Rothamsted Repository Download

B - Book chapters etc edited externally

Foulkes, J., Furbank, R. and Parry, M. A. J. 2012. Opportunities to improve genetic wheat yield potential. in: Reynolds, M., Mullan, D. and Pask, A. (ed.) Physiological breeding I: interdisciplinary approaches to improve crop adaptation Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT) Mexico. pp. 43-50

The output can be accessed at:

https://repository.rothamsted.ac.uk/item/8qq5y/opportunities-to-improve-genetic-wheat-yield-potential.

© 1 January 2012, Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT) Mexico.

23/09/2019 14:44   repository.rothamsted.ac.uk   library@rothamsted.ac.uk

Chapter 4: Opportunities to improve genetic wheat yield potential

Matthew Reynolds[1], John Foulkes[2], Robert Furbank[3], Martin Parry[4]

[1]CIMMYT. Int. Apdo. Postal 6-641, 06600 Mexico, DF, Mexico.
[2]The University of Nottingham, United Kingdom.
[3]High Resolution Plant Phenomics Centre, CSIRO Plant Industry, Australia.
[4]Rothamsted Research, Harpenden, Hertfordshire, United Kingdom.

Abstract

Wheat yield potential could be increased by 50% or more –theoretically– through the genetic improvement of radiation use efficiency (RUE). However, to achieve agronomic impacts, structural and reproductive aspects of the crop must also be improved. Attempts to increase RUE will focus on increasing the efficiency of Rubisco, introduction of C4-like traits such as CO_2 concentrating mechanisms, and improvement of light interception and photosynthesis at the spike and whole canopy levels. For extra photo-assimilates to translate into increased grain yield, reproductive aspects of growth must be fitted to a range of agro-ecosystems to ensure that stable expression of a high harvest index (HI) is achieved. Adequate partitioning among plant organs will be necessary to achieve favorable expression of HI, and to ensure that plants with heavier grain have strong enough stems and roots to avoid lodging. Trait-based crossing strategies will aim to achieve their simultaneous expression in elite agronomic backgrounds and wide crossing will be employed to augment genetic diversity where needed. Genomic selection approaches will be employed, especially for difficult-to-phenotype traits. Products will be delivered to national wheat programs worldwide via CIMMYT's international nursery systems and are expected to make a significant contribution to global food security.

Introduction

Increases in wheat productivity have been achieved worldwide as a result of adoption of Green Revolution technologies (Evenson and Gollin, 2003). Nonetheless, the challenges of increasing production to feed a world population of 9 billion by mid century are considerable. Less developed countries are particularly vulnerable in terms of food security for three main reasons: firstly, most are net importers of cereals (Dixon *et al.,* 2009). Secondly many of their national wheat programs lack sufficient capacity to meet demand (Kosina *et al.,* 2007). Finally, the majority are located in climate vulnerable regions (Lobell *et al.,* 2008). While international public wheat breeding has focused in recent decades on increasing resistance to disease and abiotic stress (Reynolds and Borlaug, 2006; Braun *et al.,* 2010), efforts to raise genetic yield potential *per se* have received little attention. In fact the fundamental bottleneck to raising productivity, namely radiation use efficiency (RUE), has barely changed.

Research in photosynthesis suggests that improvements in yield are theoretically possible (Long *et al.,* 2006; Parry *et al.,* 2007; Zhu *et al.,* 2010). These consider the inefficiency of carbon fixation in C3 crop and compare it with that of C4 crops which show up to 50% greater RUE. In wheat, genetic modification of Rubisco and its regulation are major targets to improve photosynthetic efficiency (Parry *et al.,* 2007); a more ambitious approach in rice is to introduce the characteristics of C4 photosynthesis (Furbank *et al.,* 2009). While increasing photosynthetic potential will require research to focus at cellular and sub-cellular processes, this must go in parallel with genetic modification of structural and reproductive aspects of growth, since these determine the net agronomic benefit of increased RUE. Specifically, adaptation of the reproductive processes to variation in seasonal and other environmental factors, while relatively poorly understood, determines the efficiency with which photo-assimilates are converted to yield (Reynolds *et al.,* 2009a). Furthermore, even at current levels of yield potential, a significant portion of wheat yield worldwide is already lost due to lodging (Berry *et al.,* 2004). In summary, to achieve impacts under agronomic conditions, the following broad objectives must be tackled simultaneously: (i) increase crop biomass through modification of RUE, (ii) improve targeted adaptation of reproductive processes to major wheat agro-ecosystems thereby permitting increases in RUE to be consistently translated to grain weight, and (iii) enhance plant structural characteristics to ensure that grain yield potential and quality are not sacrificed due to lodging.

To achieve these objectives, the International Maize and Wheat Improvement Center (CIMMYT) began consulting with crop experts worldwide culminating in the formation of a Wheat Yield Consortium (WYC) (Reynolds *et al.,* 2011). The remit of the WYC is, through linking ongoing research worldwide, to develop a cohesive portfolio of research activities to maximize the probability of impact in farmers' fields (Figure 4.1).

Overview of research approaches to raise the yield potential of wheat

WYC includes expertise within three linked themes:

1) Increasing photosynthetic capacity and efficiency.
2) Optimizing partitioning to grain yield while maintaining lodging resistance.
3) Breeding to accumulate yield potential traits and delivery of new germplasm.

Within each of these, a set of sub-projects (SPs) has been developed (Table 4.1) in a way that capitalizes on pre-existing knowledge and ongoing research. In the following three sections, the broad objectives of the three themes are presented in context of how research products will translate into new traits for use in breeding and eventually the delivery of new wheat cultivars. Further details for all three Themes have been published separately (Parry *et al.,* 2011; Foulkes *et al.,* 2011; Reynolds *et al.,* 2011).

Theme 1: Increasing photosynthetic capacity and efficiency

To achieve a quantum increase in crop yield potential a major improvement in photosynthetic capacity and/or efficiency will be required. In rice, potential grain number has increased markedly in the new rice types but only around 40% of these florets are fertilized and filled (Sheehy *et al.,* 2007), indicating "source" limitation by insufficient provision of photosynthate at key developmental stages. In wheat, while "sink" strength of grain and photosynthetic
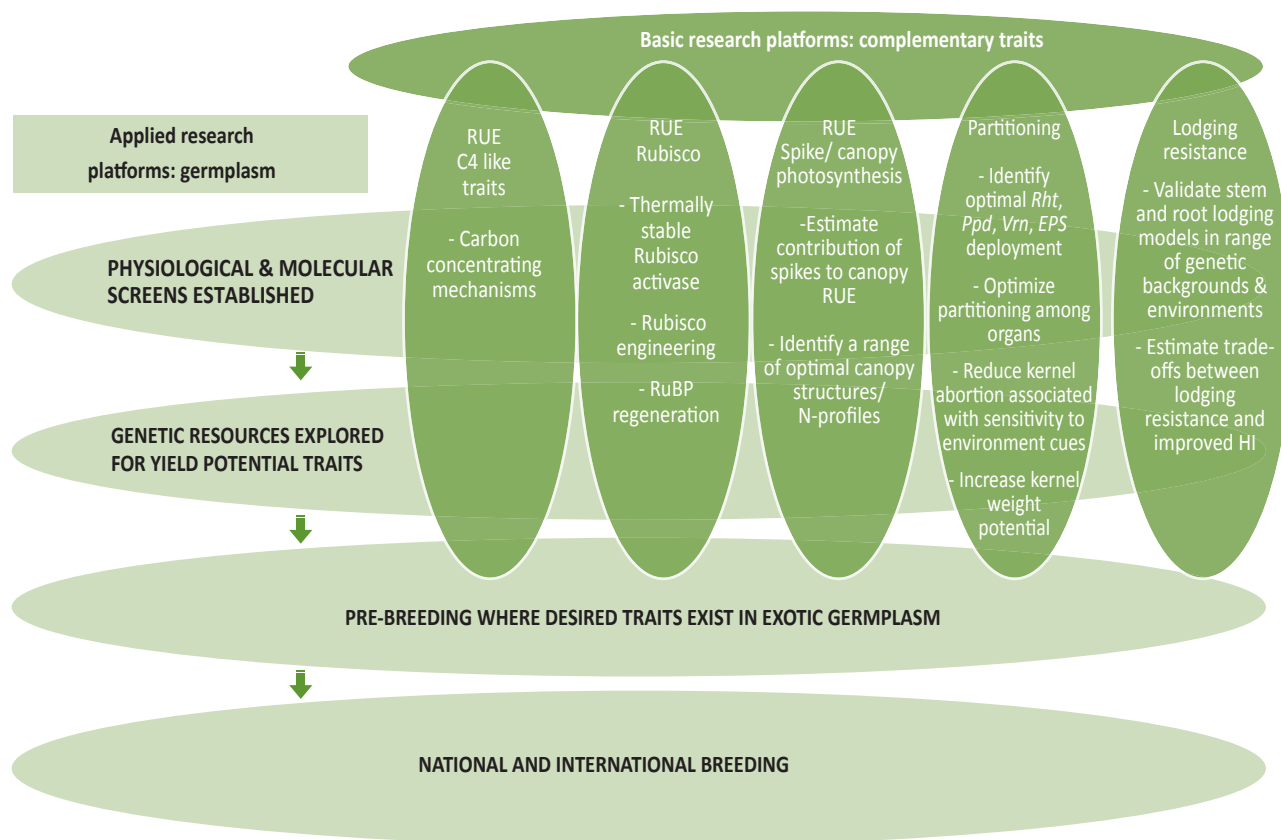

Figure 4.1. A research strategy to improve yield potential of wheat. Where: HI = harvest index; RUE = radiation use efficiency.

capacity may be more in balance, there is also evidence that historic gains in wheat yield potential have been associated with increased photosynthesis (Fischer *et al.,* 1998). Furthermore, basic research in photosynthesis has confirmed that substantial improvements are theoretically possible (Parry *et al.,* 2007; Zhu *et al.,* 2010).

Two approaches will be investigated for increasing total crop biomass. They both aim to increase photosynthetic efficiency and capacity by targeting the first step of CO_2 fixation in C3 photosynthesis, catalysed by Rubisco, and the subsequent regeneration of the co-substrate for this enzyme, Ribulose-1,5-bisphosphate (RuBP). Rubisco operates at low catalytic efficiency and also catalyses an oxygenation reaction (initiating photorespiration) which wastes carbon and energy (See Zhu *et al.,* 2010). The first approach has multiple components (Table 4.1). A component intended to achieve application in the 5-year timeframe is to target the properties of the Rubisco protein and associated photosynthetic machinery (Parry *et al.,* 2007) by phenotypic screening of diverse sources of germplasm for photosynthetic performance at the whole leaf or canopy level using direct measurement

Table 4.1. Sub-projects (SPs) of the Wheat Yield Consortium.

Theme 1: Increasing photosynthetic capacity and efficiency
SP1.1   Phenotypic selection for photosynthetic capacity and efficiency
SP1.2   Capturing the photosynthetic potential of spikes
SP1.3   Optimizing canopy photosynthesis and photosynthetic duration
SP1.4   Chloroplast CO_2 pumps
SP1.5   Optimizing RuBP Regeneration
SP1.6   Improving the thermal stability of Rubisco Activase
SP1.7   Replacement of LS Rubisco

Theme 2: Optimizing partitioning to grain while maintaining lodging resistance
SP2.1   Optimizing harvest index through increasing partitioning to spike growth and maximizing grain number
SP2.2   Optimizing developmental pattern to maximize spike fertility
SP2.3   Improving spike fertility through modifying its sensitivity to environmental cues
SP2.4   Improving grain-filling and potential grain size
SP2.5   Identifying traits and developing genetic sources for lodging resistance
SP2.6   Modeling optimal combinations of, and tradeoffs between, traits

Theme 3: Breeding to accumulate yield potential traits
SP3.1   Trait and marker based breeding
SP3.2   Wide crossing to enhance photosynthetic capacity
SP3.3   Genomic selection to increase breeding efficiency
SP3.4   Germplasm evaluation and delivery

coupled with mathematical modeling. This phenomics approach will define sets of germplasm with variation in Rubisco properties and associated regulatory proteins such as Rubisco activase (Table 4.1, SPs 1.1, 1.2 and 1.3). This will be coupled with a project to screen for improved photosynthetic capacity in spikes which can contribute a large proportion of grain carbon (see Gebbing and Schneider, 1999; Table 4.1, SP 1.2).

Genetic engineering will be used to improve RuBP regeneration, Rubisco activase (Table 4.1, SP 1.4) or to introduce Rubisco subunits with enhanced catalytic properties (Table 4.1, SP 1.6). Under conditions of low light and elevated CO_2 the regeneration of RuBP limits photosynthetic carbon assimilation. There is clear experimental evidence that manipulation of RuBP regeneration by over expressing sedoheptulose-1,7-bisphosphatase (SBPase) can increase plant productivity in controlled environments. Modeling approaches also suggest increased benefit from the over-expression of fructose-1,6-bisphosphate aldolase (FBPA). In SP 1.5 (Table 4.1), RuBP regeneration capacity in wheat will be increased by over-expressing both SBPase and FBPA which is predicted to increase yields by around 10% (Reynolds *et al.,* 2009a). For Rubisco activase, genetic variation in heat stability has been established in a range of plant species and the residues responsible mapped in *Arabidopsis* (Salvucci and Crafts-Brander 2004; Kurek *et al.,* 2007). In SP 1.6 (Table 4.1) Rubisco activase will be reengineered to increase its thermotolerance, with the aim of broadening the temperature range for photosynthesis.

Much progress has been made in identifying natural variation in the catalytic properties of Rubisco from different species and in developing the tools for introducing Rubisco genes into plants. Modeling suggests that very large increases in photosynthetic performance should be possible (Parry *et al.,* 2007) by introducing existing Rubisco variants from other plant species. In a longer term approach, SP 1.7 (Table 4.1) recognizes this potential and will develop plastid transformation for wheat.

Another approach is to mimic systems that already exist in nature which concentrate CO_2 in the compartment where Rubisco is located, eliminating photorespiration and ensuring Rubisco operates close to its catalytic optimum. These systems are present in C4 plants, where a biochemical CO_2 concentrating mechanism has evolved many times, capable of elevating CO_2 at the site of Rubisco up to 10-fold over atmospheric levels (von Caemmerer and Furbank, 2003). There is currently an International Consortium attempting to install a C4

pathway in rice (Furbank *et al.,* 2009), however, the complexity of the anatomical and biochemical traits necessary for this mechanism to operate is daunting and the minimal set of genes necessary unknown. In many algae and cyanobacteria, however, CO_2, in the form of bicarbonate, is pumped across membranes to elevate CO_2 to even higher levels than those seen in C4 plants (Price *et al.,* 2008). Only one or two genes are required for this transformation and these are now cloned and functionally validated (Price *et al.,* 2008). If these transporter proteins could be placed in the chloroplast membrane of wheat and the system functions as it does in algae and cyanobacteria, large increases in photosynthetic efficiency would result (Table 4.1, SP 1.4).

In summary a range of options –both transgenic and non-transgenic– exist to raise RUE in wheat, some of which may be physiologically complementary or genetically additive. Further exploration of genetic diversity within and outside the Triticeae tribe will eventually determine which approaches are most likely to be implemented in breeding.

Theme 2: Optimizing partitioning to grain yield while maintaining lodging resistance

Adaptation of reproductive processes to environment is still considered among the most challenging aspects of cereal improvement (Barnabas *et al.,* 2008). While increases in harvest index (HI) have been achieved since the Green Revolution period (Sayre *et al.,* 1997; Shearman *et al.,* 2005) their physiological and genetic basis is not well established. For wheat, this is in part because it is grown across widely divergent temperature regimes and latitudes, and in extreme cases, poor adaptation can result in negligible yield despite the expression of a significant crop biomass. Key physiological components include developmental response to vernalization, photoperiod, and other environmental factors that influence intra-plant competition for growth resources (Fischer, 1985; Slafer and Rawson, 1994; Ugarte *et al.,* 2007; Ghiglione *et al.,* 2008). It has been shown that spike fertility can be improved by increasing the availability of assimilates to the developing spike (Fischer, 1985), thereby reducing the early abortion of grains (Miralles and Slafer, 2007) or by increasing grain weight potential (Calderini and Reynolds, 2000; Duggan and Fowler, 2006). Both processes are affected by photosynthetic capacity, intra-plant competition between organs for assimilates, and their interaction with environmental signals that respond to photoperiod, temperature, water and nutritional

status. The photosynthetic capacity of contemporary germplasm may not even be utilized efficiently if spike fertility is not optimized (Reynolds *et al.,* 2009a).

One candidate gene that has been identified for spike fertility *per se* –Gn1a in rice– codes for cytokinin oxidase which through its regulation of cytokinin levels influence numbers of reproductive organs in the panicle (Ashikari *et al.,* 2005). The apparent involvement of growth regulators in determining grain number suggests that a better understanding of plant signaling (Davies *et al.,* 2005) may be the route to explaining the interaction of spike fertility with environment and its genetic basis.

SPs 2.1, 2.2, 2.3, and 2.4 (Table 4.1) specifically aim to better understand these interactions and identify reliable physiological and marker-based selection criteria so that improvements in RUE can be translated into greater agronomic yield potential. In this context, the use of perfect markers associated with height reduction and photoperiod and vernalization responses are expected to provide a valuable genetic underpinning to the research. A principal research target will be to maximize the partitioning of assimilates to the developing spike to increase spike fertility –i.e., potential grain number and grain weight potential. However, plants with increased photosynthetic rate and a larger biomass are likely to require more efficient if not larger root systems. Therefore, the potential tradeoffs associated with different partitioning strategies must be carefully evaluated in the context of which resource is most likely to limit yield.

Adequate partitioning among plant organs is also key to ensuring that plants with heavier grain weight have strong enough stems and roots to avoid structural failure (Berry *et al.,* 2007). Lodging is already a common phenomenon in wheat which can reduce yield by as much as 80% as well as reducing grain quality (Easson *et al.,* 1993; Berry *et al.,* 2004). Any comprehensive strategy to improve wheat yield potential must include lodging resistance since heavier yielding crops will require stronger plants (Table 4.1, SP2.5). Lodging resistance traits are prime candidates for development of molecular markers since at least some of the traits involved (e.g., crown root spread, material strength of stem) are expected to be relatively heritable, yet are not easy to phenotype in the field.

In summary, many traits are involved in optimizing agronomic performance whose genetic basis is independent of increasing biomass or RUE *per se*. Their physiological mechanisms, complex interactions, and

genetic basis will be dissected in this theme. Simulation modeling of these interactions (Table 4.1, SP2.6) will be used to refine the conceptual models used to make breeding decisions in Theme 3. The main output of Theme 2 will be a toolkit –consisting of phenotyping approaches and molecular markers– to facilitate hybridization strategies and progeny selection, such that expression of HI and lodging resistance is optimized in germplasm targeted to major wheat agro-ecosystems systems.

Theme 3: Breeding to accumulate yield potential traits

Trait selection is the foundation of plant breeding and has made continual progress through incorporating the following types of traits: simply inherited agronomic characteristics such as height and flowering time, resistance to a spectrum of common diseases, quality parameters determined by end use, and yield based on multi-location trials (Braun *et al.,* 2010). To accelerate genetic gains in yield in the future, complex physiological traits (PTs) must now be incorporated as additional criteria. The main objective of Theme 3 is to combine PTs deterministically whereby progeny will encompass both strategic traits that improve RUE with those alleles

necessary to maximize agronomic impact at the system level –including PTs associated with HI and lodging resistance– into elite agronomic backgrounds (i.e., disease resistant, appropriate quality parameters, etc). Physiological trait-based breeding approaches have been implemented successfully by CIMMYT, leading to international distribution of a new generation of elite drought adapted lines (Reynolds *et al.,* 2009b). These principles will be adapted to a conceptual platform for designing crosses that combine PTs for yield potential (Figure 4.2) whose progeny will be selected using a combination of visual criteria, precision phenotyping, and molecular marker-assisted approaches (SP3.1). Whole genome selection will also be evaluated in this context –given its utility in maize breeding (Bernardo and Yu, 2007)– since it provides a potentially powerful mechanism for accumulating alleles associated with complementary PTs (SP3.3).

The primary wheat gene pool (i.e., *Triticum aestivum*) may need to be complemented with traits from more exotic sources in cases where conventional ones lack adequate diversity. In fact, inter-specifc and inter-generic crosses within the Triticeae are already routine procedures in wheat breeding (Skovmand *et al.,* 2001;

$$\text{YIELD} = \boxed{\text{LI}} \times \boxed{\text{RUE}} \times \boxed{\text{HI}}$$

SINKS (pre-grainfill):
- **Spike fertility ($\boxed{\text{HI}}$/$\boxed{\text{RUE}}$)**
  - **grain no./weight potential**
  - **phenological pattern -Ppd/Vm-**
  - **avoid floret abortion (signals)**
- **Lodging resistance ($\boxed{\text{HI}}$)**
- **Abort weak tillers ($\boxed{\text{HI}}$)**

SOURCE (grain-filling):
- **Canopy photosynthesis**
  - **light distribution ($\boxed{\text{RUE}}$)**
  - **N partitioning ($\boxed{\text{RUE}}$)**
  - **spike photosynthesis ($\boxed{\text{RUE}}$)**
  - **stay green ($\boxed{\text{LI}}$)**

SINK (grain-filling):
- **Partitioning grain ($\boxed{\text{HI}}$)**
- **Adequate roots for resource capture ($\boxed{\text{HI}}$/$\boxed{\text{RUE}}$)**

SOURCE (pre-grainfill):
- **Light interception ($\boxed{\text{LI}}$)**
- **CO_2 fixation ($\boxed{\text{RUE}}$)***
  - **Rubisco specificity**
  - **Rubisco regulation**
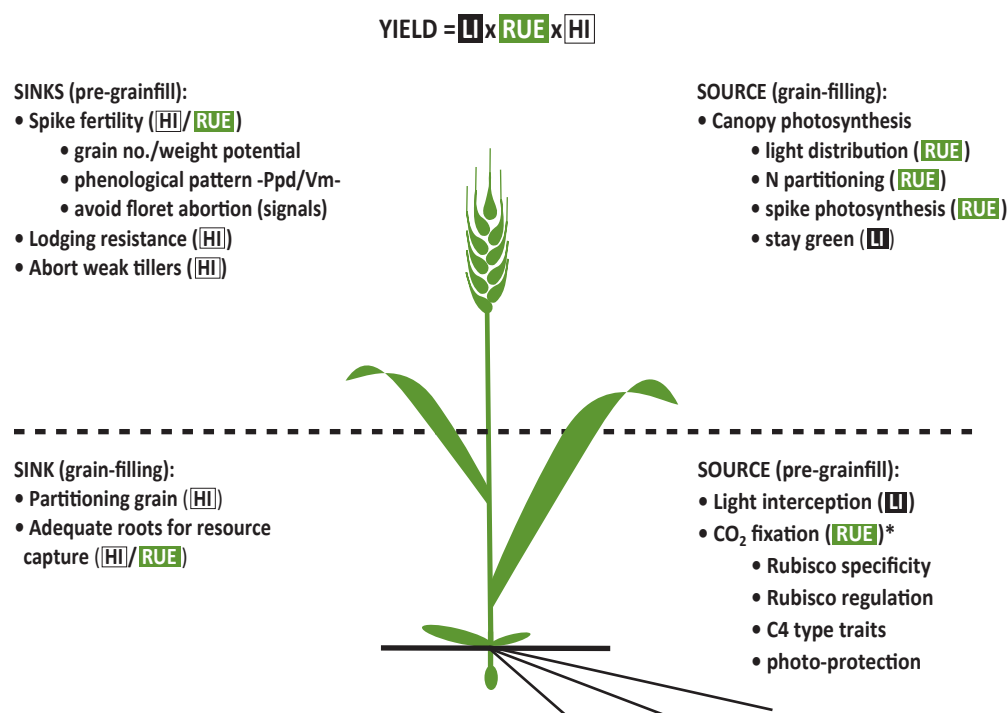 - **C4 type traits**
  - **photo-protection**

Figure 4.2. A conceptual platform for designing crosses that combine complementary yield potential traits in wheat (based on traits reviewed in Reynolds *et al*., 2009a). Traits are categorized as either net sources or sinks of photo-assimilates and their predominant expression is considered either before or during grain-filling, and in some cases both*. Where: HI = harvest index; RUE = radiation use efficiency.

Trethowan and Mujeeb-Kazi, 2008) (Table 4.1, SP3.2). In addition to the many photosynthetic traits, these might include sources of spike fertility and lodging resistance, traits for which sources are already known. Sources of other 'yield improving' traits may yet have to be identified as the limitations of current levels of expression in conventional gene pools are defined by research in Themes 1 and 2.

Both wheat/alien introgression for introducing exotic chromatin and whole genome fusion (to create synthetic polyploids) from wide crosses have had major agronomic impacts throughout the world (Ortiz *et al.,* 2008; Trethowan and Mujeeb-Kazi, 2008). While the introduction of genes from outside of the Triticeae tribe is not a routine procedure in wheat breeding, chromatin from C4 species (maize, *Zea mays* L.; and *Tripsacum dactyloides*) has been introduced into wheat but so far not proven to be stably integrated and transmitted (Laurie and Bennett, 1989; Comeau *et al.,* 1992; Li *et al.,* 1996; Brazauskis *et al.,* 2004). Greater success has been achieved in oat (*Avena sativa* L.) with the production of a complete set of disomic additions of each of the maize chromosomes (Kynast *et al.,* 2001). Expression of C4 photosynthetic enzymes in some of these oat–maize chromosome addition lines has been reported (Knowles *et al.,* 2008). These precedents and the availability of advanced molecular techniques allowing earlier, higher throughput screening and identification of putative introgressions, suggest that with appropriate investment, wide crossing may be able to introduce all of the chromatin into wheat required for full expression of C4 photosynthesis, although this would clearly require considerable effort.

The impact of the above work will depend on effective delivery of products. The International Maize and Wheat Improvement Center –the coordinating institute of the WYC– has for over 45 years coordinated an international wheat breeding effort and through its international nursery system delivers approximately 1,000 new genotypes per year, targeted to the varying needs of national wheat programs in less developed countries (Reynolds and Borlaug, 2006; Braun *et al.,* 2010). Impacts at the farm level are well documented (Lipton and Longhurst, 1989; Evenson and Gollin, 2003). These approaches will be applied and modified as necessary to ensure that new high yielding cultivars are delivered to farmers via their national programs in as short a timeframe as possible (Table 4.1, SP3.4).

References

Ashikari, M., Sakakibara, H., Lin, S., Yamamoto, T., Takashi, T., Nishimura, A., Angeles, E., Qian, Q., Kitano, H. and Matsuoka, M. (2005) Cytokinin oxidase regulates rice grain production. *Science* 309, 741–745.

Barnabas, B., Jager, K. and Feher, A. (2008) The effect of drought and heat stress on reproductive processes in cereals. *Plant, Cell & Environment* 31, 11–38.

Bernardo, R. and Yu, J. (2007) Prospects for genomewide selection for quantitative traits in maize. *Crop Science* 47, 1082–1090.

Berry, PM., Sterling, M., Spink, JH., Baker, CJ., Sylvester-Bradley, R., Mooney, SJ., Tams, AR. and Ennos, AR. (2004) Understanding and reducing lodging in cereals. *Advances in Agronomy* 84, 217–271.

Berry, PM., Sylvester-Bradley, R. and Berry, S. (2007) Ideotype design for lodging-resistant wheat. *Euphytica* 154, 165–179.

Braun, HJ., Atlin, G. and Payne, T. (2010) Multi-location testing as a tool to identify plant response to global climate change. In: Reynolds, MP. (Ed.) *Climate Change and Crop Production*, CABI, London, UK.

Brazauskas, G., Pasakinskiene, I.and Jahoor, A. (2004) AFLP analysis indicates no introgression of maize DNA in wheat × maize crosses. *Plant Breeding* 123(2), 117–121.

Calderini, DF. and Reynolds, MP. (2000) Changes in grain weight as a consequence of de-graining treatments at pre- and post-anthesis in synthetic hexaploid lines of wheat (*Triticum durum × T. tauschii*). *Australian Journal of Plant Physiology* 27, 183–191.

Comeau, A., Nadeau, P., Plourde, A., Simard, R., Maës, O., Lettre, J., Landry, B. and St-Pierre, C-A. (1992) Media for the in ovulo culture of proembryos of wheat and wheat-derived interspecific hybrids or haploids. *Plant Science* 81, 117–125.

Davies, WJ., Kudoyarova, G. and Hartung, W. (2005) Long-distance ABA signaling and its relation to other signaling pathways in the detection of soil drying and the mediation of the plant's response to drought. *Journal of Plant Growth Regulation* 24, 285–295.

Dixon, J., Braun, H-J., Kosina, P. and Crouch, J. (2009) *Wheat facts and futures.* CIMMYT, Mexico, D.F.

Duggan, BL. and Fowler, DB. (2006) Yield structure and kernel potential of winter wheat on the Canadian prairies. *Crop Science* 46, 1479–1487.

Easson, DL., White, EM. and Pickles, SJ. (1993) The effects of weather, seed rate and cultivar on lodging and yield in winter wheat. *Journal of Agricultural Science* 121, 145–156.

Evenson, RE. and Gollin, D. (2003) Assessing the impact of the green revolution, 1960 to 2000. *Science* 300, 758–762.

Foulkes, MJ., Slafer, GA., Davies, WJ., Berry, PM., Sylvester-Bradley, R., Martre, P., Calderini, DF., Griffiths, S. and Reynolds, MP. (2011) Raising yield potential of wheat. III. Optimizing partitioning to grain while maintaining lodging resistance. *Journal of Experimental Botany* 62, 469—486.

Fischer, RA. (1985) Number of kernels in wheat crops and the influence of solar radiation and temperature. *Journal of Agricultural Science* 105, 447–461.

Fischer, RA., Rees, D., Sayre, KD., Lu, Z-M., Condon, AG. and Saavedra, AL. (1998) Wheat yield progress associated with higher stomatal conductance and photosynthetic rate and cooler canopies. *Crop Science* 38, 1467–1475.

Furbank, RT., von Caemmerer, S., Sheehy, J. and Edwards, G. (2009) C4 rice: A challenge for plant phenomics. *Functional Plant Biology* 36, 845–856.

Gebbing, T. and Schnyder, H. (1999) Pre-anthesis reserve utilization for protein and carbohydrate synthesis in grains of wheat. *Plant Physiology* 121, 871–878.

Ghiglione, HO., Gonzalez, FG., Serrago, R., Maldonado, SB., Chilcott, C., Curá, JA., Miralles, DJ., Zhu, T. and Casal, JJ. (2008) Autophagy regulated by daylength sets the number of fertile florets in wheat. *The Plant Journal* 55, 1010–1024.

Knowles, RV., Walch, MD., Minnerath, JM., Bernacchi, CJ., Stec, AO., Rines, HW. and Phillips, RW. (2008) Expression of C4 photosynthetic enzymes in oat–maize chromosme addition lines. *Maydica* 53, 69–78.

Kosina, P., Reynolds, MP., Dixon. J. and Joshi, AK. (2007) Stakeholder perception of wheat production constraints, capacity building needs, and research partnerships in developing countries. *Euphytica* 157, 475–483.

Kurek, I., Chang, TK., Bertain, SM., Madrigal, A., Liu, L., Lassner, MW. and Zhu, G. (2007) Enhanced thermostability of *Arabidopsis* Rubisco activase improves photosynthesis and growth rates under moderate heat stress. *The Plant Cell* 19, 3230–3241.

Kynast, RG., Riera-Lizarazu, O., Vales, MI., Okagaki, RJ., Maquieira, SB., Chen Gang., Ananiev, EV., Odland, WE., Russell, CD., Stec, AO., Livingston, SM., Zaia, HA., Rines, HW. and Phillips, RL. (2001) A complete set of maize individual chromosome additions to the oat genome. *Plant Physiology* 125, 1216–1227.

Laurie, DA. and Bennett, MD. (1989) The timing of chromosome elimination in wheat × maize crosses. *Genome* 32, 953–961.

Li, DW., Qio, JW., Ouyang, P., Yao, QX., Dawei, LD., Jiwen, Q., Ping, O. and Qingxiao, Y. (1996) High frequencies of fertilization and embryo formation in hexaploid wheat × *Tripsacum dactyloides* crosses. *Theoretical and Appied Genetics* 92, 1103–1107.

Lipton, M. and Longhurst, R. (1989) *New seed and poor people*. London: Unwin Hyman Ltd.

Lobell, DB., Burke, MB., Tebaldi, C., Mastrandrea, MD., Falcon, WP. and Naylor, RL. (2008) Prioritizing climate change adaptation needs for food security in 2030. *Science* 319(5863), 607–610.

Long, SP., Zhu, X-G., Naidu, SL. and Ort, DR. (2006) Can improvement of photosynthesis increase crop yields? *Plant Cell and Environment* 29, 315–330.

Miralles, DJ. and Slafer, GA. (2007) Sink limitations to yield in wheat: How could it be reduced? *Journal of Agricultural Science* 145, 139–149.

Ortiz, R., Braun, H., Crossa, J., Crouch, J., Davenport, G., Dixon, J., Dreisigacker, S., Duveiller, E., He, Z., Huerta, J., Joshi, A., Kishii, M., Kosina, P., Manes, Y., Mezzalama, M., Morgounov, A., Murakami, J., Nicol, J., Ortiz-Ferrara, G., Ortiz-Monasterio, I., Payne, T., Peña, J., Reynolds, MP., Sayre, K., Sharma, R., Singh, R., Wang, J., Warburton, M., Wu, H. and Iwanaga, M. (2008) Wheat genetic resources enhancement by the International Maize and Wheat Improvement Center (CIMMYT). *Genetic Resources and Crop Evolution* 55, 1095–1140.

Parry, MAJ., Madgwick, PJ., Carvalho, JFC. and Andralojc, PJ. (2007) Prospects for increasing photosynthesis by overcoming the limitations of Rubisco. *Journal of Agricultural Science* 145, 31–43.

Parry, MAJ., Reynolds, MP., Salvucci, ME., Raines, C., Andralojc, PJ., Zhu, XG., Price, GD., Condon, AG. and Furbank, RT. (2011) Raising yield potential of wheat. II. Increasing photosynthetic capacity and efficiency. *Journal of Experimental Botany* 62, 453–467.

Price, GD., Badger, MR., Woodger, FJ. and Long, BM. (2008) Advances in understanding the cyanobacterial CO_2-concentrating-mechanism (CCM): functional components, Ci transporters, diversity, genetic regulation and prospects for engineering into plants. *Journal of Experimental Botany* 59, 1441–1461.

Reynolds, MP. and Borlaug, NE. (2006) Impacts of breeding on international collaborative wheat improvement. *Journal of Agricultural Science* 144, 3–17.

Reynolds, MP., Manes, Y., Izanloo, A. and Langridge, P. (2009a) Phenotyping for physiological breeding and gene discovery in wheat. *Annals of Applied Biology* 155, 309–320.

Reynolds, MP., Foulkes, JM., Slafer, GA., Berry, P., Parry, MAJ., Snape, J. and Angus, WJ. (2009b) Raising yield potential in wheat. *Journal of Experimental Botany* 60, 1899–1918.

Reynolds, MP., Bonnett, D., Chapman, SC., Furbank, RT., Manes, Y., Mather, DE. and Parry, MAJ. (2011) Raising yield potential of wheat. I. Overview of a consortium approach and breeding strategies. *Journal of Experimental Botany* 62, 439–452.

Skovmand, B., Reynolds, MP. and Delacy, IH. (2001) Mining wheat germplasm collections for yield enhancing traits. *Euphytica* 119, 25–32.

Slafer, GA. and Rawson, HM. (1994) Sensitivity of wheat phasic development to major environmental factors: A re-examination of some assumptions made by physiologists and modellers. *Australian Journal of Plant Physiology* 21, 393–426.

Salvucci, ME. and Crafts-Brandner, SJ. (2004) Inhibition of photosynthesis by heat stress: the activation state of Rubisco as a limiting factor in photosynthesis. *Physiologia Plantarum* 120, 179–186.

Sayre, KD., Rajaram, S. and Fischer, RA. (1997) Yield potential progress in short bread wheats in northwest Mexico. *Crop Science* 37, 36–42.

Shearman, VJ., Sylvester-Bradley, R., Scott, RK. and Foulkes, MJ. (2005) Physiological processes associated with wheat yield progress in the UK. *Crop Science* 45, 175–185.