Achieving yield gains in wheat

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ABSTRACT

Wheat provides 20% of calories and protein consumed by humans. Recent genetic gains are <1% per annum (p.a.), insufficient to meet future demand. The Wheat Yield Consortium brings expertise in photosynthesis, crop adaptation and genetics to a common breeding platform. Theory suggest radiation use efficiency (RUE) of wheat could be increased ~50%; strategies include modifying specificity, catalytic rate and regulation of Rubisco, up-regulating Calvin cycle enzymes, introducing chloroplast CO2 concentrating mechanisms, optimizing light and N distribution of canopies while minimizing photo inhibition, and increasing spike photosynthesis. Maximum yield expression will also require dynamic optimization of source: sink so that dry matter partitioning to reproductive structures is not at the cost of the roots, stems and leaves needed to maintain physiological and structural integrity. Crop development should favour spike fertility to maximize harvest index so phenology must be tailored to different photoperiods, and sensitivity to unpredictable weather must be modulated to reduce conservative responses that reduce harvest index. Strategic crossing of complementary physiological traits will be augmented with wide crossing, while genome-wide selection and high throughput phenotyping and genotyping will increase efficiency of progeny screening. To ensure investment in breeding achieves agronomic impact, sustainable crop management must also be promoted through crop improvement networks.

Key-words: food security; genetic resources; HI; partitioning; photosynthesis; physiological breeding; RUE; Wheat Yield Consortium.

INTRODUCTION

Plato stated that ‘No one can call themselves a true statesman who is ignorant of wheat’, a commodity that remains to this date a central pillar of food security. While its production has risen at approximately 7% per year since 1998, the price of wheat has increased annually by 18% in the same period (Fig. 1). It may not be entirely coincidental that social and political unrest has erupted recently in many developing countries where wheat is the number one staple food and constitutes a relatively large proportion of disposable income for most households. This review addresses the scientific basis and approaches for increasing wheat’s genetic potential as well as some of the environmental factors that can interact with its genetic expression to determine impacts at a farm level.

Imperatives to raise wheat productivity

Wheat provides 20% of the calories to the world’s population and a similar proportion of daily protein for about 2.5 billion people in less-developed countries (Braun, Atlin & Payne 2010). The future productivity of wheat will arguably have more influence on global food security than that of any other crop because it is the most widely grown, being adapted to a broad range of latitudes, temperatures, water regimes and nutritional levels. Post Green Revolution cultivars also encompass genetic resistance to a wide spectrum of diseases and other pests (Singh & Trenchevalian 2007) partly as a result of crossing with wild relatives (Ortiz et al. 2008). Nonetheless, in spite of predicted increases in demand for wheat at a rate of around 1.7% per annum (p.a.) until 2050 (Rosegrant & Ageaolii 2010), productivity is increasing globally at only 1.1% p.a. (Dixon et al. 2009) and even seems to be stagnating in some regions (Brisson et al. 2010). Factors ranging from climate change, diminishing natural resources and competition for land threaten to further reduce potential productivity (Datta & de Jong 2002; Ladha et al. 2003; Easterling 2007; Lobell et al. 2008; Battisti & Naylor 2009; Rosegrant & Ageaolii 2010). While theoretically more lands could be brought into production, this is not desirable in terms of the long-term sustainability of the global ecosystem. The most direct solution to these problems will be to increase productivity on currently cultivated land through adoption of cultivars with improved genetic potential. Yield potential (YP) is related to farm level yields (Slafer & Araus 2007; Fischer & Edmeades 2010) and genetic gains are expressed under a broad range of conditions
Recent trends in genetic improvement of wheat

In spite of some studies suggesting that genetic gains of wheat are stagnating (Acreche et al. 2008; Graybosch & Peterson 2010), recent studies measuring the impact of internationally coordinated public breeding aimed at the developing world reported genetic gains of between 0.6 and 1.0% p.a. for germplasm released between 1994 and 2010 based on data from ~1400 yield testing sites worldwide (Lopes et al. 2012a; Manes et al. 2012; Sharma et al. 2012). In spite of this achievement, the numbers still fall short of meeting the predicted demands by 2050 (Rosegrant & Agcaoili 2010), a mismatch that represents a serious challenge for future food security.

The Wheat Yield Consortium

Given concerns about the ability of our agricultural system to meet future demand (Godfray et al. 2010) and the central role of wheat in maintaining food security, the International Maize and Wheat Improvement Centre (CIMMYT) began consulting with crop experts worldwide to establish a Wheat Yield Consortium (WYC) (Reynolds et al. 2011). The overall purpose of the WYC is to raise the genetic YP of wheat by 50% within the next 20 years by bringing ongoing research efforts together to promote synergies between respective disciplines, thereby accelerating impacts in farmer’s fields. The WYC encompasses expertise within three linked themes, namely increasing photosynthetic capacity and efficiency (Parry et al. 2011), optimizing partitioning to grain yield while maintaining lodging resistance (Foulkes et al. 2011), and breeding to accumulate YP traits (Reynolds et al. 2011).

This review has the following objectives: (1) summarize state-of-the-art scientific basis for increasing YP in wheat; (2) define synergies and trade-offs that may be expected from combining different physiological mechanisms via trait and molecular breeding; and (3) outline some of the opportunities to enhance the genetic expression of improved cultivars in target environments as well as the risks and threats that may yet need to be addressed to ensure investments in research achieve their intended targets.

BREEDING FOR YP

It is axiomatic that radiation use efficiency (RUE) must be increased through crop breeding if yields are to continue to rise, as harvest index (HI) is already close to its theoretical limit (Foulkes et al. 2011). Increasing photosynthetic potential will require considerable research focused at cellular and sub-cellular processes while this must go hand in hand with genetic modification of structural and reproductive aspects of growth, as these will determine the net agronomic benefit of increased RUE. To bring these traits together through hybridization will require a multifaceted breeding effort including modelling of optimal trait combinations, screening of genetic resources combined with wide crossing and/or transgenic approaches to introduce necessary levels of trait expression, and application of phenotyping and genomic tools to increase the efficiency of progeny screening (Table 1); these approaches will be discussed next. Subsequent sections will address in detail the research needed to improve crop biomass and HI, respectively.

Trait and molecular breeding

Conventional breeding achieves incremental yield gains by recombining alleles mainly from within elite materials and selecting among thousands of progeny per cross for expression of appropriate agronomic traits, resistance to a spectrum of prevalent diseases and yield based on multi-location trials (Braun et al. 2010). While the genetic basis for improvements in biotic stress resistance of wheat is relatively well understood for the prevalent diseases (Singh & Trethowan 2007), the genetic basis of cultivar level differences in YP is largely unknown. Therefore, systematic deployment of yield-specific genes will only become the dominant breeding strategy when two conditions are met; firstly, when the wheat genome is fully sequenced so that the identification of functional polymorphisms in wheat is as achievable as it is now for rice, and secondly, when our understanding of the way genes interact to determine the expression of complex traits like yield can be modelled effectively for representative target environments; the first condition is getting closer (Paux et al. 2008), however, the second is still on the horizon. That given, in order to accelerate genetic gains from their current rate of under 1% per year, the breeding effort for the foreseeable future will depend on four main strategies: (1) strategic hybridization to combine traits associated with RUE and partitioning (Reynolds et al. 2011); (2) use of exotic germplasm – including transgenes – to complement levels of expression in...
Table 1. Estimated time frame (years) for research activities in Wheat Yield Consortium; last column represents an estimated cumulative time frame for parallel or consecutive activities towards increasing yield potential by up to 50%.

<table>
<thead>
<tr>
<th>Photosynthesis research</th>
<th>Estimated contribution to yield</th>
<th>Phenotyping, genotyping and breeding</th>
<th>Introgress traits from wild species into good agronomic backgrounds by IH</th>
<th>Develop fine markers for (i) progeny selection and (ii) genetic resource screening</th>
<th>Achieve trait expression in good agronomic backgrounds using appropriate constructs</th>
<th>Advanced lines – based on transgenics, trait/IH breeding and MAS – deployed to national programs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Improved absorption of radiation</td>
<td>Unknown but canopy reflectance + transmittance is around 5%</td>
<td>2</td>
<td>4</td>
<td>10–12</td>
<td>5–10</td>
<td>10–15</td>
</tr>
<tr>
<td>Raise leaf photosynthetic capacity (light saturation) via multiple mechanisms</td>
<td>10% depending on conditions. We assume upper canopy leaves contribute 50–75% of canopy Pn</td>
<td>3</td>
<td>4</td>
<td>N/A</td>
<td>5–10</td>
<td>5–10</td>
</tr>
<tr>
<td>Optimize Rubisco properties</td>
<td>Up to 25%</td>
<td>3</td>
<td>5</td>
<td>10–12</td>
<td>5–10</td>
<td>10–15</td>
</tr>
<tr>
<td>Reduce photorespiration</td>
<td>Up to 40%</td>
<td>3</td>
<td>5</td>
<td>N/A</td>
<td>N/A</td>
<td>10–15</td>
</tr>
<tr>
<td>Optimize distribution of photosynthetic properties in the canopy</td>
<td>Up to 30% based on example of modelling of recovery of ρCO2</td>
<td>3</td>
<td>5</td>
<td>12–15</td>
<td>10–12</td>
<td>N/A</td>
</tr>
<tr>
<td>Photosynthesis research</td>
<td>H1 &gt; 0.5–0.55 in all genotypes</td>
<td>4</td>
<td>5</td>
<td>10–12</td>
<td>5</td>
<td>N/A</td>
</tr>
<tr>
<td>Tailor phenology to diverse latitudes, temps</td>
<td>H1 &gt; 0.5 in all agro-ecosystems</td>
<td>3</td>
<td>4</td>
<td>8–10</td>
<td>0–5</td>
<td>N/A</td>
</tr>
<tr>
<td>Modulate sensitivity to pre-anthesis stress</td>
<td>H1 maintained at &gt;0.5 when conditions are unfavourable pre-anthesis</td>
<td>5</td>
<td>5</td>
<td>10–12</td>
<td>5</td>
<td>N/A</td>
</tr>
<tr>
<td>Adapt to post-anthesis stress</td>
<td>H1 maintained at &gt;0.5 when conditions are unfavourable post-anthesis</td>
<td>3</td>
<td>4</td>
<td>10–12</td>
<td>5</td>
<td>N/A</td>
</tr>
<tr>
<td>Lodging resistance</td>
<td>Lodging does not cause significant yield loss in 90% of seasons</td>
<td>2</td>
<td>3</td>
<td>8–10</td>
<td>5</td>
<td>N/A</td>
</tr>
</tbody>
</table>

H1, harvest index; IH, interspecific hybridization; MAS, marker-assisted selection; N/A, not applicable.
conventional genepools (Ortiz et al. 2008, Trethowan & Mujeeb-Kazi 2008; Parry et al. 2011); (3) high-throughput phenotyping and molecular marker-assisted breeding – including genome-wide selection (GWS) – to permit the efficient deployment of yield and other trait-linked markers as they are identified through gene discovery and GWS modelling (Bernardo & Yu 2007; Tester & Langridge 2010); and (4) conventional breeding that includes both empirical methods as well as the skill to identify from individual plant observations those phenotypes most likely to perform well in a dense agronomic canopy (while not easily incorporated into the empirical method, this kind of intuitive ability to ‘extrapolate’ is vital in industries where complex outcomes cannot be effectively modelled and remains an essential tool in plant breeding).

YP can be expressed as a function of the light intercepted (LI) and RUE, whose product is biomass, and the partitioning of biomass to yield, that is, HI:

\[ YP = LI \times RUE \times HI \]

Physiological trait (PT)-based breeding will focus on improving all three of these components. The PTs related to LI – such as stand establishment, canopy architecture and nitrogen partitioning – are relatively straightforward to phenotype on a routine basis. Although PTs related to RUE are generally more challenging to measure, the potential to increase RUE is supported by theory (Zhu, Long & Ort 2010) as well as observations of increased biomass in specific recent cultivars (Shearman et al. 2005), in some cases stemming from introgression of exotic germplasm (Singh et al. 1998; Reynolds et al. 2001). The main approaches for increasing RUE will be to modify the specificity, catalytic rate and regulation of Rubisco, up-regulate Calvin cycle enzymes, introduce CO₂ concentrating mechanisms (CCMs) in chloroplasts, optimize light and N distribution of canopies while minimizing photoinhibition, and increase the contribution of spike photosynthesis (SP). These approaches – involving both transgenic and non-transgenic strategies – will be discussed in detail subsequently.

On the other hand, HI has increased steadily during the 20th century, and with the exception of the (generally imprecise) deployment of major-effect alleles at the Rht, Ppd and Vrn loci (Sláfer & Rawson 1994; Worland et al. 1998; Mathews et al. 2006), optimal expression of HI is still achieved empirically within major agro-ecosystems and is subject to seasonal effects (Ugarte, Calderini & Sláfer 2007). A considerable genetic variation in expression of HI can be found typically in the range of 0.4–0.55 in elite cultivars worldwide (see Sayre, Rajaram & Fischer 1997; Shearman et al. 2005; Zheng et al. 2011). While improving light interception and RUE will increase crop biomass, maximum yield expression will require dynamic optimization of source: sink. This will require a better understanding of how to maximize dry matter partitioning to reproductive structures without under-investing in roots, stems and leaves on which both grain yield and lodging resistance are also dependant. The phenology of the crop should be optimized to favour spike fertility and must be tailored to different photoperiod and temperature regimes. Moreover, sensitivity to unpredictable environments including extreme weather must be modulated to prevent overly conservative responses that reduce seed set and HI. These approaches will also be discussed subsequently in more detail.

Using all information available on photosynthetic and partitioning traits and their interaction, hybridization schemes will be designed to combine PTs (Fig. 2) in such a way that the main drivers of YP (Eqn 1) are combined deterministically with the view to achieving cumulative gene action. Given limited understanding of the genetic basis of traits that contribute to yield, it is impossible to predict the outcome of combining albeit theoretically complementary characteristics. Nonetheless, it is axiomatic that a good level of PT expression in a genotype indicates a favourable – albeit unspecified – combination of positive alleles, and selecting for PTs is thereby a practical means of achieving cumulative gene action, as demonstrated by recent impacts in breeding for drought adaptation (Richards 2006; Rebetzke et al. 2009; Reynolds et al. 2009b). This approach will be complemented by marker-assisted crossing and selection as more information from genetic dissection of complex PTs becomes available (Snapes et al. 2007; Pinto et al. 2010).

Nonetheless, diagnostic markers are widely used for genes where the functional polymorphism has been identified. These include homoeoallelic series at Ppd-I (Turner et al. 2005; Beales et al. 2007), Vrn-1 (Yan et al. 2003), Vrn-3 (Yan et al. 2006) and Rht-1 (Peng et al. 1999). Diagnostic assays exist for alien introgression segments including 1BL/1RS rye translocation (Koebner 1995) and Lr19 Agropyron translocation (Prins et al. 2001). These effects are tagged with diagnostic assays, which is the ideal situation, but marker-assisted selection (MAS) can be effective using flanking genetic markers. Flanking markers from quantitative trait loci (QTL) studies are deployed in

Figure 2. Conceptual model of traits that contribute to yield potential based on evidence summarized in Reynolds et al. (2009a).
commercial breeding programs but this is not always reported. Cloning QTL will allow MAS for these effects as it is now conducted for the major height and heading date effects. Near isogenic lines (NILs) are the well-proven germplasm base for isolating genes of interest and developing ‘perfect markers’ (Yamamoto, Yonemaru & Yano 2009). Within the WYC, QTL controlling PT will be identified, validated using NILs, and close flanking markers developed for MAS. For example, the Wheat Association Mapping Initiative (WAMI) panel – consisting of 296 elite but diverse spring wheat lines with a restricted phenology range – has recently been phenotyped in more than 30 wheat growing environments worldwide, and is expected to provide information on genetic regions associated with adaption (Lopes et al. 2012b). Once genes are isolated, new opportunities exist for the identification and synthesis of novel alleles in diverse germplasm (allele mining), from mutant collections (tiling), or by transgenesis. In this way, a library of genetic variation likely to contribute to desirable PTs can be assembled from sources where the PT itself is not fully expressed. Then, by creating permutations of these alleles in a breeding programme, the library is interrogated to maximize phenotypic range for that trait. Allele mining can be performed by forward genetic screens in which lines from a population are pre-screened for the desired phenotype or by reverse genetic approaches such as tilling (Henikoff, Till & Comai 2004) or re-sequencing (Tsai et al. 2011) where the target is any sequence change in the gene of interest. For wheat, the cloning of Ppd-1 and Vrn-1 has already led to the identification of new alleles at these loci (Wilhelm, Turner & Laurie 2009; Diaz et al. 2012), which extend the ability to select for levels of photoperiod insensitive earliness and length of vernalization requirement. Often these searches are performed as a combination of forward and reverse approaches where assays for known alleles are used to reduce the target germplasm to a smaller set of lines, which are then sequenced in depth as carried out for Ppd-1, a wheat gene conferring powdery mildew resistance (Bhullar et al. 2010). Gene cloning and re-sequencing are already aided by the availability of whole genome ‘shotgun’ sequence of wheat (http://www.cerealsdb.uk.net) but absolutely require the development of contiguous whole chromosome sequence assemblies that are under development by the International Wheat Genome Sequencing Consortium (http://www.wheatgenome.org/). A long-term goal of the WYC is to clone QTL that has been validated and fine mapped and is dependent on the availability of wheat genome sequence.

While the PT approach can be used to design more strategic crosses, diagnostic markers are not yet available for the majority of PT ruling out widespread application of trait-specific MAS. Nonetheless, a few high-throughput phenotyping approaches can be applied in progeny screening. One is canopy temperature (CT) that when measured in appropriate conditions (low cloud cover, low wind speed) is well correlated with stomatal conductance and can be assessed accurately in about 10 s on field plots (Amani, Fischer & Reynolds 1996; Pinto et al. 2010). Using airborne remote sensing platforms, a range of spectral indices can be measured at high throughput, including the Normalized Vegetative Difference Index (NDVI) and the Water Index, both of which can estimate relative differences in biomass among plots at similar growth stages and are measured in the same time frame as CT (Babar et al. 2006; Gutierrez et al. 2010). Other spectral indices are sensitive to photosynthetic pigments, and the possibility of estimating photosynthetic rate has been proposed (Serbin et al. 2012).

Looking ahead, GWS offers considerable promise to increase breeding efficiency by capitalizing on the empirical association between expression of yield per se and high-density markers across the entire genome (Bernardo & Yu 2007), assuming all of the representative genetic sources are present in the ‘training’ population (Heslot et al. 2012). It is important to note, however, that GWS will not inform gene discovery or the identification of new and useful variation from diverse germplasm.

**Expanding the genetic base of wheat**

The distant relatives of wheat provide a vast reservoir of genetic variation for agronomically important traits and – given that wide crossing is already a mature discipline in wheat (Ortiz et al. 2008; Trethowan & Mujeeb-Kazi 2008) – represent a key resource in the pipeline for increasing YP (Table 1). Examples of alien introgressions include those from *Aegilops umbellulata* (Sears 1956, 1972) which saved US wheat production from catastrophic failure due to leaf rust in 1960; resistance to a range of diseases, tolerance to acid soils, increased yield and yield stability from *rye* (McIntosh 1983; Ammar, Mergoum & Rajoram 2004) (in the late 1990s, a 1B/1R translocation from rye was present in the majority of world wheat varieties and a number of the current global top varieties, e.g. ‘Rialto’, still carry it); a gene from *Ae. ventricosa* (Garcia-Olmedo, Delibes & Sanchez-Monge 1977) conferring resistance to eyespot is present in several wheat varieties; many of the top wheat varieties in Europe, for example, ‘Robigus’, are derived from unknown introgressions from *Triticum dicoccoides*; over 30% of all wheat varieties currently produced at CIMMYT are derived from crosses between normal wheat and ‘synthetic’ wheat (Dreisigacker et al. 2008) (synthetic wheat is derived from crosses between *Ae. squarrosa*, DD genome, and tetraploid wheat, AABB genomes, followed by chromosome doubling via colchicine).

Alien introgression in crop species, in its simplest form, involves the sexual hybridization of different species to form an interspecific F1 hybrid. Alien introgression occurs in the F1 hybrid (or its derivatives) when related chromosomes from the two parental species (i.e. chromosomes that carry orthologous genes in essentially the same order) recombine at meiosis resulting in the generation of interspecific recombinant chromosomes. These recombinant chromosomes are then transmitted to the next generation through the gametes. The repeated backcrossing of the F1
While the introduction of genes from outside of the Triticeae tribe is not a routine procedure in wheat breeding, chromatin from C₄ species, maize and *Tripsacum dactyloides* has been introduced into wheat but so far not proven to be stably integrated and transmitted (Laurie & Bennett 1989; Comeau et al. 1992; Li et al. 1996; Brazauskas, Pasakinskiene & Jahoor 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. It remains to be seen whether wide crossing or the transgenic approach will have impacts sooner in terms of increasing crop biomass.

**IMPROVING CROP BIOMASS**

Improvements in wheat yield in the past have been achieved largely by improvements in HI with only small changes to total biomass production (Calderini, Reynolds & Slafer 1999). However, HI values are already relatively high – around 0.5 – and it will be increasingly necessary to raise the level of total biomass production to permit higher grain yields.

**Potential biomass/RUE: theoretical considerations**

While there is evidence that biomass has increased modestly in recent years (Sayre et al. 1997; Shearman et al. 2005), and even some physiological and genetic factors identified (Reynolds et al. 2001, 2009a), theoretical considerations suggest that still more biomass can be achieved by increasing RUE. Because RUE is integrated over different processes throughout crop development it is difficult to describe mechanistically; however, net RUE can be easily measured as the amount of biomass produced per unit of radiation intercepted.

Radiation conversion has a number of steps each of which is associated with a net loss of energy (Fig. 3). These include (1) the fact that ~50% of incident radiation cannot be absorbed by leaf pigments; (2) reflection and non-photosynthetic absorption of light; (3) light saturation of photosynthesis; (4) photoinhibition and photoprotection; (5) photorespiratory flux; (6) growth and maintenance respiration; and (7) metabolism under limiting light. These processes are likely to show variation according to growing environment and stage of development, and this seems to be reflected in the reported RUE values (e.g. Sinclair & Muchow 1999). High values for measured RUE in wheat...
are likely to be in the region of 1.5 g above ground (AG) dry matter MJ\(^{-1}\) of solar radiation (close to 3 g MJ\(^{-1}\) of photosynthetically active radiation) (Yunusa et al. 1993; Sinclair & Muchow 1999), representing a little less than 3% of the energy of incident light accumulated over the cycle. Practical maxima for wheat RUE were reviewed in the context of identifying possibilities for improvement (Loomis & Amthor 1996). Quantum requirements (QRs) reported for carbohydrate synthesis in C\(_3\) species range between 10 and 30 mol CO\(_2\)\(^{-1}\) resulting in a RUE of between 4.1 and 1.1 g biomass MJ\(^{-1}\) solar radiation. Based on these theoretical calculations, Reynolds, van Ginkel & Ribaut (2000) estimated potential productivity for irrigated wheat in Northwest Mexico. For a wheat crop, best estimates of QR are in the range of 15–24 mol quanta mol\(^{-1}\) CO\(_2\), which results in a range of RUE between 1.5 and 2.6 g carbohydrate MJ\(^{-1}\) solar radiation. Measured values for AG biomass fall well below those calculated from QR showing that improvements in wheat RUE are feasible. Zhu, Long & Ort (2008) carried out an energetic study of solar radiation conversion in crops, comparing theoretical losses with measurements of RUE, and also concluded that there is capacity for improvement while proof of concept that raising net leaf photosynthesis can directly improve RUE and biomass has come from growing plants in elevated CO\(_2\) (Long et al. 2006).

The two main areas that are considered of paramount importance in terms of genetic improvement are photosynthetic efficiency at the cellular level, and canopy level light capture and photosynthesis (see Table 2) (Murchie, Pinto & Horton 2009; Zhu et al. 2010). Currently, there is an emphasis on validation of specific leaf and cell-level targets (Table 2) while Fig. 3 emphasizes the need to target major losses according to processes that are canopy position dependent. As described below, this is expected to occur via the integration of all traits and will require development of sophisticated canopy photosynthesis models.

**Light interception, canopy architecture and light dynamics**

The ideal canopy will maximize interception of solar radiation throughout the crop cycle while optimizing the distribution of light. The latter is important because photosynthesis saturates at about half the intensity of direct sunlight. Hence, the maximum rates of canopy photosynthesis are achieved by increasing the leaf area index (leaf area: ground area) to values typically above 3, and arranging leaves in a more erect posture thereby reducing the proportion of leaves in a light saturated state and increasing light penetration. In fact, light interception is generally

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**Figure 3.** Schematic figure showing the losses in radiation conversion in a wheat canopy. Major processes are listed which correspond to those in Table 2. Inset figures to the right of 1, 3 and 4 are schematic illustrations of the region of the solar spectrum corresponding to photosynthetically active radiation (PAR), the saturation of photosynthesis in a C\(_3\) photosynthesis response curve and the change in shape of the photosynthesis light response curve caused by photoinhibition, respectively.
above 95% for most wheat canopies in favourable environments – no apparent improvement was noted in the % of LI by a series of historical cultivars (Acreche et al. 2009) – and modern wheat canopies already have erect or semi-erectophile canopies (Araus et al. 1993).

However, there may be scope for further genetic alteration of leaf posture, leaf size or density to alter the architecture, and hence the in-canopy light characteristics that influence the extent and dynamics of light saturation (Murchie et al. 2009). A feature of improvement may be the manipulation of pigment and enzyme distribution even broadening the wavelengths exploited (e.g. utilizing chlorophyll D) and optimizing the response dynamics at different positions according to variation in light intensity and nitrogen content. Coordination with architecture may be required: for example, reducing the chlorophyll containing

Table 2. Summary of losses in photosynthesis alongside associated photosynthetic targets for improvement of wheat yield

<table>
<thead>
<tr>
<th>Process</th>
<th>Associated target</th>
<th>Goal</th>
<th>Bottlenecks/comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Losses of non-PAR, seasonal loss</td>
<td>Losses associated with radiation absorption: non-PAR spectral regions, canopy reflectance</td>
<td>Extend regions of absorption, for example, via chlorophylls D and F</td>
<td>Low energy of absorbed photons is barely enough to split water.</td>
</tr>
<tr>
<td>2. Light saturation of photosynthesis (not directly targeting photorespiration, see 5)</td>
<td>Rubisco</td>
<td>Improvement of Vcmax, specificity and activation (via Rubisco activase)</td>
<td>High impact on yield expected. Chloroplast transformation may be required.</td>
</tr>
<tr>
<td></td>
<td>N redistribution between Calvin cycle and other processes</td>
<td>Allocation between photosynthetic and Calvin cycle enzymes including Rubisco and RuBP regeneration</td>
<td>Knowledge of genetic regulation of intra-leaf N partitioning</td>
</tr>
<tr>
<td>3. Photoinhibition and photoprotection</td>
<td>Regulatory components of photoprotection and photoinhibitory recovery</td>
<td>Reduce proportion of canopy surface area with photoinhibitory damage and excess protective processes</td>
<td>Understanding trade-offs between canopy architecture, photoprotection, photoinhibition and CO2 assimilation</td>
</tr>
<tr>
<td>4. Photorespiratory flux</td>
<td>Photorespiratory pathway</td>
<td>Short circuit of photorespiratory pathway</td>
<td>Highest impact on yield expected under high temperatures. Non-plant genes required?</td>
</tr>
<tr>
<td></td>
<td>C4 properties</td>
<td>‘Installation’ of C4 cycle</td>
<td>High impact on yield and resource use efficiency expected under high temperatures. Dependence on anatomy uncertain. Cell specific alteration of enzyme activity and regulation required.</td>
</tr>
<tr>
<td>5. Growth and maintenance respiration</td>
<td>Respiratory metabolism</td>
<td>Removal of unnecessary respiratory flux</td>
<td>Knowledge of respiratory responses to environmental conditions</td>
</tr>
<tr>
<td>7. Integration of photosynthetic components with canopy properties</td>
<td>Lowering overall chlorophyll content for better light distribution</td>
<td>Improved light absorption and distribution in canopy</td>
<td>Appropriate targets for down-regulation of chlorophyll biosynthesis</td>
</tr>
<tr>
<td></td>
<td>Canopy position-specific metabolism</td>
<td>Target specific regions of canopy and tailor responses according to micro-environment, for example, better light harvesting at lower levels and carboxylation at exposed positions</td>
<td>Genetic regulation of canopy position effects. Possibly target photoacclimation as a means of manipulation</td>
</tr>
<tr>
<td>8. Integration of photosynthetic components with canopy properties</td>
<td>Losses in integrated photosynthesis caused by suboptimal tracking of environmental conditions</td>
<td>Improving the dynamic responses of photosynthesis in response to light fluctuation</td>
<td>Knowledge of which components are limiting in fluctuating light</td>
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</table>

PAR, photosynthetically active radiation.
photosynthesis (Zhu et al. 2010), tailoring the kinetic properties of Rubisco enzyme to different light levels (see this paper and Long et al. 2006), reducing dark respiration of tissue at low light levels, and improving photoprotective and photo-inhibitory dynamics that can reduce the quantum yield of photosynthesis (Zhu et al. 2004). Recovery of the quantum yield of CO₂ assimilation after photoinhibition within the canopy is predicted to have significant effects on canopy photosynthesis (Zhu et al. 2004), but the direct impact of all photoprotective processes on photosynthesis in fluctuating light has yet to be shown empirically. However, the potential for altering dynamics of induction and relaxation of photoprotection is clear (Murchie & Niyogi 2011).

One area of canopy photosynthesis that has not been addressed in breeding before is the potential to improve the contribution from spikes. In a dense wheat canopy, a significant proportion of incident radiation is intercepted by spikes; values typically range from 25 to 40% depending on spike architecture (López-Castañeda et al., unpublished results). Furthermore, it has been shown that SP can contribute substantially to grain filling (Tambussi et al. 2007) and shows genetic variation (Abbad et al. 2004). SP can be particularly important under high temperature and drought due to the specific structural characteristics of this organ, such as hydraulic isolation from the rest of the plant at low water potential and lower stomatal density of glumes compared with leaves (Tambussi et al. 2007). The main bottleneck to improving SP in crops is that it is especially difficult to phenotype. For example, gas exchange measurement to establish CO₂ fixation rate can be confounded by the spike’s ability to recycle respiratory carbon, and these measurements are technically difficult and slow due to the complex three-dimensional spike architecture (Tambussi et al. 2007). However, new phenomics technologies such as high-throughput chlorophyll fluorescence and high-resolution hyperspectral imaging present new opportunities to rapidly screen germplasm for SP (Munns et al. 2010). The breeding objective would be to combine improved RUE of spikes at high light intensity (because spikes are always exposed to high light levels) simultaneously with improved canopy leaf canopy photosynthesis across a range of light intensities (depending on leaf position), thereby accumulating genetic gains from both in terms of expression of total net assimilation.

Rubisco, its regulation and integration with leaf metabolism

Rubisco catalyses photosynthetic carbon fixation. Under saturating light, the rate of photosynthesis is largely determined by the abundance, kinetic properties and activation state of Rubisco. Of significance to RUE is the fact that the kinetic properties of Rubisco are not optimal for current or projected environments. Because Rubisco is a remarkably slow catalyst, large amounts are needed to sustain high photosynthetic rates, for which reason this enzyme alone accounts for approximately 25% of leaf nitrogen (Parry et al. 2003). Increasing the abundance of Rubisco further will increase photosynthesis at high irradiance and high temperatures at ambient CO₂ concentrations (Yabuta et al. 2008). However, this approach has limited appeal because it would require an increase in nitrogen fertilizer and, because at lower light intensities Rubisco would be in excess, decreasing nitrogen use efficiency. Indeed, there is strong evidence that at moderate and low light intensities there is already an over-investment in Rubisco (Ainsworth & Long 2005), and that a small decrease in the amount of Rubisco would decrease nitrogen requirements and increase nitrogen use efficiency. Thus, a Rubisco reduction of 15–20% would reduce crop nitrogen requirements by 10%, without negatively impacting on CO₂ fixation capacity at all but the highest light intensities.

Rubisco also catalyses a competing and wasteful reaction between RuBP and oxygen which leads to the loss of fixed carbon and nitrogen through photorespiration diverting captured energy away from carbon assimilation (Parry et al. 2007). C₄ crops (e.g. wheat and rice) lack the CCM found in C₃ plants, and so their productivity is compromised by photorespiration. Furthermore, the wasteful oxygenase activity is most pronounced when water supply is inadequate and when prevailing temperatures are high. Pioneering attempts to decrease or eliminate the oxygenase activity of Rubisco by site-directed mutagenesis have so far been largely unsuccessful (Parry et al. 2003). Nevertheless, considerable interspecies variation in the kinetic properties of Rubisco has been identified sufficient to suggest that it can be exploited as a means to improve crop photosynthesis. For example, replacing Rubisco in wheat with that from the Mediterranean sea lavender, Limonium gibertii, would give significant increases in photosynthesis at concentrations of CO₂ up to the current ambient concentration, and small increases even when RuBP regeneration is limiting. However, the replacement of wheat Rubisco with that of another species is technically challenging, requiring context-specific expression, assembly, post-translational modification and regulation. To achieve this, several technical hurdles need to be overcome (Parry et al. 2011). Until these issues for engineering Rubisco are resolved, an alternative approach of identifying genetic variation in Rubisco properties in wheat and wheat relatives by a physiology-based phenotypic screen is underway in the WYC (Parry et al. 2011). While potentially delivering more incremental improvements than direct engineering, the time frame for delivery is shorter (see Table 1).

Rubisco catalytic activity is regulated to match the capacity for RuBP regeneration with that for RuBP utilization. It is widely recognized that Rubisco regulation is not always optimal for crop productivity and remains an important target for crop improvement. For example, at elevated temperatures a decrease in Rubisco activity causes an undesirable decrease in photosynthetic rate (Crafts-Brandner & Salvucci 2000). Rubisco activity is modulated both by the carbamylation of an essential lysine on the large subunit and its subsequent stabilization by a Mg²⁺ ion to form an active ternary complex and also by the binding of inhibitors...
to carbamylated and non-carbamylated enzymes to block the catalytic site. The ancillary protein Rubiscoactivase facilitates the activation of Rubisco by promoting the release of inhibitors (Robinson & Portis 1988), after which the most potent of these (carboxyarabinitol 1-phosphate and pentadiulosebisphosphate) are rendered non-inhibitory by a specific phosphatase (Andralojc et al. 2012). Manipulating the amounts and activity of Rubisco-activase and targeting the degradation of inhibitors offer further opportunities not only to modulate Rubisco activity but also to control its stability.

There is strong experimental evidence that the protein and nitrogen investment in the various enzymes in leaves is not optimal. For example, overexpression of sedoheptulose-1,7-bisphosphatase (Harrison et al. 1998; Lefebvre et al. 2005; Tamoi et al. 2006) or fructose 1,6-bisphosphate aldolase (Haake et al. 1999) can ameliorate the limitation to assimilation caused by RuBP regeneration increase, both photosynthetic rate and biomass accumulation. Numerical simulation using an evolutionary algorithm to optimize the distribution of resources between enzymes of carbon metabolism where leaf nitrogen levels are kept constant supports the experimental results and further suggests that decreasing some photorespiratory enzymes would also increase photosynthetic rate (Zhu, de Sturler & Long 2007). Further decreases in the photorespiratory pathway may be made if combined with a photorespiratory bypass (Kebeish et al. 2007; Timm et al. 2008; Carvalho et al. 2012).

**C₄ and CO₂ concentrating approaches**

As discussed above, the efficiency with which CO₂ is assimilated by C₃ crop plants is severely compromised by photorespiratory activity (see Zhu et al. 2008). C₄ plants have evolved a complex biochemical mechanism to concentrate CO₂ at the site of Rubisco, reducing the energy cost of photorespiration to almost 0 and ensuring that Rubisco operates at close to its maximum catalytic capacity (see Fig. 4; Sage and Zhu 2011 and references therein). C₄ crop plants include maize, sorghum and sugarcane, but unfortunately the number of commercially cultivated C₄ species is small. In C₄ photosynthesis, photorespiration is almost eliminated and Rubisco operates close to its theoretical maximum velocity. The theoretical efficiency of conversion of total solar energy to biomass in a C₄ plant is almost 60% higher than in a C₃ cereal like wheat (see Zhu et al. 2008; Furbank et al. 2009; Parry et al. 2011). If translated into yield through appropriate whole plant carbon partitioning, this improvement could be compounded in the field by the elevated N-use efficiency and water use efficiency of C₄ crops, making the installation of C₄ photosynthesis or a modification thereof, an attractive proposition to increase cereal yields for future climate scenarios and likely limiting nutrient resources (see papers in Sheehy, Mitchell & Hardy 2007; Parry et al. 2011; Sage & Zhu 2011). Engineering biochemical C₃ pathways into C₃ plants both with and without appropriate morphological specialization is being attempted at present, focusing mostly on rice (Kajala et al. 2011; Miyao et al. 2011). A full Kranz anatomy-based C₄ system entails a considerable amount of gene discovery, genetic engineering and analysis of transgenic plants. The C₄ pathway has evolved independently more than 62 times (Sage & Zhu 2011), leading researchers to some cautious optimism as to the chances of success of this approach, and there are a wide variety of options for installation of C₄ pathway variants (Furbank 2011) and partial or ‘intermediate’ C₄ pathways in C₃ plants. These opportunities will be discussed below.

Recently, the Bill and Melinda Gates Foundation funded a major initiative to build the ‘toolkit’ necessary to install a functional C₄ pathway in rice based on a gene discovery project to identify genes responsible for anatomical specialization and a parallel engineering approach to install the enzymes and metabolite transporters in rice, sourcing many of the genes from maize (see Kajala et al. 2011). Such an
The bundle sheath is considerably higher in C4 than in C3. Similarly, chloroplast number and volume in the bundle sheath/mesophyll cell wall interface is heavily thickened and potentially provides a barrier to CO2 leakage out of the bundle sheath cells in the form of a specialized cell wall or suberised lamella is necessary for the efficient operation of the C4 pathway, and modelling suggests that organelle localization within the bundle sheath cells and diffusion path length may (see Von Caemmerer & Furbank 2003). Information on the permeability of the bundle sheath cell wall in wheat and rice to CO2 is currently unavailable. Similarly, chloroplast number and volume in the bundle sheath is considerably higher in C4 than in C3 cereals, presenting a potential obstacle for C4 wheat (see Sage & Zhu 2011).

Engineering the complex mix of morphological and biochemical specialization that exists in current C4 species may be a significant task. How much can we ‘strip down’ the C4 engine before it becomes unviable or offers no advantage in RUE over the C3 pathway? Defining this ‘minimalist’ version of C4 (that still gains a yield advantage) is a pertinent question to engineering improved RUE in wheat, and hopefully this information will be forthcoming form efforts in rice over the coming years. Putative C4 loss of function mutants has already been generated in Sorghum, potentially with both anatomical and biochemical lesions (Kajala et al. 2011), in order to find genes controlling key C4 attributes.

Two simple mechanisms for concentrating CO2 in the chloroplast have been proposed which do not theoretically require anatomical specialization, based on the mechanism present either in aquatic macrophytes or in cyanobacteria (for updates, see Miyao et al. 2011 and Price, Badger & von Caemmerer 2011). In the former case, known as ‘single cell C4’, C4 acids are synthesized in the cytoplasm of the C3 mesophyll cell, transported into the chloroplast where they are decarboxylated, theoretically elevating the CO2 concentration around Rubisco (see Fig. 5; Miyao et al. 2011). However, changes in leaf gas exchange in transgenics containing four of the necessary subsets of C4 enzymes have so far been small (Taniguchi et al. 2008; Miyao et al. 2011). Of major concern is whether a C3 chloroplast will provide sufficient resistance to CO2 diffusion for this approach to be energetically advantageous, although modelling using available data on chloroplast permeability to CO2 suggests some advantages under sub-ambient CO2 (see von Caemmerer 2003). At present, installing a full C4 pathway in wheat by a transformation approach is not considered a priority in the WYC until proof of concept has been shown in rice over the next 3–5 years. However, alien introgression is being pursued as a strategy to introduce ‘C4-ness’ into wheat as discussed above.

An alternative strategy to installing a C4-like biochemical pump into C3 plants to increase photosynthetic efficiency is to mimic the inorganic CCM present in cyanobacteria and algae (see Price et al. 2011). A plasma membrane or chloroplast envelope-localized CCM has never been observed in a terrestrial plant so, unlike the C4 mechanism, there is no ‘proof of concept’ of this approach in crop plants. This biophysical mechanism has the advantage that only a small subset of genes need to be transferred to C3 crop species and specialized anatomy and morphology may not be required. In addition, the energy costs of this type of mechanism may be inherently lower than that of the C4 pathway as approximately two additional ATPs are required per CO2 fixed in the C4 pathway to support the CCM in the mesophyll cells, compared with the C4 mechanism.

Price et al. (2011) suggest that modest elevation of CO2 levels in the C3 chloroplast would most easily be achieved by expressing a cyanobacterial HCO3 transporter on the inner envelope (Parry et al. 2011; Price et al. 2011) but would require a substantial inward Na+ gradient across the chloroplast envelope. This engineering approach has been attempted in Arabidopsis and in tobacco (Lieman-Hurwitz et al. 2003), but the transgene used has subsequently been found not to be a functional HCO3 transporter (Price et al. 2011).

In all the approaches to concentrate CO2 around Rubisco described above, the major unknown in predicting or modelling the likely impact is the diffusion properties of the chloroplast envelope and plasma membrane/cell wall in C3 plants (see von Caemmerer 2003; Evans et al. 2009). If CO2 can freely pass across the compartment where it is being
concentrated and back into the atmosphere, the cost of the CCM would likely be too high to provide and energetic benefit translatable to yield. It has been suggested that aquaporins may be involved in modulation membrane permeability to CO₂, and this raises the interesting question whether permeability could be manipulated by altering levels of these proteins (Uehlein et al. 2008). A second opportunity to reduce CO₂ permeability across the chloroplast envelope would be to reduce chloroplast surface area appressed to intercellular airspace. At present, the chloroplast surface to leaf area ratio is approximately 15 to facilitate CO₂ diffusion to Rubisco (Evans et al. 2009).

Interaction and potential additivity of photosynthesis boosting traits

Improving photosynthetic performance and the benefits to YP must be considered in a canopy context rather than at a single leaf level (see above), and it is unlikely that targeting a single photosynthetic trait would be more than a stop gap solution to reaching required yield targets (Figs 1 & 3; Table 2). From modelling of photosynthesis, improving leaf level RUE through reducing photorespiration either through Rubisco engineering or CCMs, while having large predicted impacts, would have a greater benefit under light saturated conditions where flux through Rubisco is most limiting for photosynthesis (von Caemmerer 2003) than in light-limited conditions. As discussed above, under light-limited conditions in part of the canopy, lower-shaded leaves would benefit from improvements in light harvesting. Depending on the proportion of direct versus diffuse radiation, time of day and climatic conditions, the relative contribution of Rubisco-limited versus light-limited leaves will vary (de Pury & Farquhar 1997). For this reason, stacking of genes to reduce photorespiration or improve Rubisco efficiency with improvements in light harvesting efficiency would considerably increase impact on a crop level; however, canopy models are not yet sophisticated enough to quantify this additive impact accurately.

Improving Rubisco kinetic properties and introducing CCM could be viewed as non-additive approaches, as elevating CO₂ at the active site of Rubisco alleviates the need for improved specificity for CO₂. However, engineering Rubisco for a high CO₂ environment similar to that in a C₄ bundle sheath cell could provide additive benefits and improve nitrogen use efficiency if maximum catalytic rate could be improved, even at the expense of specificity for CO₂ (von Caemmerer 2003).

Redistributing the investment in nitrogen between enzymes in the regenerative phase of the Benson–Calvin cycle, in particular overexpression of SBPase or FBPase, has a potential to be additive when combined with either CCMs or improved Rubisco kinetics (von Caemmerer 2003). As Rubisco limitation of photosynthetic flux is reduced by improving catalytic rates or increasing CO₂ concentrations, SBPase and FBPase exert more control over photosynthesis (Tamoi et al. 2006). Thus, relieving this potential bottleneck in photosynthetic carbon metabolism would in fact be necessary to extract the full benefits of improved flux through Rubisco in any engineering strategy.

Feasibility of gene stacking to improve canopy level RUE and yield depends greatly on the number of genes involved. To achieve a fully functional C₄ wheat, for example, may require a minimum of 10 transgenes encoding enzymes and transporters excluding anatomical genes (Kajala et al. 2011). Stacking these genes with another five genes underpinning other traits for improved RUE by crossing would be difficult and time consuming due to potential recombination and segregation. Single gene traits are clearly more attractive for stacking and crossing into suitable germplasm with appropriate architectural and partitioning characteristics.

ACHIEVING HIGH AND STABLE EXPRESSION OF HI

While improving light interception and photosynthetic capacity can be expected to improve crop biomass, photosynthates must be partitioned optimally during plant growth and development if the potential benefits are to be fully realized as extra grain yield. The challenge is complex because both photosynthetic capacity (source) and the various demands from plant organs for assimilate (sinks) change constantly during crop development, as well as in response to ambient conditions. The scientific challenge is first to understand the trade-offs necessary to maximize partitioning to reproductive structures without under-investing in the roots, stems and leaves needed to maintain physiological and structural integrity. The second challenge is related to the fact that the actual environment in which a cultivar will grow is unpredictable, mainly in terms of light regime and temperature profiles (both within and between crop seasons), as well as with respect to crop management factors that may additionally affect nutrition, water status, photoperiod and the microclimate of the canopy. However, to help focus research intended to ensure that HI is expressed at >0.5 across all major wheat agro-ecosystems in the normal range of seasons, the main factors considered are: (1) optimizing the partitioning of assimilates to different plant organs to maximize investment in reproductive structures without sacrificing functional integrity; (2) tailoring crop phenology to different environments – for example, genes of major effect Ppd and Vrn already determine adaptation to winter versus spring wheat mega-environments (MEs) but adaptation within these MEs is yet to be fine-tuned to ensure high and stable expression of HI; (3) modulating sensitivity to environmental cues during rapid spike growth phase – when seed number and kernel weight potential are determined – to avoid overly conservative responses that are disadvantageous under modern agronomic practices; (4) adaptation to potential stresses during grain filling that may reduce seed size; and (5) lodging resistance that may require trade-offs in terms of assimilate partitioning to avoid structural failure of the plant when spikes are fully laden with grain (see Table 3). These factors will be addressed subsequently.
Table 3. Factors affecting harvest index in relatively favourable wheat-growing environments

<table>
<thead>
<tr>
<th>Factor</th>
<th>Affect</th>
<th>Genes/QTL</th>
<th>References with main factor (bold refers to gene/QTL)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tailoring crop phenology to different environments (pre-anthesis)</td>
<td>Photoperiod from emergence to anthesis influences relative duration of reproductive growth phases and therefore affects potential grain number, while adaptation to winter temperature determines vernalization requirement; and ‘earliness per se’ allows for fine-tuning developmental rates in a wide range of conditions</td>
<td><em>Ppd</em> for adaptation to photoperiod <em>Vrn</em> for adaptation to cold winters <em>Eps</em> for fine-tuning development</td>
<td>Slifer 1996 (earliness per se) Miralles, Richards &amp; Slafer 2000 (photoperiod) Slifer et al. 2001 (photoperiod) Gonzalez et al. 2005a (photoperiod) Gonzalez et al. 2005b (<em>Ppd</em>) Ghiglione et al. 2008 (photoperiod)</td>
</tr>
<tr>
<td>Lodging resistance</td>
<td>Need for trade-offs in terms of assimilate partitioning to ensure strong enough stem and adequate crown roots to avoid structural failure</td>
<td><em>TaCM</em> associated with lignin</td>
<td>Keller et al. 1999 (<em>QTL</em>) Berry et al. 2007 (model trade-offs) Ma 2009 (<em>TaCM</em>) Acreche &amp; Slafer 2011</td>
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QTL, quantitative trait loci.

**Optimizing the partitioning of assimilates to different plant organs to maximize HI**

The grain yield increases of the first semi-dwarf cultivars during the Green Revolution were associated with higher HI due to altered competition between plant organs favouring spike growth over stem extension (Gale & Youssefian 1985). However, while there has been no systematic genetic progress in HI since the early 1990s – from values of c. 0.45–0.50 in spring wheat and c. 0.50–0.55 in winter wheat (Foulkes, Reynolds & Sylvester-Bradley 2009) – of greater concern, in the context of attempting to substantially raise YP, is that the physiological and genetic basis of partitioning is poorly understood. Large genetic ranges for dry matter partitioning among plant organs are reported, for example, at anthesis spikes show a range of 0.12–0.29, leaf lamina 0.19–0.31 and stems + leaf sheath 0.48–0.63 as a proportion of above-ground biomass in fertile shoots (Siddique, Kirby & Perry 1989; Reynolds et al. 2001; Shearan et al. 2005; Gaju et al. 2009). Genetic variation in assimilate partitioning is currently being characterized within 60 elite hexaploid bread wheat advanced lines under irrigated conditions in Northwest Mexico as part of the WYC project (Table 4). It is envisaged that optimal trait expression levels will be identified in genetic resources through phenotyping within a 5 year time frame (Table 1). By combining the lowest values

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of dry matter (DM) partitioning observed for each of the alternative sinks (true stem, leaf lamina, leaf sheath), the relative spike mass at anthesis or spike partitioning index (SPI) could theoretically be increased to 0.35 from the present maximum values of c. 0.30. However, potential trade-offs will need to be carefully assessed to avoid, for example, negative impacts on canopy photosynthetic capacity. Interestingly, these results showed the genetic range in leaf-sheath partitioning (0.15–0.22) was similar to that for leaf-lamina partitioning (0.17–0.22; Table 4) as reported by Pask (2009). However, leaf sheaths are approximately vertical, and are shaded for the majority of the grain filling period, so their actual contribution to photosynthesis is presumably much less than the lamina. There may, therefore, be scope to reduce DM investment in the leaf sheaths while maintaining photosynthetic capacity. However, the leaf sheath is also an important store of leaf N in wheat (Pask et al. 2012), so any decrease in leaf-sheath DM partitioning must also take account of possible trade-offs with N remobilization post-anthesis affecting canopy senescence rate (Gaju et al. 2011).

Overall, the WYC results showed true-stem partitioning (i.e. structure) had the highest correlation with SPI among the alternative sinks (Table 4) and was also correlated with grains m⁻². Therefore, a critical task is to quantify the minimum value to which true-stem partitioning may be decreased from current values in elite spring wheat cultivars of c. 0.30–0.40 (Table 4) and winter wheat cultivars of c. 0.45–0.50 (Pask 2009), while maintaining plant height in the optimum range of c. 60–90 cm (Miralles & Slafer 1995; Flintham et al. 1997). Optimizing the balance between true-stem structural DM and non-structural (soluble carbohydrate) DM should also be addressed in terms of maximizing grain number in general, without sacrificing grain size in specific contexts where assimilate availability during grain filling may be limited by high temperature or light. Additionally, it will be important that any reduction in true-stem structural DM does not make the plant susceptible to lodging, which will require an improved understanding of the structural biomass required in the lower internodes for lodging resistance (Berry et al. 2004; Berry, Sylvester-Bradley & Berry 2007).

Future studies should also consider the optimum partitioning to roots and infertile shoots. The root system of modern wheat may not be large enough at depth to take up sufficient water and nutrients to support future gains in biomass. Deeper root distribution could help, because root length density (root length per unit volume of soil) is often below a critical threshold for potential water and nitrate capture of 1 cm cm⁻³ (Barraclough, Kuhlmann & Weir 1989; Gregory & Brown 1989) at lower depths in the rooting profile (see Foulkes et al. 2011 for an extended discussion of optimized rooting traits for below-ground resource capture while maintaining HI, and of potential mechanisms for reducing assimilate partitioning to infertile tillers).

The complement to SPI to enhance grain number is the fruiting efficiency (FE; i.e. number of grains set per unit spike dry weight at anthesis, also termed spike fertility index; Fischer 2011; Foulkes et al. 2011; Lázaro & Abbate 2012). There is clear variability among modern cultivars in FE (Abbate et al. 1998; Fischer 2007; Gaju et al. 2009; Aisawi 2011; González, Terrile & Falcón 2011b; Lázaro & Abbate 2012). However, the relationship between SPI and FE may be negative among genotypes and trade-offs between these two physiological components are frequently observed (Gaju et al. 2009; González et al. 2011b; Lázaro & Abbate 2012). The cause of this negative relationship is still unclear. In some studies on wheat cultivars, FE was associated with the proportion of some of the spike morphological components (Slafer & Andrade 1993; Abbate, Andrade & Culot 1995; Abbate et al. 1997), whereas in other investigations no association was found (Abbate et al. 1998; Fischer 2007). The existence of a negative relationship between SPI and FE raises the question of whether selection for FE may be useful for genetic improvement. Lázaro & Abbate (2012) encouragingly reported a parallel relationship in four wheat

| Table 4. Genetic ranges for partitioning of dry matter to plant components at GS61+7 days among 60 CIMMYT spring wheat advanced lines under irrigated conditions (basins) in Ciudad Obregon, Northwest Mexico, in 2010/2011, and correlation coefficients between PI. Genetic ranges of DM partitioning at anthesis from the literature for SW and WW (table 2 of Foulkes et al. 2011) are shown for comparison. |
|-----------------|-----------------|-----------------|-----------------|
| Plant components | Ciudad Obregon Max-Min for SW, WW; | Phenotypic correlations: partitioning indices versus SPI; |
| SPI              | 0.22–0.31* | 0.12–0.27; 0.19–0.29 | –0.55* |
| LLPI             | 0.17–0.22* | 0.19–0.21; 0.25–0.31 | –0.80* |
| True stem + leaf sheath PI | 0.51–0.59* | 0.48–0.52; 0.58–0.63 | –0.80* |
| TSPI             | 0.32–0.41* | N/A | –0.60* |
| LSIPI            | 0.15–0.22* | N/A | –0.31* |

*P < 0.001,
CIMMYT, International Maize and Wheat Improvement Center; DM, dry matter; LLPI, leaf lamina PI; LSIPI, leaf sheath PI; N/A, not applicable; PI, partitioning indices; SPI, spike partitioning index; SW, spring wheat; TSPI, true stem PI; WW, winter wheat.
cultivars grown in Argentina, Mexico and France for the negative slope between spike biomass per m² at anthesis and FE suggesting the possibility to identify genotypes combining high spike biomass with a high FE.

In summary, for future improvement of SPI and HI in breeding programs, it will be critical to identify plant ideotypes with reduced structural stem DM and leaf sheath DM partitioning where trade-offs with lodging resistance and photosynthesis, respectively, are minimized. Furthermore, mechanisms to reduce chaff DM costs per grain and to minimize the trade-off between SPI and FE should be investigated. Investigations into genetic adaptation and optimization of each process will require a capacity to integrate them and anticipate their likely interactions in determining crop performance. This will require an integrated quantitative approach and will need to adopt particular partitioning traits that have high heritability to facilitate the accumulation of the favourable trait combinations in new plant ideotypes. In the WYC project, it is envisaged that traits to optimize partitioning to plant organs from wild species will be introgressed into good agronomic backgrounds by interspecific hybridization in a 10–15 year time frame; advanced lines developed through agronomic backgrounds by interspecific hybridization in a 10–20 year time frame.

**Tailoring phenology to diverse agro-ecosystems**

Crop phenology is a critical component of yield physiology as grain yield performance is strongly influenced by the timing of phenological stages in each particular environmental condition (Slater et al. 2009). The most important stage of development is the period of a few weeks immediately before to a few days immediately after anthesis, the so-called ‘critical period’ for yield determination in wheat (Fischer 1985; Reynolds et al. 2009a). This is largely due to the sensitivity of floret development, gamete formation and fertilization, and grain abortion to environmental conditions during the juvenile spike growth phase (Barnabas, Jager & Feher 2008; Fischer 2011; Gonzalez et al. 2011a and references quoted therein), notwithstanding genetic variation for this (e.g. Gale & Youssefian 1985; Miralles & Slater 1995; Reynolds et al. 2001). Thus, optimizing HI, and therefore grain yield, largely depends on the timely occurrence of anthesis.

Although determining anthesis (or heading) is relatively simple and, therefore, feasible even in large populations, for a more predictable outcome of the breeding process it is required to understand sensitivities to major environmental factors determining time to anthesis. These sensitivities are fortunately highly variable which opens room for opportunities to tailor phenology to diverse agro-ecosystems (and in fact, it is the reason for the wide adaptability of wheat to so many different climates). In the rest of this section, we will briefly recap on the major physiological and genetic determinants of wheat phenology, whose manipulation is required to tailor phenology. More comprehensive recent reviews of the genetics of wheat phenology are available (Distelfeld, Li & Dubcovsky 2009; Slater et al. 2009).

Time to anthesis is determined by the duration of the vegetative phase from sowing to floral initiation (when all the leaf primordia are initiated), the early vegetative phase up to terminal spikelet initiation (when all spikelets are initiated in each spike), and the late reproductive phase of stem elongation ending with anthesis (when the number of florets is determined) (Slater 2012). Durations of these phenophases are affected by three major environmental factors: vernalization, photoperiod and temperature per se (Slater & Rawson 1994).

There is a large degree of variability in sensitivity to vernalization from virtually insensitive spring types, through facultative types, to extremely sensitive winter types (Slater & Rawson 1994). Vernalization affects the length of the vegetative and early reproductive phases. Increasing sensitivity to vernalization slows down apex development lengthening the leaf and spikelet initiation phases. Wheat is a long-day plant, and there is also a large degree of variability in sensitivity to photoperiod (Slater & Rawson 1994). As wheat does not seem to possess a juvenile phase, plants become sensitive immediately after seedling emergence (Hay & Kirby 1991; Slater & Rawson 1995; Hay & Ellis 1998). Long photoperiod reduces the time to anthesis through reducing the duration of vegetative and reproductive phases (e.g. Rawson & Richards 1993; Slater & Rawson 1996). It has been shown that there is also a wealth of variation in earliness per se in different geographical regions (Worland, Appendino &ayers 1994; Appendino, Bartoloni & Slater 2003). Variability in earliness per se can be detected in vegetative and in reproductive phases of wheat development (Slater 1996). Therefore, it is possible to tailor phenology for a particular environmental condition through combining specific sensitivities to vernalization and photoperiod with particular earliness per se characteristics in a genotype, taking advantage of the knowledge already established on the genetic control of these determinants of phenological development (see below).

Furthermore, it may be also possible to tailor phenology patterns so that a particular time to heading may be achieved with longer reproductive and shorter vegetative phases or vice versa. This fine tuning of the developmental pattern has been suggested to have the potential to affect YP (e.g. Slater et al. 2001; Foulkes et al. 2011). This is because wheat yield is largely determined during the late reproductive phase (Slater 2003; Fischer 2011) when the florets are being developed within the growing spikes, seemingly in response to dry matter allocation to the spikes (Gonzalez, Miralles & Slater 2011a). It has been speculated that if the duration of this late reproductive phase is extended the number of grains and YP would increase (Miralles & Slater 2007; Foulkes et al. 2011). The speculation has been supported experimentally (e.g. Miralles et al. 2000; Gonzalez, Slater & Miralles 2003; Serrano, Miralles & Slater 2008).

Time to anthesis in wheat is controlled by three major groups of genes determining the vernalization response
(Vrn), the photoperiod response (Ppd) and earliness per se (Eps) (e.g. Snape et al. 2001; Slafer et al. 2009). The most significant Ppd genes in wheat distinguish photoperiod-sensitive types (Ppd-1b; requiring long days to flower) from photoperiod-insensitive types (Ppd-1a; which can flower in short or long days) (Turner et al. 2005; Beales et al. 2007; Wilhelm et al. 2009). Photoperiod-sensitive types are the ancestral (wild type) form. Photoperiod-insensitive alleles on the A and D genomes have promoter deletions while alleles on the B genome have copy number polymorphisms of the Ppd gene. These mutations cause the gene to be constitutively expressed leading to the induction of flowering locus T (FT) expression. Mutations in Vrn genes distinguish winter wheat from spring wheat. Three Vrn genes have been isolated (Yan et al. 2003, 2004, 2006). Vrn-2 is a strong repressor that inhibits flowering in unvernalized plants. Vrn-2 is likely to be suppressed by Vrn-1, which is up-regulated during cold (vernalization). The third spring habit gene, Vrn-3, is the result of a mutation within FT; the most potent floral inducer. FT is normally repressed by Vrn-2, but Vrn-3 spring habit alleles are insensitive Vrn-2 mediated repression. Spring forms of wheat commonly have mutant alleles of Vrn-1 that are expressed without exposure to cold. Genes underlying Eps QTL have not yet been isolated in wheat. However, the success in cloning relatively small effect heading date QTL and others controlling a range of traits in rice (reviewed in Miura, Ashikari & Matsuoka 2011) shows that this is also achievable in wheat. The major Vrn and Ppd loci are quickly fixed in breeding programs targeted at a specific environment. The importance of Eps effects is that they allow fine tuning of phenology within a breeding program and variation for major Eps QTL can be found in elite varieties (Griffiths et al. 2009). A number of these QTL have now been characterized as single Mendelian factors and work is underway to isolate the underlying genes.

**Modulating sensitivity to environmental cues**

In theory, an annual plant should use its full photosynthetic capacity to maximize seed production. However, in practice the proportion of assimilates invested in seeds – the HI – varies considerably, even in modern crop varieties (e.g. Sayre et al. 1997; Zheng et al. 2011). The fact that HI is typically higher in crop species than their wild progenitors provides an important clue as to why this variation exists. Seed fecundity, while an important adaptive strategy in the wild, is secondary to the imperative of finishing the life cycle with viable seed. Therefore, it seems likely that while domestication of crop species – in the context of good husbandry – has led to HI values of ~0.5, conservative survival strategies in response to environmental variables still result in variation in HI. A clear factor discussed above is response to photoperiod – a strategy to prevent untimely reproductive growth – that leads to suboptimal expression of HI when a genotype is cultivated outside of its photoperiod niche. Day length appears to act as a signal affecting developmental rate and survival of floret primordia (e.g. González, Slafer & Miralles 2005a; González et al. 2011a) with changes in sugar supply leading to programmed cell death in the juvenile spike (Ghiglione et al. 2008).

Unlike photoperiod, most other environmental factors that influence plant performance are unpredictable, including temperature, radiation levels and soil moisture. Nonetheless, plants must determine their partitioning to reproductive structures in the absence of information on growing conditions during subsequent seed filling. This has presumably led to strong selection pressure for conservative strategies especially in annual species like wheat. Plant growth regulators are known to help plants adapt to their environment (Davies, Wilkinson & Loveys 2002; Peleg & Blumwald 2011), and because they can potentially modulate the degree of response to such factors, a better understanding of their physiological and genetic basis is expected to play a key role in breeding for higher yielding crops in the future. For example, under high temperatures, ethylene appears to be involved in signalling leading to kernel abortion in wheat (Hays et al. 2007). Floral abortion in maize in response to drought appears to be controlled by a few key enzymes that are either up- or down-regulated resulting in the programmed abortion of florets (Boyer & McLaughlin 2007). A candidate gene for spike fertility has been identified in rice (Gn1a) coding for cytokinin oxidase which through its regulation of cytokinin levels influences numbers of reproductive organs in the panicle (Ashikari et al. 2005). It is well established in wheat that kernel set can be especially sensitive to environmental conditions such as moisture stress (Fischer 1980), light (Fischer 1985) and soil N levels (Ferrante, Savin & Slafer 2010). Mechanistic approaches can be applied to pinpoint the underlying physiological and genetic basis of grain set/grain abortion under the full range of growth conditions to which crops must adapt as a means to engineering plants with a less conservative strategy. While some buffering capacity is a good insurance against adversity (Evans 1993), the many factors that can reduce photosynthetic capacity in the wild – herbivory, competition for light by neighbours, water and nutrient depletion, foliar diseases, etc. – can be readily controlled with crop management. The fact that even the high-yielding cultivars of wheat can show excess photosynthetic capacity during grain filling (see later section: The Interaction of Partitioning and RUE) shows a clear need to develop cultivars that are better adapted in terms of their reproductive strategies to modern agronomic practices.

**ADAPTATION TO POTENTIAL STRESSES DURING GRAIN FILLING**

During grain filling, photo-assimilate is transported as sucrose to the growing seed where it is converted to starch. One of the enzymes involved is soluble starch synthase (SSS), which, among other key metabolic steps in the pathway, is sensitive to heat stress especially above 35 °C (Keeling, Baco & Holt 1993; Hurkman et al. 2003). As a result, decreased kernel weight due to high air temperature...
does not necessarily respond to increasing photo-
assimilates (Slafer & Miralles 1992; Denyer, Hylton & Smith 1994; Jenner 1994). Response to temperature can be quite drastic; in screening of divergent germplasm using a short, 3–4 d heat shocks (up to 40 °C), yield reductions were in some cases almost 25% (Jenner 1994; Stone & Nicolas 1994). Temperatures above 30 °C reduce both grain filling duration as well as rate, and genetic variation for both is indicated in wheat from QTL analysis (Yang et al. 2002, 2006; Gross et al. 2003; Wang et al. 2009; Mason et al. 2010; Zheng et al. 2011).

There is evidence that night temperature may be more detrimental to grain filling than day temperature in cereals. Results from rice show that high night temperature (22/34 °C) in controlled conditions compared with high day temperature (34/22 °C) reduced the final grain weight through a reduction in grain growth rate in the early-mid stages of grain filling, and also reduced the cell size in the outer part of the endosperm (Morita, Yonemaru & Takanashi 2005). Similarly, rice plants grown at two different night temperatures (27/22 and 27/27 °C) from anthesis to harvesting developed heavier kernels in the cool night treatment, in spite of the fact that there were no differences in total plant biomass. Analysis of partitioning patterns indicated that cool night temperature tended to favour carbon allocation to panicles while warmer nights led to partitioning to new tillers and other organs (Kanno & Makino 2010). These results are consistent with the idea that starch synthesis may have been inhibited, and even though assimilates were available for grain filling, they could not be remobilized to grain starch during the night.

Assuming the bottlenecks to starch synthesis can be overcome, the improvements outlined earlier in Rubisco and Rubisco activase can be expected to further buffer wheat to warmer conditions during grain filling.

LODGING RESISTANCE

Lodging, the permanent displacement of cereal stems from the vertical, may result from either failure of the stem base (stem lodging) or failure of the anchorage system (root lodging). Lodging is a persistent phenomenon in wheat which reduces harvestable yield by up to 80% as well as reducing grain quality. Therefore, strategies to raise HI must take account of lodging resistance. A validated model of the lodging process has identified the plant traits that determine stem and root lodging risk of wheat (Berry et al. 2003a,b, 2007). The lodging model has been used to estimate the dimensions of a wheat plant to make it lodging proof for the least investment of biomass in the supporting stem and root system (Berry et al. 2007). In order to increase lodging resistance, it is predicted plant breeders must increase the spread of the root plate, stem thickness and the material strength of the stem wall, while minimizing the width of the stem wall. Preliminary work has indicated that wider stems have a greater DM per unit of stem length and DM density is positively related to the material strength of the stem wall (Berry et al. 2007), which means there is a significant DM cost associated with increasing stem strength. The extent to which structural requirements compete with yield must be investigated to quantify possible trade-offs. This will depend crucially on windiness of the target environment; ultimately optimizations should aim to balance these costs against grain DM costs of lodging itself (Stapper & Fischer 1990), possibly by integrating the increasing risk of lodging as grain fill progresses, with the decreasing impact of lodging on grain yield (Foulkes et al. 2011).

THE INTERACTION OF PARTITIONING AND RUE

Recent studies have indicated that post-anthesis RUE in wheat is strongly influenced by partitioning to reproductive structures: (1) older cultivars with smaller reproductive sinks had significantly reduced RUE during this phase (Caldinari, Drecer & Slafer 1997; Acreeche et al. 2009; Acreeche & Slafer 2011); and (2) increasing sink strength during post-anthesis increased crop growth and RUE during grain filling for both $Rht$ (Miralles & Slafer 1997) and $Lr19$ introgression lines (Reynolds et al. 2001; 2009a). In the latter, substitution lines containing chromatin from *Agropyron* resulted in a 7.5% increase of light saturated photosynthetic rate of flag leaves throughout grain filling associated with increased grain number per spike, and a 10% larger AG biomass averaged across six genetic backgrounds in high-yielding environments (Reynolds et al. 2001). Following up on this result – specifically to test the hypothesis that increased sink strength could directly influence RUE during grain filling – grains/spikes were increased by artificially raising light levels during the boot stage in four elite spring wheat cultivars. The light treatment increased grain number per spike as well as increasing RUE during grain filling. Similarly, although manipulating the source : sink balance oppositely, Acreeche & Slafer (2011) showed that reducing the sink strength during grain filling, although trimming the spikes soon after anthesis, resulted in a concomitant reduction in both flag leaf photosynthesis (without affecting chlorophyll content) and RUE. The results reinforce the importance of optimizing source : sink, especially in the context of crops that are genetically improved for RUE.

PREREQUISITES TO RAISE WHEAT PRODUCTIVITY

To ensure that costly investment in the genetic improvement described above achieves its target – namely global scale productivity increases – certain prerequisites must be met in relation to technology transfer and effective crop and natural resource management. These will be addressed briefly in this section.

Networking to ensure effective technology transfer

Targeting and delivery of appropriate new genotypes to production environments requires that the latter are well
characterized so that the former achieve intended impacts. Networking among the many partners of the delivery chain is the most efficient way to achieve these objectives. 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 national breeding programs on a large scale as global public goods (Braun et al. 2010). In the case of wheat, the impacts of new wheat lines – especially in less-developed countries – are well documented (Evenson & Gollin 2003; Lantican, Pingali & Rajaram 2003) and have spread among millions of farmers (Lipton & Longhurst 1989). Nonetheless, impacts could be wider reaching if target environments were better characterized to fine-tune research targets and the delivery systems more extensive allowing for a fuller range of the available genetic diversity to be tested (Smale et al. 2002). A better coordinated and more localized approach to crop research through implementation of global crop improvement networks is proposed. Such networks could underpin agricultural research and extension by providing the following types of services (Reynolds et al. 2012); increased resolution and precision of environmental information – including meteorological data, soil characteristics, hydrological data, and identification of environmental ‘hotspots’ for a range of biotic, abiotic and socio-economic constraints; augmented research capacity – including network-based variety and crop management trials, faster and more comprehensive diagnosis of emerging constraints, timely sharing of new technologies, opportunities to better focus research efforts by linking groups with similar productivity constraints and complementary skills, and greater control of experimental variables in field-based phenotyping; and increased communication and impacts via – more effective dissemination of new ideas and products, integration of information globally to elicit well-timed local response to productivity threats, increased profile and publicity of threats to food security.

**Closing economic yield gaps and increasing the sustainability of cropping systems**

Crops and farmland should be managed with the view to realizing the full genetic potential of cultivars while protecting the natural resource base. Nonetheless, yield gaps exist between achievable and currently realized yields in almost all agro-ecosystems (Lobell, Cassman & Field 2009; Fischer & Edmeades 2010). In regions where modern technologies have been applied, biological yield gaps may be relatively small (e.g. 20–30%) and a variety of potential solutions exist to help close these gaps, assuming interventions are economically viable. Knowledge-based decision-making tools and a new generation of ‘precision agriculture’ approaches can help farmers decide when best to sow and how much fertilizer and water to apply to maximize yields and/or profit margins (Raun et al. 2005; Heng et al. 2007; Ortiz-Monasterio & Raun 2007; Tilling et al. 2007; Lobell et al. 2009). Much larger yield gaps exist in regions such as Sub-Saharan Africa where investment could provide significant productivity boosts. However, a key to success in these regions will be to apply technologies in a sustainable way (e.g. Twomlow et al. 2010). Several major cropping systems worldwide show declining productivity due to their inappropriate use (Dawe 2000; Duxbury et al. 2000; Ladha et al. 2003). Excessive soil cultivation has led to compacted or eroded soils and use of irrigation water without adequate drainage leads to toxic levels of salinity, resulting in stagnating or declining productivity (Datta & de Jong 2002). Technological solutions exist to solve these problems including better drainage to avoid salinization (Bhatta & Smedema 2007). Furthermore, the practice of conservation agriculture and other resource-conserving technologies helps stabilize soils and can lead to improvements in the fertility and productivity of cropping systems, especially those that are already fragile or have become degraded from a history of intensive cultivation (Cook 2006; Montgomery 2007; Zhang et al. 2007; Hobbs, Sayre & Gupta 2008; Verhulst et al. 2010). Practices such as reduced tillage in combination with crop residue retention can also buffer crops against severe climatic events, for example, by increasing water harvest and thereby offsetting water shortages. In addition, by improving the overall environment for root growth, such practices permit the genetic potential of improved cultivars to be more optimally expressed helping to close yield gaps that may already exist (Hobbs & Govaerts 2010). Diversification of cropping systems also helps to control soilborne diseases (Mazzola 2010). Longer-term benefits of conservation agriculture include reduced emission of greenhouse gas (GHGs) through greater precision in the application of N and water as well as reduced use of diesel fuel (Ortiz-Monasterio et al. 2010).

**CONCLUSIONS**

In conclusion, improvement of wheat yield productivity can be viewed in terms of the classical ‘strengths, weaknesses, opportunities, and threats’ analysis. Strengths include theoretical considerations which back the idea that RUE can be increased by 50%, as well as strong precedents for yield and RUE improvement that have already been achieved through classical breeding (Singh et al. 1998; Lantican et al. 2003; Lopes et al. 2012a; Manes et al. 2012; Sharma et al. 2012). The greatest weakness is the lack of information and unpredictability of target environments, especially in the context of climate change. Opportunities include the fast-growing fields of genetics, conservation and precision agriculture, as well as the existence of well-established wheat improvement networks that – with appropriate investment – could be extended to simultaneously allow testing of new genotypes and better characterization of breeding targets on a more comprehensive scale than at present. Political considerations aside, the greatest threats to achieving productivity gains are the asymmetrical investments in crop improvement. While crop management innovations are estimated to account for at least half of increases in crop
productivity (Turner 2004; Fischer 2009), research in genetics typically accounts for a much larger fraction of spending in both public and private agricultural arenas, while underfunded extension services and lack of needed subsidies or other incentives for farmers to adopt new technologies further distort the investment portfolio (Chapman & Tripp 2003; Denning et al. 2009). Nonetheless, wheat improvement remains one of the best strategies 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 (FAOSTAT 2010).

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