how they got to a certain yield level, after they had already got there, but have failed to tell them how to move to the next yield level. Combining genetics with physiology, but identifying the specific genes underlying physiological differences, can make it predictive. Molecular marker systems provide the means for doing this detailed type of genetic analysis, and marker assisted selection can allow plant breeders to move the genes around accordingly.
Application of Molecular Markers to Wheat Improvement

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Abstract
The use of conventional breeding methods has successfully improved crops within the cultivated gene pool by producing genotypes with combinations of alleles superior to either of the parents (transgressive segregation). The development of new biotechnology methods to generate, identify, characterize, and manipulate genetic variation may enhance crop improvement. Marker assisted selection (MAS) using DNA markers is being evaluated in plant breeding programs; however, MAS is limited by the effort required to generate information about map location and breeding value of genes controlling important traits. Comparative genetic maps facilitate the identification and location of gene sequences controlling specific traits in the domesticated grasses. Databases of gene sequences in related species allow directed discovery of genes and classification of alleles present within breeding germplasm. Identification of the genes controlling a trait as well as the DNA sequence would facilitate classification of variation in the germplasm pool by gene fingerprinting or by characterization of variation in key DNA sequences. Classification of the variants for a particular locus would substantially reduce the amount of work required to determine the relative breeding value and lead to the identification of superior alleles based on DNA sequence. Direct allele selection combined with conventional selection would allow more rapid and precise improvement of populations and breeding lines. Although this approach is limited by current technology, the cost can be minimized by integration of genetic information across species, the identification of highly variable genes, and focusing on the most important genes and traits for the species of interest. The challenge facing breeders is to use the appropriate tools in an integrated breeding program to create high value plant products quickly and efficiently.

Long Term Yield Trends

Several researchers have studied genetic improvement of wheat yields over time (e.g., Busch and Stuthman 1990; Schmidt 1984). Schmidt (1984) reviewed yield trends of breeding lines in regional nurseries from 1958 to 1980. He concluded that yields were generally increasing at the rate of 1% per year, but the lowest rate of increase was for the Uniform Regional Performance nursery (hard red spring) and the Southern Soft Red Nursery. The results also suggested that the rate of improvement was beginning to slow after the mid 1970s.

The American Society of Agronomy sponsored a symposium in 1994 that examined the rate of improvement in several crops including wheat. Kephart and Souza (personal communication) presented the results of analyses of yields from eight different regional nurseries in the US and the CIMMYT International Spring Wheat
Nursery. They concluded that rates of improvement varied significantly for the different nurseries. Grain yield of lines in the eastern and southern soft wheat nurseries showed a gain of about 2% per year, while lines in the Uniform Regional Performance Nursery, the Western Regional Spring Wheat Nursery, and the Western Regional Soft White Winter Wheat Nursery showed little or no yield improvement. Their analysis of the ISWYN indicated that substantial yield increases occurred up to and including the early 1980s, which coincides with the introgression of the 1B/1R translocation (Villareal et al. 1991). However, it appears that there has been very little yield improvement since then. While these studies do not indicate that wheat yields are static, they suggest that the rate of yield increase is slowing, at least in certain regions. In contrast, cross-pollinated crops such as maize and sorghum have a much higher rate of improvement.

What Is Limiting Wheat Improvement?

Breeding progress largely depends on: 1) generation of new genetic variation for agronomic traits, and 2) accurate selection of rare genotypes with new sets of attributes or superior combinations of pre-existing alleles. Biotechnology has provided us with new ways to generate genetic variation as well as methods for manipulating it. In the case of quantitative traits, superior genotypes from an elite germplasm pool represent new combinations of alleles that are better than the genotypes of either of the parents, i.e., transgressive segregation.

There is historical evidence that conventional breeding within a single germplasm pool can consistently make progress over time (Leng 1974; see Rasmusson, these proceedings). This is probably because: 1) it is very difficult if not impossible to combine all the best alleles at all loci that are segregating for a quantitative trait into a single genotype and identify it; 2) because of G x E, the ‘best’ genotype is elusive but ‘better’ genotypes can be identified; and 3) every generation there is new variation created at the DNA level. Therefore, within an elite gene pool where differences between alleles are small, progress will slow and eventually level off. The question remains: Can progress using conventional breeding continue at the same pace that it has in the past, and if so, for how much longer?

Primary Gene Pool

Recent studies indicate that, although improvement in yield potential of wheat may be slowing, genetic variation for yield in the primary gene pool of wheat is not exhausted. This leads to two questions: 1) How do we enhance breeding progress within the elite gene pool that is available? 2) Can we make more rapid breeding progress by introducing genetic variation from secondary gene pools? This paper will describe approaches that may partially answer these questions.

Testing

A comprehensive and accurate testing program is the most crucial component of any breeding program, especially when working with elite materials. In collaboration
with national programs, CIMMYT has conducted an excellent worldwide testing program. This testing program has been refined and improved over many years and is essential for identifying superior germplasm as well as for germplasm distribution. There is no alternative method for generating this information, and the testing program must not be compromised in any way. As we all know, this is a very expensive operation which limits the number of genotypes and the diversity of germplasm that can be evaluated. There are ample opportunities for error, some of which may be detected with built-in checks and screens.

New and creative methods of distributing and testing germplasm are needed. Data analysis and manipulation in the testing program promises to be one of the most productive research areas in the coming decade. Data from molecular analyses must be integrated into the databases along with pedigrees, agronomic performance, disease and insect resistance, and plant characteristics to maximize the amount of information on genotypes and gene complexes available to the breeder. In collaboration with ICARDA, we are currently gathering such information on a core durum gene pool and we are developing strategies and methods for integrating these diverse sources of information. The International Crop Information System currently being developed at CIMMYT is one of the building blocks necessary for such integration.

There are relatively few options for increasing the rate of genetic improvement within the elite gene pool given that the level of financial resources remains as in the past. One approach is to emphasize crosses between parents that are less closely related. In addition to mean parental performance, a measure of relationship such as coefficient of parentage should be used for choosing parents. This would increase the likelihood of combining new and/or different alleles to produce transgressive segregation. By reducing the number of crosses, more effort could be put into more thorough evaluation of breeding populations. A second approach is to place more emphasis on specific adaptation. This may require more sophistication in the testing program but could be especially valuable for tailoring varieties to stress environments. This will require additional effort in planning, data analysis, crossing, and selection.

**Secondary and Tertiary Gene Pool**

Efficient utilization of germplasm resources requires that under-utilized alleles be identified and combined with desirable alleles to improve elite genotypes. However, for many characters (e.g., yield) exotic germplasms have inferior phenotypes providing little evidence that they possess useful alleles. For this reason, as well as others such as linkage drag and polygenic inheritance, use of exotic germplasm is often restricted to major genes that confer disease and insect resistance, as in the case of the 1B/1R translocation. Recent evidence indicates that 1B/1R genotypes are also higher yielding (Villareal et al. 1991). Despite the apparently inferior phenotypes for many traits, exotic germplasm and even wild species contain desirable alleles for most
characters that are important in agriculture. Combining these desirable alleles with positive alleles already present in elite crop varieties may lead to genotypes with agronomic potential exceeding that of the original cultivated variety.

When the alleles come from a different species, this phenomenon is referred to as interspecific transgressive segregation and has been documented in wheat using *T. tauschii* (Cox et al. 1990) and rye (Villareal et al. 1991), in oat using *Avena sterilis* (Cox and Frey 1984; Frey 1976), and in maize using wild relatives (Reeves and Bockholt 1964; Reeves 1950). Transgressive variation for grain yield (Bramel-Cox et al. 1986; Cox et al. 1984, 1990; Lawrence and Frey 1976), protein (Cox and Frey 1985; Cox et al. 1990), and other traits in backcross populations derived from wide crosses also have been well documented.

Exotic germplasm and wild species are likely to contain positive alleles, but they may be present at low frequency and difficult to separate from the many negative alleles. Methodologies are needed for quickly locating desirable alleles and for specifically transferring them to cultivated varieties. Such strategies could result in potentially dramatic gains in crop performance. Molecular markers can facilitate the interspecific transfer of desirable quantitative alleles from the wild species into cultivated genotypes and can help selectively retain desirable alleles from the elite parent. This approach is likely to be most valuable for species where genetic variation in cultivated germplasm is known to be limited such as tomato (Miller and Tanksley 1991), soybean (Apuya et al. 1988), oat (Frey 1976), and wheat (Chao et al. 1989; Kam-Morgan et al. 1989). For these species, the secondary gene pool may be relatively more important for identification of new genetic variation if the rate of yield improvement is to be maintained or increased in the near future.

Strategies for introgression vary widely with the species. For example, wheat amphihexaploids (synthetics) constructed from crosses between durum or other AB tetraploids and *T. tauschii* are ideal genotypes for introgressing exotic germplasm because of the ease of crossing and selection (Villareal et al. 1994). A single backcross or three-way cross to an elite line results in a relatively high frequency of desirable phenotypes that can go directly into evaluation nurseries. Using these synthetic wheats, the breeder is essentially re-creating event(s) that occurred during the evolution of hexaploid wheat, thus introducing much needed genetic variation into the hexaploid wheat gene pool. Cox et al. (1990) have employed direct crosses between *T. tauschii* and *T. aestivum* to introgress disease and insect resistance genes.

**Identification of Superior Alleles**

**QTL mapping**

The theory and application of QTL mapping have been extensively covered by several authors (e.g., Paterson et al. 1991; Tinker and Mather 1995) For self-pollinated crops, doubled haploid or recombinant inbred populations are usually preferred because it is possible to replicate the genotype.
indefinitely. This is essential for QTL studies because of the need to estimate relatively small gene effects and interactions. In wide crosses where traits such as seed shattering or sterility may be a problem, one backcross followed by selfing to homozygosity can greatly facilitate testing for agronomic traits. This is because of fewer complications from undesirable traits introduced from the wild species.

Advanced backcross QTL analysis has been proposed for combining QTL analysis with variety development ( Tanksley and Nelson 1995). In this approach, elite parents are crossed with unadapted donor lines such as land races or wild species. The population is advanced with selection to the BC2 or BC3 where mapping and testing occurs and provides the data necessary for QTL analysis. Advantages include the identification of QTL in wild germplasm and the production of elite lines in a relatively short time period. The primary disadvantages are the unknown value of the few wild accessions that could be studied and the labor required for generating large numbers of cross progeny. The lack of knowledge about whether a wild accession carries superior alleles is a serious problem if desirable alleles exist in low frequency.

**Segmental populations**

Another similar approach to simultaneous QTL mapping and line development described by Paterson et al. (1990), Eshed and Zamir (1994), and others is to generate F2 or BC-derived inbred lines each of which contains a few segments from one of the parents but which collectively contain overlapping chromosome segments that cover the entire genome. Introgression lines can assist in RFLP-based gene cloning by allowing the rapid selection of DNA markers that map to specific chromosome segments. Introgression lines also provide a base population for the mapping and breeding for quantitative traits.

**Gene (pedigree) tracking**

Molecular analysis of pedigrees has been useful in soybean for verifying pedigrees, tracing loci back to ancestral parents and identifying linkages between markers and qualitative trait loci (Lorenzen et al. 1995). In this approach, modern cultivars, their parents, and all parents tracing back to land races are analyzed for RFLPs covering the entire genome. This analysis is not a substitute for a well-designed doubled haploid or recombinant inbred mapping population, but can provide useful information about which parents might be used as a source for a particular allele.

It is clear that alternative strategies are needed for identifying QTL and for determining allelic values for specific loci in large numbers of accessions that have not been used in mapping studies. With current technology, allelic value can only be determined with certainty relative to another allele in a cross population. In recent studies (Beer et al. 1996), we have tested the hypothesis that allelic values can be determined by grouping RFLP alleles and looking for association with an agronomic trait. If trait RFLP data are available for the same accessions, RFLPs can be tested for statistical association with variation for a trait. Any associations can be used to identify a subset of candidate probes with enhanced potential for use in subsequent mapping experiments.
Within the North American oat germplasm pool, surveys of quantitative trait variation and RFLPs were conducted for 64 cultivars and landraces. We performed t-tests of the hypothesis that scores for each of 13 quantitative traits were equal in lines containing a particular restriction fragment, versus those lines lacking it. Of the 157 restriction fragments with ≥5 accessions in both the 'presence' and 'absence' categories, an average of 17.4 fragments per trait produced significant t-tests (p≤0.01). Only a few of these associations corresponded to linkages of these fragments to known quantitative trait loci affecting yield or plant height in a mapping population. It appears that the effectiveness of this approach was limited by G x E interaction, disequilibria, and/or multiple alleles of different value.

**Comparative QTL Mapping**

**Identifying QTL/major gene loci**

Conventionally, the genetics for species of the Gramineae family have been studied separately. Comparative mapping using DNA markers offers a method of combining research efforts in each species. Van Deynze et al. (1995) developed consensus maps for members of the Triticeae tribe (*T. aestivum*, *T. tauschii* and *Hordeum* spp.) and compared them to rice, maize, and oat. The orders of markers detected by probes mapped in rice, maize, and oat were conserved for 93, 92 and 94% of the length of Triticeae consensus maps, respectively. This allowed homoeologous segments conserved across Triticeae species, rice, maize, and oat to be identified for each Triticeae chromosome. Several putative orthologous loci for simply inherited and quantitatively inherited traits have been identified in several Gramineae species including seed size, reduced shattering, daylength insensitivity, and osmotic adjustment (Paterson et al. 1995; McCouch and Doerge 1995).

Correspondence of these QTL with homoeologous chromosome segments indicate that the genes underlying many of these traits are identical by descent.

Rice has been the focus of an extensive effort to sequence random cDNA probes and perform subsequent homology searches in databases such as Genbank (Kurata et al. 1994). The Genbank database contains sequence information for most of the markers on the available rice maps and approximately 10,000 additional rice cDNA clones. DNA sequence searches (Altschul et al. 1990) often identify putatively orthologous genes in maize, wheat, barley, and rice, as well as more distantly related species such as tomato and *Arabidopsis*. Alignment of QTL with candidate genes is potentially a powerful approach to identification of the actual gene underlying the QTL. Placement of cloned genes on comparative maps and consideration of the functional significance of the gene product can also facilitate the identification and selection of markers for QTL.

By mapping genes that have been well-characterized with respect to function or phenotypic effect, we can transfer knowledge about specific genetic loci and/or biochemical pathways between species, extend the usefulness of species-specific and comparative maps, and associate genes with the emergent properties of plant phenotypes that are important in agriculture and plant improvement.
Results of comparative mapping using DNA markers suggest that information from barley, rice, maize, and other species may be useful for identifying additional loci controlling grain dormancy (Sorrells and Anderson 1996). For example, loci affecting grain dormancy or germination were identified for maize, barley, and wheat (Table 1).

An association between red pericarp (R) and dormancy in wheat is well known and is related to pleiotropic expression of a gene at the R locus on the long arm of group 3 chromosomes. Comparative maps indicate that the R locus in wheat is orthologous to the vivipary-1 locus in maize and the red pericarp locus in rice. While this locus may be a gene with major effects on dormancy, resistance to PHS is a quantitative character with multiple loci contributing variation in white wheat (Anderson et al. 1993) and rice (Seshu and Sorrells 1985). Association of mutants with enzymatic steps in biosynthetic pathways has been demonstrated for a number of the extreme phenotypes exhibited by maize mutants, e.g., vivipary-5-Phytoene desaturase (Hable and Oishi 1995). Additional mapping research is needed to confirm these associations, but it is clear that the location and function of loci affecting grain dormancy and other important agronomic traits have been conserved through evolution of species. This information may facilitate the mapping of these loci as well as the understanding of gene expression in divergent species.

Mapping genes that comprise a single metabolic pathway makes it possible to predict associations between these genes and previously identified QTL. Support from biochemical, physiological, developmental, and agronomic research strengthens such associations. It is apparent that genetic relationships exist among the domesticated grasses at all levels of genetic study. Comparative mapping will facilitate the integration and application of the research that is accumulating in each of the domesticated grasses.

**Marker-Assisted Selection**

Many factors affect the breeder’s choice of gene tags, e.g., how many are used, and the stage of selection or inbreeding at which they are applied. Lande and Thompson (1990) have elaborated theoretical aspects of marker-assisted selection (MAS) for improvement of quantitative traits. They concluded that the efficiency of conventional methods of phenotypic selection could be substantially enhanced by combining them with marker-assisted selection. The utility of markers for quantitative traits is limited by population sizes and environmental sampling needed to detect loci affecting traits of low heritability, and by the number of markers required to select those loci that account for a significant portion of the genetic variance for the trait.

**Table 1. Chromosome location (gene symbol) of putative orthologous loci affecting grain dormancy or germination.**

<table>
<thead>
<tr>
<th>Clone</th>
<th>Wheat</th>
<th>Barley</th>
<th>Maize</th>
</tr>
</thead>
<tbody>
<tr>
<td>BCD1434</td>
<td>1S</td>
<td>5S</td>
<td>–</td>
</tr>
<tr>
<td>CDO431</td>
<td>1S</td>
<td>–</td>
<td>1.5 (Vp2/7)</td>
</tr>
<tr>
<td>CDO795</td>
<td>4</td>
<td>4L</td>
<td>1S (Vp6)</td>
</tr>
<tr>
<td>BCD1874</td>
<td>5L</td>
<td>7L</td>
<td>7 (Vp9)</td>
</tr>
<tr>
<td>KSUG12</td>
<td>7L</td>
<td>Amy1</td>
<td>–</td>
</tr>
</tbody>
</table>
My breeding program is oriented toward integrating marker-based selection with conventional breeding. Cloning and transformation will not likely address all the needs of crop improvement but may complement marker-assisted selection and conventional methods. The cost of testing and release of genetically engineered varieties is currently well beyond most public programs.

Selection of Markers

Once a suitable mapping population (usually doubled haploid or recombinant inbred) is selected, it is grown in several environments representative of the target environment. Then the phenotypic datasets for all environments are assembled and analyzed. The association of each marker with each trait in each trial is determined by ANOVA or simple regression. Regions of the genome that are consistently associated with a trait across environments are examined for pleiotropic effects and linkage phase. The selected genomic regions and the allele and trait of interest in each are then used to screen potential parents for marker alleles in each of these regions. Because different recurrent parents differ in their strengths and weaknesses, different traits and thus markers would be used for selection.

Selection of Donor Parents

Because different recurrent parents have different combinations of alleles at selected loci, different donor lines must be used to provide the correct combination of desirable alleles. If one of the parents of the mapping population is a recurrent parent, then lines from the population with desirable alleles from the other parent are selected for incorporation. If the recurrent parents have not been used for mapping, then they must be surveyed to determine their genotype at the selected loci. Lines from the mapping population can be selected for use as source parents using an index. Typically we begin by calculating a mean rank of all lines across all trials for each trait. Then we weight the breeding value of the line according to presence of desired alleles in the genomic regions chosen. Optional weighting factors could include estimates of the locus effect or of the trait's 'economic value'. The total breeding value of each line is thus the product of the above three weights taken at each of the regions and summed across loci. Finally we sort the lines based on their breeding values and take the top few lines as donor parents.

To test allelic effects in backcrosses to unknown parents, the BC1F2 seed from selected BC1F1s can be genotyped for markers and either inbred further or tested directly in replicated micro-plots. In addition, bulked seed from plants homozygous for the desired alleles can be integrated into selection nurseries in the conventional breeding program. This allows much flexibility for improving other segregating traits using conventional breeding methods.

Potential Problems in Implementation of MAS

Identification and selection of QTL

For wheat, low polymorphism within elite germplasm is potentially a limitation;
however, the low polymorphism also facilitates the identification of homoeologous loci based on previous mapping data. Small allelic differences are difficult to map precisely in QTL studies. This may result in selection of markers that are not close to the QTL or a high probability of a crossover between the marker and the QTL. Undetected recombination between markers and trait loci can lead to backcross-derived lines that are actually inferior to the recurrent parent. Also, estimates of locus effects are subject to sampling error causing errors in assigning relative weights or in choosing loci. Locus x year effects are difficult to assess and manage because they are less predictable. Only those QTL that are relatively consistent over years and locations are likely to be sufficiently valuable for MAS.

Cost
Most economically important traits are quantitative, and allelic differences at a single locus usually account for less than 20% of the variation in a trait. Thus, following markers at several loci may require excessively large population sizes. The relative cost of marker-assisted selection at various stages of inbreeding or testing depends on the number of individuals evaluated and, to a lesser extent, on the number of markers used. In general, traits conditioned by one or very few loci will favor marker-assisted selection at advanced stages in the breeding program because a large proportion of the progeny will carry the desired allele(s) and the population can be screened for less costly traits first. However, in most situations (especially for wheat), marker-assisted selection will be most efficient in the F₂ or first backcross because these are the generations of maximum segregation. This will result in a population that is either homozygous or highly enriched for the desired alleles, depending on whether homozygotes or heterozygotes are selected. Cost of developing and using molecular markers is still relatively high compared to conventional selection methods; however, the cost of marker technologies and the infrastructure necessary for doing the research are gradually declining. Molecular markers are generally cost effective for only those traits that are difficult or costly to evaluate and are controlled by a few genes.

Parental lines of unknown genotype
The efficiency of marker-assisted selection is severely limited by unknown linkage relationships between marker and trait alleles in genotypes other than parents of mapping populations. This is because polymorphism for either the marker or the trait locus is not necessarily linked to each other, especially in unrelated germplasm. Also, QTL may be expressed differently in different genetic backgrounds. In many cases, it will be necessary to evaluate traits in intermediate generations to avoid unpleasant surprises.

Pleiotropic effects
Negative pleiotropic effects are prevalent at QTL, as might be predicted from negative correlations observed among certain traits. For example, later maturity and greater plant height are often associated with increased yield, especially if sampled in a few favorable environments. These loci are not useful for MAS if later and taller genotypes
are undesirable. Quantitative trait mapping studies must incorporate evaluation for as many traits as possible to avoid this pitfall.

**Parent building**

Probably the most conservative approach to using molecular markers is to gradually backcross desirable alleles into a few elite recurrent parents. Even if these parents become obsolete as varieties, they will remain a useful single source of several desirable alleles for crossing to new varieties. Marker-assisted selection can then be followed with conventional breeding methods and selection for other agronomic traits. If target loci of selected individuals were heterozygous, another round of screening for the markers will be necessary. If at all possible, one or more of the chosen recurrent parents should be used in QTL mapping studies so that the value of the alleles in that parent can be compared to another genotype. For qualitative traits, this is not usually necessary. Numerous mapping studies are turning up desirable alleles that may be useful for some of the mainstream CIMMYT varieties.

It is clear that today’s technology can facilitate the integration of MAS into a conventional breeding program using an index and/or culling selection (multiple stage selection) method. New large scale methods are needed for identifying favorable alleles in wild species without constructing mapping populations. Comparative maps can be used to locate trait loci and markers. Enhanced germplasm databases that combine information from various sources would enable the breeder to make more informed parental choices for the crossing block.

**References**


Questions and answers

J. Dubin:
Do you anticipate using marker-assisted selection for BYD in wheat?

M.E. Sorrells:
That depends on which source of BYDV resistance you wish to use. The gene reported to be linked to Lr34 and leaf tip necrosis may not provide a high level of resistance, but the leaf rust and leaf tip markers are already available. I don’t know if anyone has mapped it precisely. Molecular markers work well for alien chromosome segments because of the high polymorphism and low recombination with wheat.

K.J. Young:
Would you comment on the amount of polymorphism in oats? In barley, absence of polymorphism is a limiting factor.
M.E. Sorrells:
Polymorphism levels in cultivated oats are similar to or slightly higher than in barley, but this is frequently a problem in small grains.

R.A. Fischer:
The ITMI mapping population initiated by A. Mujeeb-Kazi has now been yield tested under three or four plantings in ME1. I know the QTL analysis for yield hasn't been done yet. That's a pity for this meeting. What do you think we will learn when the mapping is completed?

M.E. Sorrells: 
Since the population is derived from synthetic x Opata 85, it represents materials well removed from the best CIMMYT germplasm and the QTL information for yield potential may not be very relevant in the case of elite x elite crosses. However, the population has provided valuable information about the location and expression of Karnal bunt and rust resistance genes.
Wheat Physiology at CIMMYT and Raising the Yield Plateau

R.A. Fischer

Introduction

There are several means that CIMMYT should consider by which the efficiency of breeding for yield potential in wheat may be improved. One is the use of physiological knowledge to devise more efficient selection of parents and progeny. In doing so, I believe it is very important to consider what has already been done in this area of physiological research, especially that work done at CIMMYT itself. I make no apology for the fact that I have been involved in much of this work and that this paper may seem too much like a collection of my own work. Indeed, throughout my career as a researcher I have been involved in this theme in spring wheats. Therefore, I ought to have useful experience to offer on the subject, some over and above that which has already been published.

The Period 1970-75

Research on the physiology of yield potential determination in wheat began at CIMMYT in the 1970-71 season, soon after I had been appointed as the first physiologist-agronomist in the Wheat Program. Over the next five years (during which I was generously supported in terms of field assistants, students, and visiting scientists), two routes, both of which remain valid today, were pursued in order to identify likely yield selection criteria. The first, which I shall call the analytical or ideotype route, was to take the latest highest yielding cultivars and, through manipulation of the crops (e.g., thinning) or of their environment (e.g., shading, heating, cooling), identify stages and processes that limit the formation of yield and possible ways of removing these limitations. This work was supported by simulation modeling and ideotype exploration elsewhere (the question of erect leaves, low tillering, source-sink balance during grain filling was receiving a lot of attention in the literature at the time). The second route, which I would call the empirical route, sought to identify key traits amongst sets of historical varieties or advanced cultivars via their correlation with yield. In those early years, as is still the case at CIMMYT, we had the significant advantage relative to other groups of working in a very favorable agronomic environment (MEI) and with access to the best spring wheats available in the world. In addition, in the empirical work we had sufficient resources to permit work with never less than 20 and often more than 40 cultivars in any one experiment.

The initial results of this unprecedented amount of field physiology on wheat were put into a long internal report, a copy of

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1 Director of CIMMYT’s Wheat Program from 1988 to 1995, now at the Australian Centre for International Agricultural Research (ACIAR), GPO 1571, Canberra ACT 2601, Australia.
which I lodged in the CIMMYT library in July 1975 (Fischer 1975). Many of the findings were subsequently published, something which took several years of my time. With respect to ME1 yield potential, the main conclusions (see also Fischer 1983) from the analytical studies were as follows:

- Early plant and crop growth, at least up to terminal spikelet initiation and probably beyond, was relatively unimportant for yield determination. As a consequence it was suggested that this phase could be shortened without yield loss.

- Growth in the spike phase, especially from early boot stage until just after anthesis, was very critical for yield determination, through its effect on kernel number. Greater efficiencies in this stage should translate into higher yields, and one suggestion was to try smaller, more erect leaves, and another to try to genetically lengthen the duration of this phase.

- Growth in the grain fill stage was moderately critical for yield, depending on the particular year, and in most recent cultivars grain yield exhibited colimitation by both source and sink, with the latter (namely kernel number multiplied by the genetically-determined potential kernel weight) being the most important in most years at CIANO. Thus there seemed to be scope for the crop to fill more kernels.

The empirical correlative studies supported the above conclusions of the analytical work, showing that yield potential increase was correlated with higher harvest index and higher kernels/m², and not with change in days to anthesis or biomass. Much of the harvest index and kernel number variation was related to height reduction, usually but not always involving \( Rht1 \) and or \( Rht2 \) major genes. One study with cultivars simulated the spacing of F2 plantings confirming that harvest index in such plantings was the best predictor of yield potential in solid stand; yield per plant was of zero predictive value (Fischer and Kertesz 1976). It was also discovered in 1974-75 that leaf permeability (a surrogate for leaf stomatal conductance) in the spaced plants predicted cultivar yield potential with reasonable precision.²

A third major thrust on yield potential got underway in the CIMMYT wheat physiology section with the arrival of Dirk HilleRisLambers as a post-doctoral fellow in 1973. This approach I would call validation through incorporation of a preconceived ideotrait into current cultivars, a type of prebreeding. Dirk sought to incorporate several novel traits, but by far the greatest emphasis was on increasing leaf erectness in both bread and durum wheats. Just as with Ricardo Rodriguez and his special yield component lines, Dirk went exhaustively through the available germplasm looking for sources of the trait of interest (including using \( T. sphaerococcum \) and liguleless for erectness). He developed an initial suite of erect lines within reasonable genetic

² I cannot remember how we got on to this...I think we were measuring permeability in drought and irrigation scheduling experiments (e.g., Bob Sojka’s thesis work) and stumbled upon the fact that permeability was related to yield even under well-watered conditions....but I admit that at some stage I visited Israel, met Shimshi and Ephrat, and received an early report (to the funders, namely, the Ford Foundation) on the work they subsequently published in the Agronomy Journal in 1975.
backgrounds before leaving for IRRI in 1975. It was quite a feat in two years. Although the few yield tests run in 1975 and 1976 were inconclusive regarding the effect of leaf erectness, the breeders took over the best of Dirk’s material, crossed to it extensively, and 8-10 years later produced some outstanding bread and especially durum cultivars exhibiting the plant type initially developed by Dirk (e.g., Bacanora 88, Altar 84, and Aconchi 89).

The Period 1975-78

Pat Wall joined the agronomy-physiology section in late 1974 and stayed there until 1978. He pursued several of the leads from the above analytical studies, producing an otherwise unpublished Ph.D. thesis describing this work in detail (Wall 1978). He confirmed the earlier results and extended them in elegant field experiments, showing that the spike phase was differentially sensitive to photoperiod depending on genotype, and by showing that the importance of the spike phase was most probably related to the flux of carbon assimilates reaching the growing spikes and not to nitrogen supply (a recurring theme even today...see Abbate et al. 1996). Pat also ran the large yield trials with Dirk’s erect leaf lines. Results were not obviously conclusive, but were never fully analyzed. Pat’s most interesting contribution, however, was to actually test some indirect selection criteria for yield in breeders’ F2 populations. Over 1000 random plants from a total of eight elite by elite crosses were tagged and measured for various potential selection criteria. They were advanced without selection to F4 plot yield tests the following year at CIANO. The best predictor of F4 yield turned out to be leaf permeability at certain stages of development (r values up to 0.40). This and harvest index were clearly better than yield components, yield per plant, or breeders’ scores (the work was only written up for the 1977 CIMMYT Annual Report, p. 106-113).

The Period 1978-88

With Pat’s departure for Ecuador in 1978, this work and indeed most physiology ceased in the Wheat Program for about 10 years. A notable exception was the study of an historic set of bread and durum wheats by Steve Waddington and colleagues, which produced similar results to those seen before with the exception that Steve concluded that biomass may be increasing in the most recent cultivars (Waddington et al. 1986).

Towards the mid 1980s, after having spent considerable time analyzing and publishing the results I had collected in Mexico, results in some cases supplemented by data subsequently gathered in Australia, the process came to an end. This long gestation period did lead to some new insights and reinforced conclusions regarding kernel number determination, conclusions which were most clearly enunciated in Fischer (1983) and Fischer (1985). The model put forward then is relevant even now:

\[
\text{KNO} = \text{SDWA KNO/SDWa}, \quad \text{SDWA} = \text{Ds CGR} \times \text{Fs},
\]

where SDWA is the spike dry weight at anthesis (g/m²), Ds is the duration in days of the spike growth phase (mean of about 500 day degrees preceding anthesis), CGR (g/in²) is the crop growth rate during this period, and
Fs is the fraction of net assimilate partitioned to the growing spikes in this period (between 0.2 and 0.5, according to genotype). All these components should be reasonably independent, but this does not mean they are easy to measure. Up until the mid 1970s all genetic progress in yield and KNO derived from an increase in Fs, in turn largely associated with reduced stature.

Environmental effects on yield in ME1, however, were largely due to effects on Ds and/or CGR. These conclusions were generally confirmed by studies in the UK, although detailed work by Youssefian et al. (1992) on the nature of the effect of Rht dwarfing and recent work on nitrogen nutrition (Abbate et al. 1995; Van Heerwarden, unpublished) do leave open the possibility of direct positive effects on KNO/SDWa under potential conditions, something which merits follow up.

In the early and mid 1980s, myself, Ken Quail and colleagues undertook a major GRDC-funded project to test indirect yield selection criteria coming out of the CIMMYT work. We used random progeny of a 16-parent composite cross of largely elite CIMMYT parents and grew the F7 and F8 yield trials under irrigation in the MIA of southern New South Wales. This environment is an especially favorable version of ME1, but the results we obtained were disappointing in that none of the host of selection criteria tried in F3 spaced plants (leaf photosynthesis, leaf permeability, harvest index, etc.) were very strong predictors of plot yield (Quail et al. 1989). Useful information further debunking, at least in spring wheats, the ‘tall-dwarf’ hypothesis of PBI Cambridge was obtained (Fischer and Quail 1990). In parallel experiments in the MIA on N management, the importance of the spike phase for KNO determination received further confirmation and the influence of N nutrition on radiation use efficiency in wheat was shown, something which had already been reported for other crops.

The Period 1988-1995

Wheat physiology at CIMMYT recommenced when in the late 1980s Ken Sayre began comparing at CIANO under very optimal agronomy a more recent set of historic bread and durum wheat cultivars. He commenced some canopy temperature measurements using the infra-red thermometer. Wheat physiology at CIMMYT got a large boost with the arrival of Matthew Reynolds and Edmundo Acevedo in the early 1990s, followed soon by Debbie Rees. Edmundo commenced a selection study based on two F2 populations identified by S. Rajaram, and Matthew began looking at communalism and, from 1992 onwards, heat tolerance under hot, irrigated conditions, taking advantage of the Tlaltizapan station.

Nothing has yet been concluded from Edmundo’s selection study although critical later-generation yield trials were carried out in 1994-95. However, Matthew’s work with cultivars has been largely analyzed and presented in various fora. The communalism work has given clear-cut results regarding

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3 The genesis of the idea to use the IRT gun on fully irrigated crops deserves some investigation. Scientists at Arizona had been testing the gun for scheduling irrigation in wheat since the late 1970s and its value as a predictor of leaf conductance in wheat under a range of water stress levels had been well established, but the relationship of canopy temperature to yield potential was first revealed, I believe, by Ken in the late 1980s.
ME1 progress; these results, however, have yet to be fully understood (Reynolds et al. 1994a). His work under hot conditions has shown remarkable correlations between yield potential and canopy temperature depression, leaf conductance and photosynthetic activity (Reynolds et al. 1994b; Amani et al. 1996). The most important advance in understanding ME1 yield potential, however, has come from the work started by Debbie Rees and colleagues in 1992-93 at CIANO using Ken's historic trial as a foundation.

The recent work on the nature of yield progress at CIANO is described in Sayre et al. (1996) and Fischer et al. (in preparation), key parts of which are presented elsewhere in this volume by Sayre (see Sayre, these proceedings). Briefly the results, obtained with eight key semidwarf bread wheat cultivars grown over six seasons, showed that yield progress of 0.9% per year has been achieved, amounting to an overall yield increase of 27% between 1962 and 1988. Progress was associated with an increase in KNO and harvest index, but no change in days to anthesis or biomass, and little change in height. From the work Debbie started, it was shown over three years that yield progress was correlated with leaf conductance, leaf photosynthetic rate, canopy temperature depression, and carbon isotope discrimination. Between Pitic 62 and Bacanora 1988, leaf conductance increased 63%, photosynthesis 23%, and canopies became 0.6 degrees cooler. Unfortunately stay-green was not measured in this experiment, but anecdotal evidence suggests it too may have increased across the interval. There was also a tendency for flag leaf greenness (SPAD) at anthesis to increase.

The causal basis of all these changes is not fully understood, but it is worth noting that the results in many ways confirm those from physiological studies conducted at CIANO in the 1970-1978 period. The recent results, however, add valuable new elements. Thus progress was revealed in materials which all had major Rht dwarfing genes, so that variation in plant height was not a major explanatory variable for yield, harvest index or KNO progress. Not only did the data confirm the yield associations with leaf permeability of the 1975-78 studies, but they showed that, as expected, these were associated with greater leaf conductance and cooler canopies. Although the conclusions with respect to an increase in photosynthetic activity are less clear-cut, they are supported by a number of recent studies with wheat elsewhere. Finally, the success of this recent research on leaf traits owes much to the advances in rapid and robust field instrumentation, something which also makes the results more relevant to the ultimate objective of all this, which is to devise more efficient selection criteria. Thus Ken and Matthew have already begun some trials with the breeders to validate leaf conductance and canopy temperature as indirect selection criteria for yield. Infra-red imagery, as an even more efficient way of simultaneously recording canopy temperature across large numbers of plots, also got underway at CIANO in 1995-96.

These promising results on leaf activity traits, derived from what I have called the empirical approach, should not be allowed to obscure the fact that there are other possible avenues of yield increase arising from analytical thinking and deserving of attention. Some derive from the earlier
model of yield determination that I enunciated, although this model has not been fully validated with cultivars released beyond 1975.

This notwithstanding, it seems possible that the investment in spike dry weight at anthesis could be further increased by either lengthening the duration of the spike growth period (Ds) or further increases in partitioning to the spike (Fs), for example at the expense of the growing stem or flag leaf. Nothing much is known about the number of kernels formed per unit of spike weight (KNO/SOWa): it may be amenable to favorable change but has rarely been studied explicitly (casual observation of the latest durum cultivars suggests it is a major weakness in their yield formation...in other words at CIANO they often show significant levels of basal floret sterility). Little progress has been made on understanding why kernel weight has not increased when there still seems to be excess photosynthetic capacity during grain filling. Finally, it is to be hoped that the modeling efforts of Prem Bindraban in his thesis research will add to these earlier predictions.

Ideas from Elsewhere

Obviously not all wheat yield physiology in the period 1970-95 has been done by the largely CIMMYT sources mentioned above. However, if one sticks strictly to those publications which are relevant to MEI yield potential, there are few seemingly new or contrasting notions. Those of Youssefian et al. (1992) and of Abbate et al. (1995) have already been mentioned. The work of Colin Jenner and colleagues has added considerably to our knowledge of wheat grain growth and starch deposition, without yet showing us how to breed for greater grain filling and, hence, yield. Broadening the net to include work on other cereals under potential conditions, there are some ideas which could be relevant. I do not propose to review all of this literature but direct the reader to the books by Evans (1993), Slafer (1993) and Boote et al. (1994).

Much work has been done on carbon isotope discrimination, but the technique remains very expensive. Mobilization of stored pre-anthesis carbohydrates for grain filling has also been a popular area, but no one appears to count the opportunity cost of these reserves in terms of less spike growth and, hence, fewer kernels. There has been a couple of interesting studies on genetic variation in respiration efficiency (Briedenbach, pers.comm.) and I think these deserve follow up. There have also been two reports of exceptionally high crop RUE's in hydroponics in the field. This may have to do with root messages, a field which has received a lot of recent attention from growth physiologists in the context of plant responses to soil stress. And I continue to think valuable the notions of Don Duvick and of Thys Tollenaar (regarding the association of yield progress in maize through multilocational yield testing with a type of multiple stress resistance in leaves, something which makes them more efficient even under potential conditions, because subtle stress also operates under such conditions...see Tollenaar’s paper in Slafer 1993 and associated references). I am unaware of any significant publications in the important area of genetic resistance to lodging, except again the work on maize (and sorghum) relating resistance to
maintenance of high stem sugars during grain filling. Taken overall, our understanding of yield mechanisms remains weak in many areas, just at a time when molecular biology begins to challenge the physiologist to identify key processes at the plant physiological and biochemical level.

**Comments after the Workshop**

Did the three-day workshop at CIANO add to the above understanding of yield potential determination and of how to apply physiological knowledge to the selection process? There were lots of good ideas, but often they were not very relevant to the issue at hand, namely MEI yield potential. Thus the present level of understanding as enunciated above was not challenged.

Indeed few speakers (Richards, Slafer, Araus) were very aware beforehand of the physiology results from Mexico. It was clear that breeders do not understand them well either. And I think the breeders missed a good opportunity to focus the attention of the visitors at the outset by more fully describing their yield selection procedures, and even walking them past a few million F2 plants, a few thousand F3's, and a couple of score of yield trials. But this is a common problem for CIMMYT...it takes any new reviewer or visiting expert weeks to simply grasp the scale of things at CIMMYT and the nature of the issues.

Speakers supported the need for new techniques and approaches if yield progress is to continue (e.g., Kronstad) and supported CIMMYT’s very important global role and comparative advantage in this (several speakers). That further pursuit of yield potential might carry a penalty under severe stress levels was suggested by Blum, but even if correct, it was not suggested CIMMYT should desist in striving for higher yield potentials. Just as the recent studies by CIMMYT physiologists have revealed the power of new field measurements techniques, even more powerful ones were foreshadowed by Araus. And new breeding techniques need to be considered, with or without new physiological input (e.g., dihaploidy, heterosis). The molecular papers indicated a recent acceleration in progress in the power of markers associated with the demonstration of considerable homology between all cereals: as stated earlier, this will demand more knowledge at the physiological and biochemical level. But at the end of the day, it was really only Richards and Slafer (and Peng for rice) who got into some detail in their analyses of yield and avenues for progress. They did not contradict any earlier understanding; indeed, they reinforced it. I suspect that the discussions in the last half day were quite effective even if some found the going difficult. I do not think any significant ideas were not canvassed. Given more time and remixing of the groups we would have got down to grappling with the real issues:

- What are the priority traits for validation?
- What are the priority processes for further exploration at the physiological level?
- How should 1 and 2 be tackled, and by whom?
- Are there smart ways of getting quick answers?
- What resources are needed?

---

4 I am not implying that physiologists understand breeding and genetics any better; that's why the two groups need to communicate and, better still, collaborate.
• How can NARS and advanced institutions be most usefully involved?

And at the end of it all, how does one respond to Blum’s aphorism that consensus is a poor way to proceed? IRRI seems to be currently proceeding towards a consensus plant type for higher yield but, apart from agreement on the overall objectives, consensus has never been a strong feature of CIMMYT’s culture!

References


The Role of Crop Management Research at CIMMYT in Addressing Bread Wheat Yield Potential Issues

K.D. Sayre

In the past 45 years, remarkable progress (over 3% annual yield increase) has been achieved in increasing irrigated wheat productivity at the farmer level (Figure 1). This increase is associated with the use of succeeding generations of wheat varieties developed to a large extent from CIMMYT germplasm. Similar trends can be developed for many other developing countries such as India, Pakistan, and Egypt. However, if we study this trend curve closely we see something a bit troubling. It appears to be reaching a plateau for the latter 10 years. Table 1 breaks down the annual rate of yield increase into 10-year increments and demonstrates that this rate has decreased from 5% per year in the first 10-year period to only 0.7% in the last full 10-year period. This same pattern is also occurring for wheat yields in several other countries and poses the following question. How important is maintaining continued increases in genetic yield potential in order to provide the 'locomotive' to ensure a steady increase in productivity at the farmer level? And if the answer is, as I believe, very important, then how do we go about maintaining the momentum?

The current wheat crop management research subunit within the CIMMYT Mexico program works closely with the breeders to: 1) characterize the performance of newly developed genotypes, and 2) determine how these genotypes interact with

Table 1. Annual rate of increase in average farmer wheat yield in the Yaqui Valley for defined time periods from 1950-1991.

<table>
<thead>
<tr>
<th>Time period</th>
<th>% yield increase/year</th>
</tr>
</thead>
<tbody>
<tr>
<td>1950-1960</td>
<td>5.0</td>
</tr>
<tr>
<td>1960-1970</td>
<td>4.0</td>
</tr>
<tr>
<td>1970-1980</td>
<td>2.0</td>
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<tr>
<td>1980-1990</td>
<td>1.3</td>
</tr>
<tr>
<td>1980-1991</td>
<td>0.7</td>
</tr>
</tbody>
</table>

Figure 1. Wheat yield trends in the Yaqui Valley, 1950-96.
management factors that farmers can conceivably control and variable weather conditions that are largely beyond their control. The major emphasis is to characterize germplasm directed toward CIMMYT's mega-environment 1 (ME1, temperate, irrigated wheat production systems with high yield potential) which accounts for over 40% of wheat production in the developing world.

Whenever possible, these newly developed materials are compared with landmark varieties that have been developed over the past 40 years from CIMMYT (and its predecessors') germplasm to provide an immediate, retrospective view of how certain traits have changed over time in relation to the most recently selected high-yielding materials. Insights, therefore, may be gained to identify traits that are apparently associated with enhancing yield potential and may merit consideration as selection traits for breeders to use, provided their application results in a marked improvement in selection efficiency as compared to the use of yield per se as the selection criterion.

Figure 2 illustrates results from a trial including 16 semidwarf bread wheat cultivars derived from CIMMYT germplasm over a 25-year period that had been selected mainly for their yield potential under ME1 conditions. They were grown under a series of variable conditions at CIANO/Obregon in the 1988/89 cycle.

First, let us compare the trend lines for NOR YLD and MAX YLD. The former was produced under the trial management conditions used by the breeding programs at that time, whereas the latter involved a proposed new trial management involving use of sub-soiling and enhanced nutrient management. Two facts are of interest. First, MAX YLD management dramatically raised yields for all 16 cultivars (actually more so than achieved by 25 years of breeding at least when the cultivars are grown under the prevailing NOR YLD management practices). Second, the MAX YLD management reduced variation (see the R2 values) and obviously provided a sharper estimate of cultivar yield differences (so important to breeders). Furthermore, the

Figure 2. Bread wheat yield trends under varying conditions.
estimated annual rate of genetic gain in yield potential (the G values) was higher for the MAX YLD conditions, again, apparently providing a cleaner estimate of differences in maximum yield potential between cultivars.

The other trend lines in Figure 2 present the performance of these same sixteen cultivars under pre-anthesis drought stress (PRE-ANT DRT YLD), late heat stress by delayed planting (HEAT YLD) and post-anthesis drought stress (POST-ANT DRT YLD). It should be noted that the rate of genetic gain for this set of cultivars, which had been selected largely for high yield potential conditions, is quite high for both pre-anthesis stress and late heat conditions (the yield potential locomotive affect in action?), whereas essentially no progress was observed over the time period for these cultivars for post-anthesis stress conditions (subsequent studies with other cultivars derived from CIMMYT germplasm have, however, shown positive and significant yield potential progress under post-anthesis drought stress conditions).

Figure 3 presents a similar set of data for another historical set of bread wheat varieties, again, developed for high yield potential under high nitrogen conditions. It shows their performance when tested under varying levels of N. Again, marked genetic progress is apparent in yield expression under the high N rate, but similar progress has been made at both moderate and low N levels. These results appear clearly to refute such commonly heard statements that the new, high-yielding cultivars ‘need’ high N levels to be successful. The correct statement should be that these modern varieties are able to ‘utilize more efficiently’ higher N rates to the best advantage.

Figure 4 presents the graph of grain yields for eight bread wheat varieties (all semidwarf) that have been released in

![Graph](image)

**Figure 4. Trend in grain yield (average for five years) for bread wheat semi-dwarf varieties developed from CIMMYT germplasm over the past 30 years.**
Mexico over the past 26 years plotted against year of variety release. These yields are five-year averages for the varieties where each year the same, most optimal growth conditions possible were provided to minimize adverse biotic and abiotic stresses (including lodging by use of support nets) in order to maximize the expression of yield potential. The trend demonstrates a clear, continued increase in genetic yield potential over the period of varietal release under consideration. The same type of results is observed for total above-ground dry biomass.

Similar time trends exist for several physiological traits, including canopy temperature depression, flag leaf stomatal conductivity (Figure 5), flag leaf photosynthesis and grain C13 discrimination for the eight varieties, again plotted against year of variety release. All show significant trends towards positive improvement over the successive released varieties. Does such data enlighten us as to clarifying possible avenues to follow towards further enhancing yield potential?

When these physiological traits are compared with grain yield itself for the same eight varieties, all show interesting and significant relationships with yield (see, for example, Figure 6). Does such retrospective analysis aid our cause? Hopefully your discussions will enlighten our efforts.

What about year-to-year variation in weather conditions and its interaction with expression of yield potential? Figure 7 shows how Yaqui Valley farmer average yields, the mean yield of our on-farm trials, and the same lines planted in trials of the CIANO station have varied over the past 10 years. This includes both the record yield-setting year 1987, as well as 1992 when the lowest yields in the last 20 years were recorded. In terms of weather conditions, 1987 was a nearly perfect year, whereas it rained nearly 470 mm during the crop season in 1992. How do such dramatic year effects interact with the

Figure 5. Trend in flag leaf stomatal conductivity (average for three years) for semidwarf bread wheat varieties developed from CIMMYT germplasm over the past 30 years.

Figure 6. Relationship between canopy temperature depression and grain yield for eight semidwarf bread wheat varieties developed from CIMMYT germplasm over the past 30 years.
breeder’s steady march to develop ever higher yielding materials?

Table 2 presents the yearly mean yields for the eight bread wheat varieties that are presented in Figure 4 along with yields of sets of both durum wheat and triticale varieties that were grown each year under the same high-yield management conditions. Large, significant year-to-year effects occurred for each crop even though diseases, weeds, and pests were controlled; high, non-limiting levels of nutrients and water were provided and lodging was prevented. Weather conditions varied dramatically over the five years even in this corner of the ME1 high yield potential situation. There were varying levels of year x variety interactions (usually small but significant), but there were large year x crop interactions that are certainly intriguing and need further study. An understanding of these interactions might lead to the identification of traits that function in one crop to condition good yield performance under a certain weather situation and that could be selected for in another crop with comparatively inferior performance.

Table 2. Effect of year on grain yield (kg/ha at 12% \(H_2O\)) for several bread wheat, durum wheat and triticale cultivars produced under the same maximum yield conditions each year at CIANO/Obregon.

<table>
<thead>
<tr>
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<th>Durum wheat</th>
<th>Triticale</th>
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<tr>
<td>1990</td>
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<td>8534</td>
<td>7730</td>
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Enhancing Genetic Grain Yield Potential in Durum Wheat and Triticale

W.H. Pfeiffer, K.D. Sayre, and M. Mergoum

Introduction

Future crop improvement has to emphasize grain yield potential, yield stability, and dependability in concerted, interdisciplinary approaches, and issues of environmental sustainability must be an integral part of the research agenda. This demands a breeding strategy to enhance grain yield per se, the critical prerequisite of adaptation at the genotype level in durum wheat (*Triticum turgidum* L. var. *durum*), and triticale (*X Triticosecale* Wittmack), which capitalizes on newer empirical methods, advances in information technology, physiological marker oriented selection, and emerging biotechnology procedures. Strategies at CIMMYT to enhance the genetic yield potential of durum and triticale also involve karyotype modifications via O(A) and O(B) chromosome substitution and/or translocations, exploring heterosis, and buffering effects of mixtures. These themes are developed from recent research data in the context of linking to and building upon ‘state of the art’ breeding.

Hypothesis

Yield per se is relevant for all agroecological target zones, and hence is a priority trait. Crop improvement efforts aim to protect high genetic yield potential (GYP) as a prerequisite for adaptation through incorporating resistance to abiotic and biotic stresses. Incorporation of buffering mechanisms will simultaneously increase environmental yield potentials, yield stability (spatial, temporal, and system-dependent), and range of adaptation. Combination of yield per se associated input-responsiveness with input-efficiency at low production levels allows shifting cross-over points between low input and high GYP genotypes towards more marginal production levels. Circumstantial evidence indicates a residual effect of high GYP when environmental stress increases (Figure 1).

State of the Art

Improvements in GYP in durums (DW) resulted from higher biomass, grains per spike and grain biomass production rate per day. The increased biomass was largely partitioned into straw since the harvest index decreased significantly in the 1980s. This suggests there is scope for future gains in durum’s GYP by increasing harvest index.

Figure 1.
Comparing the performance of triticales (Tel) in the 1980s and 1990s reveals significant progress for all agronomic components except biomass, days to maturity, and grainfill duration. Existing genetic variation for relevant traits in durums and triticale suggests that rates of progress in GYP can be maintained in the future (Figure 2a, b).

Identifying Avenues-Crop Comparisons

Comparing the top three yielding DW’s and Tel’s with bread wheats (BW) reflects agronomic components with potential pay-off in raising GYP. Data suggest that the lower number of spikes/m² and associated number of grains/m² in DW compared with BW should receive special attention in future crop improvement. Past experience indicates superior BW grain yields in years favorable for number of spikes/m². In those years,

Figure 2a. Comparison of agronomic components of the highest yielding 70s and 80s durum wheat varieties evaluated in maximum yield trials at Cd. Obregon 1991-1995.

Figure 2b. Comparison of agronomic components of the highest yielding 80s and 90s triticales evaluated in maximum yield trials at Cd. Obregon 1991-1995.
there is no compensation for higher number of grains/spike in Tel or 1000-grain weight in both DW and Tel for lack of tillering capacity (Figure 3a, b).

**Empirical Approach**

The empirical approach has contributed substantially to GYP and driven improvements in computerization, experimental designs, analytical procedures, data processing, machinery, and higher breeding efficiency. This is manifested by larger total numbers of field plots, reduction in plot size and number of replications and in extended multilocalational testing. Testing efficiency at CIMMYT has doubled over the last decade due to improved crop management techniques and the adoption of more precise spatial/augmented designs. High payoff of future improvements in this areas can be expected.

**Figure 3a.** Comparison of agronomic components of modern bread and durum wheats evaluated in maximum yield trials at Cd. Obregon 1991-1995.

**Figure 3b.** Comparison of agronomic components of modern bread wheats and triticales evaluated in maximum yield trials at Cd. Obregon 1991-1995.
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 high potential in early generation screening for GYP (Figure 4).

Expansion of the Genetic Base: Probing Gene Pools

Progress in GYP and associated traits depends on existing genetic variation. Interspecific and/or intergeneric introgression is employed. Genetic base expansion 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.

Stabilizing Grain Yield Potential

Achievements in GYP can be traced to raising yield per se and stabilizing GYP. Current GYP stabilization efforts emphasize individual buffering of homozygous genotypes and population buffering effects in heterozygous populations and different population structures (Figure 5).

Karyotype Variation

Variety release and international yield nursery data indicate adaptive advantages of complete Tcls carrying a 6D(6A) chromosome substitution. In DW,
preliminary data revealed significant yield gains in Altar 84 carrying 1RS.1Bl over Altar 84 under moisture stress (R. Villareal, pers. comm.). These observations suggest the exploitation of karyotypic variability as a promising strategy to increase GYP and GYP stability in both DW and Tcl. Similar effects can be expected from other substitutions and/or translocations that are currently under study. Optimal karyotypes for enhanced GYP may emerge (Figure 6).

Dihaploid Production

Dihaploid production via the maize method and/or anther culture can substantially enhance the rhythm of breeding operations. Anther culture has been used to produce Tcl dihaploids from winter x winter crosses. Current efforts in this area emphasize the evaluation/development of methodologies to produce DW and Tcl dihaploids using the maize method.

Hybrids

Heterosis in Tcl justifies exploiting hybrids. Different pollination control mechanisms are suitable, and crop features for hybrid seed production are favorable. For DW, important floral characteristics (e.g., anther extrusion) for hybrid seed production are under study (Figure 7).

International Wheat Information System (IWIS)

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

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.
Cook and Veseth (1991) define four levels of yield: actual, affordable, attainable, and absolute yield. The first three are constrained by pests, diseases, economics and/or the environment. The last is limited by genetic potential, and that is the yield barrier this note focuses on.

Breaking the yield potential barrier will be attempted using such diverse strategies as modified ideotypes, changes in phenology and physiology, molecular biology, wide crosses, and hybrids, to name just a few. Whatever the route, our friends—the stand reducers, senescence accelerators, photosynthetic rate reducers, light stealers, assimilate sappers, tissue consumers, and turgor reducers—will be waiting to take advantage of the situation (Gaunt 1995).

Here are some points to ponder in relation to the above.

"As potential yields will increase it is tempting to conclude that crop sensitivity to disease will increase concomitantly. However, this statement is based on what we know at present. What may be discovered in the future is: Plants may be developed with greater flexibility as we learn more about the genetic, biochemical, and physiological processes of both plant growth and the effect of pathogens on these processes" (Gaunt 1995). It is not inconceivable that plants could support not only more yield but more yield in the presence of disease. The task is to understand these processes better and gain a more solid basis for disease management and the maintenance of yield. Disease is logically related to yield via radiation interception and radiation use efficiency, so reducing this effect in any way should increase yield (Gaunt 1995).

Breaking the yield potential barrier will not occur in a vacuum. A team effort will be essential and new information on disease management and the underlying genetics (including molecular) and biochemistry of resistance will need to be incorporated into the process.

References


Wheat, chiefly as bread, is the main food item in most of the developing world. It supplies the population with more energy and nutrients than any other single food source. Increasing wheat production to levels that would satisfy the food demands of the rapidly growing global population can no longer rely on expanding the wheat production area. Breaking the yield barriers in wheat must, therefore, be the main goal of breeding research associated with wheat production.

Most of the wheat produced globally (in some cases even wheat produced by subsistence farmers) is channeled toward the wheat processing industry. Therefore, developing wheat varieties with acceptable processing qualities is highly desirable and, in many cases, indispensable. Increasing yield potential while maintaining desirable industrial quality (IQ) is not an easy task because increases in grain yield usually result in decreases in grain protein, one of two major factors (the other is protein quality) defining the IQ of wheat. This constraint poses a big challenge for wheat breeders, particularly when dealing with wheat production areas in mega-environment 1 (ME1; irrigated, high yielding environment, comprising roughly 43% of the total area in CIMMYT’s ME classification). In ME1, high yielding wheat varieties generally have low to intermediate (9-12%) grain protein content. These grain protein levels may, in many cases, cause the processing industry to apply pricing penalties.

Approaches used to overcome (sometimes only partially) the impact of the negative grain yield/grain protein relationship include:

**Protein quality improvement.** This means bettering the quality of gluten protein, which in turn involves combining glutenins and gliadins that contribute to the formation of large polymeric protein aggregates; as a result, bread making quality is improved. Wheat varieties with improved gluten have better bread making quality per unit of grain (flour) protein than varieties with poor gluten quality. Improved gluten quality therefore effectively decreases the grain protein level considered by the industry as acceptable for bread making. National agricultural research systems that can afford it use this protein quality improvement approach. CIMMYT successfully breeds for improved gluten quality by using ‘good quality’ gluten proteins present in bread wheat and other novel glutenins present in wheat wild relatives (*Triticum tauschii*, for example). The introgression of novel glutenins into bread wheat also expands wheat’s genetic diversity.
Crop management. The expression of gluten quality decreases as grain protein decreases. Furthermore, differences in gluten quality among varieties tend to disappear when grain protein drops beyond the 9.0-10.0% level. This may occur when cultural practices (sowing date, sowing rate, plant spacing, irrigation regimes, crop rotations, etc.) and fertilizer management (correcting macro-and micronutrient deficiencies, N-fertilizer rates and application regimes, source of N-fertilizer, etc.) aim at increasing grain yield only. For protein quality to express in high yielding situations, it is necessary to: 1) use cultural practices that tend to improve N-use efficiency (planting in beds vs. rows, for example); 2) apply N-fertilizer in order to increase not only the grain yield, but also the amount of N translocated to the grain (rates, split applications, etc.), and 3) apply, when needed, sulfur fertilizer in amounts that ensure adequate synthesis of S-rich proteins (S-containing amino acids and S-rich glutenins play important roles in wheat's nutritional and processing qualities, respectively).

A combination of the above approaches may allow farmers to produce wheat yields as high as 9-10 t/ha while maintaining acceptable grain IQ.

Further increases in wheat's yield potential may limit the expression of IQ. Maintaining acceptable IQ in wheat while increasing yield levels above 9-10 t/ha should not rely on the use of higher fertilizer doses. Furthermore, additional increases in the already high levels of N-fertilizer used may be neither feasible nor desirable due to fertilizer costs/availability and negative environmental effects. Environmental pollution occurs because 10-40% of applied N is lost, partly into the air as nitrous oxide (N2O, which contributes to ozone breakdown and global warming) and partly into the ground as nitrate (NO3, which contaminates ground water). Breaking the yield barrier while maintaining acceptable grain protein (and quality) should come, therefore, from developing wheats with improved efficiency in translocating available nitrogen to the grain.

In order to improve N-translocation efficiency in wheat, traits associated with genotypic variations in grain protein content should first be identified and then those which can be manipulated through breeding should be targeted. Traits that may be relevant to the above include:

- Reduced late tillering: Late tillers may compete with the grain for available N.
- Glume photosynthetic capacity: There may be genotypic differences in the glumes' capacity to accumulate N and/or differences in their capacity to translocate N to the developing grain.
- Head size and grain size: Head size and grain size may be associated with the capacity of the grain sink (size) to assimilate differential amounts of translocated N.
- High protein genes: Enhance the grain's protein synthesizing ability.
At CIMMYT, efforts to manipulate the latter traits are already underway. For this, we use wheat lines derived from crosses involving a semidwarf hexaploid wheat (ND643) that possesses a major gene (located on chromosome 6B) for high protein from *T. dicoccoides*. This gene’s role in increasing grain protein is not yet known. It may either favor N-translocation to the grain or, at the grain sink level, act on the metabolic pathway of protein synthesis.

This workshop should give us the opportunity to generate workable ideas on how to tackle problems associated with the negative grain yield/industrial quality relationship in wheat.
Information Systems as Tools to Integrate Research on Yield Potential

P.N. Fox, B. Skovmand, and J. White

Discussions of strategies for increasing yield potential frequently emphasize the need for an interdisciplinary approach with full participation of breeders, agronomists, geneticists, and physiologists. CIMMYT strives to maintain interdisciplinary teams, but further integration of research on yield potential of wheat is needed.

An efficient flow of information is the heart of interdisciplinary research. Collaboration is greatly facilitated by timely exchange of data that are well documented and can be searched and retrieved in diverse user-designed formats. Recognizing this, the Wheat Program developed the International Wheat Information System (IWIS) as a database on wheat breeding.

Through the unambiguous identification of wheat germplasm, IWIS removes barriers to the association of information. The linking of a family tree to an identifier distinguishes CIMMYT identifiers from accession numbers, which may be unique but are generally ‘non-intelligent’ sequential numbers and may obscure relationships among genealogy. All information from a given source can be linked to the correct germplasm, without the problems in data sharing traditionally caused by synonyms and homonyms. In addition, field-measured data are geo-referenced.

More recently, work has started on expanding IWIS. The foremost goal is to permit managing data from other crops, which has lead to IWIS being rebaptized as ICIS, the International Crop Information System. Besides handling pedigree systems for non-self pollinating crops, ICIS will have several features that will increase its utility for yield potential research:

- Manage complex experimental designs, including generation of field books and storage of data at the replicate level.
- Store more complete environmental characterizations of trials (e.g., soil profile characteristics, details of tillage or irrigation practices, and daily weather data).
- Extract data in formats for crop simulation models.
- Manage genetic data for lines and cultivars.
- Analyze data through GIS.

Examples of uses of ICIS for yield potential research might include:

- Examining yield trends for trials from high yield potential environments.
- Identifying land races with unusual phenotypes for traits that might affect yield potential.
• Identifying which alleles of genes for physiological traits are carried by breeding lines used in physiological studies.
• Assuring that data from physiological studies are readily available to breeders and that the studies use germplasm of interest to the breeders.
• Providing data for evaluation of crop simulation models used in yield potential studies.

To ensure the success of ICIS, wheat researchers at CIMMYT and elsewhere are invited to participate in ongoing discussions on the redesign of the IWIS database schema (basic structure). They are also invited to work with the existing IWIS since it represents a valuable step in the evolution of wheat data management. Data entered in IWIS will be fully transferred to ICIS.

The capabilities of ICIS will complement other efforts within CIMMYT and across international centers to develop databases for cropping systems, biophysical and socio-economic data. Thus, use of ICIS should lead to ‘added values’ both for other aspects of wheat improvement and for wheat agronomy. Figure 1 illustrates how the various agricultural information systems might interact and influence the decision making of a range of stakeholders in CIMMYT’s activities.

![Diagram](image-url)

**Crop Information Systems**

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**Decision support tools**

- Simulation models
- Expert systems
- GIS
- COP

**Improved research decisions by CIMMYT, NARs, farmers and other stakeholders**

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ICIS = International Crop Information System  
GIS = Geographic Information Systems  
CSD = Cropping Systems Database  
COP = Coef. of Parentage (routines in ICIS)

Figure 1. How different information systems within CIMMYT interact and can lead to more efficient decision making by wheat researchers concerned with yield potential.
Introduction

Multilocation trials are important in plant breeding and agronomic research because data from such trials can be used 1) to estimate and predict grain yield of genotypes and 2) to study genotype x environment interaction and stability. Many statistical models have been developed and used to examine genotypic pattern of response across environments. Multivariate parametric methods, such as multiplicative models, are useful for assessing genotype x environment interaction.

In this study three multiplicative models were applied to the first Semi-Arid Wheat Yield Trial (SAWYT) data (29 genotypes tested in 21 sites) with the objective of studying genotype x environment interaction and genotypic adaptation. The models used are the Additive Main Effect and Multiplicative Interaction (AMMI), the Shifted Multiplicative Model (SHMM) for grouping genotypes with negligible crossover interaction, and the Site Regression Model (SREG) for clustering sites without crossover interaction.

Results

AMMI analysis

Results of AMMI analysis can be displayed in a diagram showing main effects of genotypes and environments on the abscissa and the interaction (first principal component scores, or PCA1) as the ordinates. Genotypes (or sites) that appear on a perpendicular line have similar means (horizontal axis) and those that fall on a horizontal line have similar interaction (vertical axis). Genotypes and sites with high (positive or negative) PCA1 scores have large interaction and those near zero have small interaction. Genotypes and sites with PCA1 scores of the same sign (either positive or negative) have a positive interaction. Genotypes with positive PCA1 scores and sites with negative PCA1 scores have negative interaction, as do genotypes with negative scores and sites with positive scores.

Results of AMMI analysis on the first SAWYT trial indicate that genotypes show much more variability in interaction (vertical axis) than in main effects (horizontal axis) (Figure 1), whereas sites show much variability in main effects but not much in interaction. According to the interaction (PCA1; ordinate) we can place the genotypes in three sets. Genotypes with large, positive first components (PCA1s). Set 1 had G1, G11, G13, G18, G20, G22, G23, G24, G25, G28, and G30 (mean yield=3.95 t/ha).

Sites S12 and S18 are the only ones where a 'severe' incidence of foliar diseases was reported. In site S18, average infection of stripe rust on leaf was 39%, ranging from 0%
to 80%. Stripe rust on spike was also severe in S18 with an average infection of 49%, ranging from 0% to 90%. Leaf rust infection was important in site S12 (Mexico) with an average infection of 43%, ranging from 1% to 80%.

All the genotypes in set 3 had a positive interaction with S18, that is, we expect that the yield performance of set 3 genotypes will be favored in S18. Since one of the main factors that distinguished site S18 from the others was severe infection of stripe rust on leaf and stripe rust on spike, these results suggest that set 3 genotypes should have, on average, better resistance to these diseases than the others. Indeed, the mean severity for stripe rust on leaf for genotypes in set 3 in site S18 was 22%, and the mean severity for stripe rust on spike for genotypes in set 3 in site S18 was 28%, ranging from 0% to 60%.

On the other hand, all the genotypes in set 1 had a negative yield interaction with S18 (the environment in S18 does not favor yield of genotypes in set 1). These results suggest that genotypes of set 1 would have, on average, less resistance to stripe rust on leaf and stripe rust in spike than those from set 3. In fact, the mean severity for stripe rust on leaf for genotypes in set 1 in site S18 was 79%. Similarly, genotypes of set 3 had a positive yield interaction with site S12 (although small because PCA1 of S12 is -0.05) and they showed a mean severity for leaf rust in S12 of 41% as compared with the mean severity of 50% for leaf rust showed by genotypes of set 1 in site S12.

Concerning the severity of the diseases considered in sites S18 and S12, it is expected that, on average, set 2 genotypes will show intermediate resistance as compared to

Figure 1. AMMI, diagram.
genotypes in sets 1 and 3. Indeed, for stripe rust on leaf and stripe rust in spike in S18, the mean severity of set 2 genotypes was 38% and 47%, respectively, whereas the mean severity for leaf rust in S12 was 37%.

**SHMM and SREG analyses**

The SREG clustering methods for grouping sites without crossover interaction produced the dendrogram depicted in Figure 2. A reasonable cutting off point in the dendrogram could be at the four groups level. The groups formed are: 1) Group 1 with sites S1, S8, and S15, 2) Group 2 with sites S5, S7, S9, S10, S11, S13, S14 and S17, 3) Group 3 with sites S2, S3, S4, and S6, and 4) Group 4 with sites S16, S19, and S20. Note that two sites, S12 and S18, had severe foliar diseases and negative PCA Is scores on the AMMI analysis (see Figure 1) and were left unclustered by the SREG clustering method (Figure 2).

The four groups of sites showed some degree of association with the number of days to heading (Figure 2). For example, sites of group 1 had a relatively low number of days to heading (S1=63, S8=72, and S15=87); sites in group 2 showed low to intermediate number of days to heading, S5=129, S9=118, S10=117, S11=64, S13=87, S14=94, and S17=47 (days to heading in S7 was not reported); sites in group 3 had intermediate to high number of days to heading, S2=152, S3=142, S4=115, and S6=127; in group 4, S19 had the highest number of days to heading, 154, but S16 showed 80 days to heading (in S20 days to heading was not reported).

<table>
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<tr>
<th>Code</th>
<th>Days to heading</th>
<th>Country</th>
</tr>
</thead>
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<tr>
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<td>63</td>
<td>SUDAN</td>
</tr>
<tr>
<td>S8</td>
<td>72</td>
<td>QATAR</td>
</tr>
<tr>
<td>S15</td>
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<td>S5</td>
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<td>CYPRUS</td>
</tr>
<tr>
<td>S7</td>
<td>118</td>
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<td>SYRIA</td>
</tr>
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<td>S10</td>
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<tr>
<td>S11</td>
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<td>CHINA</td>
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<td>S13</td>
<td>87</td>
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<td>S2</td>
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<td>S3</td>
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<td>S4</td>
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<td>TUNISIA</td>
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<td>S6</td>
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<td>IRAN</td>
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<tr>
<td>S16</td>
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<td>ARGENTINA</td>
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<tr>
<td>S19</td>
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<td>SPAIN</td>
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<tr>
<td>S20</td>
<td>154</td>
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<td>S12</td>
<td>154</td>
<td>MEXICO</td>
</tr>
<tr>
<td>S18</td>
<td>154</td>
<td>ECUADOR</td>
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</table>

Figure 2. SREG clustering of sites.
The SHMM group of sites were not associated with site productivity. Low yielding sites are grouped with high yielding sites. This result would indicate that there are genotypes with relatively high yield production in low yielding sites that have the potential to yield well in highly productive sites without changing relative rank.

The SHMM clustering of genotypes initially subdivided the genotypes into two main groups (Figure 3). It should be pointed out that, at the two group level, the top main branch of the dendrogram included all the genotypes of sets 1 and 2 obtained from the AMMI diagram (see Figure 1), whereas the bottom branch contains all the genotypes of set 3. However, while AMMI is unable to further partition these groups into groups with negligible crossover interaction, SHMM clustering continues the searching of those groups. A reasonable cutting off point would form seven final groups of genotypes. Group 1 with G1, G18 and G20; Group 2 with G2, G9, and G10; Group 3 with G11, G23, G13, G28, G24, G30, and G22; Group 4 with G16 and G26; Group 5 with G25 and G29; Group 6 with G3, G15, G8, G12, G6 and G7; and Group 7 with G4, G27, G14, G17, G21, and G19 (sister lines G4 and G27 are in this group).

Figure 3. SHMM clustering of genotypes.
The seven SHMM groups of genotypes showed association with the level of severity for stripe rust on leaf, stripe rust in spike and, to some degree, with leaf rust. SHMM clustering of genotypes further partitioned AMMI$_1$ set 1 in groups 1 and 3. The three genotypes in group 1 had the highest mean severity of infection for stripe rust on leaf, 77% in site S18, 54% in the mean across sites and the highest infection of stripe rust in spike in site S18, 87%. It was followed by genotypes in SHMM group 3 with mean severity for stripe rust on leaf of 60% in site S18, 34% across sites and 79% infection of stripe rust in spike in site S18.

On the other hand, SHMM clustering subdivided genotypes in AMMI$_1$ set 3 into groups 6 and 7. SHMM group 6 had the lowest infection of stripe rust on leaf in site S18 and across sites (20% and 14%, respectively). SHMM group 7 had 23% infection of stripe rust in spike in site S18. SHMM group 7 had the lowest mean percentage infection, 23%, followed by SHMM group 6 with mean infection of 32%.

For leaf rust in site S12 and across sites the trend is not as clear as for the other diseases. However, genotypes in SHMM groups 6 and 7 had lower infection levels than the other SHMM groups of genotypes (except for SHMM group 2).

SHMM clustering partitioned AMMI$_1$ set 2 into two groups, 2 and 4, with intermediate infection levels for stripe rust on leaf and stripe rust in spike. However, SHMM group 2 always showed more infection than genotypes of SHMM group 4 for stripe rust on leaf in site S18, across sites, and for stripe rust in spike in site S18 (43%, 24%, and 53% versus 25%, 13%, and 30%, respectively).

The results of this study showed that biotic stresses that affect grain yield, such as stripe rust on leaf and stripe rust in spike, and the differential level of genetic resistances of the genotypes are the major determinant of the grouping of genotypes.
Creating a Gene-Based Simulation Model to Break Yield Barriers

J. White

The ability of crop simulation models to predict growth and yield as influenced by the environment, agronomic practices and crop traits suggests that such models can identify traits to increase yield potential (e.g., de Wit 1965; Whisler et al. 1986; Boote and Tollenaar 1994). Similarly, models seem ideal for studying variation in cultivar response to environment, the genotype x environment interaction (Shorter et al. 1991; Hunt 1993; Chapman and Barreto 1994). Although models have been applied to crop improvement, use by plant breeders has been limited by several constraints:

• Where our understanding of processes of growth and development is incomplete, models often either resort to simple empirical relations or invoke poorly tested assumptions. These reduce the reliability of the extrapolations necessarily implied in yield potential research.

• Interactions among traits are often omitted or inaccurate. Leaf photosynthetic capacity is seldom coupled to leaf nitrogen content or specific leaf area, and seed composition is usually invariate.

• Cultivar differences are characterized using parameters that are unfamiliar to breeders and that are not directly measurable, having to be determined through a typically difficult and subjective calibration process.

Data on soils, weather and cultivars are not available in ‘model-ready formats,’ notwithstanding efforts to establish standards for minimum data sets (e.g., IBSNAT 1988).

Fortunately, none of these constraints are insurmountable. To increase the utility of models to crop improvement, treatment of cultivar differences is a logical first target. Simulation models can represent five levels of genetic complexity:

1. Non crop-specific.
2. Crop specific, but with no cultivar differences.
3. Cultivar differences represented by cultivar-specific coefficients (‘genetic coefficients’), which are usually traceable to field traits.
4. Actual genotypes of cultivars used to internally estimate coefficients.
5. Cultivar differences simulated directly through gene action for specific processes.

Genetic levels 1 and 2 are fairly discrete, but a single model could encompass features of levels 3 to 5. CERES Wheat (Godwin et al. 1989) corresponds to level 3, using seven coefficients to represent cultivar differences. The only level 4 model appears to be GeneGro (White and Hoogenboom 1996), which was developed for common bean
GeneGro characterizes cultivars using seven genes for growth habit, phenology, photoperiod response and seed size. Gene effects are estimated through linear functions that replace the cultivar-specific coefficients. For example, maximum pod wall growth rate (SHVAR) was estimated from additive effects of three genes for seed size (Ssz1, Ssz2 and Ssz3),

\[
\text{SHVAR} = 40.57 + 3.57 \text{Ssz-1} + 17.17 \text{Ssz-2} + 4.87 \text{Ssz-3} \quad (R^2 = 0.65**).
\]

For the calibration set of 30 cultivars grown in various trials at six locations, simulated days to maturity accounted for 85% of variation in observed data, and simulated seed yield, 31% of observed variation. With data from 14 independent trials representing over 200 treatment combinations, GeneGro explained 75% of variation in days to flower, 68% in days to maturity, and 39% in seed weight, but only 10% of variation in seed yield; however, 56% of variation in yield was accounted for when mean effect of site was removed through regression analysis (Hoogenboom et al., in review).

These results indicate the feasibility of creating a more breeder-friendly wheat model that incorporates genetic effects. Besides clarifying model inputs and outputs for wheat breeders, a gene-based wheat model should bring other benefits. By diminishing uncertainty over cultivar differences, it will help identify weak points in the physiological assumptions. Also, consideration of gene action per se can provide insights into physiological mechanisms being represented.

A logical starting point for such a wheat model is the simulation of phenology. Fairly detailed genetic information is available for photoperiod and vernalization responses (Table 1), and phenology is a basic determinant of partitioning and growth. Based on reviews of wheat phenology by Flood and Halloran (1986) and Slafer and Rawson (1994), the following points should be considered in model development:

- In vernalization, low temperatures seem to reduce activity of a system that inhibits the transition from vegetative to reproductive growth. The Vrn genes reduce the vernalization requirement, so they might increase the destruction rate of an inhibitor or decrease sensitivity to it.

- Certain cultivars posses a short-day response that reduces the vernalization requirement. Genes controlling this response should be identified.

- Once vernalization is completed, the Ppd genes determine the level of sensitivity of further reproductive development to long days.

- Under conditions that result in rapid development, and hence early time to anthesis, cultivar differences are still found. This implies inherent differences in basic developmental rate (also termed 'intrinsic earliness'), so the inheritance of this trait merits study.
• The relative sensitivity of developmental phases to photoperiod varies.

These points are sufficient to lay the foundation of a gene-based wheat phenology model, but further research will be needed. Field comparisons of cultivars of known genotypes (preferably sets of near-isogenic lines) in contrasting environments should be emphasized.

In a second phase of model development, the genes controlling dwarf or normal growth habit (e.g., *Rht1* and *Rht2*) would merit attention. Their effect on yield potential is still controversial (e.g., Araus et al. 1993), and they provide an excellent platform for considering pleiotropic effects since they not only affect plant height but cell size, leaf nitrogen concentration and leaf photosynthesis (Morgan et al. 1990).

Considerable information is available on genotypes of CIMMYT lines (Singh et al. 1989).

Parallel to modeling efforts, a renewed commitment to identifying genes affecting morphological and physiological traits is needed. Physiologists should avoid germplasm that is not fully characterized, preferably using near-isogenic lines or sets of recombinant inbred lines. A particular challenge is to adequately characterize pleiotropic effects.

### Table 1. Genes of physiological traits of hexaploid wheats that might be included in a gene-based simulation model.

<table>
<thead>
<tr>
<th>Gene</th>
<th>Description</th>
<th>Chromosome position</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Fr1</em></td>
<td>Frost resistance</td>
<td>5A</td>
<td>Sutka &amp; Snape 1989</td>
</tr>
<tr>
<td><em>Or</em></td>
<td>Osmoregulation</td>
<td>7A</td>
<td>Morgan 1991</td>
</tr>
<tr>
<td><em>Nra</em></td>
<td>Nitrate reductase</td>
<td>2DL</td>
<td>Gallagher et al. 1980</td>
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<tr>
<td><em>Ppd1</em></td>
<td>Photoperiod response</td>
<td>2BS</td>
<td>Welsh et al. 1973; Scarth &amp; Law 1983</td>
</tr>
<tr>
<td><em>Ppd2</em></td>
<td>Photoperiod response</td>
<td>2AL</td>
<td>Welsh et al. 1973; Scarth &amp; Law 1983</td>
</tr>
<tr>
<td><em>Ppd3</em></td>
<td>Photoperiod response</td>
<td>4AS</td>
<td>Allan 1970; Gale &amp; Marshall 1976</td>
</tr>
<tr>
<td><em>Rht1</em></td>
<td>Reduced height (dwarfing)</td>
<td>4AS</td>
<td>Allan 1970; McVittie et al. 1978</td>
</tr>
<tr>
<td><em>Rht2</em></td>
<td>Reduced height (dwarfing)</td>
<td>4D</td>
<td>Hu 1974; McVittie et al. 1978</td>
</tr>
<tr>
<td><em>Rht3</em></td>
<td>Reduced height (dwarfing)</td>
<td>4AS</td>
<td>Hu 1974; McVittie et al. 1978</td>
</tr>
<tr>
<td><em>Tin</em></td>
<td>Tiller inhibition</td>
<td>1AS</td>
<td>Richards, R 1988</td>
</tr>
<tr>
<td><em>Vrn1</em></td>
<td>Vernalization</td>
<td>5AL</td>
<td>Pugsley 1972; Maystrenko 1980; Law et al. 1976</td>
</tr>
<tr>
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<td>5DL</td>
<td>Maystrenko 1974; Law et al. 1975</td>
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<td>[Vrn4]</td>
<td>Vernalization</td>
<td>5B</td>
<td>Lbova &amp; Cherniy</td>
</tr>
</tbody>
</table>

For complete citations and additional references see: McIntosh, R.A. Catalogue of gene symbols for wheat.

Stelmakh (1987) concluded that *Vrn4* does not exist and was mistakenly proposed based on parents that were incorrectly characterized.
CIMMYT is well positioned to develop a gene-based wheat model due to its:

• Strong interdisciplinary approach, including close ties to molecular marker research.

• Access to diverse germplasm, including special genetic stocks.

• Access to diverse growing environments.

• Experience with data bases of field data (e.g., IWIS) that might be used with simulation models.

Such an effort will not lead to overnight surpassing of yield barriers, but it will provide a solid platform for integrating knowledge from physiology, plant breeding and molecular biology.

References


Quantitative Understanding of Wheat Growth and Yield for Identifying Crop Characteristics to Further Increase Yield Potential

P.S. Bindraban

Introduction

In the past, breeders have obtained major success in increasing wheat yield potential with a rate of increase of around 1% per year; however, a declining tendency is currently being noted (Sayre 1990; CIMMYT 1995). As increasing wheat yield potential will remain a major component of required increase in world wheat production, all means to sustain or even accelerate the rate of increase will have to be explored to support breeding efforts. Systems analysis has been useful in various disciplines in agricultural production systems research, but has not been much applied in conjunction with breeding. This paper describes an analysis, demonstrating possible means of formulating recommendations to breeders based on quantitative understanding of wheat growth and yield.

Material and Methods

Experiments

Three cycles of experiments were conducted at the CIANO experiment station in the Yaqui Valley in northwestern Mexico. Wheat yield potential was determined under optimum management conditions for optimum (30, 30 and 26 Nov.: exp. 1) and late (18, 17 and 4 Jan.: exp. 2) planting dates for cycles I, II, and III, respectively, with an additional late planting on 2 Feb. (exp. 3) in cycle III only. A similar experiment (exp. 4) was conducted at the INIFAP experiment station near Celaya, Mexico, in cycle III only. In exp. 5 a range of growth conditions was obtained by varying N fertilization rate. Four bread wheat cultivars were grown in exps. 1 to 4, while 16, 4 and 4 cultivars were grown in exp. 5 in cycle I, II, and III, respectively. Observations of various cultivars in a yield potential trial (exp. 6) (see Sayre, these proceedings) and two cultivars in an experiment with different timing of nitrogen application (exp. 7) were also included in this analysis. Monthly average temperatures are presented for all cycles in Table 1.

One or two destructive biomass samples were taken around anthesis and biomass; yield and yield components were determined at maturity. Leaf area index (L) and leaf nitrogen content of upper leaves (N) were determined throughout growth in all experiments. Stem carbohydrate concentrations were measured in the course of crop growth in exp. 1 in cycles I and II and in exps. 2 and 5 in cycle II only. The decline in total amount of carbohydrates from a week after anthesis to maturity was calculated from these data.

Spikes were degrained in three different ways at anthesis in exps. 1 to 4 in cycle III to study grain growth. In treatment A, all
spikelets, except four central ones, were removed by scissors. Eight central spikelets were left in treatment B, with distal kernels removed by tweezers, leaving two proximal kernels per spikelet in place. Also eight central spikelets were left in treatment C, however, with the proximal kernel removed by tweezers, and the remaining one or two, seldom three, distal kernels left in place. These treatments resulted in approximately 80% reduction in grain number, needed to obtain unlimited supply of carbohydrates (Fischer and HilleRisLambers 1978). Kernel weights (KW) at maturity were compared to weights of kernels in similar positions in untreated spikes. Proximal and distal kernels in treatment A were observed separately. Responses have been expressed as percentage increase over control KW, averaged for four cultivars common to all four experiments.

**Growth and yield analysis**

A simple algorithm was developed to calculate daily biomass accumulation (G) during crop growth, based on the amount of radiation intercepted by the crop ($I_{abs}$) and the conversion efficiency of radiation (R) (Monteith 1977). Incoming radiation ($I_0$) extinguishes exponentially with increasing L, with an extinction coefficient (k) of 0.44 (Van Heemst 1988). The relative impact of leaf N on R ($N_c$) increases linearly from zero at N is 2% to unity at 3.2%, remaining constant at higher values. R and the relative impact of N on R have been derived from exp. 5.

$$G = I_{abs} * R * N_c$$

$$I_{abs} = I_0 * (1- e^{-k*L})$$

0 for 2% > N

$$N_c = (N-2)/1.2$$ for 2% < N > 3.2%

1 for N > 3.2%

Actual realization of yield occurs during grain filling, but the first week after anthesis can be excluded for various reasons. Grain filling is still in its lag phase, final KNO is still being determined (Fischer 1985), and assimilates are allocated to many other sinks, like stem and spike structures and the reserve pool of carbohydrates in the stem. Biomass accumulation during this yield realization period should reflect observed yield so that both have been related. However, as approximately 10% of the yield is realized during the lag phase, to account for exclusion of the first week after anthesis.

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<td>12.9</td>
<td>11.3</td>
<td>8.1</td>
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</table>
in growth calculations, yields are expressed at 90% for an objective comparison.

Results

Growth and yield
Calculated biomass relates well to values of biomass measured both during growth and at maturity (Bindraban et al. 1996). Therefore, this procedure could be applied to calculate growth during any period of time throughout growth. Calculated growth during the yield realization period relates to observed yield as shown in Figure 1 for cycle I, with an eyefitted curve through the data. Similar patterns are found for the other cycles (Figure 1). Calculated biomass accumulation during the yield realization period is lower than observed yield for yields below 5-7 t ha\(^{-1}\), indicating that current assimilation must have been supplemented by additional sources, like stem carbohydrates. At yields exceeding 5-7 t ha\(^{-1}\), calculated biomass accumulation exceeds yield, indicating that sink rather than source might have limited yield.

Translocation of carbohydrates
Changes in stem carbohydrate during the yield realization period as related to observed yield are given in Figure 2. Strongest declines occur at relatively low yields (3-4 t ha\(^{-1}\)), while declines are lower at higher yields. Although absolute decline was small at lower yields, they were important in relative terms.

Decline in stem carbohydrates yield realization period (kg ha\(^{-1}\))

![Figure 2. Decline in stem carbohydrate during yield realization period at different (90%) yield levels.](image)

Estimated biomass accumulation yield realization period (kg ha\(^{-1}\))

![Figure 1. Estimated biomass accumulation during the yield realization period at different levels of observed yield (90%). Actual data with hand-drawn curve are given for cycle I, while hand-drawn curves only are given for cycles II and III.](image)
Responses of KW to degraining

Degraining treatments were imposed to identify factors limiting grain growth. Relative responses of the degraining treatments in relation to average temperatures during grain filling are given in Figure 3. Proximal kernels in treatments A and B show relatively small responses in KW to increasing average temperature during grain filling of 6% at 17°C to 15% at 25°C. Kernels in distal positions in treatment A show similar responses to the proximal kernels at lower temperatures (exps. 1 and 4), but these responses become stronger at higher temperatures (exps. 2 and 3). Distal kernels in treatment 3 show strongest responses at all temperatures, with responses increasing rapidly with temperature.

Discussion

Biomass accumulation is largely determined by leaf area index, governing radiation interception, and leaf nitrogen content, which governs conversion efficiency of radiation. Yield realization is much more complex, with translocation of carbohydrates and storage capacity of kernels as major processes to be considered as well. Translocation of carbohydrates mainly stored in the stem is an additional source for yield under lower yielding conditions. Translocation is known to be of particular importance when post-anthesis stresses occur, hampering assimilate supply (Kiniry 1993). Disease infestation (Evans 1993), drought (Bidinger et al. 1977) or rapidly declining leaf nitrogen content during grain filling due to translocation of N to the kernels (see also Sinclair and de Wit 1976), all result in significant amounts of carbohydrates to be translocated to the grains. Absolute required amounts of carbohydrates translocated in this study, as can be derived from Figure 1, are larger than observed amounts (Figure 2). However, water soluble carbohydrates do not represent all stem carbohydrates, and storage occurs in leaves as well. Trends in calculated requirement and actual demand are nevertheless similar and comparable to trends described by Yoshida (1972) and Gallagher et al. (1975).

Though no translocation is needed at higher yield levels, some reduction in total amount of stem carbohydrates is observed. No accumulation of stem carbohydrates has been reported in the literature to occur in the last weeks of grain filling, while decrease in
carbohydrates can be ascribed to losses caused by wasteful respiration. Large amounts of carbohydrates can be lost through this process, especially when carbohydrates are abundantly available (Lambers et al. 1991; Lambers, pers. comm.).

Both biomass and stem carbohydrate analysis indicate potential yield under cool conditions to be limited by the storage capacity of kernels rather than the supply of carbohydrates, while source supply may limit yield under warmer growth conditions.

Results of the degraining treatments provide additional data on factors limiting yield. Proximal kernels in treatments A and B show relatively small responses in KW, though supply was increased approximately 5-fold by degraining. Distal kernels in treatment A show similar responses as the proximal kernels in the same spikelet at lower temperatures, while the distal kernels in treatment C respond much more strongly in the absence of the proximal kernels. This discrepancy in response of the distal kernels with and without the presence of the proximal kernels indicates the relatively favorable position of the proximal kernels in the competition among kernels in the spikelet for available carbohydrates.

At higher temperatures, responses of distal kernels in treatment A are stronger than responses of proximal kernels. As proximal kernels are situated in more favorable positions, they would suffer less from declining supply in carbohydrates than distal kernels. Degraining under these higher temperatures does result in a response of distal kernels to increased availability of carbohydrates. Responses are especially strong for distal kernels in treatment C, as both competition and source limitation have been alleviated.

Differential responses to competition among kernels within a spikelet and in different spikelets (central vs. top) (see also Bremner and Rawson 1978; Radley and Thorne 1981) suggest differences in availability of carbohydrates among kernels. Proximal kernels are shown by Hanif and Langer (1972) to be supplied by principal vascular bundles from the rachilla, while distal kernels are supplied by sub-vascular bundles, derived from the principal vascular bundles. Under any condition, proximal kernels have priority access to available carbohydrates, while distal kernels will suffer strong competition, especially under source-limiting conditions.

To further increase yield potential under sink-limiting conditions, growth conditions for kernels in distal positions should be improved through alleviation of competition. Anatomically, kernels in distal positions may need to be supplied by principal vascular bundles. Morphologically, a more open and vigorous spike structure might result from such an adjustment and this would be an easy trait to evaluate under field conditions. For instance, KW in wheat may vary from 15 to 60 mg, while kernels of rice, having an open panicle structure, have been found to vary very little, from 19 to 21 mg. Rawson and Ruwali (1972) have indeed shown more uniform kernel weights to be obtained in branched wheat spikes. Alleviation of competition among kernels in current cultivars would increase sink
capacity by at least one t ha\(^{-1}\). Analyses currently being performed with lines of large spikes (R. Rodríguez' crosses at CIMMYT) show encouraging variation with respect to kernel size distribution.

Sink capacity can be increased also through increased KNO (see Sayre, these proceedings), the yield component that correlates strongly to spike weight (Brooking and Kirby 1981; Fischer 1983; Fischer 1993). Spike weight could be increased through a prolonged spike growth period (see Slafer, these proceedings) or through a more favorable allocation of carbohydrates to the spike, which competes with stem growth (Fischer and Stockman 1986; Kirby 1988).

Source-limiting conditions tend to occur under higher temperature, most probably due to accelerated leaf death (Van Keulen and Seligman 1978). Yield increase under these conditions could be achieved through increased leaf area duration through prolonged leaf life span or leaf greenness.

**Conclusions**

This quantitative analysis of growth and yield indicates that adaptations required to further increase wheat yield potential depend on environmental conditions. These conditions force wheat cultivars to have specific adaptations to prevailing environmental conditions. Under optimum management conditions, supply of carbohydrates under relatively cool temperatures exceeds sink capacity which limits yield, while accelerated LAI decline caused by high temperatures during grain filling reduce source supply, limiting yield. Yield, limited by source supply under warm conditions (exps. 2 and 3) could be increased through increasing LAD and leaf greenness, while these adjustments would not increase yield whenever limited by sink capacity (exps. 1 and 4). Sink capacity can be increased either through increased KNO, discussed elsewhere in these proceedings (see Sayre's and Slafer's contributions, these proceedings) or by improving carbohydrate availability to kernels in distal positions. This last improvement could be achieved through a morphologically more open spike structure, a trait relatively easy to evaluate in breeding trials.

**References**


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