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Applying physiological strategies to improve yield potential

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SUMMARY – Genetic gains in yield have increased by 0.9% per year over the last 30 years. Yield progress has been associated with improved harvest index and grain number, and in very recent cultivars higher biomass too. However, global demand for wheat is predicted to increase by 1.6% per year over the next 20 years hence physiological strategies such as improving radiation use efficiency (RUE), manipulating source-sink balance, and application of rapid early generation selection tools are being considered to accelerate the rate of breeding progress. In the area of RUE, several studies have indicated good associations between yield and leaf photosynthetic rate (A_n). While A_n was not always associated with higher RUE, A_n and related traits such as stomatal conductance (g_s) and canopy temperature depression (CTD) have potential application in breeding to screen for physiologically superior genotypes. Canopy photosynthesis may be improved by optimizing leaf architecture and the distribution of the photosynthetic apparatus in the canopy. Prolonged green-leaf area duration is another trait with the potential for improving RUE. Improving source-sink balance offers the opportunity to further improve grain number, and thereby raising the possibility of increasing RUE through increased sink demand. One way to achieve this may be to increase the relative duration of the juvenile spike growth phase, and hence provide a greater supply of assimilates during the critical spike growth period. By combining information on the physiological basis of yield limitation with new physiological selection tools such as CTD, g_s, and spectral reflectance, the probability of accelerating the rate of genetic progress through plant breeding should be significantly increased.

Key words: Wheat breeding, selection traits, radiation use efficiency.

RESUME – *"Application de stratégies physiologiques pour améliorer le potentiel de rendement". Le gain génétique du rendement a augmenté de 0,9% par an sur les 30 dernières années. Les progrès du rendement ont été associés à un meilleur indice de récolte et du nombre de grains, et dans les cultivars très récents également à une biomasse plus élevée. Cependant, il est prévu que la demande globale de blé augmente de 1,6% par an sur les 20 prochaines années, de là que les stratégies physiologiques telles qu'une meilleure efficacité de l'utilisation du rayonnement (RUE), la manipulation du bilan source-puits, et l'application d'instruments de sélection rapide des premières générations, soient considérées pour accélérer le taux de progrès de l'amélioration génétique. En ce qui concerne la RUE, plusieurs études ont indiqué de bonnes associations entre le rendement et le taux photosynthétique foliaire (A_n). Tandis que A_n n'était pas toujours associé à une RUE plus élevée, A_n et les caractères liés tels que la conductance stomatique (g_s) et la dépression de température de la voûte (CTD) présentent une application potentielle en amélioration pour un criblage pour des génotypes physiologiquement supérieurs. La photosynthèse de la voûte peut être améliorée en optimisant l'architecture des feuilles et la distribution de l'appareil photosynthétique dans la voûte. La durée prolongée de surface verte foliaire est un autre caractère avec un certain potentiel pour améliorer la RUE. L'amélioration du bilan source-puits offre l'opportunité d'améliorer encore le nombre de grains, et donc donne lieu à la possibilité d'augmenter la RUE à travers une demande augmentée du puits. Une façon d'y parvenir serait d'augmenter la durée relative du stade de croissance juvénile des épis, et donc de réaliser un plus grand apport d'assimilats pendant la période critique de croissance des épis. En combinant l'information sur la base physiologique de la limitation du rendement avec de nouveaux instruments de sélection physiologique tels que CTD, g_s, et réflectance spectrale, la probabilité d'accélérer le taux de progrès génétique à travers l'amélioration génétique végétale devrait augmenter de façon significative.*

Mots-clés : *Amélioration génétique du blé, caractères de sélection, efficacité de l'utilisation du rayonnement.*

Introduction

Reviews of progress made in wheat breeding reveal a number of interesting trends. In the first place genetic gains in yield seem to have remained relatively steady over the last 30 years, averaging a little under 1% per year in favorable environments (Calderini *et al*., 1999). In addition, while yield progress is strongly associated with improved partitioning of assimilates to grain, little progress appears to have been made in improving biomass (Slafer *et al*., 1994; Calderini *et al*., 1997). Reduced height (*Rht*) genes have had the greatest impact on wheat yield, and studies in near isogenic backgrounds have shown, that yield improvement attributable to the *Rht* genes are associated with higher harvest index. In contrast, radiation use efficiency (RUE) and light interception characteristics have remained unaffected (Miralles and Slafer, 1997). Nonetheless, recent examination of yield progress in irrigated spring wheat showed that biomass has been increased approximately 10% in the latest CIMMYT cultivars (Reynolds *et al.*, 1999); in one case being associated with the introgression of disease resistance gene *Lr19* from a wild grass species.

Although encouraging, these results do not indicate any acceleration in the rate of genetic yield gains in recent years, while global demand for wheat is predicted to increase by 1.6% per year over the next 20 years (Rosengrant *et al.*, 1995). Given the environmental implications associated with increasing land use, and the cost and complexity of further reducing the relatively small yield gaps in high production areas (Pingali and Heisey, 1999), improving genetic yield potential of wheat may be the most cost-effective solution for meeting future demands. To keep pace with global demand for wheat, The International Maize and Wheat Improvement Center (CIMMYT) and its collaborators are considering a number of new interdisciplinary approaches. These are based on physiological evidence accumulated over a number of years and attempt to accelerate breeding progress (Reynolds *et al.*, 1999, 2000).

A summary of these ideas is presented. Attention is given to traits that may improve RUE, a trait which is especially important in the light of the theoretical limit to harvest index, estimated at approximately 60% (Austin *et al.*, 1980). The issue of manipulating source-sink balance is addressed, since it may impact on both partitioning to grain yield as well as RUE. The integration of rapid physiological screening tools as standard breeding procedure into breeding programs is addressed as a means of improving the efficiency of breeding and hence the probability of identifying new combinations of genes which interact favorably in different genetic backgrounds.

Radiation use efficiency

Selection for leaf photosynthetic rate

In breeding studies where progeny have been selected for greater leaf photosynthetic (net assimilation, A_n) rate, the trait was shown to be heritable, but not generally associated with genetic gains in yield (Nelson, 1988). Increased photosynthesis would not be expected to improve performance where yield is not primarily assimilate limited, and there is evidence to support that this is the case in many crops. In addition, yield and biomass are determined by the integration of many metabolic processes, including canopy photosynthesis of which individual leaf photosynthesis is one component representing a single snap-shot in time.

Nonetheless, a small number of studies have indicated an association between yield of spring wheat lines and A_n (see Fischer *et al.*, 1998). When A_n was measured under temperate conditions on a series of eight lines representing breeding progress at CIMMYT from 1962 to 1988, it was associated with yield improvement (both yield and A_n increased approximately 25% over the series), but not with greater biomass (Fischer *et al.*, 1998). Although yield was not associated with biomass, there was an association with increased harvest index and grain number. This indicates that higher A_n measured during grain filling was probably a pleiotropic effect of improved partitioning driven by the larger grain number of more modern lines. This conclusion is supported by work using isogenic lines contrasting in the *Rht* gene. The *Rht* gene is well documented to improve the partitioning of assimilates to grain yield in comparison to non-grain biomass (Gale and Youssefian, 1985). In our study, a total of 16 pairs of spring wheat isolines were grown in replicated yield plots, and canopy temperature depression (CTD) was measured approximately every 7 days between canopy closure and approximately 15 days after heading. CTD values were larger for the better yielding *Rht* isolines only after grain filling had commenced. Given that CTD has been shown to be associated with stomatal conductance and A_n (Reynolds *et al.*, 1994; Fischer *et al.*, 1998), the results suggest that greater sink demand during grain filling associated with the *Rht* allele led to increased rates of A_n.

However, for wheat cultivars grown in a warm, irrigated environment, higher A_n was associated with both higher yield and biomass indicating that A_n may have reflected a higher overall rate of net canopy photosynthesis (Reynolds *et al.*, 1994). More recent work in the same environment showed genetic gains in yield in response to selection for flag leaf photosynthetic rate and stomatal conductance in F_5 sister lines (Fig. 1). The percentage increases in A_n and yield was of a similar magnitude, and increased A_n was associated with biomass and stomatal conductance (Table 1).

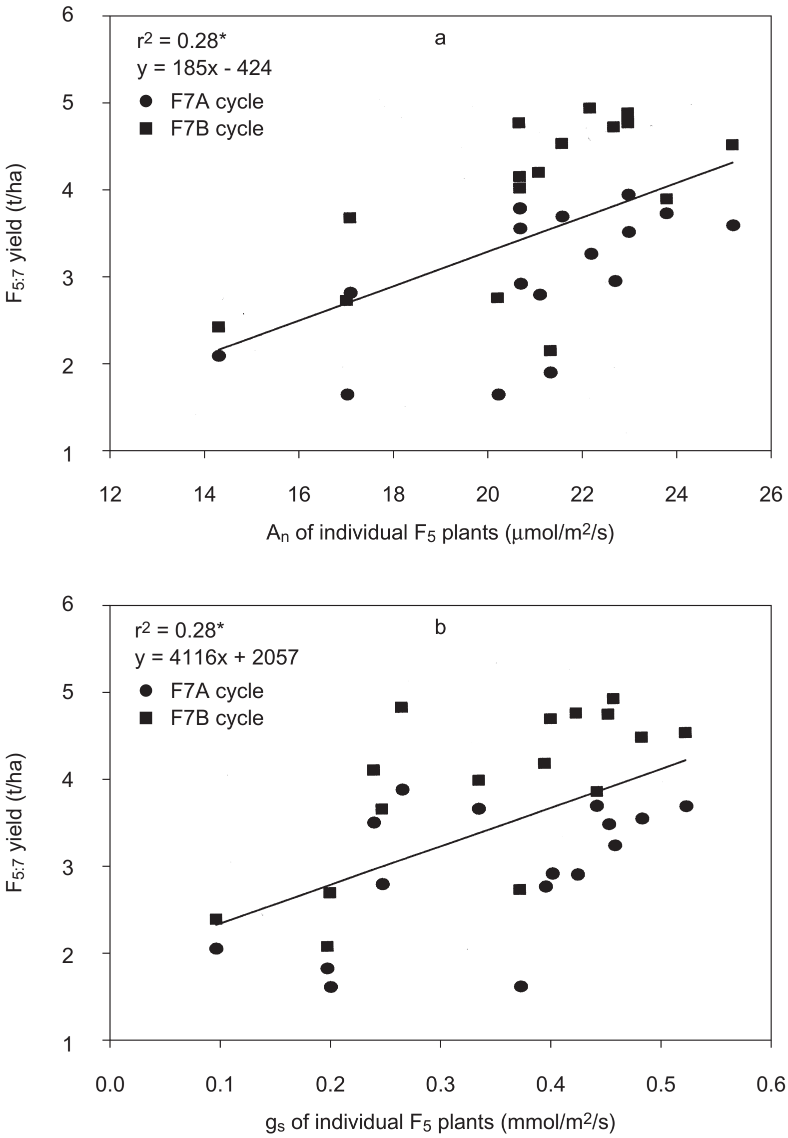

Fig. 1. (a) Relationship between $F_{5:7}$ grain yield and leaf photosynthesis rate (A_n) of individual F_5 plants. (b) Relationship between $F_{5:7}$ grain yield and stomatal conductance (g_s) of individual F_5 plants. (*) Significant at p = 0.05 (Gutiérrez-Rodríguez *et al.,* 2000).

Table 1. Correlation between photosynthetic traits measured of 16 individual F_5 plants and performance in $F_{5:7}$ yield plots, 1995-1996, Tlaltizapán, Mexico

Individual F_5 plants (grain filling)	$F_{5:7}$ yield plots		
	Yield	Biomass	A_n
A_n	0.66**	0.67**	0.68**
Stomatal conductance	0.65**	0.68**	0.68**
Intercellular CO_2 concentration	0.70**	0.65**	0.55*

The demonstration of an association between A_n and yield is of considerable relevance to breeding because photosynthesis or related traits could be used as early generation selection criteria to identify higher-yielding genotypes among segregating generations. This issue will be addressed in a subsequent section.

Canopy photosynthesis

Erectophile leaf canopies are believed to increase crop assimilation rates, especially in high radiation environments, and several lines of evidence have supported this idea (Innes and Blackwell, 1983; Araus *et al.*, 1993). Germplasm collections were screened for erect leaves at CIMMYT in the early 1970s, and the trait introgressed into the wheat germplasm pool. More erect leaf canopy types are characteristic of many of CIMMYT's best yielding wheat lines. Genetic manipulation of leaf angle is not complex and is thought to be controlled by only two to three genes. However, an important question is whether manipulation of leaf angle will permit further gains in RUE over current high yielding agronomic types. Indirect evidence supports this notion. For example, when comparing two of the highest yielding CIMMYT cultivars, Bacanora 88 and Baviacora 92, the former has a partially erectophile leaf canopy, while the latter, which has a higher biomass, has lax leaves.

Another way of improving canopy photosynthesis may be optimising the composition of the photosynthetic apparatus and N distribution throughout the canopy, so that leaf photosynthesis is equally efficient at different light intensities. Studies with lucerne (Evans, 1993) showed a clear trend for reduced total leaf N at greater depth in the canopy. In addition, chlorophyll *a:b* ratios declined with depth, indicating an increased ability to capture scarce light by increasing investment in chlorophyll associated with the light harvesting antennae, relative to the reaction centers. This was consistent with a lower total N to chlorophyll ratio, reflecting a smaller investment in soluble protein associated with CO_2 fixation. Consequently, lower leaves had a reduced overall photosynthetic capacity in normal light, but equally efficient RUE per unit of N at the light intensities experienced towards the bottom of the canopy. Crop models support the advantage of optimizing vertical distribution of canopy nitrogen in wheat.

Stem reserves and green leaf area duration

There are a number of additional physiological traits that have implications on yield potential and are related to increasing assimilate (i.e. source) availability. One is the ability to reach full ground cover as early as possible after emergence to maximize the interception of radiation (Richards, 1996). Another is remobilization of soluble carbohydrates (stem reserves) during grain filling (Stoy, 1965). A third is the ability to maintain green leaf area duration "stay green" throughout grain filling. Direct evidence for the contribution of these traits to high yield potential is lacking. Stem reserves apparently make a greater contribution to performance in relative low yielding lines where contrasting lines have been examined (Stoy, 1965). It has also been suggested that utilization of stem reserves and stay green may be mutually exclusive, since loss of chlorophyll and stem reserve mobilization seem to be consequences of plant senescence. A greater understanding of the genetics of these traits is warranted to establish the potential for breaking such linkage. As yield potential is raised by improving reproductive sinks, additional assimilation capacity will become more important. In theory, extra assimilates gained by increasing early ground cover could contribute to increased stem reserves and be tapped at later reproductive stages to enhance potential kernel number and size. A longer stay green period would improve the likelihood of realizing that potential.

Manipulation of source-sink balance

Source versus sink limitation

Many studies have been conducted in wheat to investigate whether source or sink were the principle yield limiting factor. A quantitative analysis was made by Slafer and Savin (1994) to establish a relationship between assimilate supply and response of grain mass in wheat using data from 15 studies where source-sink balance was manipulated by degraining or shading treatments. When comparing the relative change in assimilate supply with the relative change in grain mass, a 1:1 response was not apparent. The relationship suggested that yield was either entirely sink limited (i.e. no response to assimilate supply) or co-limited by sink and source (i.e. proportionally lower response of grain weight in comparison to change in assimilate supply). Studies on cultivars representing historical yield gains indicate that while modern cultivars are still largely sink limited, they appear to have less excess assimilate than older cultivars (Kruck *et al.*, 1997).

If yield gains are to be achieved through increasing RUE, one route may be through simultaneously increasing capacity for both photo-assimilation capacity as well as sink strength (Richards, 1996; Kruck *et al.*, 1997). The way to achieve this may be to focus on improving assimilate supply during spike development thereby increasing sink capacity, which itself would drive higher assimilation rates during grain filling. Most experiments indicate that yield, as determined by grain number, is limited by growth factors during the period of juvenile spike development prior to anthesis.

Manipulation of phenology

The rapid spike growth phase (RSGP) which has a duration of approximately 20 days in irrigated spring wheat, is critical in determining wheat yield potential. It is when final grain number is set, not only determining the partitioning of photo-assimilates to yield, but also influencing photosynthetic assimilation rate during seed filling. The relative duration of the juvenile spike growth period shows genetic variability (Slafer and Rawson, 1994). This variation is determined by the different alleles present for *Ppd* and *Vrn* genes (conferring photoperiod and vernalization sensitivity respectively) as well as those influencing earliness *per se*, and how they interact with photoperiod and temperature. Slafer has hypothesised that final grain number and yield potential may be improved by manipulating these genes so as to increase the relative duration of RSGP. The idea stems from the notion that increased partitioning of photo-assimilates to spike growth will increase floret survival. Comparison of different radiation regimes during juvenile spike growth lend support to the hypothesis (Slafer *et al.*, 1994; Abbate *et al.*, 1997). Recently, the duration of RSGP has been manipulated using short day photoperiod treatment on wheat and barley, showing a highly significant relationship between its duration and number of fertile florets per spike (Miralles and Richards, 1999). Other recent work has shown the potential for grain weight potential to be increased when assimilate supply to developing grains was increased during the latter part of RSGP by selectively removing grains within the spikelet (Calderini and Reynolds, 2000). Increasing the duration of RSGP may, therefore, improve grain weight potential in addition to grain number.

Modifying spike anatomy

Wheat breeders have succeeded at increasing the crop sink capacity by manipulation of the spike morphology. Dencic (1994) crossed genotypes with branched tetrastichon (two spikelets per node of the rachis) with high yielding lines that contained other desirable traits. After ten years of breeding and selection, four lines were developed with 13% higher yields (approximately 1 t/ha) than the standards. This was related to improvement in the following traits, spike length (16%), number of spikelets/spike (10%), grains/spikelet (9%), and grains/m^2 (18%). The fact that the original tetrastichon donor lines had severe problems of sterility and low kernel weight, indicates that through exhaustive recombination and selection, the high sink potential of the tetrastichon trait was complemented by other (unknown) traits, permitting it to be expressed through higher yield potential. The multiovary trait is another character, which could be exploited in a similar fashion.

Analysis of genotype by environment interaction

Manipulation of source-sink balance is a likely avenue to achieve gains in RUE given that even modern cultivars still seem to be more sink than source limited. However, the critical and difficult task will be to optimize the balance of source and sink throughout the life cycle of the plant. During its life cycle wheat experiences a wide range of environmental conditions, to which, almost by definition, it cannot be equally well adapted to. The fact that genotypes can be sensitive to relatively small changes in environmental conditions is indicated by the genotype by environment interaction for yield that is frequently observed within similar cropping environments.

Statistical analyses were performed to help elucidate the physiological basis of genotype by environment interaction in spring wheat by partitioning the interaction term to environmental data (i.e. meteorological measurements collected during the growth cycle) using partial least squares analysis (Vargas *et al.*, 1998). For varieties grown under irrigation, either in the same environment over years (temperate environment) or in similar environments within a defined agro-climatic region (warm environment), genotype by environment interaction for yield in both cases was best associated with variation in night temperatures during the spike growth phase. This result confirmed the critical nature of spike growth in determining yield. One might speculate further that the differential genetic sensitivity to higher night temperatures is related to acceleration of developmental rate and/or high dark respiration rates, either of which could prejudice spike growth at high temperature. For genotypes grown under temperate conditions, interaction in the performance was also explained by differences in radiation, while in the warmer regions maximum temperature had a more significant effect. This makes sense, since radiation is the principal yield limiting factor in temperate sites, while in warmer regions temperature are more likely to limit photosynthetic rates. Such analyses provide important clues as to which mechanisms are sensitive to environment and may therefore be restricting genetic yield potential. They also suggest that interaction of genotype with environment can be related to both source and sink constraints.

Empirical approaches to breeding using physiological strategies

Breeding for complex traits

The interaction of genotypes with environment discussed above illustrates how complex the issue of crop improvement is. Even the modification of a single process such as photosynthetic rate is not a simple genetic exercise due to its metabolic complexity, involving many enzymes. This is almost certainly why empirical plant selection has been successful, and ideotype breeding not so. The power of empirical selection for raising yield potential is that by crossing diverse high yielding parents with good combining ability, there is a good probability of creating new synergistic gene combinations. After selecting progeny in early generations based on knowledge of high yielding "agronomic types", favorable epistatic or additive gene action can then be identified in subsequent yield trials. Since good agronomic performance in a genotype requires complementarity among many different traits, recombinant lines are usually inferior to both parents (traits conferring superior agronomic performance not having been fixed during the evolution of the genome). However, there is a small chance that new allelic combinations at target genes will be identified which outperform the parents. As additive effects are fixed in a mature breeding program, progress for complex traits like yield and RUE will depend more on epistasis or background effects, therefore making genetic progress more difficult to attain. The use of physiological selection tools to help improve the efficiency of empirical breeding may be one approach to improve the likelihood of success.

Using stomatal aperture related traits to select for yield

Physiological criteria in general have seldom been successfully used as selection criteria in breeding programs (Slafer *et al.*, 1994). However, with modern apparati physiological parameters are relatively simple to measure in the field. Stomatal conductance (g_s) and canopy temperature depression which are easier to measure than A_n, have been demonstrated to be associated with performance of irrigated wheat under high radiation levels (Reynolds *et al.*, 1994; Fischer *et al.*, 1998). Because both g_s and canopy temperature depression are influenced through feedback mechanisms by a number of physiological processes such as photosynthesis, vascular transport, and source-sink relationships, these traits may give an indication of a line's physiological adaptation to a given environment, a factor that is difficult to assess visually. In addition, because such traits can be measured rapidly and non-destructively they have potential in breeding. Given the scale of most breeding programs, traits that can indicate physiological fitness in small plots or in individual plants in early generations could significantly improve selection efficiency.

Canopy temperature depression

When water evaporates from the surface of a leaf it becomes cooler, and the rate of evaporative cooling is affected directly by stomatal conductance, which itself is affected by feedback mechanisms of other processes such as photosynthetic metabolism and vascular transport. Canopy temperature depression, therefore, is a good indicator of a genotype's physiological fitness, since a high value will be indicative of good expression for all of those traits under a given set of environment conditions. The trait can be measured in a few seconds with an infrared thermometer, which measures the surface temperature of a field plot. Since the reading integrates the temperatures of plant organs over a small area of the canopy, error associated with plant to plant variability is reduced. CTD measured on irrigated yield trials showed a good association with plot performance, but in addition to being a good predictor of yield *in situ*, CTD showed a significant association with performance of the same lines grown at a number of target breeding locations (Reynolds *et al.*, 1994). Further work confirmed the potential for making genetic gains in response to selection for CTD in recombinant inbred lines. Recently CIMMYT breeders successfully used CTD measured on small plots in their heat tolerance nurseries to identify the highest yielding entries. Genetic correlation coefficients of 0.6-0.8 were observed between final yield and CTD measured during grain filling, indicating the potential of this technique to pre-screen for physiological potential, prior to the execution of expensive yield trials (van Ginkel *et al.*, unpublished data).

Aerial infrared imagery

Recent results from NW Mexico showed that aerial infrared (IR) images collected at a height of 800 m had sufficient resolution to detect CTD differences on relatively small plots (1.6 m wide). The data, collected from an IR radiation sensor mounted on a light aircraft, showed positive correlations with final grain yield for a set of random derived recombinant inbred lines as well as a set of advanced breeding lines (Table 2). The results indicate the potential of aerial IR imagery as a means of screening thousands of breeding lines in a few hours for CTD (Reynolds *et al.*, 1999).

Table 2. Comparison of CTD data from aerial IR imagery with hand-held IR thermometers, Obregon 1996-1997, NW Mexico (adapted from Reynolds *et al.,* 1999)

Trial	n	Correlation of CTD with yield			
		Aerial		Hand-held	
		Phenotypic	Genetic	Phenotypic	Genetic
RILs (Seri82*7C66) random derived sisters	81	0.40**	0.63**	0.50**	0.78**
Advanced lines bread wheat	58	0.34**	–[†]	0.44**	–

**Statistical significance at 0.01 level of probability.

[†]– Genetic correlations not calculated due to design restrictions.

Spectral reflectance

Another technique which may have application in screening for physiologically superior progeny is spectral reflectance (SR) which can be used to estimate a range of physiological characteristics including canopy chlorophyll content, absorbed PAR, leaf area index, and plant water status (Araus, 1996). These traits are associated with absorption of very specific wavelengths of radiation (e.g. water absorbs energy at 970 nm). Solar radiation reflected by the crop is measured, and calibrated against light reflected from a white surface. Different coefficients can be calculated from specific bands of the crop's absorption spectrum, giving a semi-quantitative estimate (or index) of a number of such characteristics. Preliminary studies showed significant associations between crop performance and a number of SR indexes (Reynolds *et al.*, 1999).

An integrated approach to plant breeding

By combining information on the physiological basis of yield limitation with new physiological selection tools, the probability of accelerating the rate of genetic progress through plant breeding should be significantly increased. Parents can be selected for improved physiological and anatomical traits and crossed to high yielding agronomically elite materials. Good performance in a genotype requires complementarity among a number of different traits so that better performance can be expressed. By promoting a large numbers of progeny in the breeding process there is a chance of identifying phenotypes where favorable interactions among genes permit the expression of higher yield. The probability of selecting these lines can be enhanced by: (i) eliminating inferior agronomic phenotypes visually in early generations; (ii) selecting superior physiological phenotypes using rapid detection techniques such as IR thermometry in intermediate generations; and (iii) selecting for higher performance in yield trials in advanced generations.

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