

REVIEW PAPER

# Raising yield potential of wheat. I. Overview of a consortium approach and breeding strategies

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Received 22 June 2010; Revised 8 September 2010; Accepted 13 September 2010

## Abstract

Theoretical considerations suggest that wheat yield potential could be increased by up to 50% through the genetic improvement of radiation use efficiency (RUE). However, to achieve agronomic impacts, structural and reproductive aspects of the crop must be improved in parallel. A Wheat Yield Consortium (WYC) has been convened that fosters linkage between ongoing research platforms in order to develop a cohesive portfolio of activities that will maximize the probability of impact in farmers' fields. Attempts to increase RUE will focus on improving the performance and regulation of Rubisco, introduction of C<sub>4</sub>-like traits such as CO<sub>2</sub>-concentrating mechanisms, improvement of light interception, and improvement of photosynthesis at the spike and whole canopy levels. For extra photo-assimilates to translate into increased grain yield, reproductive aspects of growth must be tailored to a range of agroecosystems to ensure that stable expression of a high harvest index (HI) is achieved. Adequate partitioning among plant organs will be critical to achieve favourable expression of HI, and to ensure that plants with heavier grain have strong enough stems and roots to avoid lodging. Trait-based hybridization strategies will aim to achieve their simultaneous expression in elite agronomic backgrounds, and wide crossing will be employed to augment genetic diversity where needed; for example, to introduce traits for improving RUE from wild species or C<sub>4</sub> crops. Genomic selection approaches will be employed, especially for difficult-to-phenotype traits. Genome-wide selection will be evaluated and is likely to complement crossing of complex but complementary traits by identifying favourable allele combinations among progeny. Products will be delivered to national wheat programmes worldwide via well-established international nursery systems and are expected to make a significant contribution to global food security.

**Key words:** Adaptation, food security, genetic resources, harvest index, lodging, partitioning, phenology, photosynthesis, physiology.

## Introduction

Wheat (*Triticum* spp) is the most widely grown of any crop and an essential component of the global food security mosaic, providing one-fifth of the total calories of the world's population (Food and Agricultural Organization of the United Nations, 2010). Since the 1960s, increases in productivity have been achieved as a result of wide-scale

Abbreviations: CGIAR, Consultative Group on International Agricultural Research; CIMMYT, International Maize and Wheat Improvement Center; DArT, diversity array technology; DH, doubled haploids; EGS, early generation selection; FBPA, fructose-1,6-bisphosphate aldolase; GS, genomic selection; HI, harvest index; LI, light intercepted; MARS, marker-assisted recurrent selection; MAS, marker-assisted selection; PT, physiological trait; QTL, quantitative trait locus; RUE, radiation use efficiency; SBPase, sedoheptulose-1,7-bisphosphatase; SP, subproject; USAID, United States Agency for International Development; WYC, Wheat Yield Consortium; YP, yield potential.

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adoption of Green Revolution technologies (Evenson and Gollin, 2003). However, in spite of growing demand (Rosegrant and Agcaoili, 2010), the challenges of increasing production to feed an estimated world population of 9 billion in 2050 are still considerable. Less developed countries are particularly vulnerable in terms of food security for three main reasons: (i) most are net importers of cereals (Dixon *et al.*, 2009); (ii) many of their national agricultural research services lack sufficient capacity for timely delivery of agricultural technologies (Kosina *et al.*, 2007); and (iii) the majority are located in regions that are vulnerable to climate change (Lobell *et al.*, 2008). While internationally coordinated public wheat breeding efforts have 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 scant attention. In fact the fundamental bottleneck to raising productivity, namely utilization of solar radiation per unit of dry matter production [radiation use efficiency (RUE)], has barely changed in the modern era of wheat breeding.

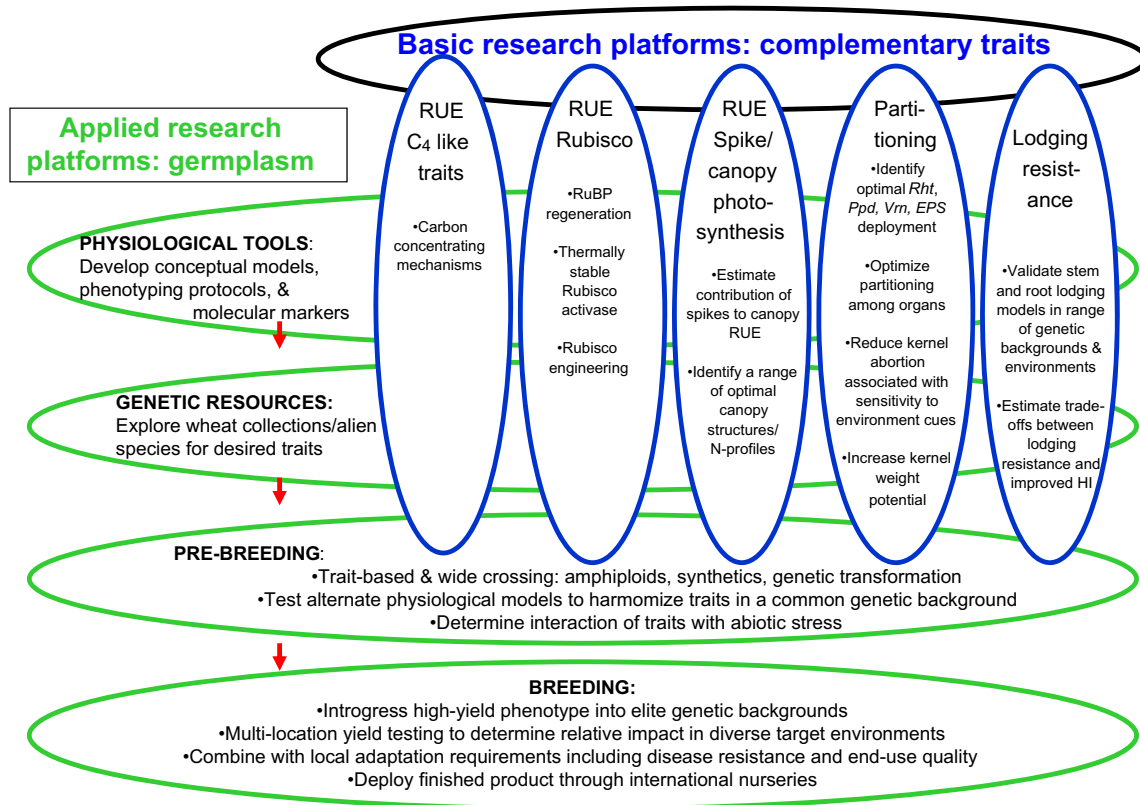
Ongoing basic research in photosynthesis suggests that substantial improvements in yield are theoretically possible (Long *et al.*, 2006; Parry *et al.*, 2007; Zhu *et al.*, 2010). These consider the fundamental inefficiency of carbon fixation in so-called C<sub>3</sub> crops (wheat, rice, beans, potatoes, and most vegetables) and compare it with that of C<sub>4</sub> crops (maize, sorghum, millet, sugar-cane) which show up to 50% greater RUE. In wheat, genetic modification of the enzyme responsible for C fixation—Rubisco—and its regulation are major targets to improve photosynthetic efficiency (Parry *et al.*, 2007); a more ambitious approach in rice is to introduce all of the characteristics of C<sub>4</sub> photosynthesis (Furbank *et al.*, 2009). While increasing photosynthetic potential will require considerable research focused on cellular and subcellular processes, this must go hand in hand with genetic modification of structural and reproductive aspects of growth, since these will determine the net agronomic benefit of increased RUE. First, adaptation of the reproductive processes to variation in seasonal and other environmental factors is relatively poorly understood yet determines the efficiency with which photosynthesis is converted to yield (Reynolds *et al.*, 2009a). Secondly, even at current levels of yield potential, a significant portion of the world's wheat crop is still lost to lodging damage each year (Berry *et al.*, 2004). Therefore, research aimed at raising the yield potential of wheat under agronomic conditions must achieve the following broad objectives 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 translated to grain weight; and (iii) enhance the structural characteristics of wheat plants to ensure that grain yield potential and quality are not sacrificed due to lodging. A large body of basic and applied research supports the notion that a multidisciplinary team focused on genetic gains in wheat yield would have a high probability of success (Berry *et al.*, 2007; Miralles

and Slafer, 2007; Reynolds *et al.*, 2009a; Tester and Langridge, 2010; Zhu *et al.*, 2010).

Given the urgency of the current food crisis (Godfray *et al.*, 2010), coupled with the threat of climate change to productivity, the International Maize and Wheat Improvement Centre (CIMMYT) began consulting with crop experts worldwide, culminating in the first meeting of a Wheat Yield Consortium (WYC) in November 2009. The remit of the WYC thus far has been to determine how linkage between ongoing research areas can achieve synergy in terms of raising the yield potential of wheat, and develop a cohesive portfolio of research activities to maximize the probability of impact in farmers' fields (Fig. 1). The main objective of this set of linked reviews (including Foulkes *et al.*, 2011; Parry *et al.*, 2011) is to present the scientific basis of the proposed research. While it is unconventional to publish the elements of a research proposal, authors are in broad agreement that the implications of food insecurity are serious enough, especially in the developing world, to permit a breach of normal protocol in order to bring this matter into immediate focus with scientific peers. By publishing these documents, the consortium seeks feedback from a cross-section of the scientific community, with the following objectives: firstly, through the formal peer-review process, to seek endorsement of the approaches to be adopted in the WYC, thereby lending scientific credibility to its foundation. Secondly, through *JXB* readership, to stimulate feedback on current approaches, thereby assisting the longer term WYC agenda to evolve (the WYC is expected to require at least 20 years to achieve its goals). Thirdly, through broader dissemination of these ideas, to bring wider attention to the role of publically funded research to generate essential global public goods.

## Overview of research approaches to raise the yield potential of wheat

The WYC encompasses expertise within three linked themes: Theme 1, *increasing photosynthetic capacity and efficiency*; Theme 2, *optimizing partitioning to grain yield while maintaining lodging resistance*; and Theme 3, *breeding to accumulate yield potential traits and delivery of new germplasm*. Within each of these themes, a set of subprojects (SPs) has been developed (Table 1) in a way that capitalizes on pre-existing knowledge and the strengths of qualified research laboratories worldwide. In the following three sections, the broad objectives of the three themes are presented in the context of how research products will translate into new traits for use in breeding and eventually the delivery of new wheat cultivars. Further details of Themes 1 and 2, including their theoretical basis and main research goals, are presented in the accompanying papers (Foulkes *et al.*, 2011; Parry *et al.*, 2011). Full details of Theme 3 are presented in a final section of this article. Coordination activities will also run in parallel to the three main research themes to maximize research efficiency not just in terms of use of inputs and outputs, but also to



**Fig. 1.** A research strategy to improve yield potential of wheat.

**Table 1.** A consortium to raise the yield potential of wheat: subproject (SP) structure.

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 <sub>2</sub> pumps
SP1.5	Optimizing RuBP regeneration
SP1.6	Improving the thermal stability of Rubisco activase
SP1.7	Replacement of large subunit 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	Modelling optimal combinations of, and trade-offs 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

maintain relevance and accelerate impact; these will be described later.

### *Theme 1: increasing photosynthetic capacity and efficiency*

There is increasing evidence that to achieve a quantum boost to cereal 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 ~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 the ‘sink’ strength of grain and photosynthetic 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 main approaches will be pursued to provide new genetic stocks for increasing total crop biomass. Both aim to increase photosynthetic efficiency and capacity by targeting the first step of CO<sub>2</sub> fixation in C<sub>3</sub> photosynthesis, catalysed by Rubisco, and the subsequent regeneration of the co-substrate for this enzyme, ribulose-1,5-bisphosphate (RuBP). Rubisco, which is the most abundant protein in C<sub>3</sub> plants, 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 1). A component intended to achieve application in the 5-year time frame 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 a variety of high-throughput measurements of photosynthesis, coupled with mathematical modelling. This phenomics approach will allow the establishment of defined sets of germplasm with demonstrated variation in Rubisco amount, and properties and variation in associated regulatory proteins such as Rubisco activase, important in heat tolerance of photosynthesis, especially in climate-changed environments [Table 1, sub-projects (SPs) 1.1, 1.2, and 1.3]. There is strong evidence for genetic variation in both photosynthetic efficiency and capacity in cereals, although a comprehensive screening approach has not been attempted in wheat. This will be coupled with a project to screen for improved photosynthetic capacity in non-leaf tissues, which can contribute up to 25% of grain carbon (see Gebbing and Schnyder, 1999; Table 1, SP1.2) and improve nitrogen distribution and photosynthetic capacity over the entire life cycle of the plant (Table 1, SP1.3)

Genetic manipulation will be used to engineer RuBP regeneration and Rubisco activase (Table 1, SP1.4), or to introduce Rubisco subunits with enhanced catalytic properties (Table 1, SP1.6). Under conditions of low light and elevated CO<sub>2</sub> the regeneration of RuBP limits photosynthetic carbon assimilation. There is irrefutable experimental evidence that manipulation of RuBP regeneration by overexpressing sedoheptulose-1,7-bisphosphatase (SBPase) can increase plant productivity in laboratory conditions and may also enhance stress tolerance. In addition, modelling approaches suggest increased benefit from the overexpression of fructose-1,6-bisphosphate aldolase (FBPA). In SP1.5 (Table 1), RuBP regeneration capacity in wheat will be increased by overexpressing both SBPase and FBPA, which is predicted to increase yields by ~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-Brandner, 2004; Kurek *et al.*, 2007). In SP1.6 (Table 1) Rubisco activase will be re-engineered to increase its thermotolerance, with the aim of broadening the efficient temperature range for photosynthesis.

Considerable progress has been made in identifying natural variation in the catalytic properties of Rubisco from different species and in developing the tools for introducing both novel and foreign Rubisco genes into plants. Modelling 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, SP1.7 (Table 1) recognizes this potential and will develop plastid transformation for wheat.

The second approach is to mimic systems present in nature which concentrate CO<sub>2</sub> in the compartment where Rubisco is located, eliminating photorespiration and ensuring Rubisco operates close to its catalytic optimum. These systems are present in C<sub>4</sub> plants, where a biochemical CO<sub>2</sub>-concentrating mechanism has evolved many times in nature, capable of elevating CO<sub>2</sub> at the site of Rubisco up to 10-fold over atmospheric levels (von Caemmerer and Furbank, 2003). While there is currently an International Consortium attempting to install a C<sub>4</sub> pathway in rice (Furbank *et al.*, 2009), 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<sub>2</sub>, in the form of bicarbonate, is pumped across membranes to elevate CO<sub>2</sub> to even higher levels than those seen in C<sub>4</sub> 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 1, SP1.4).

This first theme builds on the synergies of germplasm mining and candidate gene approaches. The top-down mining of germplasm for improved photosynthesis, across the entire life cycle, in leaves and in other organs, does not rely on a hypothetical 'target' gene but on established mechanistic relationships between photosynthetic performance and leaf biochemistry. This will allow identification of new mechanisms and parents for crosses and for this information and germplasm to be fed into Theme 3. The candidate gene approaches do not depend on existing genetic variation but seek to create it. The time frame is longer but the potential gains much larger.

### *Theme 2: optimizing partitioning to grain yield while maintaining lodging resistance*

Notwithstanding the global impact of dwarfing genes on improving yield and crop harvest index (HI) (Mathews *et al.*, 2006), adaptation of reproductive processes to the environment is still considered among the most challenging aspects of cereal improvement (Barnabas *et al.*, 2008). While increases in HI have been achieved in the post-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 latitudes and temperature regimes, 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 photoperiod, vernalization, 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). There is clear evidence 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 cues such as 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 of the few candidate genes that has been identified for spike fertility *per se*—*Gn1a* in rice—codes for cytokinin oxidase which, through its regulation of cytokinin levels, influences the number 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 signalling (Davies *et al.*, 2005) may be the route to explaining the interaction of spike fertility with the environment and its genetic basis.

SPs 2.1, 2.2, 2.3, and 2.4 (Table 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, photoperiod, and vernalization responses is 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; that is, potential grain number and grain weight. However, plants with increased photosynthetic rate and a larger biomass are likely to require more efficient if not larger root systems. Therefore, the potential trade-offs 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 crucial to ensure that plants with heavier grain weight have strong enough stems and roots to avoid structural failure (Berry *et al.*, 2007). Lodging is already a persistent 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 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 none is especially easy to phenotype in field plots.

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 modelling of these interactions (Table 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

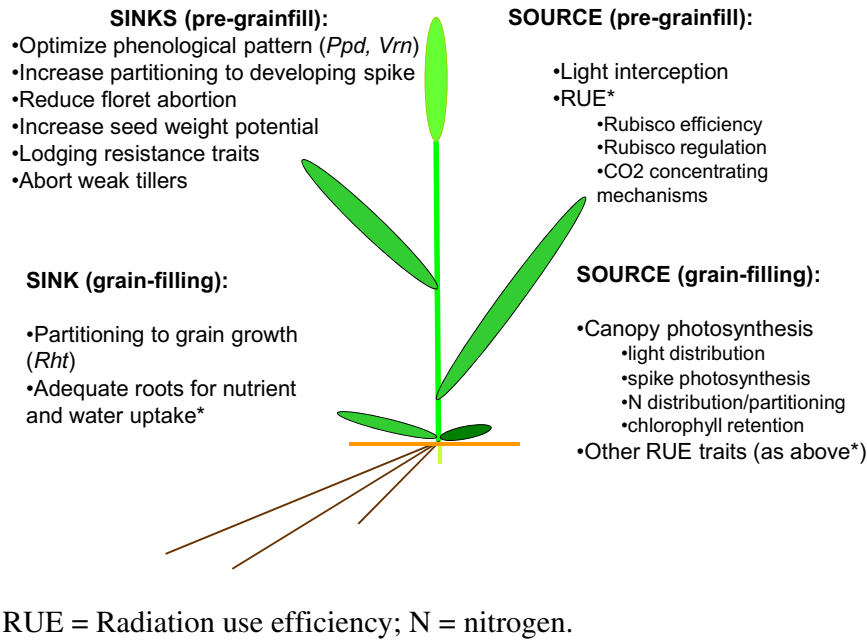
markers—to facilitate hybridization strategies and progeny selection, such that expression of the HI and lodging resistance is optimized in germplasm targeted to major wheat agro-ecosystems.

### Theme 3: breeding to accumulate yield potential traits

Trait selection is the cornerstone of modern 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 prevalent diseases; quality parameters determined by end use; and yield based on multilocation 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 and those alleles necessary to maximize agronomic impact at the system level—including PTs associated with HI and lodging resistance—in elite agronomic backgrounds (i.e. disease resistant, appropriate quality parameters, etc.). PT-based breeding approaches have been implemented successfully in Australia (Rebetzke *et al.*, 2009) as well as 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 (Fig. 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).

Given the ambitious nature of this project, the primary wheat gene pool (i.e. *Triticum aestivum*) may need to be complemented with traits from more exotic sources in cases where conventional sources lack adequate diversity. In fact, inter-specific and inter-generic crosses within the *Triticeae* are already routine procedures in wheat breeding (Skovmand *et al.*, 2001; Trethowan and Mujeeb-Kazi, 2008) (Table 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. Nonetheless, 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). Whole-genome fusion has even been used to create a totally new species, triticale ( $\times$ *Triticosecale* Wittmack), a wheat $\times$ rye amphidiploid, which is cultivated on 3.6 million ha worldwide and has



**Fig. 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 photoassimilates, and their predominant expression is considered either before or during grain filling, and, in some cases, both (\*). Genes of major affect known to be implicated are mentioned parenthetically.

yields comparable with those of the best wheat cultivars, good yield stability, and often produces exceptional biomass (Ammar *et al.*, 2004). While the introduction of genes from outside of the *Triticeae* tribe is not a routine procedure in wheat breeding, chromatin from C<sub>4</sub> 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 C<sub>4</sub> photosynthetic enzymes in some of these oat–maize chromosome addition lines has been reported (Kowles *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 needed for full expression of C<sub>4</sub> photosynthesis, although this would clearly require considerable effort.

The impact of research and breeding will depend on effective delivery of products. CIYMMT—the coordinating institute of the WYC—has for >45 years coordinated an international wheat breeding effort and through its international nursery system delivers ~1000 new genotypes per year, targeted to the varying needs of national wheat programmes 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 programmes in as short a time frame as possible (Table 1, SP3.4).

#### Coordination and facilitation of research

It is now broadly accepted that genetic dissection of traits aided by precision phenotyping to identify consistent levels of expression and associated genetic markers can accelerate their deployment in breeding (Tuberosa and Salvi, 2006; Rebetzke *et al.*, 2009; Reynolds *et al.*, 2009b; Pinto *et al.*, 2010). Efforts will be made to maximize the synergy between the three research themes in this regard; for example, to identify, facilitate access to, and develop, where appropriate, shared research platforms such as germplasm panels, phenotyping protocols, and genotyping approaches. Efforts to assist with this are already underway and will be addressed in more detail in the next section. Other facilitation roles of the WYC will include: training in the use of common research platforms and technologies; timely sharing of results among participants; monitoring and reviewing WYC activities and linkages in order to maintain relevance; and publicizing and promoting WYC outputs to ensure adoption by breeding programmes and farmers worldwide.

#### Crop management and crop productivity

Although beyond the scope of this review—and outside of the current remit of the WYC—improved methods of crop management are expected to play a crucial role in increasing wheat productivity, for two main reasons: (i) improvements

in genetic yield potential are more fully expressed where crop husbandry is optimized; and (ii) the practice of conservation agriculture and other resource-conserving technologies help stabilize soils and can lead to improvements in the fertility and productivity of cropping systems, especially those which are already fragile or have become degraded from a history of intensive cultivation (Cook, 2006; Montgomery, 2007; Hobbs *et al.*, 2008).

### Breeding to accumulate yield potential traits in wheat (Theme 3)

The need to accelerate genetic progress in the yield potential of crops is widely acknowledged (Royal Society, 2009; Phillips, 2010). Increased demand for food, the multiple challenges associated with climate change, and declining crop productivity due to attrition of natural resources are all reasons for concern. The fact that rates of genetic gains resulting from breeding have decreased in recent decades for most staple crops has led to a sense of urgency (Fischer and Edmeades, 2010; Graybosch and Peterson, 2010). To date, genetic progress in yield *per se* has been achieved mainly through the innovative use of both germplasm and crossing strategies, followed by empirical selection for grain yield at multiple locations (Braun *et al.*, 2010). The future challenge to increase genetic gains could take a number of directions. For example, given the advances that have been made in molecular marker technology, genome-wide marker-trait association has become feasible as an empirical selection tool for complex traits such as yield (Bernardo and Yu, 2007). It could complement (and potentially replace) marker-assisted selection (MAS) platforms that function well for genes of relatively large effect—typically associated with resistance to biotic stresses (Bonnet *et al.*, 2005; William *et al.*, 2007). On the other hand, advances in genome sequencing offer opportunities to identify potentially new sources of allelic variation for the purpose of widening the gene pool available for hybridization (e.g. Latha *et al.*, 2004; Kaur *et al.*, 2008). While neither of these platforms (genome-wide selection or sequence-based discovery of novel allelic diversity) are yet routinely applied in crop breeding, their potential to increase rates of genetic gains is indisputable. The strength of the current project is that genomic approaches will be developed in conjunction with hybridization and selection strategies that are based on a physiological understanding. As outlined earlier, this understanding points to the need to improve simultaneously three groups of PTs, namely (i) those associated with RUE; (ii) the optimized partitioning of assimilates to yield; and (iii) lodging resistance, in order that genetic gains are realized as agronomic impacts across a wide range of wheat-growing environments. Therefore, the WYC is structured so that outputs of research from Themes 1 and 2 will be channelled directly into the breeding effort of Theme 3 (Box 1). The components of this breeding effort are described next.

#### Box 1. WYC Theme 3: Key Deliverables

- Conceptual models of PTs targeted to major wheat agro-ecosystems.
- Products of inter-specific hybridization expressing superior RUE and other PT traits available for crossing with wheat.
- Whole genome selection methodology developed to complement phenotypic and genotypic selection for PTs.
- A new generation of wheat genotypes that encompass a range of PT traits made available to breeders worldwide through international nurseries.

#### Combining PTs to achieve cumulative gene action

Yield potential (YP) can be expressed in its simplest form as a function of the light intercepted (LI) and RUE, whose product is biomass, and the partitioning of biomass to yield; that is, the HI:

$$YP = LI \times RUE \times HI \quad (1)$$

PT-based breeding will focus on improving all three of these components. Theme 1 of the current proposal aims to identify PTs that will increase LI and RUE, while Theme 2 focuses on optimizing the expression of HI, thereby ensuring that improved LI and RUE are translated into yield. The PTs related to LI—such as stand establishment, canopy architecture, and nitrogen partitioning—which have not generally been selected for yet are relatively straightforward to phenotype on a routine basis. Potential to increase RUE is supported by both theoretical calculations (Zhu *et al.*, 2010) and reports of increased biomass in advanced breeding lines, in some cases stemming from introgression of exotic germplasm (Singh *et al.*, 1998; Reynolds *et al.*, 2009a). HI has increased steadily during the 20th century but, with the exception of the (generally imprecise) deployment of major-effect alleles at the *Rht*, *Ppd*, and *Vrn* loci (Slafer and Rawson, 1994; Worland *et al.*, 1998; Matthews *et al.*, 2006), optimal expression of HI is still achieved empirically within major agro-ecosystems and is subject to seasonal affects (Ugarte *et al.*, 2007). Even among current elite materials, a considerable genetic variation in expression of HI can be found typically in the range of 0.4–0.55 (Sayre *et al.*, 1997; Shearman *et al.*, 2005).

The starting point for Theme 3 will be to identify the current limitations of PTs in current gene pools of the major wheat agro-ecosystems to help determine new target levels of expression. This information will help fine-tune research priorities in Themes 1 and 2 as well as suggesting potentially complementary PTs in extant gene pools. Hybridization schemes will be designed to combine PTs (Fig. 2) in such a way that the main drivers of yield potential (Equation 1) are improved systematically. The PT-based breeding strategies will be based on precedents in breeding for drought adaptation of wheat (Richards, 2006;



Rebetzke *et al.*, 2009; Reynolds *et al.*, 2009b) and will be complemented as far as possible by MAS (Bonnet *et al.*, 2005; William *et al.*, 2007; Collard and Mackill, 2008; Wang *et al.*, 2009; Tester and Langridge, 2010). Development of F<sub>1</sub> hybrid cultivars will also be explored as an approach to combine complementary traits rapidly. With this objective in mind, an international public–private consortium is being developed to make available a GM-based hybrid wheat breeding system that will provide a high level of hybrid purity combined with economically viable seed production costs (H. J. Braun, personal communication). The design of PT-based crosses (whether for hybrid or inbred lines) will evolve as new genetic stocks and understanding of PT interactions becomes available through research (Table 1).

### Progeny selection

Where relatively efficient screening protocols exist, early generation selection (EGS) and MAS of progeny will enrich populations in terms of desirable traits and their markers. Until genome selection becomes routine it is likely that EGS will rely mainly on (i) visual selection; (ii) a handful of integrative phenotyping approaches such as spectral reflectance and canopy temperature; and (iii) MAS on a set of relatively heritable traits.

### Breeding research platforms

To accelerate gene deployment, two key locations will be the main focus of research and breeding effort, one for spring wheat and the other for winter wheat. The following are strategies that will be adopted to maximize timely and efficient delivery of new germplasm initially at the spring wheat hub. Parallel models will be adopted for the winter wheat breeding hub as well as at locations that emerge as WYC outputs better define the key environmental characteristics of major breeding target regions:

- (i) A research and breeding hub will be established at the Normal E Borlaug Experiment Station (CENEB) in NW Mexico, representing the environmental conditions of a number of high-yielding wheat agro-ecosystems worldwide. This has been confirmed through analysis of yield performance of thousands of advanced breeding lines tested at hundreds of locations worldwide over several decades (Trethowan *et al.*, 2003; Braun *et al.*, 2010). The station is located at the centre of a high yield wheat agro-ecosystem in Sonora's Yaqui Valley which produces well over 1 million t of wheat annually, with farm yields recently averaging 6.4 t ha<sup>-1</sup> and maximum yields sometimes exceeding 10 t ha<sup>-1</sup> in a 5 month cycle (Sayre *et al.*, 1997).
- (ii) Core breeding research panels are being identified that encompass the following categories of germplasm: (a) genetically diverse advanced lines with high and stable yield expression from a range of production systems; (b) landmark wheat ideotypes that have become well represented in the pedigrees of improved germplasm; (c)

exotic-derived advanced lines that incorporate alien chromatin, for example 1B.1R (Villareal *et al.*, 1998) and 7Ag.7DL (Singh *et al.*, 1998), and lines derived from products of interspecific hybridization such as 'resynthesized' hexaploid wheat (Trethowan and Mujeeb-Kazi, 2008); and (d) mapping populations that are controlled for agronomic traits (e.g. Pinto *et al.*, 2010). These panels, representing a full range of genetic diversity in agronomic backgrounds of proven value, will provide a common research platform available to all SPs (Table 1).

- (iii) Core data sets representing key PTs as well as standard agronomic traits will be established to standardize and, therefore, maximize the usefulness of research outputs across themes.

The advantages of focusing research in this manner are: (i) by collecting data on common environmental and germplasm platforms, cross-referencing is easy and research resources are used more efficiently; (ii) results will be representative of major wheat production environments; and (iii) research and breeding will be conducted side by side, encouraging maximum accountability of both.

### Increasing RUE of wheat through wide crossing

In breeding, continual reselection within restricted gene pools is likely to lead to diminishing returns, so it is imperative to introduce new allelic diversity by exploiting non-conventional sources. Allelic diversity for any number of traits impacting on yield potential may exist outside of the primary wheat gene pool, and molecular tools to exploit such molecular diversity are now reasonably well developed, with the rapid progress in genome sequencing providing powerful new opportunities for tracking and characterizing such introgressions. An understanding of the underlying physiology of some key target traits related to yield potential can complement these tools by guiding hybridization and selection strategies for these relatively heritable component traits, for example some or all of the traits associated with C<sub>4</sub> photosynthesis. While this is an ambitious aim, it seems feasible based on current understanding and tools. The possibility of introgressed C<sub>4</sub> genes being expressed in wheat is supported by findings of the expression of C<sub>4</sub> photosynthetic enzymes in oat–maize chromosome addition lines (Kowles *et al.*, 2008).

Like oat, wheat is a polyploid, is tolerant of alien chromatin introgressions, and crosses of wheat with certain C<sub>4</sub> species can produce viable plants through embryo rescue (Inagaki and Mujeeb-Kazi, 1995). The chromosomes of C<sub>4</sub> species are typically eliminated in the early mitotic divisions during embryo development in crosses with wheat, and indeed this phenomenon has been exploited to develop doubled haploids (DHs) (Laurie and Bennett, 1986, 1989). However, a number of studies of wheat by C<sub>4</sub> species crosses have reported retention of chromosomes of the latter in later stages of haploid plant development. Maize chromosomes were identified in haploid plants by Comeau



*et al.* (1992) and in *Tripsacum dactyloides* chromosomes by Li *et al.* (1996). The fate of the *Tripsacum* chromosomes was not reported, but the maize chromosomes were shown to not be transmitted to the progeny of colchicine doubled plants. In both of these studies, relatively small numbers of plants were checked for the presence of chromosomes from the C<sub>4</sub> species using cytology and Southern blots. In studies using PCR-based molecular techniques, one group reported introgression of maize chromatin in wheat×maize DH plants (Chen *et al.*, 1997, 2000) while another group failed to find any evidence of retention of maize chromatin (Brazauskas *et al.*, 2004). These studies screened small numbers of plants for the presence of maize chromatin. Although large numbers of DH plants are produced around the world using the wheat×maize system, cytological confirmation of the chromosome number of such DHs is not routine because of the effort involved, and the fertility and phenotype of DH plants are usually a good indicator of a euploid chromosome complement. Screening specifically for the presence of maize chromatin in DHs would rarely, if ever, be done. However, given modern molecular methods, screening new or existing DH populations for introgression of maize chromatin is a relatively low-cost opportunity.

An increased probability of recovering maize introgressions would be afforded by a targeted, large-scale wheat×maize crossing programme. From such an effort, the chance of recovering plants carrying one or more maize chromosomes is probably acceptably high, although the frequency of transmission to the next generation following chromosome doubling will be another hurdle. Considering that retention of maize chromosomes in oat appears to occur at a higher frequency than in wheat but still required pollination of almost 60 000 oat florets to recover a complete set of maize disomic addition lines, the effort required in wheat will probably need to be of a greater scale (Kynast *et al.*, 2001). In the case of the oat–maize addition lines, both the oat and maize genotypes had an effect on the frequency of introgression of maize chromosomes (Rines *et al.*, 2009), which suggests that testing a range of wheat and maize genotypes in different cross combinations may identify some that have a higher frequency. It is possible that genotypic effects may have contributed to the differences between studies on retention of maize chromatin in wheat–maize crosses (Laurie and Bennett, 1989; Comeau *et al.*, 1992; Chen *et al.*, 2000; Brazauskis *et al.*, 2004). The observation of >21 chromosomes in some wheat×*T. dactyloides* hybrids by Li *et al.*, (1996) suggests that wheat×*T. dactyloides* crosses would also be worth further effort. Successful crosses of wheat with pearl millet and sorghum are another avenue (Inagaki and Mujeeb-Kazi, 1995). Regardless of C<sub>4</sub> donor species, wheat lines with additions of C<sub>4</sub>-related genes will be key resources for analysis of components of C<sub>4</sub>-type photosynthesis in SP1.1.

A second target of the SP will be to explore the potential of rye introgressions to increase RUE. An increase in RUE and the possibility of transferring this trait to wheat is suggested by the increase in biomass commonly observed in triticale (Ammar *et al.*, 2004). A focus on rye is also

strongly supported by the success of the 1BL.1RS translocation present in almost all wheat cultivars in the Middle East and west Asia (most of these CIMMYT derived), and in a significant proportion of cultivars in the USA, China, and Europe (Stokstad, 2007). The wide distribution of these wheats can be attributed to their high yield in diverse environments (Villareal *et al.*, 1998), perhaps due to demonstrated effects of 1BL.1RS on yield, drought tolerance, and nitrogen-use efficiency (Ehdaie *et al.*, 2003) despite all of the known disease resistance genes on the 1RS segment no longer being completely effective. Considering that this represents only one chromosome arm from one rye variety, ‘Petkus’, that was originally transferred to wheat in the 1930s, the potential to increase yield potential with introgressions from other rye chromosomes, or even introgressions of 1RS from other rye varieties, must be high.

The potential for donor genes from rye has long been recognized by many researchers who have made efforts to develop wheat germplasm incorporating a range of rye chromosome segments from a range of rye germplasm (USDA, 2010; GrainGenes website <http://wheat.pw.usda.gov/GG2/germplasm.shtml>). The resulting germplasm base is a valuable resource for this initiative and will allow assessment of the potential of different rye segments in a much shorter time than would be possible if it was necessary first to develop the introgression stocks. Many rye chromosome additions and single arm translocations have been assembled at CIMMYT, some of these in the background of CIMMYT wheat Pavon 76. The existing set includes several 1BL.1RS translocations with different rye origins, some of which have already been shown to have positive effects on yield and nitrogen-use efficiency related to root characters (Villareal *et al.*, 1998; Ehdaie *et al.*, 2003; Hysing *et al.*, 2007). To be comprehensively evaluated, rye introgression stocks should be updated into the best recent varieties.

A further attraction of rye is that it differs from most other ‘alien’ relatives of wheat in being a cultivated species grown in similar environments, and having a history of considerable breeding effort directed at improvement of yield potential. Elite rye varieties and hybrids therefore offer a potential longer term source of alleles for improved yield potential in wheat. Breeding and research efforts in rye also provide a range of molecular tools that can be used to track introgressed rye segments in routine breeding efforts, determine the size of rye introgressions, and identify new recombinant rye segments from crosses of existing translocation lines to triticales or new rye sources.

In addition to the traits and approaches mentioned above, wide crossing has the potential to introgress variation for other traits—such as lodging resistance or spike fertility—that will be important in higher yielding wheat. Increasing genomic knowledge and the cloning of important genes in crop species provides tools to uncover novel and potentially superior allelic variants previously inaccessible among the vast collections of wheat and its relatives (Latha *et al.*, 2004; Kaur *et al.*, 2008). The knowledge generated by gene cloning and allele mining will

unlock considerable genetic potential from germplasm collections for a range of traits and allow more effective targeting of wide hybridization efforts.

#### *Increasing rates of genetic gain using molecular markers—genomic selection*

Genetic mapping has provided information about the genetic control of many traits in wheat, enabling wheat breeders to use molecular markers in selection for disease resistance, adaptation, and end-use quality (Kuchel *et al.*, 2007; Landjeva *et al.*, 2007; William *et al.*, 2007). Yield of bread wheat is a quantitative trait controlled by many genes, of both large and small effects (Kumar *et al.*, 2007). Within elite×elite breeding crosses, quantitative trait loci (QTLs) with large effects may be already fixed, and further genetic gain must rely on the continuous accumulation of small-effect alleles at other loci (Crosbie *et al.*, 2006; Singh *et al.*, 2007). Rather than relying only on investigation of simple crosses, breeding programmes are increasingly using their entire collections of phenotypic, genotypic, and pedigree data to estimate the effects of multiple alleles available for selection (Christopher *et al.*, 2007; Crossa *et al.*, 2007). This approach allows further exploitation of effective alleles that have already been selected in breeding programmes.

Conventional field selection, although proven to provide consistent genetic gains for yield potential, can fix only a few new favourable effects per breeding cycle. To accelerate the accumulation of favourable alleles, maize and soybean breeders have implemented marker-assisted recurrent selection (MARS). MARS involves a QTL discovery step, followed by cycles of intercrossing and selection based purely on genotypic information (Eathington *et al.*, 2007). However, in this approach, only a portion of the genetic variance is taken into account (Goddard and Hayes, 2007), and effects retained for the model may be greatly overestimated (Beavis, 1998). Genomic selection (GS, or whole-genome selection) uses the entire marker information to predict phenotypic performance and calculate breeding values (Meuwissen *et al.*, 2001; Heffner *et al.*, 2009). It captures more of the variation due to the smaller effects than MARS (Heffner *et al.*, 2009). GS has been implemented in animal breeding and reported to improve prediction of genotype performance (Hayes *et al.*, 2009). In public-sector plant breeding research, it has been tested only by simulation, and has been reported to provide higher genetic gains than MARS (Bernardo and Yu, 2007).

Implementation of GS relies on the availability of high-throughput, high-density marker technology at a low cost. For wheat, the highest density multiplexed marker system currently available is diversity array technology (DArT) (Akbari *et al.*, 2006), which currently provides several thousand data points per DNA sample, at a cost of ~US\$50 per sample. In future, array-based genotyping technologies could be replaced by systems based on next-generation high-throughput sequencing. With genotyping by sequencing, the cost of detecting hundreds of thousands of polymorphisms may be reduced to <US\$10 per DNA

sample, allowing large-scale implementation of GS in wheat breeding.

This SP will design, implement, and evaluate GS as an approach to increase genetic gain for yield potential in wheat. The first step of GS is the estimation of marker effects and the design of genomic prediction models from a set of genotypes with both genotypic and phenotypic information available, called the training population. Model design will rely on historical data from CIMMYT's international trials in an approach similar to that used by Crossa *et al.* (2007) and on new data from an association genetic set assembled specifically to map yield genes under drought and heat. The second step will be a 'rapid cycling' phase consisting of two or three cycles of early-generation genotypic selection and intercrossing, with the aim of quickly accumulating favourable alleles. Advanced lines derived from GS and from a parallel conventional selection stream will be evaluated in yield trials and phenotyped PTs for studied in Themes 1 and 2. Rates of genetic gain will be assessed and compared between breeding methods. Assuming the proof of concept succeeds, GS will be incorporated into the effort to raise yield potential.

Since GS relies on the assessment of the existing genetic variability in the breeding programme, it is expected to increase efficiency of breeding for yield potential in elite×elite crosses, but it is not designed to introduce new genetic variability into the most adapted backgrounds. Trait-based breeding will combine and introgress yield potential traits coming from various genetic resources into the most adapted spring and winter wheat backgrounds. New elite lines produced from trait-based breeding will enter CIMMYT international yield trials. As genomic prediction models will be updated every year from new international data, the new regions coming from trait-based pre-breeding will be integrated into the GS indexes. With appropriate bioinformatic tools available, the breeder will be able to visualize the most important regions related to trait expression, and to combine genotypic and phenotypic trait information to design optimal elite×elite crosses. In addition, GS will permit genetic gains to be made in early generations without necessarily having to confirm the phenotypic expression of PTs—a highly labour-intensive process which may not even be feasible for all target traits on very large populations—since marker information would presumably indicate where additive gene action for yield is expressed as a result of favourable trait combinations.

#### *Evaluation and delivery of new germplasm*

Over the last 40 years or so, international nursery evaluation networks—coordinated by crop centres of the Consultative Group on International Agricultural Research (CGIAR) and partnering with thousands of breeders worldwide—have delivered new crop genotypes to developing countries on a large scale as freely available global public goods (Braun *et al.*, 2010). The impact of this work on the livelihoods of resource-poor farmers in less developed countries is well documented (Evenson and Gollin,

2003). The value of the international wheat breeding effort coordinated by CIMMYT is estimated at several billion dollars of extra revenue annually (Byerlee and Traxler, 1995; Lantican *et al.*, 2003), spread among millions of farmers (Lipton and Longhurst, 1989). While the impact of the so-called Green Revolution cultivars was initially in relatively favourable environments, subsequent breeding and dissemination effort has resulted in economic benefits in more marginal environments, including those affected by drought and heat stress (Lantican *et al.*, 2003).

This breeding–evaluation–delivery pipeline encompasses the following elements: (i) free exchange of germplasm with national agricultural research services worldwide; (ii) a centralized breeding effort that focuses on generic needs, i.e. yield potential, yield stability, genetic resistance to a range of biotic and abiotic stresses, and consumer-oriented quality traits; (iii) distribution of international nurseries—that are specifically targeted to a number of major wheat agro-ecosystems—via national wheat programmes in >120 countries; (iv) analysis of international yield trials and global disease monitoring to ensure relevance of current local, regional, and global breeding activities; and (v) capacity building and training of research partners (Reynolds and Borlaug, 2006; Braun *et al.*, 2010). Regular contact is also maintained among research partners to help identify the latest technology needs (Kosina *et al.*, 2007). As a result, the international nursery networks have generated massive phenotypic data sets—with data voluntarily contributed by cooperators throughout the North and South—that have allowed breeders to identify germplasm with either specific adaptation to local challenges and diseases or broad adaptation over many different seasons and cropping systems. The proposed delivery and coordination model for the WYC thus encompasses hundreds of national wheat research institutions and will promote best-practice collaborative mechanisms to ensure timely and effective delivery of new high-yielding cultivars as they become available.

## Conclusions

The WYC represents a new model to tackle global food security at the level of crop productivity. For the first time the fundamental bottleneck to yield potential in this  $C_3$  species, that is RUE, is being seriously addressed in a breeding context. However, the WYC also takes a global approach, combining research focused at the cellular level with genetic modification of structural and reproductive aspects of growth to ensure net agronomic benefits. The WYC also represents an unprecedented willingness of experts to share ideas within a consortium, and to leverage new networks of wheat researchers across the production systems. Outputs of the WYC are expected to include a new generation of wheat genotypes with the following characteristics:

- (i) 10–50% increased biomass depending on environment and breeding time frame (10–25 years).

- (ii) Effective partitioning of assimilates to grain yield so that HI is maintained above 0.5 at new levels of expression of biomass in all targeted wheat environments.
- (iii) Improved lodging resistance so that structural failure is improbable in at least 90% of years under the most optimistic yield scenarios.
- (iv) Simultaneous expression of all of the above characteristics such that genetic gains are realized as improved agronomic performance in the shortest time frame possible, leading to farm-level productivity increases in most major wheat agro-ecosystems.

A little over 70% of the wheat produced in developing countries comes from near-optimal environments—the major target of this proposal. However, it has been shown that improvement in yield potential is expressed across a wide range of conditions, including those affected by abiotic stress factors (Lantican *et al.*, 2003). Therefore, while the outputs of the WYC are aimed at the major breadbaskets worldwide, spillover effects into marginal production regions can be anticipated. In summary, the outputs of this initiative are expected to reduce the number of hungry and malnourished in the world and thereby contribute to stated goals of the 2009 World Summit on Food Security (Food and Agriculture Organization of the United Nations, 2010).

## Acknowledgements

The authors are grateful to Perry Gustafson, Ian King, and Ron Phillips for their helpful comments about this manuscript. The generous support of the United States Agency for International Development (USAID) and of the UK's Biotechnology and Biological Sciences Research Council (BBSRC) in helping to convene the Wheat Yield Consortium is also gratefully acknowledged.

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