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Raising yield potential in wheat

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Abstract

Recent advances in crop research have the potential to accelerate genetic gains in wheat, especially if co-ordinated with a breeding perspective. For example, improving photosynthesis by exploiting natural variation in Rubisco's catalytic rate or adopting C_4 metabolism could raise the baseline for yield potential by 50% or more. However, spike fertility must also be improved to permit full utilization of photosynthetic capacity throughout the crop life cycle and this has several components. While larger radiation use efficiency will increase the total assimilates available for spike growth, thereby increasing the potential for grain number, an optimized phenological pattern will permit the maximum partitioning of the available assimilates to the spikes. Evidence for underutilized photosynthetic capacity during grain filling in elite material suggests unnecessary floret abortion. Therefore, a better understanding of its physiological and genetic basis, including possible signalling in response to photoperiod or growth-limiting resources, may permit floret abortion to be minimized for a more optimal source:sink balance. However, trade-offs in terms of the partitioning of assimilates to competing sinks during spike growth, to improve root anchorage and stem strength, may be necessary to prevent yield losses as a result of lodging. Breeding technologies that can be used to complement conventional approaches include wide crossing with members of the Triticeae tribe to broaden the wheat genepool, and physiological and molecular breeding strategically to combine complementary traits and to identify elite progeny more efficiently.

Key words: Complex traits, crop breeding, gene discovery, genetic resources, lodging, phenology, photosynthesis, *RUE*, source:sink, spike fertility.

Introduction

Wheat is grown on more than 200 million hectares of land worldwide, and provides approximately one-fifth of the total calorific input of the World's population (FAO, 2003). Steady increases in productivity since the Green Revolution are associated with genetic improvements in yield potential, resistance to diseases, and adaptation to abiotic stresses (Sayre *et al.*, 1997; Donmez *et al.*, 2001; Brancourt-Hulmel *et al.*, 2003; Shearman *et al.*, 2005; Reynolds and Borlaug,

2006) as well as better agronomic practices (Evenson and Gollin, 2003). However, challenges to production are still considerable as highlighted recently at a Symposium involving scientists from 30 wheat-producing countries (Reynolds *et al.*, 2007*a*). Since global demand for wheat is predicted to increase at a faster rate (Rosegrant and Cline, 2003) than the annual genetic gains that are currently being realized (Shearman *et al.*, 2005; Fischer, 2007; Miralles

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and Slafer, 2007), it is broadly agreed that improvement in genetic yield potential will need to be accelerated in order to avoid encroachment into natural landscapes or the over-intensification of current agro-ecosystems. Two additional factors reinforce the need for genetic interventions to boost crop production; climate change (Neelin *et al.*, 2006; IPCC, 2007) and environmental concerns associated with intensive agriculture (Beman *et al.*, 2005; Montgomery, 2007; WBCSD, 2008). Climate change makes agricultural productivity less predictable, while serious concerns about the environment highlight the need to develop more input-use efficient cropping systems. Increasing the genetic yield potential of cultivars may contribute to solving both problems at the same time, since it has been proven empirically that wheat yield potential is expressed across a wide range of environments (Calderini and Slafer, 1998; Slafer and Araus, 2007) including those affected by water deficit (Richards, 1992; Trethowan *et al.*, 2002), high temperatures (Reynolds *et al.*, 1998), and salinity (Richards, 1995; Isla *et al.*, 2003). High yielding varieties also express their genetic potential at low N levels (Ortiz Monasterio *et al.*, 1997), and when combined with genetic disease resistance, a routine procedure in most wheat improvement programmes, is also expressed in the absence of disease control applications (Sayre *et al.*, 1998).

In the last two decades, significant progress has been made in a number of research areas that have the potential to boost wheat productivity through genetic interventions. These include (i) increasing the efficiency of carbon fixation in C_3 species (Parry *et al.*, 2003a, 2007; Long *et al.*, 2006; Zhu *et al.*, 2008); (ii) a substantial body of work pointing to the pivotal role of spike fertility in determining yield potential (Fischer, 1985, 2007; Slafer and Savin, 1994; Reynolds *et al.*, 2005; Shearman *et al.*, 2005; Miralles and Slafer, 2007); (iii) the first comprehensive mechanistic model of physical processes that cause lodging in wheat (Berry *et al.*, 2007); and (iv) genetic tools that can take these physiological platforms closer to breeding application (Snape, 2004; Collins *et al.*, 2008).

The authors recognize that improved crop management will also play a crucial role in stabilizing and increasing crop yields and, while beyond the scope of this review, readers are referred to the following (Govaerts *et al.*, 2005; Cook, 2006; Matthiessen and Kirkegaard, 2006; Fereres and Soriano, 2007; Hobbs, 2007; Montgomery, 2007; Morison *et al.*, 2008; Reynolds and Tuberosa, 2008).

Current understanding of genetic constraints to wheat yield potential

Yield potential (*YP*) can be expressed in its simplest form as a function of the light intercepted (*LI*) and radiation-use efficiency (*RUE*), whose product is biomass and the partitioning of biomass to yield, i.e. harvest index (*HI*):

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

Genetic gains in wheat during the 20th century have been associated with increased *HI* not only as an immediate result of the introgression of *Rht* genes (Gale and Youssefian, 1985; Calderini *et al.*, 1995) but also as a result of continued selection for yield in the post-Green Revolution period (Kulshrestha and Jain, 1982; Waddington *et al.*, 1986; Calderini *et al.*, 1995; Sayre *et al.*, 1997). Despite a theoretical limit to *HI* of 62% in wheat (Austin, 1980) comparisons of genetic progress in *HI* over time in spring wheat indicate no systematic progress since the mid-1980s from values of approximately 50% (Sayre *et al.*, 1997; Reynolds *et al.*, 1999).

Traits related to *LI*, stand establishment and delayed senescence, show significant genetic variation in conventional gene pools and are highly amenable to visual selection, suggesting that they are probably not currently major bottlenecks for improving yield potential. Therefore attention has turned to increasing *RUE* in crops.

Calculations of theoretical limits to *RUE* indicate that there is still considerable potential to increase the biomass of C_3 species (Loomis and Amthor, 1999; Long *et al.*, 2006). Increases in above-ground biomass of wheat have been reported in recent years (Singh *et al.*, 1998; Reynolds *et al.*, 1999; Donmez *et al.*, 2001; Shearman *et al.*, 2005), in some cases as a result of using exotic germplasm in breeding, including alien introgressions such as *7Ag.7AL* (Reynolds *et al.*, 2001).

Various approaches for improving *RUE* have been reviewed (Reynolds *et al.*, 2000; Long *et al.*, 2006; Parry *et al.*, 2007; Zhu *et al.*, 2008; Murchie *et al.*, 2008) focusing largely on increasing leaf/cellular level photosynthesis—see next section. At the canopy level, modification of leaf architecture may improve *RUE* by permitting a light distribution profile that reduces the number of leaves experiencing wasteful and potentially destructive supersaturated light levels, while increasing light penetration to canopy levels where photosynthesis responds linearly to light (Duncan, 1971). The erectophile leaf trait was introduced from sources such as *T. sphaerococcum* and modern wheat frequently shows more erectophile canopies (Reynolds *et al.*, 2000; Fischer, 2007). Nonetheless, modelling suggests that there may still be scope for further optimization of both light and N distribution in the canopy (Dreccer *et al.*, 2000; Long *et al.*, 2006; Mussgnug *et al.*, 2007). Measurement of the relative contribution of spike photosynthesis (Tambussi *et al.*, 2007) to overall canopy photosynthesis has never been considered as a selection criterion despite the large proportion of light that spikes intercept during grain filling. However, recent comparative studies of the integrated contribution of spike photosynthesis to grain weight showed highly significant genetic effects (MP Reynolds *et al.*, unpublished data).

At the level of plant growth and development a more optimal balance between source and sink is expected to improve overall *RUE* (Richards, 1996; Slafer *et al.*, 1996; Kruk *et al.*, 1997). In fact, an ever-increasing body of evidence suggests sink strength is still a critical yield-limiting factor in wheat (Fischer, 1985; Slafer and Savin, 1994; Abbate *et al.*, 1995; Miralles *et al.*, 2000; Borras *et al.*, 2004; Miralles and Slafer, 2007) and that improving

the balance between source and sink is a highly promising approach for raising *RUE*, biomass and yield (Calderini *et al.*, 1997; Reynolds *et al.*, 2001, 2005; Shearman *et al.*, 2005). Key to achieving progress in this complex area will be obtaining a better understanding of the genetic and molecular control of how the partitioning of assimilates at key developmental stages affects spike fertility and hence the determination of grain number and sink strength. [Although, in this review, increasing the number of fertile florets and grains m^{-2} is addressed as the main avenue to increase sink strength, it is also possible that sink strength could be improved by increasing the carpel size of florets, thereby boosting potential grain weight (Calderini *et al.*, 1999b, 2001; Calderini and Reynolds, 2000; Ugarte *et al.*, 2007).]

The rest of this review will summarize 'state of the art' understanding in key research areas related to wheat yield potential including lodging resistance. Approaches for understanding the genetic basis of complex traits will also be discussed and a final section will address how the technologies developed may be brought together to impact on breeding to raise the yield threshold of wheat.

Increasing photosynthetic capacity

Rubisco, which catalyses the assimilation of CO_2 by the carboxylation of RuBP in the Calvin Cycle, is the most obvious target for attempts to improve photosynthetic rate. This is because Rubisco is such a slow catalyst that large amounts are needed to sustain high photosynthetic rates; it is not uncommon for 50% of soluble leaf protein and 25% of leaf nitrogen to be in the form of Rubisco[1]. Studies with transgenic plants with decreased amounts of Rubisco demonstrated that, under field conditions or with high or variable irradiance and ambient CO_2, photosynthetic rate is tightly correlated with Rubisco amount. Increasing the catalytic rate of the enzyme would increase photosynthetic rate and yield. Rubisco also catalyses the wasteful oxygenation of RuBP, initiating the process of photorespiration and the consequent release of CO_2, NH_3, and energy expenditure. Since CO_2 and O_2 compete to react with RuBP bound to the catalytic site of Rubisco, the relative amounts of carboxylation and oxygenation depend on the concentrations of O_2 and CO_2 present. The discrimination between the two gases is determined by inherent properties of Rubisco and is expressed as the specificity factor (described by the equation $SF=V_cK_o/V_oK_c$). This value is low when the oxygenase activity is favoured and high when the carboxylase activity is favoured. The oxygenase activity of Rubisco (and therefore photorespiration) has been shown to become more significant at higher temperatures, relative to the carboxylation of RuBP (Long *et al.*, 2006), making the dual

specificity of Rubisco a more significant problem at higher temperatures. Furthermore, the dual specificity of Rubisco seriously impacts upon water use efficiency: stomatal closure leads to a lower internal CO_2/O_2, making carbon assimilation less efficient; conversely, the unrestricted exchange of gases through fully open stomates would exacerbate water loss (Parry *et al.*, 2005). Although the carbon concentration mechanisms of C_4 plants have largely overcome this problem, an alternative strategy would be to introduce forms of Rubisco with higher relative specificity for CO_2.

Whilst the availability of high resolution 3-D structures of Rubisco and the characterization of site-directed mutants and chimaeric enzymes for cyanobacterial, algal, and bacterial forms of Rubisco have greatly enhanced our understanding of the catalytic mechanism, no substantial increase in the carboxylase relative to oxygenase activity or catalytic rate has yet been achieved by this approach (Parry *et al.*, 2003a, 2007). Whilst studies of Rubisco kinetic properties have focused on cultivated plants, some plants have evolved forms of the enzyme that discriminate more strongly against O_2 and, amongst C_3 plants, the specificity factor varies from 80–110. (Delgado *et al.*, 1995; Galmés *et al.*, 2005). Although comparatively small, the differences demonstrate that natural variation could be exploited to improve both Rubisco specificity and catalytic rate and thus CO_2 assimilation in crop plants (Parry *et al.*, 1987, 2007). For example, theoretical models indicate that replacing native wheat Rubisco with that from the species *Limonium gibertii* will give a 60% increase in net photosynthesis and thus increase yield (Table 1). Although much progress has been made to develop the tools for introducing genes into the nuclear genome of elite cultivars of wheat (Pastori *et al.*, 2001; Shewry and Jones, 2005), transformation of the plastid genome is still slow and limited to model species (Maliga, 2004). Furthermore, the additional complexities of assembling copies of the large and small polypeptide subunits of Rubisco into a functional holoenzyme *in vivo* (requiring high levels of expression, interaction with chaperonins, post-translational modification, and interaction with Rubisco activase) remains a major challenge.

In C_4 plants (e.g. maize) there is Kranz anatomy and segregation of biochemistry. In these plants CO_2 is initially fixed in the mesophyll by phospho*enol*pyruvate carboxylase (PEPC). The C_4 acids thus produced are transported from the mesophyll cells into the bundle sheath (BS) cells. Rubisco is confined to the BS cells which also have a suberized outer cell wall to decrease leakage of CO_2. When the C_4 acids are decarboxylated in the BS cells, the CO_2 released is mostly captured by Rubisco. In addition, because the C_4 cycle maintains a high CO_2 concentration in the BS cells, the oxygenase activity of Rubisco is suppressed. An alternative approach to overcoming the limitations of Rubisco in C_3 crops is to increase the CO_2 concentration at the catalytic site. On a global scale, atmospheric CO_2 is increasing but not sufficiently even to counteract the temperature-dependent increases in Rubisco oxygenase activity and associated photorespiratory losses.

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[1] As N invested in Rubisco is readily remobilized and constitutes the major source of N for grain proteins in wheat, increased efficiency may have a negative consequence on grain quality, in the absence of additional N inputs.

Table 1. Possible increases in net photosynthesis that may be achieved by selected modifications to current C_3 crops, and speculated time for adoption into breeding programmes

The prediction assumes that water and nutrients would not be limiting (adapted from Long *et al.*, 2006, and reproduced by kind permission of Wiley-Blackwell).

Modification	Predicted increase (%)	Time scale (years)
Increased RuBP regeneration	10	5
Increased stomatal and mesophyll conductance	5	5
Rubisco increased specificity factor and increased K_{cat}	60	15
Rubisco without oxygenase and high K_{cat}	100	25
Optimized Rubisco regulation	10	10
CO_2 pump	10	10
CO_2 pump with Kranz anatomy	50	20

However, if important C_3 crop plants, such as wheat, possessed a C_4 mechanism of carbon concentration, then very large increases in yield would be expected. The complexities of C_4 'Kranz' anatomy and the segregation of biochemistry has deterred researchers from attempting to introduce such a system into C_3 plants. Nonetheless, given the vast amount of diverse germplasm available for rice and wheat it may be possible to identify and select for features of Kranz anatomy. Indeed, the International Rice Research Institute (IRRI) is currently screening genetic resources for C_4 characteristics (Hibberd *et al.*, 2008).

Recently, the discovery of CO_2 pumps that operate within a single cell of some species (e.g. *Hydrilla verticillata*) has encouraged a number of biotechnological approaches to introduce a single cell CO_2 pump into C_3 crop plants (e.g. rice and wheat (Leegood, 2002; Taniguchi *et al.*, 2008). Theoretical analysis suggests that, whilst energy requiring, such systems would be of greatest benefit under drought or other conditions that lead to stomatal closure and low intercellular CO_2 (von Caemmerer, 2003). Much like the adoption of C_4 photosynthesis, this approach would require the co-ordinated, targeted expression of many transgenes, the assembly of gene products at the correct cellular and subcellular location, together with the appropriate regulation of the component enzymes and transporters. This has yet to be achieved (Leegood, 2002) and, even if successful, additional structural changes may be required to maximize yield potential.

In photorespiration, the deamination of glycine leads to the generation of ammonia. An important energy 'cost' of photorespiration is the reassimilation of this NH_3 (1 ATP and 1 NADPH equivalent per NH_3, or 3 of each per molecule of sucrose). Biotechnological approaches are being explored to introduce bacterial enzymes to short-circuit the photorespiratory pathway, eliminating the photorespiratory release of NH_3 (Parry *et al.*, 2003b; Bari, 2004). A pathway which converts chloroplastic glycolate directly to glycerate without the involvement of NH_3 has been introduced into *Arabidopsis* and releases CO_2 in the chloroplast. This new pathway decreased the flux of metabolites through the photorespiratory pathway in the peroxisomes and mitochondria and increased both shoot and root biomass. This is consistent with an increase in photosynthesis, partly due to increased CO_2 at the catalytic site of Rubisco (Kebeish *et al.*, 2007). Short-circuiting photorespiration, irrespective of where the CO_2 is released, will save energy which will be beneficial in low light (e.g. improve photosynthetic performance of lower leaves in the canopy).

Under moderate heat stress, photosynthesis and Rubisco activity decline. The loss of Rubisco activity is a consequence of Rubisco deactivation caused by the thermal inactivation of Rubisco activase (Salvucci *et al.*, 2001). *In vitro*, the loss of Rubisco activity can be overcome by increasing Rubisco activase concentrations and *in vivo*, by over-expression of Rubisco activase, or making activase more stable, enabling it to sustain photosynthetic rate under moderate heat stress. Although there is variation in the thermal stability of Rubisco activase from different species, which, in principle, could be exploited, the extent of variation within a single species has yet to be determined. A number of tight binding inhibitors of Rubisco occur *in vivo* which are responsible for low Rubisco activities (e.g. CA1P; Gutteridge *et al.*, 1986; Keys *et al.*, 1995) and accumulate under stress conditions (Medrano *et al.*, 1997). The release of these inhibitors requires Rubisco activase. However, although such inhibitors decrease the activity of Rubisco they also confer protection from oxidative or proteolytic damage (Khan *et al.*, 1999). New opportunities to modulate Rubisco activity and stability may result from altering the abundance of these inhibitors, by targeting their synthesis or degradation. The elucidation of the biosynthetic and degradative pathways of these inhibitors is an important new area for research (Andralojc *et al.*, 1996, 2002; Parry *et al.*, 2008).

Another approach to increasing total photosynthesis is to decrease the down-regulation of photosynthesis, encouraging the existing capacity to be more fully utilized (Parry *et al.*, 1993). Since down-regulation is essentially a mechanism for protecting the photosynthetic apparatus from excess radiation when dark reactions become a bottleneck to energy transduction, it is necessary to consider not only the inherent properties of the system but also indirect factors such as sink capacity, stomatal and mesophyll resistance, water availability, temperature etc. (Flexas *et al.*, 2004). Nonetheless, genetic variation in rate of xanthophyll cycling, a reversible adaptation to excess radiation that thermally dissipates energy at the thylakoid level, was associated with improved *RUE* in rice under conditions of intermittent cloud and bright sunshine and theoretical calculations suggest that selection for more rapid recovery from the photoprotected state would substantially increase carbon uptake by crop canopies in the field (Zhu *et al.*, 2004). Other targets for the improvement of photosynthetic rate impact upon the capacity for RuBP regeneration and include other Calvin cycle enzymes, principally

sedoheptulose *bis*phosphatase (Lefebvre *et al.*, 2005), and components of electron transport and light capture (Long *et al.*, 2006). In conclusion, there are several different and potentially complementary approaches to increase photosynthesis in wheat and their impact will depend on the time scale and magnitude of investments made (Table 1). However, it will be necessary to ensure that increased *RUE* and biomass are converted to grain yield. The complexity of partitioning and spike-fertility, coupled with evidence for underutilized photosynthetic capacity in modern cultivars, reinforces the need for better understanding of the processes determining grain number.

Factors influencing partitioning of assimilates to reproductive growth and spike fertility

Candidate traits for improving spike fertility come from a number of studies. Bingham (1969) suggested that increasing the relative partitioning of assimilates to the developing spike before anthesis, i.e. spike index, might increase grain set and the trait was later shown to be associated with yield improvement in comparisons of landmark wheat cultivars (Austin *et al.*, 1980; Calderini *et al.*, 1999a). Work looking at the association between spike index and resources available during the spike growth stage showed the critical importance of this period in determining final grain number (Fischer, 1985, 1993; Slafer *et al.*, 1990; Savin and Slafer, 1991; Abbate *et al.*, 1995; Demotes-Mainard and Jeuffroy, 2004). As yield is more dependent upon grain number (specifically grains m^{-2}) than upon the weight of the grains, raising spike dry matter at anthesis is an obvious target for genetic improvement.

Based on an examination of the relationship between photoperiod and changes in relative duration of phenological phases, Slafer *et al.* (1996, 2001) proposed that increasing the relative duration of spike growth through the manipulation of genetic sensitivity to photoperiod is a means to achieve larger spike mass. Another way to increase investment in spike growth is to increase pre-anthesis *RUE* and therefore biomass at anthesis, making more assimilates available to increase spike mass. Association between these traits has been shown in winter wheat cultivars (Shearman *et al.*, 2005) and random inbred lines from spring bread wheat crosses (Reynolds *et al.*, 2007b).

Elucidation of the genetic basis of the physiological processes determining spike fertility, including its interaction with (i) crop phenology, (ii) partitioning of assimilates to the growing spike versus other competing sources, and (iii) environmental constraints, are expected to lead to the development of a new generation of wheat cultivars that show a more optimal balance between partitioning of assimilates to competing growth processes and a full utilization of the canopy's photosynthetic capacity. The exercise becomes even more crucial to new generations of wheat, representing a quantum jump in photosynthetic capacity, if their true yield potential is to be realized under agronomic conditions.

Modifying crop phenology and spike fertility

As mentioned, Slafer *et al.* (1996, 2001) hypothesized that one alternative approach to achieving genetic gains in spike dry matter at anthesis, and thus further raise the number of grains m^{-2}, is to lengthen the stem elongation phase (Fig. 1A, B). The rationale has been that unlike spike development, which is very active from relatively early in the developmental stages of floral initiation (Slafer and Rawson, 1994), spike growth takes place during a rather short window of phenological time (Fig. 1A) starting about 20 d before ear emergence, in parallel with stem growth and elongation (Kirby, 1988). Thus, if the stem elongation phase (embracing the spike growth period) is longer, accumulated crop growth during stem elongation would be greater (as more radiation would be intercepted by the canopy). This would result in a heavier spike in this period, provided that dry matter partitioning to the growing spikes does not change in response to the lengthened duration (Slafer *et al.*, 2005; Fig. 1B).

As the objective would be to raise yield potential of the best (elite) material available, and these normally have an optimized time of anthesis, for this hypothesis to be viable there must be a way of lengthening the stem elongation phase without producing major changes in the total period from sowing to anthesis. A scheme of this alternative is provided in Fig. 2. There must not only be variability in the length of the stem elongation phase, but this variability must also be independent of any variability in the duration of phases from sowing to the onset of stem elongation. Although most large-scale screens of germplasm collections for developmental attributes have focused on the duration of the whole phase (either pre-anthesis or grain filling) a recent screening of commercial cultivars of wheat reported by Whitechurch *et al.* (2007) shows a wealth of variation in the duration of stem elongation, in line with previous observations in wheat (Slafer and Rawson, 1994) and barley (Kernich *et al.*, 1997). This is unrelated to the length of the period from seedling emergence to the onset of stem elongation (Fig. 2, top). In addition, it may be speculated that an even wider range of variation may exist in exotic germplasm.

The fact that there is variation in the length of the stem elongation phase means that cultivars may differ in either their intrinsic earliness, or earliness *per se*, for this phase and/or in their sensitivity to photoperiod during the stem elongation phase. Although most literature on intrinsic earliness analysed the trait in terms of time to anthesis (again without discerning differences in sub-phases of time to anthesis), there are indications that the intrinsic earliness for different sub-phases may be independent of each other (Slafer, 1996). In other words, a particular genotype may be intrinsically early in time to the onset of stem elongation and at the same time intrinsically late for the stem elongation phase. However, there has been negligible effort
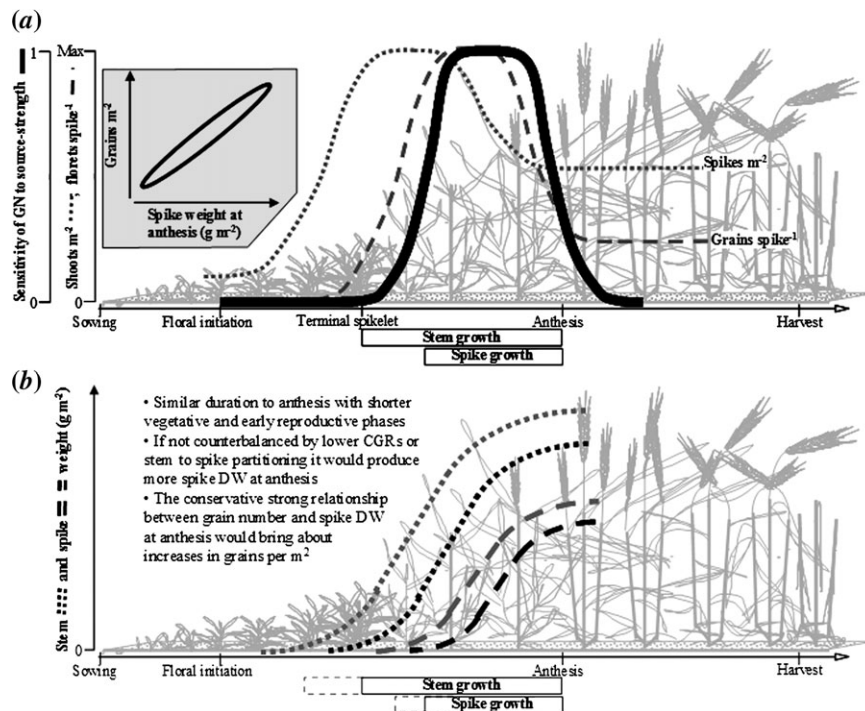
Fig. 1. (a) A simplified schematic diagram of wheat development, showing the relative sensitivity of grains m^{-2} to source strength at different stages throughout the growing season (thick line), together with the total number of shoots m^{-2}. The curve ends with the number of spikes m^{-2} (dotted line) and the total number of floret primordia per spike becoming fertile florets and then grains (dashed line), in both cases in relative scales from zero to their maximum values. Below the abscissa two boxes show the length of the period of stem and spike growth (inset box is the frequently reported relationship between grain number per unit land area and the spike weight at anthesis). (b) Schematic of the hypothesis proposed: lengthening the duration of the stem elongation phase at the expense of the duration of earlier phases such that time to anthesis is unaffected. Adapted from Miralles and Slafer (2007), copyright Cambridge University Press and reproduced with permission.
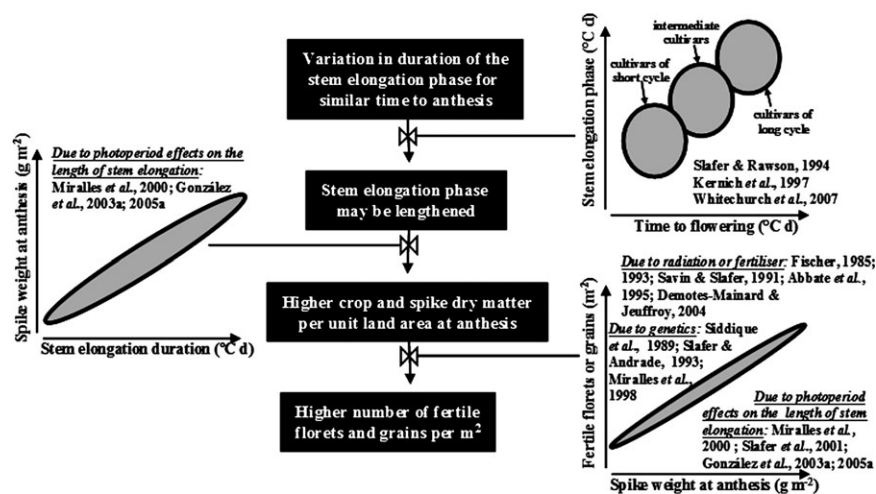

Fig. 2. Schematic illustration of the hypothesized avenue for improvement in grain number through manipulating the proportion of developmental time allocated to the stem elongation phase, describing some reported relationships supporting the hypothesis. Adapted from Slafer *et al.* (2005) and reproduced by kind permission of Wiley-Blackwell.

systematically to examine genetic variation in earliness *per se* of different sub-phases. More research has been devoted to elucidating photoperiod effects on the stem elongation phase. Although most agronomic models assume that photoperiod sensitivity is restricted to the relatively early phases of leaf and spikelet primordia initiation, and that the

stem elongation phase might not be responsive, a large body of evidence from physiological studies unequivocally demonstrates that this late reproductive phase is responsive to photoperiod (e.g. Slafer and Rawson, 1994). Not only is there genetic variation in this sensitivity, but this variation is also independent of variation in the sensitivity of previous

phases (Slafer and Rawson, 1996; González *et al.*, 2002). Subsequent work by Miralles *et al.* (2000) in a phytotron and by González *et al.* (2003*a*, 2005*a*) under field conditions, in which duration of spike growth phase was modified through manipulation of photoperiod exclusively during this phase (i.e. beyond any responsiveness of earlier phases) showed that grain set could be increased by lengthening the spike growth phase. Furthermore, the mechanism of increased grain number was an increased spike dry weight at anthesis (Miralles *et al.*, 2000; González *et al.*, 2003*a*; Serrago *et al.*, 2008; Fig. 2, centre), and this was equivalent to the effect that could be achieved by modifying radiation intensity during the stem elongation phase (González *et al.*, 2005*a*). The longer the duration of the phase, the more floret primordia can develop towards potentially fertile florets (González *et al.*, 2003*b*, 2005*b*), again a process seemingly related to the acquisition of dry matter by the spike immediately before anthesis (Fig. 2, bottom), in line with what can be observed by altering incoming radiation (González *et al.*, 2005*b*) or dry matter partitioning towards growing spikes (Miralles *et al.*, 1998) during the few weeks preceding anthesis.

To make use of this characteristic, it will be necessary to understand the genetic basis of photoperiod sensitivity during stem elongation. So far, there have been only a few efforts to identify which genes might be more relevant in determining the sensitivity to photoperiod in this late reproductive phase. Studies using isogenic lines or recombinant populations for major *Ppd* genes have provided little information because results have been inconsistent (Scarth *et al.*, 1985; Whitechurch and Slafer, 2001, 2002; Foulkes *et al.*, 2004; González *et al.*, 2005*c*). This lack of consistency may be due to the fact that only the effects of a few major genes for photoperiod sensitivity have been examined, while other, as yet unidentified, photoperiod genes in wheat are expected to exist (Snape *et al.*, 2001). Alternative approaches to identify candidate genes include searching for genes that are down- or up-regulated in response to photoperiod during this phase (Ghiglione *et al.*, 2008), and finding QTLs related to this particular developmental phenomenon in mapping populations (Dwivedi *et al.*, 2008).

Altering sinks that compete with spike fertility

Spike index could theoretically be increased by reducing competition from alternative sinks during stem elongation: roots, leaves, stems, and infertile shoots. Genetic variation in spike index is reported in the range of 0.12–0.29 (Siddique *et al.*, 1989; Reynolds *et al.*, 2001; Shearman *et al.*, 2005; Gaju, 2007; Acreche *et al.*, 2008). Potential avenues for raising spike index are discussed below with regard to decreasing partitioning to roots, stems (i.e. stems and attached leaf sheaths) and infertile shoots—the reduced allocation of assimilate to the leaf lamina may be incompatible with maintaining light interception and/or *RUE*. The potential competition of awns with spike fertility is also considered. Genetic ranges for partitioning coeffi-

cients for respective plant organs at anthesis reported in the literature are summarized in Table 2.

Root partitioning: The root dry weight ratio (root dry weight/total dry weight, *RDW*) of wheat is typically *c*. 0.30 during early vegetative growth decreasing to *c*. 0.10–0.15 by anthesis (Lupton *et al.*, 1974; Gregory *et al.*, 1978; Miralles *et al.*, 1997). One avenue to reduce *RDW* could be through accelerated development rate, since nodal root production is synchronized with leaf and tiller production (Gómez-McPherson *et al.*, 1998). However, this would be incompatible with the optimized phenology for increasing spike dry matter at anthesis as discussed above. Effects of increasing plant height in *Rht* near-isogenic lines (NILs) are generally either neutral or negative on *RDW* (Siddique *et al.*, 1990; McCaig and Morgan, 1993; Miralles *et al.*, 1997). Some caution is required when suggesting decreasing *RDW* as a strategy to increase spike index, since future genetic gains in yield seem likely to depend on raising biomass which, in turn, may require increased access to water and nutrients. Therefore, some attention should be focused on optimizing rooting systems for more efficient water and nutrient capture. In this respect, deeper root distribution could help, since root length density (root length per unit volume of soil) is often below a critical threshold for potential water and nitrate capture of *c*. 1 cm cm^{-3} (Barraclough *et al.*, 1989; Gregory and Brown, 1989) at lower depths in the rooting profile (Ford *et al.*, 2006; Reynolds *et al.*, 2007*c*). The use of synthetic wheat derivatives, incorporating genes from the diploid wild species *T. tauschii* (D genome), may help in the development of cultivars with such optimized rooting systems since they have similar *RDW* compared to recurrent parents, but roots which are distributed relatively deeper in the rooting profile (Reynolds *et al.*, 2007*c*).

Stem partitioning: Stem dry matter is partitioned between structural dry matter in the stem walls and soluble carbohydrate storage in the pith. Increased spike index in semi-dwarfs compared with tall controls appears to be due to reduced competition from the growing stem (Fischer and Stockman, 1986; Siddique *et al.*, 1989). Reducing structural stem dry matter further by decreasing plant height below current values of *c*. 70–90 cm may reduce grain yield by association with lower biomass (Richards, 1992; Miralles and Slafer, 1995; Flintham *et al.*, 1997), due to a suboptimal source: sink balance and/or light distribution within the canopy. Alternatively, reduced structural stem dry matter may be achieved by reducing the peduncle length, whilst maintaining the height of the leaf canopy (Richards, 1996). Strategies to reduce partitioning to the structural dry matter must be optimized with those to improve lodging resistance with regard to potential trade-offs with stem thickness and material strength of the stem wall, as discussed further below.

By flowering, reserves of soluble carbohydrates, mostly as fructans, have accumulated in the stems of the crop. Much of this carbohydrate is remobilized to the grain even under favourable post-anthesis conditions (Gebbing *et al.*, 1999;

Table 2. Genetic ranges for dry matter partitioning coefficients of wheat at anthesis (reported in the literature)

Reported ranges are from field investigations (except Ehdaie *et al.*, 2006; greenhouse).

Plant component[a]	Genetic range (sig.)[b]	Plant material[c]	Country	References
Spike	0.12–0.21***	WW, 8 cvs	UK	Shearman *et al.*, 2005
Spike DM/AGDM	0.15–0.27***	WW and SW, 99 DH lines	UK	Foulkes (unpublished)
	0.16–0.29***	SW, 17 cvs	Australia	Siddique *et al.*, 1989
	0.19–0.21**	SW, +/- 7Ag.7DL isolines (6 pairs)	Mexico	Reynolds *et al.*, 2001
	0.22–0.27***	SW, 2 F7+s and 1 cv	Mexico	Gaju, 2007
Competing sinks				
Roots	0.12–0.17*	WW, 6 cvs	UK	Lupton *et al.*, 1974
Root DM/Total DM	0.09–0.14**	SW, 3 Rht isolines	Argentina	Miralles *et al.*, 1997
	0.06–0.08	SW, synthetic/rec. parent (2 pairs)	Mexico	Reynolds *et al.*, 2007c
Leaf lamina	0.19–0.21*	WW, 8 cvs	UK	Shearman, 2001
Lam DM/AGDM	0.25–0.31**	SW, 2 F7+s and 1 cv	Mexico	Gaju, 2007
Stem and leaf sheath (SS)	0.58–0.63**	WW, 8 cvs	UK	Shearman, 2001
SS DM/AGDM	0.48–0.52*	SW, 2 F7+s and 1 cv	Mexico	Gaju, 2007
WSC DM/SS DM	0.24–0.43***	WW, 8 cvs	UK	Shearman *et al.*, 2005
	0.20–0.28*	WW and SW, 10 cvs	USA	Ehdaie *et al.*, 2006
	0.11–0.21***	SW, 20 cvs	Australia	Ruuska *et al.*, 2006
Infertile shoots	0.03–0.05*	WW, 8 cvs	UK	Shearman, 2001
In. shoot DM/AGDM	0.01–0.02	SW, 2 F7+s and 1cv	Mexico	Gaju, 2007

[a] DM, dry matter; AG, above ground; WSC, water soluble carbohydrate in stem and leaf sheath.
[b] *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.
[c] WW, winter wheat; SW, spring wheat.

Foulkes *et al.*, 2007). Genetic variation in water-soluble carbohydrate (*WSC*) as a proportion of the stem and leaf sheath dry matter shortly after anthesis is reported in the range of 0.11–0.43 (Foulkes *et al.*, 2002; Ehdaie *et al.*, 2006; Ruuska *et al.*, 2006). The field study of Beed *et al.* (2007) showed that the response of stem *WSC* to shading during the stem-elongation period was proportionally greater than that of the spike or the structural stem dry matter, suggesting that stem *WSC* tends to accumulate mainly once the sink demand of the spike and structural stem has been satisfied. This implies that reduced partitioning to stem *WSC* may be less useful in raising spike index than reduced partitioning to structural stem dry matter. The relationship between stem *WSC* accumulation and yield potential appears to depend on location, with neutral (Ruuska *et al.*, 2006; Reynolds *et al.*, 2007c) and positive (Foulkes *et al.*, 2002; Shearman *et al.*, 2005) associations reported. This may reflect that yield potential is more light-limited in some countries than others and stem reserves are, consequently, a more important post-anthesis source under these conditions. Ruuska *et al.* (2006) reported large broad-sense heritability ($H=0.90\pm0.12$) for stem *WSC* accumulation, indicating that breeding for high/low stem *WSC* should be possible.

Infertile tiller partitioning: Improved tiller economy could potentially favour partitioning to the spike by minimizing assimilate wasted in non spike-bearing shoots. In favourable environments with adequate water supply, non-surviving shoots are considered to be detrimental to crop performance, i.e. there is no net redistribution of assimilate to surviving shoots after their death (Simons, 1982; Berry *et al.*, 2003a). The effects of the tiller inhibition (*tin*) gene located on chromosome 1A (Spielmeyer and Richards, 2004) were investigated by Duggan *et al.* (2005) examining +*tin*/–*tin* NILs in Australia. They observed under irrigation a reduction in non-productive tiller number in +*tin* lines compared to their commercial near-isogenic counterparts, and that +*tin* lines showed increased grains per spike by 14%, but decreased grain yield by 9%. Similarly, Gaju (2007), examining a +*tin* F$_{7+}$ advanced line compared to a check cultivar under irrigation, observed the +*tin* line to decrease the number of non-productive tillers and increase grains per spike (+4%), but decrease grain yield (–8%). In both studies, reduced tillering with the *tin* gene boosted spike fertility but decreased grains per unit area. Overall, the potential to raise spike index through improved tiller economy may be moderate as the proportion of dry matter in non-spike bearing shoots at anthesis appears to be relatively low in modern elite wheat cultivars, for example, 0.01–0.05 (Shearman, 2001; Gaju, 2007).

The contribution of awns: Few and inconsistent effects of awns on bread wheat yield potential were reported when awnless/awned NILs were compared (McKenzie, 1972; Weyhrich *et al.*, 1994). Results of field experiments in the UK examining awnless/awned lines in a Beaver×Soissons DH population under irrigation showed that chaff weight per grain was increased by 1.1 mg with the presence of awns (MJ Foulkes, unpublished data), but grain yield was unaffected (Foulkes *et al.*, 2007). The selection of awnless phenotypes appears, therefore, not to be a priority for increasing spike fertility under high-output conditions.

In summary, it appears there is scope to fine-tune partitioning of assimilate to roots and infertile tillers below current values at anthesis of *c.* 0.01–0.15 and 0.01–0.05%, respectively, to raise spike index at anthesis, but that only moderate gains seem possible through these avenues. The principal target to raise spike index appears to be reduced partitioning of assimilate to the structural stem dry matter which presently accounts for *c.* 40–45% of above-ground biomass at anthesis (Table 2). In this respect, reducing peduncle length may offer one strategy for future progress. There is scope for the development and use of whole plant physiology and crop modelling approaches and simulation analysis to investigate the joint optimization of the distribution of assimilate between root, leaf, and stem and trade-offs in breeding (Hammer *et al.*, 2005). The availability of information on genetic variation for biomass partitioning will be crucial to this exercise, as well as knowledge on: (i) the developmental basis of the duration of the spike growth period, (ii) the leaf dry matter necessary for photosynthetic function, (iii) the stem dry matter required to resist lodging, and (iv) the contribution of storage of redistributable dry matter in the stems to grain dry matter. Such models calibrated and validated for a range of target environments may be of use to detect prospective traits for selection for raising spike fertility whilst avoiding a greater risk of lodging. Further advances will also require an improved understanding of the genetics of stem partitioning and underlying traits and the development of screens for beneficial traits including molecular markers.

Maintenance of spike fertility under unpredictable environments

Direct evidence for the 'conservative behaviour' of modern wheat varieties in terms of grain set came from observations of *7Ag.7DL* chromosomal substitution lines grown in a high-yield environment. In contrast to the six recurrent parents, the presence of *7Ag.7DL* was associated with average increases of 12.8% in grains/spike, 7.5% in flag-leaf light-saturated photosynthetic rate, and 9.2% in post-anthesis biomass accumulation—yield and biomass were increased by 13% and 10%, respectively (Reynolds *et al.*, 2001). To test the hypothesis that increased sink strength could directly influence *RUE* during grain filling, grains/spike were increased artificially with a 12 d light treatment during the boot stage in four of the highest yielding spring wheat cultivars available (Reynolds *et al.*, 2005). Very much like the effect of *7Ag.7DL*, the light treatment increased sink strength by increasing spike index and grains/spike as well as increasing light-saturated rates of flag leaf photosynthesis and *RUE* during grain filling; yield and biomass were increased by 20% and 18%, respectively (Table 3).

This raises the question of why elite cultivars carry apparently excess photosynthetic capacity, or the corollary, why elite cultivars express sub-optimal spike fertility. The explanation is likely to be associated with the fact that wheat is a self-pollinating species, which depends on the production of viable seed for evolutionary survival. Open pollinated species, on the other hand, can propagate genes through both seed set on the mother plant as well as through pollen dispersal to receptive neighbours (Bolaños and Edmeades, 1993). Therefore, grain number determination in primitive wheat (and its self-pollinating ancestors) would have evolved in response to two conflicting selection pressures, the need to produce enough seed to survive versus the need to adjust seed number to ensure viability (Sadras, 2007). However, while seed number is fixed around anthesis (Fischer, 1985) seed viability is determined by a number of subsequent events that are somewhat unpredictable including radiation levels, soil water status, competition from neighbouring plants for growth resources, as well as loss of photosynthetic tissue due to foliar diseases, insects, or herbivores. Therefore, plants would have been under selection pressure to evolve a relatively conservative strategy for determining seed number which could explain why, under well-managed conditions, even modern wheat cultivars show an apparent excess photosynthetic capacity (Table 3). In other words, given the fact that throughout most of its domestication wheat was cultivated under highly variable agronomic and environmental conditions, it is probable that this conservative tendency has become relatively genetically fixed, and may represent a bottleneck for achieving genetic gains in optimal environments. [Some mechanisms considered to be 'conservative' under favourable and well-managed environments are, however, likely to confer buffering capacity to environmental stresses in more marginal situations (Blum, 2005).]

A working hypothesis is that increased genetic capacity to set a larger number of grains/spike would result in a more efficient use of photosynthetic capacity during grain filling in favourable environments giving a substantial boost to yield potential. Two potentially complementary means to achieving this are outlined below. The first involves an empirical approach to increase the genetic variability of modern wheat varieties by introducing genes from wild ancestors. Interspecific hybridization between the ancestral genomes of wheat occurred spontaneously an estimated 10 000 years ago, creating a genetic bottleneck that resulted in restricted genetic diversity in the bread wheat genome (Trethowan and Mujeeb-Kazi, 2008). Wide crossing techniques have recreated this event and so-called 're-synthesized' or 'synthetic' wheats have already provided new sources of disease resistance (Villareal *et al.*, 1994) and drought adaptive traits (Reynolds *et al.*, 2007c). To increase spike fertility in bread wheat, donor genomes (AB-durum wheat and D-*Aegilops tauschii*) could be screened for favourable expression of the trait and the products of interspecific hybridization used as genetic sources. The feasibility of this approach is supported by past success in transferring traits from the D genome to cultivated bread wheat (Reynolds *et al.*, 2007c) and the fact that the alien introgression of *Lr19* for leaf rust into bread wheat from *Agropyron* (7Ag.7DL) resulted serendipitously in increased spike fertility, yield, biomass, and *RUE*, as discussed.

Secondly, mechanistic approaches can be applied to pinpoint the underlying physiological and genetic basis of

Table 3. Effects of increasing sink strength (using a 12 d extra light treatment during boot stage) on biomass and spike index at anthesis, yield components, grainfill rate, and stomatal conductance (g_s), and C fixation (A_{max}) of light-saturated flag leaves, averaged for four elite wheat cultivars over two cycles, NW Mexico, 2001–2002 (adapted from Reynolds *et al.*, 2005)

Cultivars used were three bread wheats: Siete Cerros 66, Baviacora 92, Babax/Lr24//Babax, and the durum wheat: Atil 2000.

	Effect of light treatment		Yield components[a]			RUE effects during grainfilling[a]		
	Biomass-anthesis (g m^{-2})	Spike index (ratio)	Yield (g m^{-2})	Biomass (g m^{-2})	Grains/spike	Grainfill rate (g m^{-2} d^{-1})	g_s (mmol m^{-2} s^{-1})	A_{max} (μmol m^{-2} s^{-1})
Check	1020	0.255	790	1800	40.3	19.2	559	25.9
Extra sink	1170	0.270	950	2,125	43.3	23.0	668	28.6
% Effect	15	6	20	18	8	20	19	10.4
P main effect	0.01	0.05	0.01	0.01	0.03	0.01	0.01	0.01
P interaction	0.25	0.50	0.00	0.03	0.37	0.01	0.85	0.50

[a] No significant effects were found for kernel weight, harvest index, leaf chlorophyll or leaf internal CO_2 concentration.

grain set/grain abortion as a means to engineering plants with a less conservative strategy, better adapted to modern agronomy. 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 probably soil N levels (Abbate *et al.*, 1997). This suggests that signalling may be involved in response to these environmental factors, especially at the critical growth stage when final grain number is determined through the abortion of potential florets (Fischer, 1985). In fact, signalling in plants is well established and regulatory mechanisms appear to be highly sophisticated involving long-distance electrical signals and the intercellular transport of macromolecules that help to optimize energy use and regulate plant development and defence pathways, including transcriptional activators, RNA molecules, and phytohormones (Brenner *et al.*, 2006; Rolland *et al.*, 2006; Malladi and Burns, 2007). Some argue that these are equivalent to neural networks that can receive, store, and process information related to biotic and abiotic cues (Brenner *et al.*, 2006; Baena-Gonzalez *et al.*, 2007; Smith and Stitt, 2007). For example, when plant roots detect a drying of the soil profile, signals are sent to leaves resulting in a reduction in transpiration rate mediated by reduced stomatal conductance; the signal appears to be complex but involves transport of ABA from the roots to the aerial parts (Davies *et al.*, 2002). The important point is that these signals are pre-emptive; by relaying information about soil water status in advance of adverse effects on plant water relations, growth rate is reduced and water use efficiency increased.

If plants have evolved complex pre-emptive signalling strategies to optimize water use better, then it is possible that they integrate information on other potentially limiting resources, such as nitrogen, or the presence of neighbours that could eventually compete for light and other resources (Ballaré *et al.*, 1990). 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 and McLaughlin, 2007). In wheat, day length has been shown to influence the number of fertile florets by regulating sugar supply leading to programmed cell death (Ghiglione *et al.*, 2008), while under high temperature stress ethylene appears to be involved in signalling leading to kernel abortion (Hays *et al.*, 2007). Since the *7Ag.7DL* translocation in wheat is associated with reduced floral abortion in high yield environments, it may be a suitable model for studying the cues which determine final grain number, for a number of reasons such as the effects on spike fertility are relatively large and consistent across genetic backgrounds (Reynolds *et al.*, 2001); the types of environment in which increased spike fertility is expressed are well documented (Monneveux *et al.*, 2003); and trait expression is focused on a specific tissue (immature spike) at a well-defined growth stage (rapid spike-growth stage). At least one candidate gene for spike fertility already exists in rice (*Gn1a*) coding for cytokinin oxidase which, through its regulation of cytokinin levels, influence numbers of reproductive organs in the panicle (Ashikari *et al.*, 2005)

However, any comprehensive strategy to improve wheat yield potential must consider the fact that heavier more fertile spikes will increase yield losses associated with lodging unless traits associated with stem strength and root anchorage are simultaneously improved.

Physical processes associated with lodging and key traits for genetic improvement

Lodging is a persistent phenomenon in wheat which reduces yield by up to 80% (Stapper and Fischer, 1990; Easson *et al.*, 1993) as well as reducing grain quality. A validated model of lodging has identified the characters that determine stem and root lodging risk of wheat (Baker *et al.*, 1998; Berry *et al.*, 2003b). The steps involved in calculating lodging risk and the equations used to link the characters are described in Berry *et al.* (2003b). The risk of stem and root lodging is calculated in terms of the wind speeds required to cause failure of the stem base and the anchorage system. Stem lodging is predicted when the

wind-induced leverage of a single shoot exceeds the strength of the stem base. Root lodging is predicted when the wind-induced leverage of all shoots belonging to a single plant exceeds the anchorage strength. The wind-induced leverage of a shoot is calculated from its height at the centre of gravity, the rate at which the shoot sways (natural frequency), and the projected area of the ear. In turn, these characters can be calculated from the height to the ear tip, grain yield per unit area, and shoot number per unit area (Berry *et al.*, 2004). The strength of the stem is calculated from the diameter, wall width, and material strength of the stem wall. Root anchorage strength is calculated from the spread and depth of the root plate and the shear strength of the surrounding soil.

The model described above has been used with information about the dry matter costs of improving lodging traits to calculate 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). The plant characteristics required to give an 8 t ha^{-1} yielding crop (with 500 shoots m^{-2} and 200 plants m^{-2}) a lodging return period of 25 years, include a height of 0.7 m, a root plate spread of 57 mm, and for the bottom internode a wall width of 0.65 mm with a diameter/material strength combination ranging from 5.86 mm with a material strength of 20 MPa to a diameter of 4.00 mm with a material strength of 50 MPa (Fig. 3). It is estimated that this ideotype would require 7.9 t ha^{-1} of stem biomass and would have a harvest index of 0.42. Observations of a wide range of varieties grown in the UK using crop management to maximize lodging resistance without reducing yield potential showed that the root plate of the best variety was 7 mm less than the ideotype target, the stem character targets were achieved but not all in one variety, and the height target was achievable with the use of plant growth regulators. Plant breeders must therefore focus on selecting for a wider root plate and combining the appropriate stem strength characteristics.

It is clear that plant breeders must improve the spread of the root plate, stem thickness, and the material strength of the stem wall, whilst minimizing the width of the stem wall. To achieve this, the genetic control of these traits must be understood, pleiotropic effects identified, and methods of rapidly screening for them must be developed. One of the key assumptions in the analysis of Berry *et al.* (2007) was that the minimum height compatible with high yields is 0.7 m. Many empirical observations support this (Allan, 1986; Kertész *et al.*, 1991; Richards, 1992; Baylan and Singh, 1994; Miralles and Slafer, 1995; Flintham *et al.*, 1997). However, further work must investigate why there appears to be a minimum height for high yield and whether this barrier can be overcome. If shorter crops can be found which are compatible with high yields then this would significantly reduce the amount of dry matter that must be partitioned to the stem and roots to support the crop. A key question arising from the analysis is to what extent the development of the traits that determine stem and anchorage strength may compete with yield formation. The
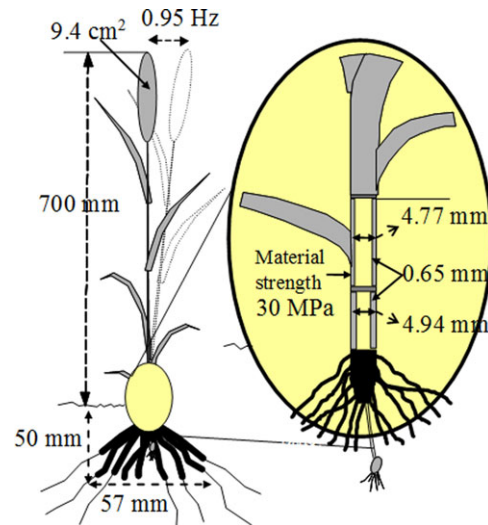

Fig. 3. Dimensions of a lodging-proof wheat plant.

development of the root and stem characters associated with lodging continues until anthesis (Crook *et al.*, 1994). Lodging characters may, therefore, compete for resources with the development of grains m^{-2} and with the production of soluble stem reserves that are later relocated to the grain. Further work must investigate how important this competition is and to what extent it can be minimized.

The analysis of Berry *et al.* (2007) predicts that the maximum harvest index for a lodging-proof crop yielding 8 t ha^{-1} is 0.42 rising to 0.50 for a crop yielding 16 t ha^{-1}. It was assumed within this prediction that the yield increase is brought about by increasing ear size rather than increasing ear number. If yield is increased from 8 t ha^{-1} to 16 t ha^{-1} by increasing ear number then harvest index will remain largely unchanged at 0.42. These predictions illustrate that yield improvements probably need to be accompanied by increases in total biomass to avoid greater risk of lodging. Furthermore, trade-offs in terms of partitioning of assimilates to competing sinks during spike growth, to improve root anchorage and stem strength, will need to be considered carefully when determining the optimal strategy for partitioning of assimilates to reproductive organs.

Genetic tools to take physiological platforms to breeding applications

While genetic variation exists for most of the traits discussed it cannot be selected for easily based on Mendelian inheritance due to its quantitative nature. However, using genetic markers in segregating mapping populations is now a facile procedure for QTL discovery. Nonetheless, there is a bottleneck in marker development because data from current mapping populations are confounded by genetic variation in flowering date. This is not generally considered to be problematic if the population's overall maturity class fits the target environment. However, this is often a false assumption and the most likely reason why

QTL studies frequently identify *Ppd* and *Eps* loci as those most strongly associated with yield; while differential sensitivity to photoperiod is a component of yield potential, it is self evident that effects of major genes must be controlled when trying to determine the more subtle influence of minor genes on yield potential traits (Reynolds and Tuberosa, 2008). It is well established in wheat that key developmental processes such as kernel set are determined within relatively narrow developmental windows and can be especially sensitive to environmental conditions (Fischer, 1980, 1985; Abbate *et al.*, 1997). Therefore, genotypes growing side by side, but which pass through key developmental stages on different dates, are likely to trigger different signal transduction pathways and different adaptive responses at the whole plant level due to variation in simple weather parameters. Hence the only way to eliminate this confounding factor is to minimize differences in flowering time in the experimental population. There are different ways in which this can be done. Firstly, by using subsets of RILs or doubled-haploids from particular crosses where the lines are chosen to have similar genetic make-up for phenology by using perfect markers at the major gene loci of *Vrn-1* and *Ppd-1* to select the subsets with the same alleles. Confirmation is then needed, based on phenotypic expression and G×E for flowering time, in the appropriate range of target environments. The development of populations with negligible differences in flowering time will substantially increase the precision with which QTLs for yield-related traits can be identified and subsequent gene discovery. Secondly, a cohort of lines with similar flowering time can be used for association genetics mapping. The latter approach has the additional advantage that populations can be assembled using exclusively agronomically improved material, thereby minimizing the probability of identifying QTLs associated with yield that have already been optimized by plant breeding, in contrast to the random inbred line approach.

While new populations using these criteria are in development, a number of mapping populations already exist that can be used to study these traits including CIMMYT populations Bacanora/Weebil, a cross between two high yield/*RUE* parents that contrast in yield components; Seri/Babax, progeny of a broadly adapted high yield line and a high *RUE* line with a restricted range of phenology (Olivares *et al.*, 2007); and adapted European winter wheat populations including Spark/Rialto and Beaver/Soissons. Preliminary data have already indentified putative QTLs associated with spike fertility and *RUE*. With good phenotypic and genotypic data, statistical tools can also be used to permit candidate genes to be analysed in terms of gene×background as well as gene×environment interaction (Vargas *et al.*, 2006) permitting the optimum deployment of markers to economically important target environments

Integration of new technologies into breeding

Given the genetic complexity of yield, it is apparent that a comprehensive and multidisciplinary approach to crop improvement has the greatest probability of achieving impact on productivity in farmer's fields (Fig. 4). Although crop scientists now have greater challenges than in past (climate change, water shortage, restricted land area, degraded soils) there is also unprecedented access to new technologies. Selection for grain yield using conventional empirical approaches will continue to see modest improvements, a consequence of much current genetic variability having been captured by previous breeding activities. However, there is a need to broaden the genetic base as well as developing new approaches to revisit the physiological basis of grain production. The proposals outlined in this review present some new and radical opportunities. Increased biomass must be considered to be the highest
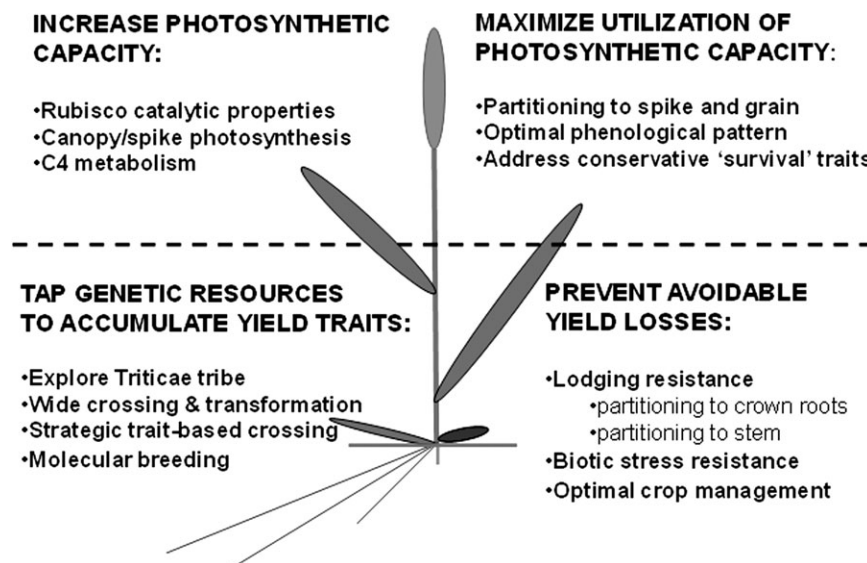
INCREASE PHOTOSYNTHETIC CAPACITY:

•Rubisco catalytic properties
•Canopy/spike photosynthesis
•C4 metabolism

MAXIMIZE UTILIZATION OF PHOTOSYNTHETIC CAPACITY:

•Partitioning to spike and grain
•Optimal phenological pattern
•Address conservative 'survival' traits

TAP GENETIC RESOURCES TO ACCUMULATE YIELD TRAITS:

•Explore Triticae tribe
•Wide crossing & transformation
•Strategic trait-based crossing
•Molecular breeding

PREVENT AVOIDABLE YIELD LOSSES:

•Lodging resistance
 •partitioning to crown roots
 •partitioning to stem
•Biotic stress resistance
•Optimal crop management

Fig. 4. Complementary strategies to increase wheat yield potential.

priority and be addressed by manipulating photosynthetic efficiency. If this resulted in a 10% increase in biomass (and 6% yield), on a current 600 million tonne world crop this would be a staggering 36 million tonnes of wheat—twice the current output of a country like the UK.

Broadening the genetic base of wheat

In order to achieve significant increases in yield and biomass the genetic base of current wheat gene pools needs to be broadened further and ample scope exists using closely related taxa (Table 4); the approach has already proved highly successful. For example, the 7Ag.7DL introgression is associated with both increased yield and biomass/*RUE* in different wheat backgrounds (Reynolds *et al.*, 2001); it is especially attractive to breeders since it can be tracked with the genetic marker for *Lr19*. Recent work at the John Innes Centre has identified the non-glaucous trait introduced from *Triticum dicoccoides* conferred by *Vir*; the phenotype is associated with delayed senescence leading to prolonged grain-filling duration (Simmonds *et al.*, 2008). The success of the CIMMYT 'synthetic' programme further illustrates the potential impact of broadening the genetic base using wide crossing (Trethowan and Mujeeb-Kazi, 2008). However, there is always a risk of 'linkage drag' when introducing chromatin from non-agronomic species, as was the case for the introduction of resistance to eyespot (*Pseudocercosporell herpotrichoides*) using *Aegilops ventricosa*; although eyespot resistance was achieved its linkage with low yield has yet to be overcome.

Nonetheless, there must be a well-defined strategy to develop wide crosses. Crossing 'blindly' in the hope that 'something will turn up' is both inefficient and unlikely to deliver benefits. For too long breeders have looked at genetic resources in terms of relatively simple characters, such as disease resistance. There are a wide number of physiological traits for which genetic resources can be characterized and integrated selectively into breeding programmes, and a vast pool of genetic resources that remain largely untapped (Table 4) despite their potential value (Hajjar and Hodgkin, 2007).

In terms of broadening the gene pool, genetic transformation represents the final frontier and is almost certain to be necessary if *RUE* is to be raised by figures approaching 50%. The technology is attractive to breeders, at least where the value of the transgene is unequivocal, since they can be tracked using marker assisted selection.

Trait-based breeding

Over the last 40 years progress in 'crop ideotype' selection has concentrated on the gross morphological changes manifest by the introduction of the major dwarfing genes *Rht1-D1* and *Rht-B1*. Nonetheless, there are a range of other dwarfing genes available (Rebetzke *et al.*, 2007) which could contribute to 'fine-tuning' wheat ideotypes. For example, work by Law *et al.* (1978) suggested that improvements could be made by adopting a 'tall dwarf' strategy, by crossing semi-dwarf varieties with taller counterparts and reselecting for the presence of the dwarfing gene in the tall background. This route has been successful in the UK with a movement towards slightly taller varieties, although still with either *Rht1-D1* and *Rht-B1*. This can be enhanced by the use of molecular markers to identify lines with the new but appropriate height reduction genes, neutral in their effect on yield but positive for height reduction (Rebetzke *et al.*, 2007), combined with early generation culling of lines prior to field evaluation for other traits.

However, to achieve quantum leaps in yield the ideotype approach must focus on a range of key characteristics for use in strategic crossing to combine complementary traits that will result in cumulative gene action. Trait-based physiological breeding has been used successfully to improve performance in drought-prone environments (Reynolds and Tuberosa, 2008) and is well suited to the current objectives in which a number of complex traits (*RUE*, spike fertility, lodging resistance) must be combined in the absence of comprehensive information of their genetic basis. Once achieved, the next priority from the breeder perspective will be to understand the more subtle physiological and genetic basis of broad adaptation, or yield stability, in the face of the inevitable variation in environmental factors among sites and years.

Molecular breeding

Although the evolution of laboratory-based molecular techniques has led to a revolution in genotyping breeding material, there is still a significant gap between the breeding community and the creators of the technology. Facile and high-through-put phenotyping technologies lag behind those of genotyping at present, and the characters being used so far in breeding programmes represent the 'easier targets' such as major disease resistance, alien introgressions or dwarfing genes. Whilst these are commendable they are generally still working within the genetic pool currently being utilized by the breeding community. The task is now to develop

Table 4. Number of accessions of wheat wild relatives available in world collections and the number already used in wide crossing

Compiled by Kishii M (personal communication) using data from Konopka and Valkoun (2005).

	Genome	CIMMYT	World	Utilized
Triticum dicoccum	AABB	779	–	24
Triticum dicoccoides	AABB	880	1390	3
Triticum timopheevii	AAGG	280	640	2
Triticum monococcum	AA	880	1520	120
Triticum urartu	AA	392	516	21
Aegilops speltoides	(~BB) SS	140	540	34
Aegilops bicornis	(~BB) SbSb	14	28	0
Aegilops longissima	(~BB) SlSl	10	59	2
Aegilops tauschii	DD	400~600	1144	400
Total		3875	~7400	~8%

Table 5. Prioritization of traits and technologies in a current wheat breeding programme, 1 = high

	Wide crosses	Transformation	Physiological trait breeding	Molecular markers	Doubled haploids	Hybrids
Increasing biomass	1	1	2	2	2	2
Partitioning	1	3	1	2	2	2
Adaptation	2	3	1	1	2	3
Lodging	3	2	1	1	1	2

a strategy incorporating a wide range of disciplines in order to develop populations for phenotyping and consequential genotyping. Populations currently available should only be used if they express traits of high physiological significance. Techniques, now routine, such as doubled haploid production should be used to establish these target populations.

With increasing numbers of markers and traits, breeders will be faced with a mass of information that, under current systems, would be too difficult to integrate into a coherent strategy. It is thus imperative that, at the same time as an integrated strategy is implemented, there are bioinformatic tools available to allow the breeder to refine selection criteria and prioritize those traits of high value (Bonnet *et al.*, 2005; Wang *et al.*, 2009). With some traits, such as photosynthetic efficiency, once the genes for enhanced efficiency are fixed within the current gene pool, efforts can be devoted to other 'yield enhancing' physiological traits. This is very much in line with current practice whereby breeders do not screen for genes known to be homozygous within the populations under selection. Key strategies can be applied to fix some of the traits prior to the all-important field selection. This can be done effectively in three-way crosses whereby 'genetic enrichment' can be practised on F_1 seed top-crossed with a third parent.

Table 5 presents a view of traits and technologies and their prioritization for the current needs of a wheat breeding programme; hybrid wheat is highlighted since it is believed that problems of seed production will soon be overcome given novel approaches to plant manipulation, either through conventional means or transgenesis. While there is optimism amongst plant breeders, physiologists, and geneticists that progress can be made in increasing yield potential in wheat, and at a pace to keep up with demand, it will require a multi-disciplinary approach and close co-operation between fundamental and strategic research, on the one hand, and applied plant breeding on the other, to create a 'pipeline' for discoveries to go from the laboratory to the field. In recent years, such pipelines have been broken and there is a need to ensure that they are rebuilt and effectively utilized in the future.

Conclusions

In summary, it is proposed that, while improvement of the photosynthetic capacity of wheat may be achieved through genetic modifications at the cellular and whole plant level (Table 1), increased spike fertility, achieved at least partially via more optimal partitioning of assimilates to the growing spike, appears to be necessary fully to realize photosynthetic potential during grain filling. A better understanding of how crops respond to environmental cues, such as photoperiod and availability of growth inputs, may help to design crops that balance source and sink potential to maximize yield in favourable environments. However, trade-offs in terms of how additional biomass is partitioned to root and stem versus reproductive growth will be necessary to construct lodging-proof crops. The wheat gene pool can be broadened using interspecific hybridization with wild relatives or transgenes from alien taxa. In addition to an exploration of genetic resources, trait-based strategic crossing, use of physiological and molecular markers for early generation selection, and doubled haploid breeding, can be used to accelerate rates of genetic gains (Fig. 4).

Acknowledgements

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