Wheat Special Report No. 12

Increasing the Yield Potential of Irrigated Bread Wheat

Basis for Physiological Research at CIMMYT

E. Acevedo, Leader
Crop Management and Physiology

November 1992
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Preface

R.A. Fischer
Director, CIMMYT Wheat Program

In 1989, CIMMYT's Wheat Program estimated that 42.7% of developing spring wheat production, representing 36.1 million ha, was being produced in mega-environment (ME) 1. The desirable level of resource allocation for this ME was calculated to be 45% according to CIMMYT's strategic plan criteria. The past large yield increases in farmers' fields in this ME have paralleled increases in yield potential (YP), meaning yield in the absence of abiotic and biotic stresses and under optimal management.

Thus, increasing YP of bread wheat in ME1 is not only a continuing challenge for breeders, agronomists, and physiologists, but it is of worldwide importance and of high potential returns to CIMMYT's investment. There is a positive correlation between increases in YP in CIANO, and ME1, and increases in farmers' yields. Furthermore, higher YP lines are more efficient and more responsive to agronomic management and tend to yield better even in environments with moderate abiotic stress. The rate of increase in YP of bread wheat has had a tendency to decrease in the last 10 years at CIMMYT, even though the long-term trend (20-30 years) is still in the order of 1%/year. The progress achieved so far has been essentially through intensive crossing, direct empirical selection for plant type, and extensive testing for yield. But as YP increases, such a program becomes more difficult and it is possible that, among other alternatives, the use of indirect selection traits will improve efficiency.

This wheat special report provides a physiological framework geared to improving bread wheat YP for ME 1. Hopefully, it provides some approaches to understanding this complex issue thereby facilitating further progress.

Note on Citing this Wheat Special Report

By sharing research information in this Wheat Special Report on Increasing the Yield Potential of Irrigated Bread Wheat, we hope to contribute to the advancement of wheat breeding and to the importance of shared knowledge. However, the information in this report is shared with the understanding that it is not published in the sense of a refereed journal.

Introduction

Yield potential (YP) is defined as the "yield of a cultivar grown in environments to which it is adapted when nutrients and water are nonlimiting, and when pests, diseases, weeds, lodging, and other stresses are effectively controlled" (Evans 1987).

Rajaram and Fischer (1989) described seven world wheat mega-environments (MEs). They are distinct niches of the developing world with an area that, by definition, is greater than 1 million hectares. After weighting wheat production within an ME according to per capita income, likely breeding progress and strength of the National Agricultural Research System, Fischer and Rajaram (1990) gave a priority assessment for CIMMYT wheat research (Table 1). ME1 (irrigated) had the highest percentage of developing world wheat production and it also had the highest priority for research.

It has been found that varieties with high yield potential in ME1 usually yield more in other MEs, even at moderate levels of stress. The past yield increases in ME1 have paralleled increases in YP for this ME.

CIMMYT has the responsibility of maintaining and increasing YP in a framework of a world mandate, therefore understanding and researching YP is a priority task. There are several aspects of YP that merit our attention:

• How is it determined?
• What morphological and physiological characters and in what combinations is expression maximized?
• What is the genetic variability in YP and traits related to it?
• How are these characters transmitted from one generation to the next?
• How can high YP genotypes be selected as early as possible in the improvement process and in an efficient and cost effective way?

In what follows, we provide a physiological research framework geared to bread wheat YP improvement for ME1.

Approaches to Understanding and Advancing YP

Retrospective analysis

Retrospective analysis shows the progress made by breeders and the trends in characters associated with yield improvement. Waddington et al. (1986) studied the genetic YP of bread wheat cultivars released in northwestern Mexico over the 1950-82 period. They observed an average increase for the period of 59 kg/ha per year or about 1.1%/yr. Prior to 1970, Fischer and Wall (1976) had estimated a 2% increase per year. A comparison to pre-1970 cultivars indicated that increases in YP were associated to increases in grain number per unit area, mostly due to increased grain number per spike, 1000-grain weight being reduced slightly in the modern cultivars. Interestingly, the modern (post-1970) genotypes had, on average, 16% greater above-ground biomass. Forty three percent of the variation in grain yield was attributable to biomass, but grain yield and HI were not correlated. High grain number per m² was strongly, positively associated with higher biomass and hence to an improved grain sink size as well as strongly related to longer duration of the genotypes. HI in the most modern wheats in Waddington's study was low (30-44%), indicating the scope for increasing this value.
Recent data obtained at CIMMYT (K. Sayre, unpubl.) studying bread wheat genotypes released between 1962 and 1988 show a significant positive correlation \( r = 0.44 \) between grain yield and days to heading. The pre-heading period has increased with time while the grain filling period has decreased and it is negatively related to grain yield \( r = -0.23 \). These findings support the idea that increasing the spike growth period may produce a better sink for assimilate (Evans 1987) and indirectly induce a higher photosynthetic rate during grain filling. The net result has been an increase in crop duration with time accompanied by an increase in radiation use efficiency (kg/ha per day), primarily in the post-heading period. The grains per m\(^2\) have increased significantly explaining a large proportion of grain yield variation \( r = 0.75 \), while the number of spikes per m\(^2\) and thousand grain weight have low \( r = 0.17 \) and -0.10, respectively correlations with grain yield. The total above-ground biomass has increased in the period studied.

In a similar study, Austin et al. (1989) showed a higher yield in modern English winter wheat cultivars, associated with shorter stature, earlier flowering, and longer grain filling period, but similar total above-ground biomass. Modern cultivars tended to have more ears and grains per m\(^2\) than their predecessors. Winter wheat improvement in the UK has led to different physiological changes than spring wheat improvement at CIMMYT.

It is of interest to analyze durum wheat improvement at CIMMYT. While most bread wheat selection has been done by selecting for grain yield per se, in the case of durum wheat, breeding for high yield occurred, in part, by selecting for grain yield, but also by adopting the ideotype approach, that is by selecting for morphological characters considered to contribute to high grain yield (Waddington et al. 1987). The characters included reduced plant height, more erect leaf posture, and larger grain sink size resulting in a higher number of grains/spikelet. At the same time, above-ground biomass and HI increased during the period under study. Grain yield was correlated with biomass; harvest index; duration of the grain filling period; and number of spikes/m\(^2\), grains/m\(^2\), and grains/spike. The growing cycle was 4 to 5 days longer in the recent genotypes but most importantly, the period from emergence to anthesis was 8-13 days longer. An increased rate of biomass production was highly associated with grain yields as well as associated number of grains/m\(^2\) coming from an increased number of grains per spikelet and spike.

Slow spike development (where a large spike is produced with many florets of similar size) and the ability of the spike to compete successfully for assimilates (primarily with the stem during the period of rapid spike growth prior to anthesis) are considered keys to a high spike growth rate, a high number of grains, and, therefore, a high grain yield (Evans 1981). The more erect leaves in durum wheat presumably increase the assimilate supply to the plant during the period of rapid spike growth to anthesis. Fischer et al. (1981) provided evidence that spikes with a large number of grains are associated with higher leaf photosynthetic rates and more rapid accumulation of dry matter after anthesis in bread wheat in northwestern Mexico. Selections for a higher ratio of spike dry weight to above-ground dry weight around anthesis may help to identify genotypes with higher sink (maybe a longer period from emergence to anthesis while maintaining the spike growth rate). Selection for specific physiological traits appears to be associated with higher yields in durum wheat. A more erect canopy structure and a high number of grains per spikelet, in addition to selection of grain yield per se, need more definitive studies to prove that improved grain yields are a result.

**The ideotype approach**

Donald (1962) was probably the first to recognize the limitations and difficulties of yield component analysis due to the compensations between components. He proposed a dry
matter-based approach, i.e., mainly only increases in total biomass and the harvest index (HI) would result in an increase in seed yield.

Later, Donald (1968) proposed the concept of an ideotype as a general plant model that performs in a predictable manner in a given environment and as an aid to early generation selection. The ideotype identifies characters that have direct meaning for plant breeders as selection criteria,

Table 1. Statistics of wheat mega-environments in developing countries as used by CIMMYT Wheat Program in 1989 to calculate an allocation index for the bread wheat breeding effort, 1984-86 statistics.

<table>
<thead>
<tr>
<th>Mega-Environmenta</th>
<th>Area (m ha)</th>
<th>Production (m t)</th>
<th>Per capita income ($/yr)</th>
<th>Rate of progress %/yr</th>
<th>Calculated Allocn. index %d</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperate, wet</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ME1 Irrigated</td>
<td>36.1</td>
<td>42.7</td>
<td>390</td>
<td>1.0</td>
<td>44.9</td>
</tr>
<tr>
<td>ME2 High rainfall</td>
<td>8.5</td>
<td>10.4</td>
<td>1,220</td>
<td>1.0</td>
<td>7.3</td>
</tr>
<tr>
<td>ME3 Acid soil</td>
<td>1.9</td>
<td>1.3</td>
<td>1,640</td>
<td>1.0</td>
<td>0.4</td>
</tr>
<tr>
<td>Temperate, dry</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ME4A Winter rain</td>
<td>6.1</td>
<td>2.3</td>
<td>1,990</td>
<td>0.7</td>
<td>1.2</td>
</tr>
<tr>
<td>ME4B Transitional</td>
<td>3.6</td>
<td>2.1</td>
<td>2,110</td>
<td>0.7</td>
<td>0.5</td>
</tr>
<tr>
<td>ME4C Residual mois.</td>
<td>4.9</td>
<td>2.5</td>
<td>300</td>
<td>0.7</td>
<td>1.9</td>
</tr>
<tr>
<td>Hot</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ME5A Hot, low vpd</td>
<td>4.4</td>
<td>4.9</td>
<td>540</td>
<td>1.0</td>
<td>5.0</td>
</tr>
<tr>
<td>ME5B Hot, high vpd</td>
<td>3.6</td>
<td>1.5</td>
<td>380</td>
<td>0.7</td>
<td>1.1</td>
</tr>
<tr>
<td>Cold-very cold</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ME6A Facult., wet</td>
<td>6.2</td>
<td>9.8</td>
<td>350</td>
<td>1.3</td>
<td>13.4</td>
</tr>
<tr>
<td>ME6B Facult., dry</td>
<td>5.1</td>
<td>2.0</td>
<td>990</td>
<td>1.0</td>
<td>1.8</td>
</tr>
<tr>
<td>ME6C Winter, wet</td>
<td>7.4</td>
<td>9.2</td>
<td>570</td>
<td>1.3</td>
<td>11.6</td>
</tr>
<tr>
<td>ME6D Winter, dry</td>
<td>6.7</td>
<td>4.6</td>
<td>780</td>
<td>1.0</td>
<td>3.6</td>
</tr>
<tr>
<td>Extremely cold</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ME7 High lat.</td>
<td>5.5</td>
<td>6.8</td>
<td>310</td>
<td>1.0</td>
<td>6.9</td>
</tr>
<tr>
<td>Total</td>
<td>100</td>
<td>100</td>
<td></td>
<td>100</td>
<td></td>
</tr>
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a See text.

b For allocation index weighed as follows:
0-400=3.0, 400-1000=2.3, 1000-1500=1.7, 1500=1.0.

c Projected for 1990-99.

d Calculated by product of % production, and income, rate of progress, and strength of NARS weights for each ME, then dividing by the total of all MEs. Strength of NARS weights not shown because vary little between weak (1.3) and strong (1.0).

Source: Fischer and Rajaram 1990.
and are also susceptible to physiological analysis. Donald (1981) proposed a crop or communal ideotype that was an erect, sparsely tillered plant with small erect leaves, able to survive and produce in a competitive situation surrounded by plants of the same form. By definition, this ideotype performed very poorly in a wide spacing situation. The crop ideotype would have minimal resources invested in structure, and hence a higher HI. The ideotype plant was a weak competitor and it would take a minimum demand on resources per unit of dry matter produced, i.e., maximum efficiency in resource use. The low competitive ability with like neighbors would then be associated in a crop stand to a high efficiency of conversion of resources (light, nutrients, carbon, and water) to dry matter and yield. Of interest, studies in an historical series of CIMMYT bread wheat genotypes appear to show that, when grown under optimum conditions, the higher yielding ones respond less to reduction in the level of competition for light and soil resources than the earlier, lower yielding ones (Reynolds, unpubl.). This may imply that bread wheat improvement is developing genotypes that are less exploitative of space but more efficient resource users.

The attributes, suggested by the work of Donald and co-workers that would provide a high biological yield and high harvest index associated to low competitive ability, were summarized by Sedgley (1991) as:

- Tolerance of similar plant forms in high density sowings.
- Economy in the use of resources, i.e., optimum HI with minimal investment in morphological structure.
- Sensitivity to cultural practices (row spacing, weed control, other).
- As many florets as are necessary to ensure that the ear has sufficient capacity to accept all photosynthates.
- In many respects, this is a plant form that may be overlooked in the process of visual selection.

The suggested characters for a weak competitor are: short, strong stems, single culm, erect leaves, few small leaves, large ear, erect ear, and presence of awns.

Inherent in this approach is the aim to reduce the amount of empiricism in plant breeding by using more analysis (Sedgley 1991). In breeding practice, however, early generation selections are often done in plants planted widely spaced (F2-spaced plants) and also in competition environments (F3 bulks) for the crop. As indicated, under these conditions the crop ideotype would perform very poorly because the preferred plants should be weak and poor competitors. Selections would be difficult in early generations (Marshall 1991) and those for vigor and biomass production may be counterproductive (Evans 1981, Donald 1981).

The relationship between yield performance of cultivars (as crops) at high density versus that at low density or mixed culture is likely to be reversed; and as mentioned, the genotypes are exposed to low density and mixed culture during early selection stages to be grown later in dense pure cultures. Donald (1968) concluded that the actual development of crop ideotypes would have to depend initially on recognizing their morphology and their harvest index and not their success in competing with other genotypes. Early generation selections should be oriented to higher harvest index and for proven characters which are controlled by relatively few genes (Rasmusson 1987).
Based on his experience with ideotype breeding in barley, Rasmusson (1991) suggested that, since plant breeders have selected and will continue to select for ideotype traits (maturity, height, kernel number and weight, head number, leaf area, angle, and duration), they might benefit from going a step further and specifying the desired goal or phenotype for each trait. He has found that pleiotropy, trait compensations, and inferior donor germplasm have slowed progress in ideotype breeding, but that good progress has been achieved for several traits (short stature, kernel number, kernel weight, and erect leaf angle) in his program. A major challenge is to identify traits worthy of an ideotype breeding effort. Ideotype traits should be tried in many gene combinations and incorporated into good genetic background; once freed of deleterious linkages, they should be valuable to a large number of researchers (Rasmusson 1991).

Evans (1984, 1987, 1991), in a forward looking perspective, has analyzed opportunities for increasing the YP of wheat. He argues that "there is no sign yet of an approaching yield plateau in either the UK or USA, and the gains from hybrid wheat and other advances have yet to be exploited." He cautions, however, that the increase in YP of wheat has been achieved without any increase in the rates of growth or photosynthesis hence without much change in aerial biomass, i.e., with weaker plants with a reduced investment in stems, leaves, roots, and reserves. He analyzed 5 areas of opportunity (Evans 1987) for increasing the YP of wheat: 1) growth and photosynthesis, 2) the timing of the reproductive cycle, 3) shift in biomass allocation, 4) regulatory processes, and 5) environmental responses.

Evans recognized that each characteristic interacts not only with the environment, but also with the rest of the genome (e.g., with the Rht genes). He came to the conclusion that, for wheats with longer growing periods, the following are promising avenues to explore in future YP improvement:

- Increased activity of RUBISCO (if variation is found);
- Selection for local adaptation in the timing of the reproduction cycle such that there is an optimum balance between the main stages of the life cycle;
- Further shifts in biomass allocation allowed by continued agronomic support to the crop such that HI may reach up to 60%; and
- Selection for higher grain number (indirectly for faster or more prolonged photosynthesis during grain growth).

A conceptual model for the determination of YP

The transformation of solar energy into harvestable plant parts can be logically and conveniently divided into three major processes:

- Interception of incident solar radiation by the leaf canopy;
- Conversion of the intercepted radiant energy to chemical potential energy (plant dry matter); and
- Partitioning of the dry matter produced between the harvested parts and the rest of the plant.

A wheat crop with high YP needs to carry out these three processes efficiently and in a balanced way. A simple equation illustrates these processes (Hay and Walker, 1989):
Y = Q * I * E * H  

where: Y is the harvestable plant part(s) or yield, Q is the total quantity of solar radiation received by the crop over the growing period, I is the fraction of Q intercepted by the crop canopy, E is the overall photosynthetic efficiency (total dry matter produced per unit of intercepted radiant energy), and H is the HI or the fraction of the total dry matter harvested as yield.

Wheat is physiologically and genetically capable of much higher productivity and photosynthetic efficiency than has been recorded in field environments. Loomis and Williams (1963) calculated the maximum potential productivity for a single leaf to be about 1.78 g/mol of photosynthetic photons (PAR) or 8.20 g/MJ (assuming the average energy content of photosynthetic photons to be about 217 KJ/mol). Monteith (1981) estimated a conservative photosynthetic efficiency of 1.28 g/mol of PAR or 5.89 g/MJ with a quantum requirement of 20 mol of photons per mol of CO₂ fixed. Ehleringer and Pearcy (1983), however, obtained a quantum requirement of 13.7 at 16°C in normal CO₂ conditions and their data suggested that a quantum requirement of 13 might be achievable in C₃ plants at about 13°C.

Bugbee and Salisbury (1988), by assuming a quantum requirement of 13, an absorption of the incident PAR of 95%, a respiratory carbon use efficiency of 75%, and 40% carbon in that plant mass, calculated a maximum crop growth rate of 1.64 g/mol of PAR (7.55 g/MJ PAR). This growth rate would be possible only with low-lipid plants in which the respiratory carbon use efficiency can be high. They grew wheat in a growth cabinet at 1200 ppm CO₂ and reached the calculated growth rate.

Assuming a PAR of 43.2 mol/m² per day (500 cal/cm² per day), the potential crop growth rate at 1.64 g/mol would be about 71 g/m² per day. Monteith (1978) reportedly obtained maximum short-term crop growth rates of 34 to 39 g/m² per day for C₃ crops and 51 to 54 g/m² per day for C₄ crops. For the period from heading to maturity, values of 22.2 g/m² per day are obtained in well managed wheat plots in Cd. Obregon in northwestern Mexico (K. Sayre, unpub.), about 65% of the maximum short-term values reported by Monteith (1978).

From equation 1, it can be seen that there are at least two major ways in which the rate in crop photosynthesis might be increased. One possibility is to increase the interception (I) of PAR by the canopy through the growing season by a faster approach to full cover. The other way is to increase the efficiency of conversion of PAR into dry matter, perhaps by improving the distribution of PAR among the various leaves by modifying the canopy structure.

Radiation interception by the canopy—For cereals and other crop species, there is a linear relationship between total dry matter and intercepted solar radiation (Monteith 1977). The extent to which the canopy intercepts the available radiation depends largely on leaf area index and to some extent on characteristics such as leaf angle and the arrangement of leaves in space.

The optimum canopy architecture for maximum radiation interception and high rates of canopy photosynthesis and crop growth is necessarily different at various stages of the growth of a crop stand and at different levels of irradiance. In the early stages of growth, horizontal leaves would be an advantage in a row crop like wheat. There may be an advantage in switching to erect upper leaves after stem extension, but keeping the horizontal posture of the early lower leaves, particularly at high leaf area indices. This
architecture is common in cereals and small advantages in canopy net photosynthesis have been found for erect leaf posture (Austin et al. 1976).

The second major element of radiation interception on accumulated dry matter is the duration of the crop, with longer duration of crops intercepting more radiation.

**Photosynthetic efficiency**—Quantum yield (the slope of the line of photosynthesis on radiation at low radiation) and the rate of photosynthesis at light saturation (Pmax) define the light response of photosynthesis at the leaf level. It appears that little genetic variation exists in quantum yield (Charles-Edwards 1978) being around 5 g CO₂/MJ PAR (Ehleringer and Pearcy 1983).

The relation between biomass accumulation and photosynthetic rates is complex. It includes variation in photosynthetic rates among individual leaves, light distribution within the leaf canopy, and respiratory activity. The relationship between photosynthetic efficiency or radiation use efficiency and Pmax (Sinclair and Hoire 1989) predicts that, in C₃ plants, increases in light-saturated CER above 1.3 mg CO₂/m²/s will not have large effects on canopy photosynthetic efficiency and consequently on crop biomass accumulation. Decreased values of light saturated photosynthesis, however, have important effects on photosynthetic efficiency. This conclusion indicates that it would be difficult to derive crop yield responses to genetic selection for high Pmax. On the contrary, at a Pmax below 1.2 mg CO₂/m²/s, CER has an important effect on photosynthetic efficiency.

Other reasons for the little increase in yield with increased Pmax are pleiotropic effects on leaf area (reductions in leaf area and duration) and possible sink limitations. Significant increases in maximum photosynthesis per unit leaf area have been observed in wild diploid wheat ancestors (Evans and Dunstone 1970) and genes of these species can be transferred to wheat. The higher photosynthetic rate of the diploids appears to be related to smaller leaves with a higher mesophyll area to leaf area ratio. Notwithstanding Sinclair and Horie's conclusions, recently it has been reported that amphiploids derived from T. durum x T. urartu have shown significantly higher biomass. (Austin 1990).

Photorespiration accounts for 25 to 50% of the CO₂ fixed by a number of C₃ species (Zelitch 1980). However, genotypes with low CO₂ compensation points have not been found in wheat. Furthermore, there appears to be little scope to modify RUBISCO to decrease the oxygenase activity relative to the carboxylase activity (Austin 1989). However, by selecting for genotypes that do not have the cyanide resistant or alternative pathway of respiration, there is some hope that close to 45% of dark respired photosynthates may be reduced (Lambers 1985, Amthor 1989, Hay and Walker 1989). Selection for plants with lower mature leaf respiration per unit dry weight may result in higher yields (Wilson 1975, Day et al. 1985). The alternative respiration pathway (Lambers 1985) may be wasteful.

**Harvest index**—Increases in HI have been considered the major cause for wheat yield increases during this century (Austin et al. 1980). Even though European winter wheats are getting close to a calculated maximum of around 60% (R.B. Austin, pers. comm.), the spring wheats produced at CIMMYT have an HI of around 45%, which still allows ample room for improvement. This route of improvement appears to be particularly interesting considering that most modern varieties at CIMMYT appear to have increased biomass and even lower HI (K. Sayre, unpub.). As mentioned before, spike growth and development during the pre-anthesis period (which may be source-limited) appear to be one of the keys to increase potential yields in spring wheat (Fischer 1983). Source limitation during ear development and the early part becomes the dominant sink.
Conclusions
It appears that the basic concept of Donald for improving selection efficiency for early generation is still valid. His proposed ideotype may be right in some aspects, but 20 years after his proposal, it is still controversial (Sedgley and Belford 1991). It seems that a challenge we still face today is the identification of traits and trait combination(s) that are worthy of an ideotype breeding effort for YP.

From the retrospective analysis, it appears that a slow spike development rate accompanied by a higher number of grains per spike has an important effect on grains per unit area, grain yield, and photosynthetic efficiency for post-anthesis growth. The low, but consistently negative correlations between grain yield and kernel weight appear to indicate that, in recent spring bread wheat cultivars, the sink limitation to grain yield is being relaxed and we could expect that, in time, a source limitation may become dominant. Ways to continue to increase the spike sink size should be explored, together with increased source intensity and duration. The literature appears to indicate that there is still room to improve radiation interception, I (early ground cover, longer crop duration), the photosynthetic efficiency, E (appropriate phenology, canopy architecture), and the harvest index, H, for spring bread wheat. Present field yields are within 30 to 40% of theoretically attainable yields, hence, there appears to be scope for YP improvement in ME1.

Relationship between CIMMYT's Physiology and Bread Wheat Breeding Programs
The relationships between crop and plant physiology work at CIMMYT and the bread wheat breeding program are close. Efforts have been almost continuous in:

• Suggesting crop management practices for specific environments;

• Improving the basic understanding of achievements in breeding; and

• Providing a better understanding of the effects of soil and environment on plants.

Now, we are proposing to intensify the efforts by:

• Testing the efficiency of using indirect selection traits in early generations;

• Helping to identify parental material for high YP in breeding; and

• Helping to understand the potential for crop improvement under particular environments.

CIMMYT's current strategy for wheat breeding in ME1
To cope with developing world needs, CIMMYT's wheat breeding strategies are designed for various agroecological zones or MEs. Wide adaptation is a predominant aim for the material sent to a given ME. Selections to address the needs of specific agroecological niches within an ME are the responsibility of the National Agricultural Research Systems (NARSs). The primary goal is, therefore, the development of broadly adapted disease-resistant, high yielding, and stable germplasm within the context of each ME. Shuttle breeding within Mexico and international multilocation testing allow combining wide adaptation with a high YP.
The breeding objectives for ME1 are high YP, lodging resistance including maintenance of Rht1 and/or Rht2 dwarfing genes, improved industrial quality, and durable resistance to the rusts. Salinity and high temperature resistance and resistance to aphids and powdery mildew are additional targets for this ME.

The parents used for crosses of material intended for ME1 are generally varieties released in different countries, elite CIMMYT germplasm identified from international and CIMMYT testing, or advanced lines exhibiting good expression of a specific trait or traits. Specifically, the genotypic constitution of the ME1 optimum environment germplasm is the following:

- High yielding varieties and advanced lines (CIMMYT widely adapted varieties and CIMMYT high yielding lines);
- Subcontinent varieties (India, Pakistan, Nepal, Afghanistan);
- Leaf rust resistant lines;
- Good industrial quality (bread type and cookie type); and
- High yielding under heat.

With 1000 to 1200 crosses made each season, the selection program involves:

<table>
<thead>
<tr>
<th>Generation</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>F₁</td>
<td>1000-1200</td>
</tr>
<tr>
<td>F₂ Obregon</td>
<td>500 pop x 1000-1500</td>
</tr>
<tr>
<td></td>
<td>plants/pop</td>
</tr>
<tr>
<td>F₃ Toluca</td>
<td>10,000-15,000</td>
</tr>
<tr>
<td>m. bulk</td>
<td></td>
</tr>
<tr>
<td>F₄ Obregon</td>
<td>4000-5000</td>
</tr>
<tr>
<td>m. bulk</td>
<td></td>
</tr>
<tr>
<td>F₅ Toluca</td>
<td>2000-2500</td>
</tr>
<tr>
<td>m. bulk</td>
<td></td>
</tr>
<tr>
<td>F₆ Obregon</td>
<td>1000</td>
</tr>
<tr>
<td>select plants</td>
<td></td>
</tr>
<tr>
<td>F₇ Toluca</td>
<td>1000</td>
</tr>
<tr>
<td>bulked</td>
<td></td>
</tr>
<tr>
<td>PYT Obregon</td>
<td>1000</td>
</tr>
<tr>
<td>YT Obregon</td>
<td>500 x 3 reps</td>
</tr>
<tr>
<td>IBSWN</td>
<td>200-300</td>
</tr>
<tr>
<td>ESWYT</td>
<td>30</td>
</tr>
</tbody>
</table>

In the selection methodology, individual plants selected from the F₆ are bulked in the F⁷ to form PCs (small plots). These PCs are also sown as PYTs (unreplicated preliminary yield trials) during the Obregon winter cycle, providing information on YP, agronomic type (on a large-plot basis), and disease resistance (from PC inoculation). In the PYTs, the bottom end of the yield distribution is eliminated. Plots are 5 m x 8 rows, which give an effective harvest area of 5 m².
Yield trials (YT) have three replications and are conducted in Obregon. The best lines are distributed in International Screening Nurseries (IBWSN) and International Yield Trials (ESWYT). Early generation selection for YP may improve the efficiency of selecting high yielding material from the F_2 through F_5 generations.

**Possibilities for improving selection efficiency**

Grain yield being the target of selection, the logical parameter to select for is yield itself. It is known, however, that yield-based selections are only possible in the more advanced generations because it needs to be done in plots, therefore, some high yielding individuals present in the early generations (F_2s, F_3s) may escape recognition, thus decreasing the efficiency of the selection process. It also appears that most plant breeders have a conceptual model of the plant type that they consider to be ideal and much discussion continues to evolve around the ideotype concept (Sedgley and Belford 1991). Indeed, selections based solely on yield appear to be rare, morphological traits usually being incorporated, though yield is always the dominant selection criterion. The incorporation of analytical traits other than yield appears to be generally a product of experience more than the result of any systematic research effort.

Other than the difficulty in selecting for yield in early generations, a factor decreasing efficiency in breeding programs is their increase in size as yield improves and progress becomes more difficult. Under these circumstances, it appears appropriate to examine whether the efficiency of selection can be increased by using morphophysiological characters in a systematic way and their associated genetic parameters. The problem reduces to two major topics:

- Identification, assessment, and verification of characters for indirect selection; and

- Their possible use in early generation selection.

**Trait identification and testing**—Indirect selections are better based on traits chosen at the appropriate level of integration due to the complexities associated with plant growth and development (Acevedo and Ceccarelli 1989). It is usually possible to link two neighboring hierarchical levels of plant organization that are close to each other, but it is a more difficult task to relate yield to distant processes such as intermediate products of metabolism (e.g., Pearson et al. 1987). Other than the distance in organizational level associated with the hierarchical plant order, there is a time and space consideration to take into account. Short-term responses are unlikely to be directly related to yield. Metabolic responses take minutes and occur at microscopic distances, while the formation of yield takes months and occurs in the field. But choosing traits at the proper level of integration, say plant organs such as spikes, leaves, and tillering is not enough. The combined effect of various traits is unlikely to be the result of a their linear combination. Classical examples are the number of established plants and tillering of cereals, and compensation among yield components (ears per plant, grains per ear, and grain size).

Indirect selection for yield is necessary in the early stages of a breeding program. Selection criteria are required if the selection is to be better than taking a random subset of individuals (Wall 1978). The traits used in indirect selection must, additionally, satisfy a number of criteria:

- The character should be easier to assess than yield.
• There should be genetic variation for the trait in the population to be screened. The heritability of the trait should be high.

• The trait should be causally related to yield, its correlation with yield being strong.

• It should be assessed rapidly and inexpensively.

Many traits have been proposed for indirect selections for yield (Clarke 1987, Wall 1978, Quail et al. 1989) although very few of them have been shown to comply with the required criteria and hence be of use in breeding programs. The number of traits that have been verified, alone or in combination, is even lower.

Acevedo and Ceccarelli (1989) suggested a procedure later expanded on by Ceccarelli et al. (1991) to identify, assess, and verify single traits or a combination of traits to assist in yield selection. It involved the development of an ideotype by assembling a nursery of genotypes with enough diversity in the postulated traits to assess their worth for indirect selection for yield. Finally, verification of the traits was to be done through selection experiments using the experimental genotypes.

They suggested conducting a selection experiment for different combinations of traits with the objective to develop all possible recombinants between the opposite expressions of the traits under investigation. In their barley example, four putative characters were chosen on the basis of their relationships with a stress resistance index (Acevedo and Ceccarelli 1989), namely growth habit (GH), prostrate vs. erect; growth vigor (GV), poor vs. good; leaf color (LC), dark vs. pale; and days to heading (DH), early vs. late. Crosses were suggested between genotypes with highly contrasting expressions of all four characters, for example:

\[
\text{GH}^+ \text{ LC}^+ \text{ GV}^- \text{ DH}^- \times \text{GH}^- \text{ LC}^- \text{ GV}^+ \text{ DH}^+
\]

where: plus and minus signs indicate contrasting expressions of each character. A population of about 2000 \(F_3\) families representing an unselected \(F_2\) population should permit the identification of \(F_3\) families showing the following 16 phenotypes:

<table>
<thead>
<tr>
<th>GH</th>
<th>LC</th>
<th>GV</th>
<th>DH</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>2.</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>3.</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>4.</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>5.</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>6.</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>7.</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>8.</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>GH</th>
<th>LC</th>
<th>GV</th>
<th>DH</th>
</tr>
</thead>
<tbody>
<tr>
<td>9.</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>10.</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>11.</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>12.</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>13.</td>
<td>-</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>14.</td>
<td>-</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>15.</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>16.</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

Two additional groups—one selected for low yield and one for high yield—are needed to measure relative efficiency of selection. One unselected (random) group is needed to obtain estimates of response to selection free of bias due to genetic drift. The comparison between about 10 \(F_3\) families for each of the 19 groups will provide contrasts to measure the efficiency of different selection criteria on grain yield. For example, the contrast (where the numbers refer to the phenotypes listed above):

\[ [1,2,3,4,5,6,7,8] \text{ vs. } [9,10,11,12,13,14,15,16] \]
will give unbiased estimates of the effect of contrasting expressions of growth habit on grain yield at all combinations of the other three characters. Similarly, the contrasts:

\[ [1,2,3,4,13,14,15,16] \text{ vs. } [5,6,7,8,9,10,11,12] \]
\[ [1,2,5,6,11,12,14,16] \text{ vs. } [3,4,7,8,9,10,13,14] \]
\[ [1,3,5,7,10,12,14,16] \text{ vs. } [2,4,6,8,9,11,13,15] \]

will measure the efficiency of contrasting expressions of leaf color, growth vigor, and days to heading, respectively.

The genetic structure of the F3 families makes it possible to measure the effect of combinations of two and three characters. For example the contrast:

\[ [1,2,3,4] \text{ vs. } [9,10,11,12] \]

will measure the combined effect on grain yield of prostrate growth habit and pale green leaves as opposed to erect habit and dark green leaves. Again, the contrast is independent of both growth vigor and days to heading.

Many other contrasts including trait interaction can easily be built to test a number of alternative architectures.

The efficiency of each selection criterion (single traits as well as combinations of traits) is measured by the ratio between the difference in grain yield (\(GY\)) associated with a given contrast and the yield difference between the two groups selected for low (\(GY[LY]\)) and high (\(GY[HY]\)) grain yield. For example:

\[ \frac{(GY[1-8] - GY[9-16])}{(GY[HY] - GY[LY])} \]

measures the efficiency of using growth habit as a selection criterion relative to grain yield. The value of this ratio as an alternative selection criterion to grain yield will depend on the nature of the selection criterion itself. A weighting factor has to be introduced to take into account the substantial differences that may exist in the cost associated with different selection criteria.

Such an experiment would also generate the genetic information associated with a selection experiment, the most relevant being realized heritability of the individual traits measured as:

\[ h^2 = \frac{R}{S} \]

where: \(R\) (response to selection) is measured against the random group and \(S\) is the selection differential.

The comparison of the genotypes generated by such a selection experiment would need to be validated across years and locations.

Other methods can be used for trait validation. Near isogenic lines has been used successfully to test the effect of single traits (e.g., Quarrie 1981). Many isogenic pairs in different genetic backgrounds would be required to fully validate a trait and it would be extremely difficult if not impossible to test a combination of traits.
Another method is work with random lines. To test if a selection made for a trait in an early generation (F2) will relate to yield in an advanced generation, Wall (1978) reported on work done with 150 plants randomly selected out of 10 bread wheat populations. He measured 26 potential traits in the F2 plants and observed their correlation with F4 plot yields. He observed that F2 leaf permeability 3 weeks after anthesis, plant height, HI, leaf fire, kernel weight, leaf width, and kernels per main spike had a significant correlation with F4 yields. In a similar but more comprehensive work, Quail et al. (1989) tested 220 F3 lines taken at random from a multiple convergent cross among 16 parents representing elite CIMMYT germplasm. Yield was measured in the F8. The best correlation between F3 traits, and grain yield in F8 were plant height, kernel weight, HI, leaf angle and spike number.

CMP project underway--Research project MPBW9101 (Appendix 1) in the Crop Management and Physiology Subprogram commenced in November 1991. We believe it is a concrete attempt to study this indirect selection concept to increase the efficiency of selection for YP in ME1.

Acknowledgments

The author thanks R.A. Fischer, Craig Meisner, Matthew Reynolds, and Gene Hettel for reviewing the manuscript and making helpful suggestions.

References Cited


Appendix 1-- Project ID No.: MPBW9101

Title: Identification, assessment and verification of early selection criteria to increase the efficiency of selection for yield potential in ME1

Original Description

Original description prepared: August 1991
Project to commence: November 1991
Planned termination: October 1996

Type of project: Physiology, upstream, core

Investigators: E. Acevedo, P. Stefany, S. Rajaram, M. van Ginkel, J. Crossa, R.A. Fischer, and V. Calixto

Germplasm description: Spring bread wheat

Ecology/mega-environment: ME1

Background:

The search for indirect selection traits to increase yield potential (YP) is not new at CIMMYT and can be traced back to the early 1970s. Works reported by Fischer (1975), Wall (1978), Waddington et al. (1986, 1987), and Sayre (1991) show an almost continuous effort to assess the contribution of various morphological components to potential yields. The results point to various degrees of success, and even though it is usually stated that use of these traits by breeders is rare (e.g., Fischer 1989), in reality many of them are being used in the bread wheat selection process (S. Rajaram, pers. comm.) This is encouraging and justifies further effort on this subject, especially as new understanding and techniques continuously accrue. We have to recognize that, notwithstanding
exceptions, we are at the beginning of our understanding of the effects of single morphophysiological traits on YP. A continued concerted effort is required in this area if CIMMYT is to continue to break barriers in YP improvement having an appropriate understanding of what are the underlying causes. In addition, the application of RFLP technology to yield improvement will likely depend on such an understanding.

Objectives:

To determine whether there are morphophysiological traits which, when assessed in early generation in populations derived from crosses between elite high yielding parents, are useful indirect selection criteria for yield potential in spring bread wheat. To assess usefulness in terms of progress per unit cost as compared to traditional methods, and in terms of consistency of success across a range of elite germplasm and ME1 situations.

Materials and methods:

A base nursery will be assembled with approximately 100 bread wheat genotypes. These genotypes represent a wide range of morphological, developmental, and presumably other physiological characters. The genotypes include an historical series of bread wheats released in the Yaqui Valley of northwestern Mexico--the best lines derived from the bread wheat programs at CIMMYT and ICARDA, bread wheat lines studied in a line source sprinkler at CIANO/Mexico for yield potential and drought resistance and the best and lowest yielding lines of the 1990/91 yield trials at CIANO. Morphophysiological traits related to yield potential will be identified in this nursery by growing entries in optimally managed plot experiment in CIANO, commencing 1991-92.

An assessment of the morphophysiological traits presently being used by the bread wheat program will be done through a divergent selection experiment using the F2 populations grown in BV91 of two crosses (GPO/PR6/Vee 6 and PFAU/HAHNX2/PRL). The parents of these crosses differ in the traits under consideration.

After initial trait observations at CIANO, the possibility of identifying ideotraits or building and ideotype for ME1 will be studied based on the trait correlations with grain yield, as in Craufurd et al. (1991). The traits will be assessed individually by the strength of their correlation with grain yield following a methodology similar to the one described by Acevedo et al. (1991). The verification of the traits will be done by crossing diverse parents and using divergent selection experiments as proposed by Acevedo and Ceccarelli (1989) and expanded by Ceccarelli et al (1991). In these selection experiments, individual as well as the most important combinations of traits will be tested.

Literature cited:


CIMMYT Wheat Special Reports, Completed or In Press
(As of Nov. 1, 1992)


