

REVIEW PAPER

Raising yield potential of wheat. III. Optimizing partitioning to grain while maintaining lodging resistance

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Abstract

A substantial increase in grain yield potential is required, along with better use of water and fertilizer, to ensure food security and environmental protection in future decades. For improvements in photosynthetic capacity to result in additional wheat yield, extra assimilates must be partitioned to developing spikes and grains and/or potential grain weight increased to accommodate the extra assimilates. At the same time, improvement in dry matter partitioning to spikes should ensure that it does not increase stem or root lodging. It is therefore crucial that improvements in structural and reproductive aspects of growth accompany increases in photosynthesis to enhance the net agronomic benefits of genetic modifications. In this article, six complementary approaches are proposed, namely: (i) optimizing developmental pattern to maximize spike fertility and grain number, (ii) optimizing spike growth to maximize grain number and dry matter harvest index, (iii) improving spike fertility through desensitizing floret abortion to environmental cues, (iv) improving potential grain size and grain filling, and (v) improving lodging resistance. Since many of the traits tackled in these approaches interact strongly, an integrative modelling approach is also proposed, to (vi) identify any trade-offs between key traits, hence to define target ideotypes in quantitative terms. The potential for genetic dissection of key traits via quantitative trait loci analysis is discussed for the efficient deployment of existing variation in breeding programmes. These proposals should maximize returns in food production from investments in increased crop biomass by increasing spike fertility, grain number per unit area and harvest index whilst optimizing the trade-offs with potential grain weight and lodging resistance.

Key words: Alien introgression, crop breeding, dry mass partitioning, gene-discovery, genetic-resources, grain size, grain weight, lodging resistance, marker assisted selection, phenology, quantitative trait locus, spike-fertility, wheat.

Abbreviations: ABA, abscisic acid; ACC, 1-aminocyclopropane-1-carboxylic acid; DAA, days after anthesis; DM, dry matter; GA, gibberellin; GM, genetically modified; HI, harvest index; IAA, indole-3-acetic acid; NIL, near isogenic line; NUE, nitrogen use efficiency; QTL, quantitative trait loci; RLD, root length density; RUE, aerial biomass per unit radiation interception; SFI, spike fertility index; SPI, spike partitioning index; SSC, soluble stem carbohydrate; WGIN, Wheat Genetic Improvement Network; WYC, Wheat Yield Consortium.

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Introduction

The UN forecasts that the world human population will reach 9.4 billion by 2050. The world must therefore develop the capacity to feed 10 billion within the next 40–50 years. Most of this capacity will need to result from greater yields on existing cropland. If we can achieve this without proportionate increases in the use of water or fertilizer (sustainable intensification), and within the context of climate change (Hirel *et al.*, 2007; Cattivelli *et al.*, 2008; Foulkes *et al.*, 2009a; see also Royal Society, 2009), the detrimental environmental effects of expanding the global cropped area will be minimized. A substantial increase in yield and in crop stress resistance is therefore required, along with better use of water and fertilizer, to ensure food security and environmental protection in future decades. Improved efficiency of nitrogen (N) use (nitrogen-use efficiency; NUE) will be particularly crucial as part of the dynamic to allow greater biomass production to be sustained. Yield potential is the yield of a cultivar when grown in environments to which it is adapted (solar radiation, temperature, day length) with nutrients and water non-limiting and with pests, diseases, weeds, and other stresses effectively controlled (Evans and Fischer, 1999). The attainable yield is close to the yield potential ceiling and is the best yield achieved through skillful use of the best available technology; on-farm yields normally realize from 60 to 80% of attainable yield (Foulkes *et al.*, 2009b). Yield potential remains the principal target for breeders as it is directly linked to both attainable and on-farm yields (Slafer and Calderini, 2005; Fischer and Edmeades, 2010), even under conditions that are frequently stressful during grain filling (Acreche *et al.*, 2008). Selection for greater yield potential has frequently resulted in higher production in environments subject to abiotic stress (usually water and heat) in wheat as well as in unstressed environments (Calderini and Slafer, 1999; Slafer *et al.*, 1999; Richards *et al.*, 2002; Araus *et al.*, 2002; Reynolds and Borlaug, 2006; Foulkes *et al.*, 2007). Therefore, an important outcome of breeding for yield potential is higher attainable yields under relatively favourable conditions, as well as under moderate abiotic stresses. Although to date improvement of yield potential has been based mainly on yield *per se*, there is strong evidence that understanding traits at the physiological level will help to identify trait interactions and indirect selection criteria that could accelerate breeding progress (Jackson *et al.*, 1996; Araus *et al.*, 2002; Slafer, 2003; Reynolds and Borlaug, 2006; Reynolds *et al.*, 2009). An understanding of traits at the physiological level will help to predict synergies (between new environments and breeding, between agronomy and breeding, and between biomass and partitioning traits). Moreover, knowledge of the genes that regulate these traits will facilitate their assembly in new genotypes. Such an integrated approach will complement empirical breeding and hasten progress to increased wheat production, particularly in regions of the world predicted to become more climatically suited to cereal production under climate change. Trait-based physiological breeding has been used

successfully to improve drought adaptation of wheat in Australia and by the International Maize and Wheat Improvement Centre (CIMMYT), including higher transpiration efficiency, greater early vigour, reduced tillering, and dehydration avoidance (Richards *et al.*, 2002; Reynolds and Tuberosa, 2008), and is well suited to the current objectives in which a number of complex traits (spike fertility, potential grain size, and lodging resistance) must be combined.

In wheat, grain yield improvement has been highly associated with grain number per unit area (Canevara *et al.*, 1994; Sayre *et al.*, 1997; Brancourt-Hulmel *et al.*, 2003; Shearman *et al.*, 2005; Peltonen-Sainio *et al.*, 2007). Evidence suggests that grain sink strength remains a critical yield-limiting factor (Fischer, 1985; Slafer and Savin, 1994; Abbate *et al.*, 1998; Miralles *et al.*, 2000; Borrás *et al.*, 2004; Miralles and Slafer, 2007) and that sink capacity will need to be improved if improvements in biomass and radiation-use efficiency (aerial biomass per unit radiation interception; RUE) are to be fully exploited as increased harvestable yield (Reynolds *et al.* 2001, 2005, 2009; Acreche and Slafer, 2009). Increased partitioning of assimilates to the developing spike and grain has historically had the single greatest impact on improving yield potential in wheat (e.g. Calderini *et al.*, 1999a), not only under high-yielding conditions (e.g. Brancourt-Hulmel *et al.*, 2003) but also under stressful conditions such as those of Mediterranean regions (e.g. Loss and Siddique, 1994; Acreche *et al.*, 2008). Although greater biomass appears to be contributing to genetic yield progress in modern cultivars released since about 1990 (e.g. Donmez *et al.*, 2001; Shearman *et al.*, 2005), there are clear indications that yield of modern wheats is still more sink than source limited during grain filling (e.g. Borrás *et al.*, 2004). A mirror image of this sink limitation is that the current or improved photosynthetic capacity during grain filling may not be fully exploited if it is not matched by adequate spike fertility (Reynolds *et al.*, 2005). For example, photosynthesis during the post-anthesis period (at both leaf and canopy levels) seems to be responsive to increases in strength of the sink, via source/sink manipulation treatments imposed around anthesis, even in modern cultivars with high grain numbers (e.g. Reynolds *et al.*, 2005; Acreche and Slafer, 2009). Therefore, for improvements in photosynthesis to result in additional crop yield, extra assimilates must be partitioned to developing spikes and grains and/or potential grain size must be increased to accommodate the extra assimilate.

Yield increases associated with the introduction of semi-dwarf cultivars during the Green Revolution of the 1960s and 1970s were associated with reduction in stature, reduction in lodging, and also reduced competition from the growing stem resulting in greater spike growth, more grains per unit area, and higher harvest index (HI) (Fischer and Stockman, 1986). Despite a hypothetical limit to HI of ~0.62 in wheat (Austin, 1980; and see below) comparisons of genetic progress in HI over time indicate no

systematic improvement since the early 1990s from values of ~50% in spring wheat (Sayre *et al.*, 1997; Reynolds *et al.*, 1999) and 55% in winter wheat (Shearman *et al.*, 2005). Future yield gains in modern semi-dwarfs through HI will require further gains in grain number. These may be achieved by increased partitioning to spikes during stem elongation but, if increased assimilate is not available for this, care must be taken that decreased stem partitioning does not decrease lodging resistance (see below) or potential grain size. The genetic and physiological interdependence of these traits will need to be established for easier deployment in breeding and to optimize any trade-offs.

Past breeding for grain yield has increased the efficiency of nutrient use, but nutrient requirements, as defined by the economic optimum amount of nutrient fertilizer, have also increased; in particular requirements for N have increased where conditions enabled high yields (e.g. Foulkes *et al.*, 1998; Sylvester-Bradley and Kindred, 2009). It is important that, particularly in these high-yielding conditions, work to enhance wheat yields is associated with ongoing research programmes to improve nutrient-use efficiency (e.g. Martre *et al.*, 2007; Foulkes *et al.*, 2009a; Sylvester-Bradley and Kindred, 2009). Additionally, strategies to optimize developmental pattern to overcome limitations to spike fertility and grain size should take account of the cropping system and/or rotational requirements, e.g. in cropping systems in which wheat is as a component of more than one crop in a year, to maximize yield of the system. Additionally, it is recognised that in some eastern Mediterranean countries straw may be as important as grain yield.

The overall strategy of the international Wheat Yield Consortium (WYC) is described in the accompanying article by Reynolds *et al.* (2010), and three linked themes

were introduced: Theme 1, increasing photosynthetic capacity and efficiency; Theme 2, optimizing partitioning to grain while maintaining lodging resistance; and Theme 3, trait and gene deployment through combining wide crosses and marker-assisted selection with trait-based breeding. In Theme 2, a set of six sub-projects has been developed (Reynolds *et al.*, 2010; Fig. 1; Box 1). This article makes a critical analysis of the research area for Theme 2 and then justifies appropriate research approaches (Box 1) together with the key deliverables (Box 2). We stress that it is crucial for improvements in partitioning and lodging aspects of growth to go hand in hand with increases in photosynthesis and biomass (Parry *et al.*, 2010) if the net agronomic benefits of this physiological approach are to be maximized.

Strategies to overcome limitations to spike fertility and HI

Optimizing developmental pattern to improve spike fertility

Many physiological studies have demonstrated that increasing the number of grains set in wheat brings about almost parallel increases in yield and that the number of grains is strongly related to the dry weight of the spikes at around anthesis (disregarding whether the source of variation is genetic or environmental, e.g. Slafer, 2003). As spike growth takes place in a rather short period within pre-anthesis development, mostly coincident with stem elongation, it has been suggested that modifying the duration of the stem-elongation phase could bring about improvements in spike dry matter (DM) at anthesis and in the number of

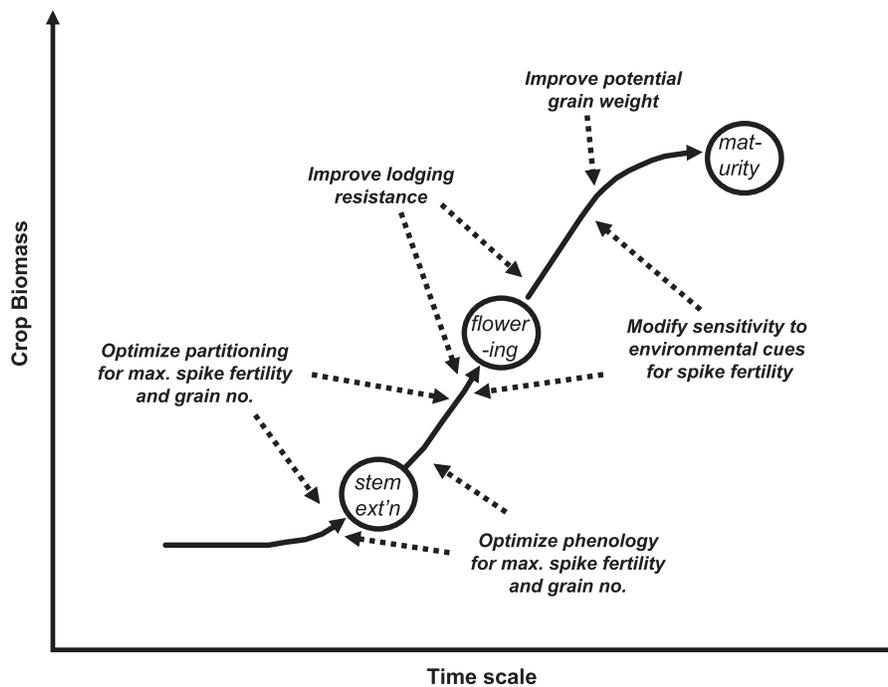


Fig. 1. Schematic diagram of relationship between the research approaches adopted in Theme 2: optimizing partitioning to grain while maintain lodging resistance.

Box 1. WYC approaches to optimizing partitioning to grain while maintaining lodging resistance

Optimizing harvest index through increasing partitioning to spike growth and maximizing grain number

Optimizing developmental pattern to maximize spike fertility

Improving spike fertility through modifying its sensitivity to environmental cues

Improving potential grain size and grain filling

Identifying traits and developing genetic sources for lodging resistance

Modelling optimal combinations of, and trade-offs between, traits

Box 2. WYC key deliverables in a 5-year time-frame

New sources of germplasm with maximized grain number per m² through a variety of phenology and partitioning (DM and N) mechanisms

New sources of germplasm with increased potential grain weight and lodging resistance

New sources of germplasm with increased NUE

Determine the physiological, structural, and biochemical bases for high grain number per unit ground area through optimized phenology and partitioning (DM and N)

Determine the physiological and biochemical bases for high potential grain weight

A model of optimum phenology and partitioning of high-yielding wheat in different environments with a focus on spike fertility, taking into account damage through lodging

A model explaining the trade-off between grain number and grain weight

New tightly linked molecular markers for spike fertility and component traits for deployment in breeding

New tightly linked molecular markers for lodging resistance and potential grain weight for deployment in breeding

High-throughput screens for partitioning, potential grain weight, and lodging resistance characteristics for deployment in breeding

grains (Slafer *et al.*, 2001). In wheat the grain number response to duration of stem elongation mainly relates to the fate of floret primordia during the short period when a large proportion of the developed floret primordia die; the remaining proportion (~40%) develop normally until they achieve the fertile floret stage (Kirby, 1988; Slafer *et al.*, 2009). For instance, the thermal time for the stem-elongation

phase is shortened by longer photoperiods and the proportion of surviving floret primordia is reduced in parallel with reductions in spike DM at anthesis (González *et al.*, 2003, 2005; Serrago *et al.*, 2008; Bancal, 2008). This corroborates evidence that the introgression of dwarfing genes improved partitioning to the juvenile spikes, reduced the rate of degeneration of floret primordia, and increased the number of fertile florets that could produce grains (Siddique *et al.*, 1989; Miralles *et al.*, 1998).

This evidence indicates that it will be important to identify the genetic basis by which the stem-elongation phase (or spike development within it) may be further extended. Ongoing research has demonstrated a clear link between photoperiod sensitivity, the duration of spike development, and spike fertility (Slafer *et al.*, 2005; Miralles and Slafer, 2007 and references quoted therein), but analysis of the scale of variability available has been scarce (e.g. Whitechurch *et al.*, 2007). Furthermore, the few attempts to elucidate the genetic bases of that variability have not yet been successful (e.g. González *et al.*, 2005). Both the identification of variation and knowledge of its genetic basis are critically required before breeding can be facilitated. It would seem important that alternatives to photoperiod sensitivity genes and evaluation of genotypic differences in earliness *per se* during the stem-elongation phase (Slafer, 1996) should be explored. The 'optimal phenological pattern' might be achieved by manipulating not only photoperiod sensitivity genes but also earliness *per se* genes. In recent quantitative trait loci (QTL) meta-studies (Hanocq *et al.*, 2007; Griffiths *et al.*, 2009) a number of robust earliness *per se* effects detected in multiple environments and genetic backgrounds were identified, largely in Western European winter wheat varieties. A number of these QTL have now been introgressed into uniform genetic backgrounds to develop near isogenic lines (NILs). These precise genetic stocks are essential for the transition from quantitative to qualitative genetics. This may allow the specific phenological effects of allelic variation at each of these loci to be defined and the genes responsible to be cloned using a strategy similar to that employed by Yano *et al.* (2001) for rice.

Potential research approaches include characterizing the variability in developmental time between phases occurring before and after the onset of stem elongation, and the degree of dependence of this variability on the environment, and to what degree the variability identified is due to differences in sensitivity to photoperiod or in earliness *per se*. A quantitative framework of optimum phenology and grain yield in different environments with a focus on spike fertility should be developed. Additionally, for the key attributes determining improvements in grain number through optimizing the phenological pattern, the trait analysis should drive marker development where it is deemed necessary to help with traits that are difficult to phenotype. Precise phenotyping of bi-parental populations and/or multiple backcross populations should identify consistent traits, and genotyping utilizing appropriate marker platforms should be implemented for fine mapping,

to identify genetic markers that can accelerate deployment of phenology traits in breeding.

Optimizing partitioning to improve spike fertility

The degree of partitioning of above-ground DM to grain yield, i.e. HI, is genetically complex. During the Green Revolution of the 1960s and 1970s, the yield increases of the first semi-dwarf cultivars were associated with reduction in stature, reduction in lodging, and hence a greater responsiveness to high soil fertility and irrigation. In the absence of lodging, yield was also higher due to altered competition between plant organs resulting in greater spike growth, more grains per spike (and grains per unit area), and higher HI (Gale and Youseffian, 1985). Since the Green Revolution, yield potential has continued to increase mainly due to improvements in HI (Reynolds *et al.*, 1999; Abeledo *et al.*, 2002). Despite a hypothetical limit to HI of ~ 0.62 in wheat (Austin, 1980), there has been no systematic progress since the early 1990s from values of ~ 0.50 – 0.55 . Austin (1980) predicted a maximum theoretical HI of 0.62 in winter wheat based on an extrapolation from the mean value (0.49) observed for the four most modern winter wheat cultivars characterized by Austin *et al.* (1980) in the UK. This assumed no change in above-ground DM, leaf lamina (physiological); and chaff (structural) DM cannot be decreased, stem and leaf sheath DM can be reduced by 50%, and chaff DM can be increased pro rata to accommodate extra grain. A more recent investigation of breeding progress in winter wheat in the UK demonstrated that biomass increased by 17% amongst seven semi-dwarf cultivars released from 1980 to 1995 (Shearman, 2001; Shearman *et al.*, 2005) over the 15-year period. Moreover, the ratio of chaff to grain decreased by 38 mg chaff g grain⁻¹ over the 15-year period. Extrapolating from the mean value of the four most modern cultivars characterized by Austin *et al.* (1980) and making the same assumptions as Austin (1980) except that: (i) above-ground biomass may be increased by 10% and (ii) the ratio of chaff to grain may be decreased from the value assumed by Austin (1980) of 202 mg chaff g grain⁻¹ to that of the most recent cultivar characterized by Sherman *et al.* (2005) of 195 mg chaff g grain⁻¹, the theoretical maximum HI increases to 0.63. Assuming that the ratio of chaff to grain may be decreased by a further 10% to 175 mg chaff g grain⁻¹, and holding all the other assumptions the same, HI could theoretically be increased to 0.64 (Table 1). Strategies for optimizing assimilate partitioning to raise HI towards this theoretical maximum value of ~ 0.64 are now considered.

Increased partitioning to grains could theoretically be increased by reducing competition from alternative sinks, especially during stem elongation when grain number is determined (Fischer, 1985; Kirby, 1988). These competing sinks include roots, leaves, stems (structural and soluble carbohydrate), and infertile tillers. The genetic range for partitioning to the respective plant organs at anthesis reported in the literature was recently reviewed by Reynolds *et al.* (2009): in summary, the range for spikes was

Table 1. Comparison of above-ground DM (AGDM) and DM partitioning at harvest

Crop component	Austin (1980) (four most modern) ^a		Austin (1980) theoretical max. HI ^b		HI theoretical max. calc. 1 ^c		HI theoretical max. calc. 2 ^d	
	g m ⁻²	%	g m ⁻²	%	g m ⁻²	%	g m ⁻²	%
Grain	707	49	895	62	992	63	1007	64
Chaff	143	10	181	13	193	12	177	11
Leaf lamina	139	10	139	10	153	10	153	10
Stem + sheath	453	31	226	15	249	15	249	15
AGDM	1442	–	1441	–	1586	–	1586	–

^a Mean of four most modern winter wheat cultivars reported by Austin *et al.* (1980).

^b Winter wheat crop corresponding to a theoretical maximum HI of 0.62 reported by Austin (1980).

^c Winter wheat crop calculated on the basis of Austin (1980) except AGDM increased by 10% and chaff to grain ratio decreased from 202 to 195 mg chaff g grain⁻¹.

^d Winter wheat crop calculated on the basis of Austin (1980) except AGDM increased by 10% and chaff to grain ratio decreased from 202 to 175 mg chaff g grain⁻¹.

0.12–0.29, for leaf lamina 0.19–0.31, and for stems and leaf sheaths 0.48–0.63 as a proportion of above-ground biomass. The DM lost in infertile tillers was 0.02–0.15 as a proportion of above-ground biomass (Berry *et al.*, 2003a) and the DM in roots was 0.06–0.17 as a proportion of total biomass (Table 2). These data suggest the possibility for increasing partitioning to spikes at the expense of other plant organs. Some caution is required when suggesting decreasing root partitioning as a strategy to increase spike partitioning index (SPI: spike DM/above-ground DM) at anthesis, since future genetic gains in yield seem likely to depend on raising biomass which, in turn, may require increased access to water and nutrients. Reducing partitioning to the leaf lamina may also have negative effects in the context of improving photosynthetic capacity. However, decreasing leaf partitioning may be possible if combined with agronomic compensation by increasing plant density. On the other hand, reduced partitioning to the stem and infertile shoots may not have negative effects, although decreasing stem partitioning should take account of any effects of compacting the leaves of the canopy, decreasing the vertical light distribution and RUE. Before discussing strategies to optimize stem partitioning, strategies to optimize the root system for more efficient water and nutrient capture without increasing partitioning of assimilate to roots will be briefly considered.

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, possibly because wheat breeders do not presently select for root characters. 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 (RLD: root length per unit volume

Table 2. Genetic ranges for DM partitioning coefficients of wheat at anthesis reported in the literature. Reported ranges are from field investigations, except Ehdaie *et al.* 2006 (glasshouse), after Reynolds *et al.* (2009).

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

SW, spring wheat; WSC, water-soluble carbohydrate in stem and leaf sheath; WW, winter wheat.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

of soil) is often below a critical threshold for potential water and nitrate capture of $\sim 1 \text{ cm cm}^{-3}$ (Barracough *et al.*, 1989; Gregory and Brown, 1989) at lower depths in the rooting profile (Ford *et al.*, 2006; Reynolds *et al.*, 2007; Lynch, 2007). In maize genomic regions controlling RLD at depth can also determine yield, particularly when water is in short supply (e.g. Tuberosa *et al.*, 2002). In wheat, the use of synthetic wheat derivatives, incorporating genes from the diploid wild species *Triticum tauschii* (D genome) with roots distributed relatively deeper (Reynolds *et al.*, 2007) may help in the development of cultivars with such optimized rooting systems. In addition, the rye–wheat translocations of group 1 translocations have been observed to have increased root biomass at depth (Ehdaie *et al.*, 2003). This is not to say that bigger roots *per se* will produce more yield since it is the spatial distribution of the roots in the soil (and not root mass) that defines the capacity of a root system to take up water (e.g. Manschadi *et al.*, 2006). Higher RLD can be beneficial when evaporative demand increases and soil water reserves decrease. Ultimately, however, too high a RLD will result in an allocation of photosynthates without any significant increase in water uptake. In any significant plant improvement programme, an assessment of RLD distribution with depth will be essential as it is the primary determinant of water and nutrient uptake at depth, and a variable that will potentially impact significantly on yield.

Although gains in SPI at anthesis may not be possible through reducing root or leaf lamina partitioning, and only small gains seem likely through reducing partitioning to infertile tillers, reducing allocation of assimilate to the structural stem, which presently accounts for ~ 40 – 45% of above-ground biomass at anthesis, may offer much greater scope. In this respect, reducing peduncle length may offer

one strategy for future progress. This could favour spike partitioning without altering the height of the flag leaf and the other yield-forming leaves of the canopy, the height of which appears to be close to optimum in modern canopies of plant height in the range 80–100 cm, e.g. in Connecticut (Gent and Kiyomoto, 1997), California (Ehdaie and Waines, 1994), Argentina (Miralles and Slafer, 1995b), and the UK (Flintham *et al.*, 1997). Turning to consider the soluble stem carbohydrate (SSC) DM, evidence suggests that reducing partitioning to SSC reserves may be less useful in raising SPI than reducing partitioning to structural stem DM. For example, larger responses to shading during the stem-elongation period were observed for the SSC DM than for either the spike or the structural stem DM (Beed *et al.*, 2007). This indicates that the structural stem and the spike may be prioritized sinks for assimilate. Also significant amounts of SSC are accumulated outside the rapid spike growth phase, i.e. either before early booting in the lower internodes or after anthesis in the peduncle. Wide genetic variation in SSC percentage of the stem and leaf sheath DM shortly after anthesis is reported in the range 0.05–0.43 (Foulkes *et al.*, 2002; Ehdaie *et al.*, 2006; Ruuska *et al.*, 2006; Reynolds *et al.*, 2007), indicating that breeding should be possible for this trait in agro-ecological regions where stem reserves are important for post-anthesis source. Optimizing the balance between structural stem and SSC DM should 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. Further advances will also require an improved understanding of structural biomass required in the lower internodes for lodging resistance—and must be coupled with an increase in the material strength of the stem wall to resist lodging (see

later)—and of the genetics of stem partitioning and underlying traits, and of the leaf lamina and sheath DM necessary for photosynthetic function.

Strategies to boost spike growth by reducing assimilate partitioning to alternative sinks are complementary to those described above for phenological partitioning. Optimizing phenology will mainly extend the duration of spike growth in the pre-anthesis phase, whereas optimizing partitioning amongst the plant organs to favour the spike will mainly increase the rate of spike growth. Therefore, there are synergies between these two approaches. Alongside optimizing assimilate partitioning between plant components, other recent work suggests that trade-offs between tiller number associated with the *tin1A* gene (Spielmeyer and Richards, 2004) and spike size and architecture may be important targets in designing new ideotypes with improved HI. Significant genetic variation has been established for spike size (Gaju *et al.*, 2009) and molecular markers are in development (Ribas-Vargas *et al.*, 2008).

An important further consideration is to quantify the trade-off between SPI and spike fertility index (SFI: grains per gram spike DM, at anthesis). There is generally a negative relationship between these two determinants of grain number per unit area (Gaju *et al.*, 2009; Foulkes *et al.*, 2009b) and it will be crucial to identify opportunities to break this negative relationship. One possible avenue may be to allocate a higher proportion of spike DM to reproductive (developing florets) rather than structural (rachis, glumes, and paleas) organs within the spikes, as shown by Slafer and Andrade (1993). Overall new ideotypes in which source and sink are more or less simultaneously increased and exploiting traits that affect grain number without affecting grain size, and vice versa, will be key to improving HI. From a physiological perspective, competition between stem and the spike is seen as the cause of shortage of assimilate for developing florets, with floret death imposing a ceiling on grain number. From an evolutionary perspective, the combination of programmed floret death by starvation and simultaneous storage of stem carbohydrate reserves suggests that plants adjust the number of seeds to allow for a narrow range of seed size favouring maternal fitness under most conditions (Sadras and Denison, 2009). This analysis suggests a route for increasing yields under favourable conditions, in that upper limits on seed size may be a side-effect of maternal mechanisms to suppress genomic conflict (parent-offspring), and it may be possible to relax those limits for genetically uniform crops (see below).

Finally, it will be important to consider N partitioning within strategies to optimize assimilate partitioning, as increasing biomass implies greater crop N uptake and/or NUE (grain yield/N available from fertilizer and/or soil). Optimizing canopy N dynamics could provide an additional route to increase canopy photosynthesis and biomass by prolonging green area in the post-anthesis period, to complete the approaches outlined in Theme 1 of the WYC (Parry *et al.*, 2010). Nitrogen dynamics are an important factor in the maintenance of green leaf area in sorghum,

with the onset and rate of leaf senescence amongst three hybrid lines in Australia explained by a supply–demand framework for N dynamics, in which individual grain N demand was sink determined and was initially met through N translocation from the stem and rachis, and then if these N pools were insufficient, from leaf N translocation (van Oosterom *et al.*, 2010a,b). Genetic variation in the stay-green trait has been reported in bread wheat (Silva *et al.*, 2000; Verma *et al.*, 2004; Foulkes *et al.*, 2007), and the underlying mechanisms are presently under investigation at laboratories of the WYC (see below).

The research approaches should include characterizing genetic variability in partitioning indices amongst plant organs at key stages including anthesis and SFI underlying spike fertility in multi-location trials, and responses to source–sink manipulation treatments imposed around anthesis to investigate prioritized sinks and to benchmark the source–sink balance in the post-anthesis period. Improved understanding of how partitioning of assimilates at key developmental stages may enhance RUE in the post-anthesis period as a result of improved grain sink will be crucial. These approaches should be integrated with those to optimize phenological partitioning with the use of common germplasm and hub sites where appropriate. The trait dissection should drive marker development where it is deemed necessary to accelerate the deployment of key partitioning traits in breeding. In addition, the potential of alternative Rht resources (e.g. Rht8) using Rht NILs to increase spike partitioning and HI in different environments should be investigated. In all experiments, plant N should be measured whenever DM is measured, and research activities should be integrated with the genetically modified (GM) and non-GM approaches to improving NUE that are ongoing around the world at the moment, and with which WYC members are closely associated [UK Department for Environment, Food and Rural Affairs (DEFRA)- and Biotechnology and Biological Sciences Research Council (BBSRC)-funded research at University of Nottingham and ADAS, UK; and INRA-funded research at INRA Clermont Ferrand, France]. These strategies to optimize canopy N dynamics and enhance the stay-green trait should be coordinated with the approaches for increasing canopy photosynthesis and biomass proposed in Theme 1 of the WYC (Parry *et al.*, 2010).

Improving spike fertility through modifying its sensitivity to environmental cues

Work demonstrating excess photosynthetic capacity during grain filling in modern wheat (Reynolds *et al.*, 2005) suggests that wheat produces fewer fertile florets and/or aborts more pollinated fertile florets than could potentially be exploited. This may be a result of an overly conservative response to environmental cues due to genetic bottlenecks associated with evolutionary pressures and the historic cultivation of wheat in stressful environments. In general, all grain crops produce a larger number of primordia than the number of grains they will possess afterwards—even in

non-stressful conditions—and in most cases grain filling is only slightly or not source limited (as discussed above). This may be why variation in grain weight tends to be much smaller than variation in grain number [Peltonen-Sainio *et al.*, 2007; and see also Sadras (2007) for a more extensive discussion on this subject].

Signalling in plants is well established and regulatory mechanisms appear to be highly sophisticated involving long-distance electrical signals and intercellular transport of macromolecules that help to optimize energy use and regulate plant development and defence pathways (Brenner *et al.*, 2006), and are thus obvious targets for genetic modification. In wheat, photoperiod has been shown to influence the number of fertile florets (Miralles *et al.*, 2000) in relation to spike growth (González *et al.*, 2005) probably by regulating sugar supply leading to programmed cell death (Ghiglione *et al.*, 2008). When temperature is high around anthesis, yield losses can be very significant (Semenov and Shewry, 2010). Here, stress ethylene appears to be involved in signalling leading to grain abortion (Hays *et al.*, 2007). Ethylene may also be involved in the drought stress response of growth, development, and functioning of plants under ozone stress (Wilkinson and Davies, 2009) and abscisic acid (ABA)/ethylene ratios can be important in determining spikelet fertility (maize—Wang *et al.*, 2002; rice—Yang *et al.*, 2006) and the rate of grain filling in wheat (Yang *et al.*, 2006). The photo-environment and the nutrient status of plants, both of which significantly impact plant growth, development, and grain yield can do so through modification of hormone signal transduction chains (e.g. Pierik *et al.*, 2004).

Several studies have characterized post-anthesis changes in hormone concentration in wheat grains [ABA, 1-aminocyclopropane-1-carboxylic acid (ACC)—Yang *et al.*, 2006; ABA, gibberellin (GA), indole-3-acetic acid (IAA)—Gutam *et al.*, 2008] but there is little information on the physiological roles of these changes in hormone content of developing wheat grains in response to environmental factors. Post-anthesis application of ABA and/or ethylene biosynthesis inhibitors directly to developing grains increased the ratio of ABA to ethylene and increased the grain-filling rate (Yang *et al.*, 2006). This observation, and that excessive ethylene production results in wheat grain abortion under high temperature stress (Hays *et al.*, 2007), suggests that grain ABA accumulation in wheat is a desirable trait (as in rice). Further investigation is important here, however, as there is a clear indication that accumulation of ABA in developing grains of maize can result in grain abortion (Wang *et al.*, 2002).

Pinpointing the underlying genetic basis of floret survival and grain set/abortion in wheat will permit the development of genotypes with a less conservative strategy for determination of grain number, better adapted to modern agronomy. The *7Ag.7DL* translocation (Reynolds *et al.*, 2001; Miralles *et al.*, 2007) in wheat is associated with reduced floral abortion and improved utilization of photosynthetic capacity in high-yield environments, and is for a number of reasons a suitable model for studying the cues that

determine final grain number: effects on spike fertility are relatively large and consistent across genetic backgrounds; the types of environment in which increased spike fertility is expressed is well documented and trait expression is focused on a specific tissue—immature spike—at a well-defined growth stage (Reynolds *et al.*, 2005). Furthermore, at least one candidate gene for spike fertility already exists in rice (*Gn1a*) coding for cytokinin oxidase, which through its regulation of cytokinin levels influences the number of reproductive organs in the panicle (Ashikari *et al.*, 2005).

Research approaches should combine developmental, physiological, and histological studies with genetic analysis to strengthen understanding of the genetic controls of spikelet fertility. Particular emphasis should be put on defining the nature and impact of hormonal and sugar signalling. Meristem/spikelet hormone concentration (ABA, ACC, IAA, cytokinins) needs to be measured at key stages of plant development (floret initiation, terminal spikelet initiation, anther lobe formation, meiosis, floret degeneration—determined by dissection of the elongating stem) and sugars analysed by HPLC in all plant parts. To characterize hydraulic signalling, mid-day leaf water potential (and osmotic potential to calculate leaf turgor) should be measured, and to characterize chemical signalling, plants should be harvested to profile a range of leaf hormones in the leaf-elongation zone and in the developing meristem. During the period of maximum grain-filling rate, these same hormones can be measured in the grains. Gene networks involved in the regulation of spikelet fertility could be inferred from transcriptomic data in parallel genetic, developmental, and physiological studies.

Strategies to overcome limitations to potential grain weight and size

A complementary approach to optimize grain yield is to increase grain weight. In most conditions assimilate availability (combining actual photosynthesis and remobilization of soluble carbohydrate accumulated earlier) does not limit grain growth, and the frequently reported negative relationship between grain number and average grain weight does not necessarily reflect competition among grains for limited assimilates (Miralles and Slafer, 1995a; Acreche and Slafer, 2006). In other words, the photosynthetic capacity of vegetative organs and the storage capacity of the grains cannot fully account for genetic and environmental variations in grain weight as clearly demonstrated by effects of artificial changes of plant source–sink ratio (Simmons *et al.*, 1982; Slafer and Savin, 1994). Therefore, increasing the potential size of the grains may be critical in raising actual average grain weight.

The final grain size and weight of several species, including wheat (Calderini and Reynolds, 2000; Calderini *et al.*, 1999b), barley (Scott *et al.*, 1983), and sorghum (Yang *et al.*, 2009), were found to be positively related ($r > 0.95$) to the size and weight of the maternally derived ovary from which the pericarp develops. In wheat, rapid expansion of floret carpels, which form the ovary, occurs

between booting and anthesis (i.e. during the 2–3 weeks preceding anthesis) and this period has been shown to be very critical in the determination of grain weight (Calderini *et al.*, 1999b,c, 2001; Ugarte *et al.*, 2007). After anthesis, the development of the albumen is characterized by a short syncytial phase [from ~0 to 3 days after anthesis (DAA)] followed by the spatially regulated formation of cell walls associated with active cell divisions (from ~4 to 14 DAA) leading to the complete cellularization of the endosperm. The total number of cells in the endosperm at the end of the cellularization phase is closely associated with final grain weight and has been hypothesized as the main factor controlling the rate of starch accumulation during the linear grain-filling phase (Brocklehurst, 1977). The grain acquires most of its final dimensions during the cellularization phase. The expansion of the grain during this phase is allowed by the expansion of the pericarp cells sustained by a rapid accumulation of water in the endosperm which itself is by the continuous import of osmoticum (Rogers and Quatrano, 1983). The grain achieves its maximum water content at the end of the cellularization phase and several studies have shown a close correlation between grain water content at that time and the final grain weight (e.g. Schnyder and Baum, 1992; Saini and Westgate, 2000; Slafer *et al.*, 2009).

These observations have led to the hypothesis that the expansion of maternally derived tissues delimits a volume available for the growth of the endosperm and for the subsequent accumulation of starch in wheat and other crops (Calderini *et al.*, 1999a; Cantagallo *et al.*, 2004; Haughn and Chaudhury, 2005; Berger *et al.*, 2006; Yang *et al.*, 2009). The association ($0.40 < r < 0.75$) between final grain size and the volume of the floret cavity (Millet, 1986) also suggests that the early development of the grain may be influenced by mechanical constraints. This hypothesis may provide an explanation for the strong maternal influence on final grain weight reported for several species (Jones *et al.*, 1996; Millet and Pinthus, 1980). The control of grain size by the growth of inner integument during ovary and early phases of grain development has recently been demonstrated for the model plant species *Arabidopsis thaliana* (Adamski *et al.*, 2009), supporting the hypothesis that potential weight of grains may be controlled by outer grain tissues.

The importance of the pericarp on early grain development has long been recognized (Rijven and Banbury, 1960), but the physiological processes through which the pericarp controls the final size of the grain are only starting to be understood (e.g. Léon-Kloosterziel *et al.*, 1994; Garcia *et al.*, 2005; Schruff *et al.*, 2006; Song *et al.*, 2007). Recent results suggest that the expansion of the pericarp may be controlled by the rheological properties of the cell wall through the action of expansins (Lizana *et al.*, 2010), proteins that allow the loosening of cell walls (McQueen-Mason *et al.*, 1992). Hormones also play a major role in the coordination of grain tissue expansion and in the integration of both endogenous (e.g. mechanical, trophic) and environmental (e.g. temperature, soil water deficit) signals (Schruff *et al.*, 2006; and see above). For example,

in rice it has been shown that the final grain weight and the endosperm cell number at different positions within the panicle for genotypes of contrasting potential grain size are related, with a unique relation to the endosperm concentration in cytokinins during the period of active cell division (Yang *et al.*, 2002), while the ABA to ethylene ratio was positively associated with endosperm cell division and grain-filling rates (Yang *et al.*, 2006). The effect of hormones on grain development is intimately related to sugar metabolism and signalling (Cheng *et al.*, 1996; Cheng and Chourey, 1999). Recent results in rice and in the model species *A. thaliana* have clearly established the central role of several transcription factors and E3 ubiquitin ligases in sugar and hormone signalling networks controlling the early stages of grain development (e.g. Schruff *et al.*, 2006; Song *et al.*, 2007).

The ability of the crop to achieve its potential grain weight and yield may be limited even by mild environmental constraints, particularly temperature, immediately before (Calderini *et al.*, 1999a; Ugarte *et al.*, 2007) or after (Calderini *et al.*, 1999c; Nicolas *et al.*, 1984; Tashiro and Wardlaw, 1990a,b) anthesis, despite favourable environmental conditions during most of the grain-filling period. The sensitivity of the period before anthesis has been recently reinforced since even moderately high temperature (i.e. maximum daily temperature $<28^{\circ}\text{C}$ degree) during the 15 days prior to anthesis can cause substantial loss in grain yield due to reduction in final grain size (Ferrise *et al.*, 2010). This highlights the need for improving our understanding of grain weight potential determination. The physiological mechanisms involved in the response of grain size and weight to temperature and especially the role of maternal tissues/pericarp in this response could be the key to advancing our knowledge of the physiology of grain weight potential determination.

Understanding the physiological and genetic bases of potential grain size may allow breeders to develop strategies to increase yield potential *per se* and to break the inverse relationship between grain number and grain weight, especially by considering the period immediately pre-flowering which accounts for both grain number and grain size (Ugarte *et al.*, 2007). It is encouraging in this regard that, for a range of different wheat crosses, some QTL controlling grain yield have been found to work primarily through individual grain weight without pleiotropic effects on grain number (Snape *et al.*, 2007; Gegas *et al.*, 2010; McIntyre *et al.*, 2010). Similarly, it has been shown (Gegas *et al.*, 2010) that grain length and grain volume are controlled independently. Possible physiological objectives are to understand and modify the signalling pathways responsible for cell division and expansion modulations in response to environmental (e.g. temperature) and endogenous (e.g. sugar availability, hormonal balances) signals during the period of ovary and grain expansion.

It is expected that the increase in sink size (through grain number and grain weight) will improve NUE ($\text{g biomass g N uptake}^{-1}$) as in the past (Austin *et al.*, 1980; Ortiz-Monasterio *et al.*, 1997; Calderini *et al.*, 1999a), but negative effects on

grain protein concentration are also likely. The knowledge of N dynamics and partitioning during the grain-filling period will be the key to avoiding negative effects of sink size on quality traits of grains (Bertheloot *et al.*, 2008). Maintaining active root N uptake during the grain-filling period should also be an important objective in maintaining grain protein concentration (Bogard *et al.*, 2010).

Research approaches should combine developmental, physiological, histological, and molecular studies with genetic analysis to strengthen understanding of the genetic controls of potential grain size. Particular emphasis should be placed on the role of the biochemical and structural properties of the ovary and pericarp cell walls and on hormonal and sugar signalling during the 2 weeks before and after ovary fecundation. Detailed analysis should identify traits associated with grain weight and size stability and adaptation to the range of conditions encompassed in generally favourable environments. Hormone analysis should be localized to specific tissues and compartments, as described above. Gene networks involved in the regulation of ovary and pericarp growth could be inferred from transcriptomic data linked to parallel genetic, developmental, and physiological studies. Particular emphasis should be placed on the grain transcription factors and the ubiquitin 26S proteasome proteolytic pathway involved in cell wall formation and the structure and control of its bio-rheological properties to establish patterns of co-regulation and gene networks. In parallel, N economy during grain filling should be monitored to identify key traits to avoid the trade-off between sink size and N concentration of grains.

Maintaining and improving lodging resistance

Lodging, the permanent displacement of cereal stems from the vertical, should result from either plastic failure of the stem base (stem lodging) or failure of the anchorage system (root lodging). Lodging is a persistent phenomenon in wheat that reduces harvestable yield by up to 80% as well as reducing grain quality. Therefore, any comprehensive strategy to improve wheat yield potential must include 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.*, 2003b,c, 2007). 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 (rotational moment) of a single shoot exceeds the elastic modulus 'approximating to stem strength' of the stem base. Root lodging is predicted when the rotational moment of all shoots belonging to a single plant exceeds the anchorage strength. The rotational moment of a shoot is calculated from its height at centre of gravity which defines the point of resultant force, the rate at which the shoot sways (natural frequency), the area of the spike, and the wind speed. In turn, these plant characteristics can be calculated from the height to the spike 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 strength of the surrounding soil.

The lodging model described above has been used with preliminary datasets describing the DM costs of improving lodging traits 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). The characteristics required to give a crop yielding 8 t ha^{-1} with 500 shoots m^{-2} and 200 plants m^{-2} an average lodging frequency of once every 25 years in a UK environment 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, a stem diameter of 4.94 mm, and a material strength of 30 MPa. For a typical plant population of 200 plants m^{-2} the average plant spacing will be 71 mm. Depending on the row spacing this will probably be larger between rows than within rows. Root plate spread is measured as the average of the maximum and minimum spread of the root plate. Therefore we expect that plants can achieve an average root plate spread of 57 mm within a typical plant population. Observations of a range of cultivars grown in the UK showed that the root plate of the best variety was 7 mm less than the ideotype target, and the widest stem was 0.5 mm below the ideotype target. Targets of other stem characteristics were achieved but not all in one cultivar, and the height target was achievable with the use of plant growth regulators.

It is estimated that this lodging-proof ideotype will require 7.9 t ha^{-1} of stem biomass and 1.0 t ha^{-1} of root biomass within the top 10 cm of soil, which will give an above-ground HI of only 0.42. Note that the maximum HI of 0.62 derived by Austin (1980) did not account for lodging effects. Preliminary work has indicated that DM density is positively related to the material strength of the stem wall which means there is a significant DM cost associated with increasing this strength parameter. The contribution made by the node and leaf sheath to stem strength is unknown. Investigations are therefore required to verify the DM cost of increasing stem strength in a range of environments. The development of the root and stem characters associated with lodging continues until anthesis and may therefore compete for resources with the development of grain number and the production of soluble stem reserves.

Further work should investigate why there appears to be a minimum height for high yield, whether this barrier can be overcome, and whether the minimum height varies between environments. In order to increase lodging resistance, plant breeders must increase the spread of the root plate, stem thickness, and the material strength of the stem wall, whilst minimizing the width of the stem wall. The exact values of the traits will vary between environments (due to different wind and rain conditions) and will depend on further investigations to assess and validate the minimum crop height, the DM costs associated with the lodging traits, and the possible trade-offs with yield

formation. Future research should aim to identify sets of traits for lodging proofness that are applicable to different environments and validate them using field trials.

It is likely that some of the lodging traits, e.g. the spread of the root plate, will not be found within elite germplasm and therefore wide crosses with novel germplasm might be required to achieve the target traits. A recent analysis of two bi-parental mapping populations by Berry and a study of a wheat × spelt cross by Keller *et al.* (1999) have identified more than one QTL for each of the traits and indicated that they are controlled by several genes. Further work should therefore be carried out to better understand the genetic control of the traits and to investigate whether reliable genetic markers can be identified that work across a range of genotypes and environments and have a sufficiently large effect to be useful. Phenotypic screens and assessment methods (e.g. Berry *et al.* 2003d) should also be investigated to assess whether they can offer an alternative method for selecting germplasm in case genetic markers with a large effect prove difficult to identify.

Estimating potential trade-offs between phenology, partitioning, and lodging resistance to optimize yield expression

Photosynthesis, phenology, and partitioning of wheat interact to determine final crop performance. Investigations into genetic adaptation and optimization of each process, as described above, will benefit from a capacity to integrate them and anticipate their likely interactions in determining crop performance. Conventional crop models commonly seek to simulate environmental variation in performance of single cultivars, using fixed parameters for traits deemed to be unaffected by environment; examples are responsiveness to photoperiod or vernalization, light extinction by the green canopy, or conversion of intercepted radiation to DM. Since these fixed traits are (intentionally or inadvertently) deemed to be heritable, it has been suggested that an inverse approach might be taken (Riffkin and Sylvester-Bradley, 2008; Sylvester-Bradley and Riffkin, 2008) whereby conventional simulation modelling routines for crop growth would be used to vary key traits through the range observed in bread wheat, especially phenology and partitioning, to reveal the inter-trait trade-offs in terms of a final optimized yield. There appears to be no existing model that takes this approach, but an attempt has been initiated by Sylvester-Bradley and Riffkin (2008); this would depend on adopting particular traits, e.g. those concerned with phenology and morphology having high heritability; eventually its outputs should be optimized ideotypes for specific environments defined in terms of quantitative traits deemed to be 'heritable'.

An optimization capacity should allow field experimenters to interrelate their hypotheses and integrate their findings, at least on a semi-quantitative basis. A possible hypothetical approach to trait optimization is set out below, based on the relevant literature; this is likely to complement the more

sophisticated modelling approaches to genetic improvement (e.g. Hammer *et al.*, 2005, 2006; Chapman, 2008).

Growth during certain critical stages in wheat's life cycle—e.g. the onset of stem extension and flowering—is particularly susceptible to damage by frost. Hence, an initial step in specifying optimum ideotypes for an environment according to climate data is to deduce the basic limits on phenology that dictate feasible lifespans for an ideotype, and feasible duration of successive phases of growth, which in turn will set boundaries for DM production and partitioning that are feasible in each environment.

Conventional modelling approaches can provide relatively robust estimates of DM growth from meteorological and soil data (Jamieson *et al.*, 1998; Porter *et al.*, 1993; McCown *et al.*, 1996; Ferrise *et al.*, 2010). For each wheat-growing environment, photosynthetic conversion coefficients for available radiation and water dictate expectations of DM growth in each phenological phase. For improvements in photosynthesis to result in additional crop yield, extra assimilates must be partitioned to developing spikes, and directly or indirectly (i.e. via redistributable reserves largely held in stems) to grains.

A maximum HI will be determined by the minimum requirements for support (unharvested) materials. There will be an interdependence between minimum support DM and grain yield since, as described above, support DM is required for: (i) roots to resist lodging (due to anchorage failure) and capture soil resources, (ii) stems to maintain stature and resist lodging (due to internode failure), (iii) leaves to sustain photosynthesis, and (iv) inflorescences (chaff) to support the grain. The potential for reducing quantities of support DM can be estimated either from minima determined empirically (e.g. through observations of the SFI) or from physical models (as in the case of lodging; Berry *et al.*, 2003b, 2004, 2007), or according to economic criteria, as in the case of leaves (Sylvester-Bradley *et al.*, 1997).

Changes in leaf area are primarily determined by fertilizer N use (Lemaire, 2007), so the optimum leaf canopy (Sylvester-Bradley *et al.*, 1997), hence leaf DM requirement, can be derived according to expected grain yield and the N:grain price ratio through empirical observations of specific leaf weight (g DM m⁻² leaf; Stapper and Fischer, 1990). Direct measurements of the DM necessary to form an economically optimum leaf canopy optimum 'leaf' DM appear small (2–3 t ha⁻¹; Sylvester-Bradley *et al.*, 2008) compared with 'stem' DM (6–7 t ha⁻¹). However, leaves are usually measured as lamina only, whilst leaf sheaths are included with stems. Recent data (Pask, 2009) show sheath biomass to be similar to lamina biomass, hence total leaf DM must be considered similar in magnitude to true stem DM. The functional value of sheaths is unclear so it will be important to investigate whether leaf DM could be reduced by minimizing sheath DM (through shorter or thinner sheaths) so increasing DM available for more vital organs, and to incorporate the repercussions for yield here.

At present it seems best to take chaff DM requirements directly from empirical data for estimation of SFI

(according to chaff DM rather than spike DM at anthesis; mg chaff grain⁻¹) without acknowledging any genetic or environmental effects. Further work on floret fertility and on DM partitioning to (and within) the spike is needed to quantify genetic targets for SFI and to enable more sophisticated estimates of the DM trade-offs between root, stem and leaf DM, and spike fertility.

The model of Berry *et al.* (2003b, 2004) estimates risks of stem and root lodging in terms of wind speeds required to cause failure of the stem base and the anchorage system, as described above. Optimizations of stem DM requirements could be based on a meta-analysis of the lodging model, because relationships with grain yield appear to be relatively simple. Height clearly proves crucial in dictating stem DM requirements, so it will probably prove best to recognize empirical observations of a minimum height (0.7 m) compatible with maximum observed grain yields and a range of environments (Richards, 1992; Miralles and Slafer, 1995b; Flintham *et al.*, 1997). Given that stem DM requirements are large, further work is required to examine this finding and build in explanations. Possible explanations are that height determines the capacity for storage of water-soluble carbohydrates which ultimately transfer to the grain (Beed *et al.*, 2007), or improves light distribution in the canopy (Miralles and Slafer, 1997), or that height delays disease progress by separating new leaves from inoculum on older leaves (Lovell *et al.*, 2002). Work carried out within the UK Wheat Genetic Improvement Network (WGIN) on the winter wheat Avalon×Cadenza doubled haploid population has identified six QTL influencing crop height (www.wgin.co.uk), which segregate in wheat germplasm. Their cumulative additive effects are significantly greater than individual major dwarfing genes currently used. In most cases these height QTL are coincident with grain yield QTL where, except in the case of *Rht-D1b*, height-reducing alleles also reduce yield. However, two QTL reduce height with a neutral yield effect. This result was confirmed by a wider meta-analysis of elite Western European germplasm (Griffiths *et al.*, 2009). This work exemplifies how direct selection of a trait, in this case height, is inadequate because of disruptive (balancing) selection and that specific selection of allelic combinations is essential for directed manipulation. Work will also be required to incorporate optimization of DM investment in roots into the calculations.

It has been suggested that a more optimal balance between source and sink could improve overall RUE (Richards, 1996; Kruk *et al.*, 1997; Reynolds *et al.*, 2009). This would suggest that there may be periods during the growing season when RUE is reduced indirectly by sink limitation, and that genetic modification of the source–sink balance could result in a better use of otherwise underutilized photosynthetic capacity. Experiments with both genetic and physiological treatments in spring wheat lend strong support to this idea (Reynolds *et al.*, 2005) and suggest that improving the balance between source and sink is a highly promising approach for raising RUE (Calderini *et al.*, 1997; Reynolds *et al.*, 2001, 2005; Shearman *et al.*, 2005). Key to achieving progress in the development of

ideotypes with improved crop performance will be obtaining data to build a quantitative understanding of how partitioning of assimilates at key developmental stages may enhance RUE in the post-anthesis period as a result of improved grain sink.

The DM costs of lodging resistance depend crucially on windiness of the target environment; ultimately optimizations should aim to balance these costs against grain DM costs of lodging itself (Stapper and Fischer, 1990), possibly by integrating the increasing risk of lodging as grain-fill progresses, with the decreasing impact of lodging on grain yield.

Since support DM must first support itself, maximum HI of ideotypes will almost inevitably increase with total DM, i.e. an increase in total DM, say due to improved RUE, will cause a larger increase in grain yield (in percentage terms). It remains to be seen how significant this effect will be over a range of environments.

Conclusions

Even without improved photosynthetic conversion of intercepted radiation to DM (Parry *et al.*, 2010), there is evidence that wheat is often sink limited, i.e. that yields would benefit from greater grain numbers brought about by greater partitioning of assimilates to spikes during their development. The need for improved grain numbers will be increased further by any improvements in photosynthetic rates. The WYC has identified several complementary approaches (Box 1) that have the potential to optimize partitioning and maximize grain number per unit area whilst avoiding undesirable trade-offs, for instance with grain weight or lodging resistance. These involve increasing grain number by: (i) prolonging spike development without increasing the overall crop life cycle, (ii) prioritizing partitioning of DM to spikes rather than stems (or other organs) while not sacrificing capacity for resource capture by roots for example. Additional work areas are: (iii) defining the nature and impact of hormonal and sugar signaling controls of spikelet fertility, (iv) seeking independent controls of grain weight, possibly relating to maternal grain tissues laid down before anthesis, and (v) features of lodging resistance that minimize structural DM requirements. Maximizing lodging resistance in physiologically improved genotypes will be a particularly important objective and will require the quantification of trade-offs between lodging-associated traits and DM partitioning indices amongst plant organs at key stages for improving spike fertility.

Optimum partitioning between anchorage roots, stems, leaves, spikes, and ovaries before anthesis will differ depending on whether the potential yield is 4 or 12 t ha⁻¹ so a means for quantitative optimization between organs (vi) is included.

The approaches proposed will identify priority traits for particular environments. This will be coupled to the discovery of genetic variability for prioritized traits, and the development of diagnostic markers or new phenotyping

tools for traits that are currently difficult to phenotype (Box 2). Traits may relate to partitioning itself, or to the chemical signals determining spike fertility and potential grain weight. The availability of diagnostic haplotypes and cloned genes will facilitate the mining of new allelic variants from non-adapted hexaploid and alien germplasm for enrichment of breeding programmes for the target environments.

These objectives complement those of research in Theme 1. Indeed, the approach proposed to optimize canopy N dynamics and the stay-green trait should directly contribute to enhanced photosynthetic capacity of the canopy. The acceleration of future yield progress will depend crucially on enhancing the synergy between increases in photosynthetic capacity and grain sink capacity, and hence will require trait-based breeding programmes. Because trait-based breeding adds complexity to conventional breeding approaches, the impact of such programmes will be depend on successful application of high-throughput precision phenotyping, and/or implementation of associated marker-based selection. Strategies for screening traits must factor in how precisely the traits can be measured, and how far they are affected by environmental variation. The most complex effects relating to a high degree of environmental variation will mean that it is harder to accumulate the favourable trait combinations and will require genetic tools to accelerate introgression of traits into elite cultivars.

Increased photosynthesis and increased grain partitioning both ostensibly offer to improve water productivity and nutrient productivity, but if grain quality is maintained, crop nutrient requirements will nevertheless increase as grain size improvement would only partially compensate the N dilution effect. Hence it will be important that the research proposed here is complemented by successful research elsewhere to ensure more efficient provision of nutrients (particularly N) necessary to maintain grain quality (particularly protein content), that can work with lower grain nutrient content.

If there is to be faster progress than is currently achieved in breeding wheat for yield, it will be increasingly important to take an integrated quantitative approach in the design of breeding strategies that anticipates the climatic changes expected in the decades ahead. Hence, strategies will need to pay closer attention to mechanisms of yield determination, and they will need to include consideration of agronomic requirements.

An integrated approach to the coordination of the research strands adopted in Theme 2, as well as the interactions with the activities in Themes 1 and 3, of the WYC will be taken as described in the accompanying article (Reynolds *et al.*, 2010). In summary, maximum efficiency in the proposed activities, including the ability to integrate results across sub-projects and the delivery of standardized data sets in the experiments carried out in the laboratories of the partners, will be achieved through the use of hub sites, core germplasm sets, and a core trait set. An intensive integrated international approach is now urgently required to make progress towards delivering greater food security.

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References

- Abbate PE, Andrade DH, Lazaro L, Baraitti JH, Beradocco HG, Inza VH, Marturano F.** 1998. Grain yield in recent Argentine wheat cultivars. *Crop Science* **38**, 1203–1209.
- Abeledo LG, Calderini DF, Slafer GA.** 2002. Physiological changes associated with genetic improvement of grain yield in barley. In: Slafer GA, Molina-Cano JL, Savin R, Araus JL, eds. *Barley science: recent advances from molecular biology to agronomy of yield and quality*. New York: Food Product Press, 361–386.
- Acreche M, Briceño-Félix G, Martín Sánchez JA, Slafer GA.** 2008. Physiological bases of genetic gains in Mediterranean bread wheat yield in Spain. *European Journal of Agronomy* **28**, 162–170.
- Acreche M, Slafer GA.** 2006. Grain weight response to increases in number of grains in wheat in a Mediterranean area. *Field Crops Research* **98**, 52–59.
- Acreche M, Slafer GA.** 2009. Grain weight, radiation interception and use efficiency as affected by sink-strength in Mediterranean wheats released from 1940 to 2005. *Field Crops Research* **110**, 98–105.
- Adamski NM, Anastasiou E, Eriksson S, O'Neill CM, Lenhard M.** 2009. Local maternal control of seed size by KLUH/CYP78A5-dependent growth signaling. *Proceedings of the National Academy of Sciences USA* **106**, 20115–20120.
- Araus JL, Slafer GA, Reynolds MP, Royo C.** 2002. Plant breeding in C3 cereals: what should we look for? *Annals of Botany* **89**, 925–940.
- Ashikari M, Sakakibara H, Lin S, Yamamoto T, Takashi T, Nishimura A, Angeles ER, Qian Q, Kitano H, Matsuoka M.** 2005. Cytokinin oxidase regulates rice grain production. *Science* **309**, 741–745.
- Austin RB.** 1980. Physiological limitations to cereals yields and ways of reducing them by breeding. In: Hurd RG, Biscoe PV, Dennis C, eds. *Opportunities for increasing crop yields*. London: Association of Applied Biology/Pitman, 3–9.
- Austin RB, Bingham J, Blackwell RD, Evans LT, Ford MA, Morgan CL, Taylor M.** 1980. Genetic improvement in winter wheat yield since 1900 and associated physiological changes. *Journal of Agricultural Science, Cambridge* **94**, 675–689.
- Bancal P.** 2008. Positive contribution of stem growth to grain number per spike in wheat. *Field Crops Research* **105**, 27–39.
- Barracough PB, Kuhlmann H, Weir AH.** 1989. The effects of prolonged drought and nitrogen fertiliser on root and shoot growth and water uptake by winter wheat. *Journal of Agronomy and Crop Science* **163**, 352–360.
- Beed FD, Paveley ND, Sylvester-Bradley R.** 2007. Predictability of wheat growth and yield in light-limited conditions. *Journal of Agricultural Science, Cambridge* **145**, 63–79.

- Berger F, Grini PE, Schnitger A.** 2006. Endosperm: an integrator of seed growth and development. *Current Opinion in Plant Biology* **9**, 664–670.
- Berry PM, Spink JH, Foulkes MJ, Wade A.** 2003a. Quantifying the contributions and losses of dry matter from non-surviving shoots in four cultivars of winter wheat. *Field Crops Research* **80**, 111–121.
- Berry PM, Spink JH, Gay AP, Craigon J.** 2003c. A comparison of root and stem lodging risks among winter wheat cultivars. *Journal of Agricultural Science, Cambridge* **141**, 191–202.
- Berry PM, Spink JH, Sterling M, Pickett A.** 2003d. Methods for rapidly measuring the lodging resistance of wheat cultivars. *Journal of Agronomy and Crop Science* **189**, 390–401.
- Berry PM, Sterling M, Baker CJ, Spink JH, Sparkes DL.** 2003b. A calibrated model of wheat lodging compared with field measurements. *Agricultural and Forest Meteorology* **119**, 167–180.
- Berry PM, Sterling M, Spink JH, Baker CJ, Sylvester-Bradley R, Mooney SJ, Tams AR, Ennos AR.** 2004. Understanding and reducing lodging in cereals. *Advances in Agronomy* **84**, 217–271.
- Berry PM, Sylvester-Bradley R, Berry S.** 2007. Ideotype for lodging resistant wheat. *Euphytica* **154**, 165–179.
- Bertheloot J, Martre P, Andrieu B.** 2008. Dynamics of light and nitrogen distribution during grain filling within wheat canopy. *Plant Physiology* **148**, 1707–1720.
- Bogard M, Allard V, Brancourt-Hulmel M, Heumez E, Machet J-M, Jeuffroy M-H, Gates P, Martre P, Le Gouis J.** 2010. Deviation from the grain protein concentration–grain yield negative relationship is highly correlated to post-anthesis N uptake in winter wheat. *Journal of Experimental Botany* <http://jxb.oxfordjournals.org/content/early/2010/08/02/jxb.erq238>.
- Borras L, Slafer GA, Otegui ME.** 2004. Seed dry weight response to source-sink manipulations in wheat, maize and soybean. A quantitative reappraisal. *Field Crops Research* **86**, 131–146.
- Brancourt-Hulmel M, Doussinault G, Lecomte C, Bérard P, Le Buanec B, Trottet M.** 2003. Genetic improvement of agronomic traits of winter wheat cultivars released in France from 1946 to 1992. *Crop Science* **43**, 37–45.
- Brenner ED, Stahlberg R, Mancuso S, Vivanco J, Baluska F, Van Volkenburgh E.** 2006. Plant neurobiology: an integrated view of plant signaling. *Trends in Plant Science* **11**, 413–419.
- Brocklehurst PA.** 1977. Factors controlling grain weight in wheat. *Nature* **266**, 348–349.
- Calderini DF, Abeledo LG, Savin R, Slafer GA.** 1999b. Effect of temperature and carpel size during pre-anthesis on potential grain weight in wheat. *Journal of Agricultural Science, Cambridge* **132**, 453–459.
- Calderini DF, Abeledo LG, Savin R, Slafer GA.** 1999c. Final grain weight in wheat as affected by short periods of high temperature during pre- and post-anthesis under field conditions. *Australian Journal of Plant Physiology* **26**, 453–458.
- Calderini DF, Dreccer MF, Slafer GA.** 1997. Consequences of plant breeding on biomass growth, radiation interception and radiation use efficiency in wheat. *Field Crops Research* **52**, 271–281.
- Calderini DF, Reynolds MP.** 2000. Changes in grain weight as a consequence of de-graining treatments at pre- and post-anthesis in synthetic hexaploid lines of wheat (*Triticum durum* × *T-tauschii*). *Australian Journal of Plant Physiology* **27**, 183–191.
- Calderini DF, Reynolds MP, Slafer GA.** 1999a. Genetic gains in wheat yield and main physiological changes associated with them during the 20th century. In: Satorre EH, Slafer GA, eds. *Wheat: ecology and physiology of yield determination*. New York: Food Product Press, 351–377.
- Calderini DF, Savin R, Abeledo LG, Reynolds MP, Slafer GA.** 2001. The importance of the period immediately preceding anthesis for grain weight determination in wheat. *Euphytica* **119**, 199–204.
- Calderini DF, Slafer GA.** 1999. Has yield stability changed with genetic improvement of wheat yield? *Euphytica* **107**, 51–59.
- Canevara MG, Romani M, Corbellini M, Perenzin M, Borghi B.** 1994. Evolutionary trends in morphological, physiological, agronomical and qualitative traits of *Triticum aestivum* L. cultivars bred in Italy since 1900. *European Journal of Agronomy* **3**, 175–185.
- Cantagallo JE, Medan D, Hall AJ.** 2004. Grain number in sunflower as affected by shading during floret growth, anthesis and grain setting. *Field Crops Research* **85**, 191–202.
- Cattivelli L, Rizza F, Badeck F, Mazzucotelli E, Mastrangelo A-M, Francia E, Mare C, Tondelli A, Stanca M.** 2008. Drought tolerance improvement in crop plants: an integrated view from breeding to genomics. *Field Crops Research* **105**, 1–14.
- Chapman SC.** 2008. Use of crop models to understand genotype by environment interactions for drought in real-world and simulated plant breeding trials. *Euphytica* **161**, 195–208.
- Cheng WH, Chourey PS.** 1999. Genetic evidence that invertase-mediated release of hexoses is critical for appropriate carbon partitioning and normal seed development in maize. *Theoretical and Applied Genetics* **98**, 485–495.
- Cheng WH, Taliercio EW, Chourey PS.** 1996. The Miniature1 seed locus of maize encodes a cell wall invertase required for normal development of endosperm and maternal cells in the pedicel. *Plant Cell* **8**, 971–983.
- Donmez E, Sears RG, Shroyer JP, Paulsen GM.** 2001. Genetic gain in yield attributes of winter wheat in the Great Plains. *Crop Science* **41**, 1412–1419.
- Ehdaie B, Alloush GA, Madore MA, Waines JG.** 2006. Genotypic variation for stem reserves and mobilization in wheat I. Postanthesis changes in internode dry matter. *Crop Science* **46**, 735–746.
- Ehdaie B, Waines JG.** 1994. Growth and transpiration efficiency of near isogenic lines for height in a spring wheat. *Crop Science* **34**, 1443–1451.
- Ehdaie B, Whitkus RW, Waines JG.** 2003. Root biomass, water-use efficiency, and performance of wheat-rye translocations of chromosomes 1 and 2 in spring bread wheat ‘Pavon’. *Crop Science* **43**, 710–717.
- Evans LT, Fischer RA.** 1999. Yield potential: its definition, measurement, and significance. *Crop Science* **39**, 1544–1551.
- Ferrise R, Triossi A, Stratonovitch P, Bindi M, Martre P.** 2010. Sowing date and nitrogen fertilisation effects on dry matter and nitrogen dynamics for durum wheat: an experimental and simulation study. *Field Crops Research* **117**, 245–257.

- Fischer RA.** 1985. Number of kernels in wheat crops and the influence of solar radiation and temperature. *Journal of Agricultural Science, Cambridge* **105**, 447–461.
- Fischer RA, Edmeades GO.** 2010. Breeding and cereal yield progress. *Crop Science* **50**, S85–S98.
- Fischer RA, Stockman YM.** 1986. Increase kernel number in Norin 10-derived dwarf wheat: evaluation of the cause. *Australian Journal of Plant Physiology* **13**, 767–784.
- Flintham JE, Borner A, Worland AJ, Gale MD.** 1997. Optimizing wheat grain yield: effects of Rht (gibberellin-insensitive) dwarfing genes. *Journal of Agricultural Science, Cambridge* **128**, 11–25.
- Ford KE, Gregory PJ, Gooding MJ, Pepler S.** 2006. Genotype and fungicide effects on late-season root growth of winter wheat. *Plant and Soil* **284**, 33–44.
- Foulkes MJ, Hawkesford MJ, Barraclough PB, Holdsworth MJ, Kerr S, Kightley S, Shewry PR.** 2009a. Identifying traits to improve the nitrogen economy of wheat: recent advances and future prospects. *Field Crops Research* **114**, 329–342.
- Foulkes MJ, Reynolds M, Sylvester-Bradley R.** 2009b. Genetic improvement of grain crops: yield potential. In: Sadras VO, Calderini D, eds. *Crop physiology applications for genetic improvement and agronomy*. The Netherlands: Elsevier, 235–256.
- Foulkes MJ, Scott RK, Sylvester-Bradley R.** 2002. The ability of wheat cultivars to withstand drought in UK conditions: formation of grain yield. *Journal of Agricultural Science, Cambridge* **138**, 153–169.
- Foulkes MJ, Sylvester-Bradley R, Scott RK.** 1998. Evidence for differences between winter wheat cultivars in acquisition of soil mineral nitrogen and uptake and utilization of applied fertiliser nitrogen. *Journal of Agricultural Science, Cambridge* **130**, 29–44.
- Foulkes MJ, Sylvester-Bradley R, Weightman R, Snape J.** 2007. Identifying physiological traits associated with improved drought resistance in winter wheat. *Field Crops Research* **103**, 11–24.
- Gaju O, Reynolds MP, Sparkes DL, Foulkes MJ.** 2009. Relationships between large-spike phenotype, grain number, and yield potential in spring wheat. *Crop Science* **49**, 961–973.
- Gale MD, Youseffian S.** 1985. Dwarfing genes in wheat. In: Russell GE, ed. *Progress in plant breeding*. London: Butterworths, 1–35.
- Garcia D, FitzGerald JN, Berger F.** 2005. Maternal control of integument cell elongation and zygotic control of endosperm growth are coordinated to determine seed size in *Arabidopsis*. *Plant Cell* **17**, 52–60.
- Ghiglione HO, Gonzalez FG, Serrago R, Maldonado SB, Chilcott C, Curá JA, Miralles DJ, Zhu T, Casal JJ.** 2008. Autophagy regulated by day length determines the number of fertile florets in wheat. *Plant Journal* **55**, 1010–1024.
- Gregory PJ, Brown SC.** 1989. Root growth, water use and yield of crops in dry environments: what characters are desirable? *Aspects of Applied Biology* **22**, 234–243.
- Griffiths S, Simmonds J, Leverington M, et al.** 2009. Meta-QTL analysis of the genetic control of ear emergence in elite European winter wheat germplasm. *Theoretical and Applied Genetics* **119**, 383–395.
- Gegas VC, Nazari A, Griffiths S, Simmonds J, Fish L, Orford S, Sayers L, Doonan JH, Snape JW.** 2010. A genetic framework for grain size and shape variation in wheat. *Plant Cell* **22**, 1046–56.
- Gent MPN, Kiyomoto RK.** 1997. Physiological and agronomic consequences of Rht genes in wheat. *Journal of Crop Production* **1**, 27–46.
- González FG, Slafer GA, Miralles DJ.** 2003. Floret development and spike growth as affected by photoperiod during stem elongation in wheat. *Field Crops Research* **81**, 29–38.
- González FG, Slafer GA, Miralles DJ.** 2005. Pre-anthesis development and number of fertile florets in wheat as affected by photoperiod sensitivity genes *Ppd-D1* and *Ppd-B1*. *Euphytica* **146**, 253–269.
- Gutam S, Nath V, Srivastava GC.** 2008. Endogenous hormonal content during grain development in hexaploid and tetraploid wheat. *Bangladesh Journal of Agricultural Science, Cambridge* **33**, 493–502.
- Hammer G, Chapman S, van Oosterom E, Podlich D.** 2005. Trait physiology and crop modelling as a framework to link phenotypic complexity to underlying genetic systems. *Australian Journal of Agricultural Research* **56**, 947–960.
- Hammer G, Cooper M, Tardieu F, Welch S, Walsh B, van Eeuwijk F, Chapman S, Podlich D.** 2006. Models for navigating biological complexity in breeding improved crop plants. *Trends in Plant Science* **11**, 587–593.
- Hanocq E, Laperche A, Jaminon O, Lainé AL, Le Gouis J.** 2007. Most significant genome regions involved in the control of earliness traits in bread wheat, as revealed by QTL meta-analysis. *Theoretical and Applied Genetics* **4**, 569–584.
- Haughn G, Chaudhury A.** 2005. Genetic analysis of seed coat development in *Arabidopsis*. *Trends in Plant Science* **10**, 472–477.
- Hays DB, Do JH, Mason RE, Morgan G, Finlayson SE.** 2007. Heat stress induced ethylene production in developing wheat grains induces kernel abortion and increased maturation in a susceptible cultivar. *Plant Science* **172**, 1113–1123.
- Hirel B, Le Gouis J, Ney B, Gallais A.** 2007. The challenge of improving nitrogen use efficiency in crop plants: towards a more central role for genetic variability and quantitative genetics within integrated approaches. *Journal of Experimental Botany* **58**, 2369–2387.
- Jackson P, Robertson M, Cooper M, Hammer G.** 1996. The role of physiological understanding in plant breeding: from a breeding perspective. *Field Crops Research* **49**, 11–37.
- Jamieson PD, Semenov MA, Brooking IR, Francis GS.** 1998. Sirius: a mechanistic model of wheat response to environmental variation. *European Journal of Agronomy* **8**, 161–179.
- Jones RJ, Schreiber BM, Roessler JA.** 1996. Kernel sink capacity in maize: genotypic and maternal regulation. *Crop Science* **36**, 301–306.
- Keller M, Karutz C, Schmid JE, Stamp P, Winzler M, Keller B, Messner MM.** 1999. Quantitative trait loci for lodging resistance in a segregating wheat×spelt population. *Theoretical and Applied Genetics* **98**, 1171–1182.

- Kirby EJM.** 1988. Analysis of leaf, stem and ear growth in wheat from terminal spikelet initiation to anthesis. *Field Crops Research* **18**, 127–140.
- Kruk BC, Calderini DF, Slafer GA.** 1997. Grain weight in wheat cultivars released from 1920 to 1990 as affected by post-anthesis defoliation. *Journal of Agricultural Science, Cambridge* **128**, 273–281.
- Lemaire G.** 2007. Is crop N demand more closely related to dry matter accumulation or leaf area expansion during vegetative growth? *Field Crops Research* **100**, 91–106.
- Léon-Kloosterziel KM, Keijzer CJ, Koornneef M.** 1994. A seed shape mutant of arabidopsis that is affected in integument development. *Plant Cell* **6**, 385–392.
- Lizana XC, Riegel R, Gomez LD, Herrera J, Isla A, McQueen-Mason SJ, Calderini DF.** 2010. Expansins expression is associated with grain size dynamics in wheat (*Triticum aestivum* L.). *Journal of Experimental Botany* **61**, 1147–1157.
- Loss SP, Siddique KHM.** 1994. Morphological and physiological traits associated with wheat yield increases in Mediterranean environments. *Advances in Agronomy* **52**, 229–276.
- Lovell DJ, Parker SR, Paveley ND, Worland AJ.** 2002. Understanding field resistance mechanisms for improved control of *Septoria tritici*. *Plant Protection Science* **38**, 165–169.
- Lupton FGH, Oliver RH, Ellis FB, Barnes BT.** 1974. Root and shoot growth of semi-dwarf and taller winter wheats. *Annals of Applied Biology* **77**, 129–144.
- Lynch JP.** 2007. Roots of the second green revolution. *Australian Journal of Botany* **55**, 493–512.
- Manschadi AM, Christopher J, DeVoil P, Hammer GL.** 2006. The role of root architectural traits in adaptation of wheat to water-limited environments. *Functional Plant Biology* **33**, 823–837.
- Martre P, Semenov MA, Jamieson PD.** 2007. Simulation analysis of physiological traits to improve yield, nitrogen use efficiency, and grain protein concentration in wheat. In: Spiertz JHH, Struik PC, Van Laar HH, eds. *Scale and complexity in plant systems research: gene-plant-crop relations*. Berlin: Springer, 181–201.
- McCown RL, Hammer GL, Hargreaves JNG, Holzworth DP, Freebairn DM.** 1996. APSIM: a novel software system for model development, model testing, and simulation in agricultural systems research. *Agricultural Systems* **50**, 255–271.
- McIntyre CL, Mathews KL, Rattey A, Chapman SC, Drenth J, Ghaderi M, Reynolds MP, Shorter R.** 2010. Molecular detection of genomic regions associated with grain yield and yield-related components in an elite bread wheat cross evaluated under irrigated and rainfed conditions. *Theoretical and Applied Genetics* **120**, 527–541.
- McQueen-Mason SJ, Durachko DM, Cosgrove DJ.** 1992. Two endogenous proteins that induce cell wall extension in plants. *Plant Cell* **4**, 1425–1433.
- Millet E.** 1986. Relationships between grain weight and the size of floret cavity in the wheat spike. *Annals of Botany* **58**, 417–423.
- Millet E, Pinthus MJ.** 1980. Genotypic effects of the material tissues of wheat on its grain weight. *Theoretical and Applied Genetics* **58**, 247–252.
- Miralles DJ, Katz SD, Colloca A, Slafer GA.** 1998. Floret development in near isogenic wheat lines differing in plant height. *Field Crops Research* **59**, 21–30.
- Miralles DJ, Resnicoff E, Carretero R.** 2007. Yield Improvement associated with Lr19 translocation in wheat. In: Spiertz JHH, Struik PC, van Laar HH, eds. *Scale and complexity in plant systems research: gene-plant-crop relationships*. The Netherlands: Springer, 171–178.
- Miralles DJ, Richards RA, Slafer GA.** 2000. Duration of stem elongation period influences the number of fertile florets in wheat and barley. *Australian Journal of Plant Physiology* **27**, 931–940.
- Miralles DJ, Slafer GA.** 1995a. Individual grain weight responses to genetic reduction in culm length in wheat as affected by source–sink manipulations. *Field Crops Research* **43**, 55–66.
- Miralles DJ, Slafer GA.** 1995b. Yield, biomass and yield components in dwarf, semidwarf and tall isogenic lines of spring wheat under recommended and late sowings dates. *Plant Breeding* **114**, 392–396.
- Miralles DJ, Slafer GA.** 1997. Radiation interception and radiation use efficiency of near isogenic wheat lines with different height. *Euphytica* **97**, 201–208.
- Miralles DJ, Slafer GA.** 2007. Sink limitations to yield in wheat: how could it be reduced? *Journal of Agricultural Science, Cambridge* **145**, 139–150.
- Miralles DJ, Slafer GA, Lynch V.** 1997. Rooting patterns in near-isogenic lines of spring wheat for dwarfism. *Plant and Soil* **197**, 79–86.
- Nicolas ME, Gleadow RM, Dalling MJ.** 1984. Effects of drought and high-temperature on grain-growth in wheat. *Australian Journal of Plant Physiology* **11**, 553–566.
- Ortiz-Monasterio JI, Sayre KD, Rajaram S, McMahom M.** 1997. Genetic progress in wheat yield and nitrogen use efficiency under four nitrogen rates. *Crop Science* **37**, 898–904.
- Parry M, Reynolds M, Salvucci M, Raines CA, Andralojc PJ, Zhu Xg, Price GD, Condon AG, Furbank RT.** 2010. Raising yield potential of wheat: (II) increasing photosynthetic capacity and efficiency. *Journal of Experimental Botany* **62**, 453–467.
- Pask A.** 2009. Optimising nitrogen storage in wheat canopies for genetic reduction in fertiliser nitrogen inputs PhD thesis, University of Nottingham, UK.
- Peltonen-Sainio P, Kangas A, Salo Y, Jauhiainen L.** 2007. Grain number dominates grain weight in temperate cereal yield determination: evidence based on 30 years of multi-location trials. *Field Crops Research* **100**, 179–188.
- Pierik R, Whitelam GC, Voesenek LACJ, de Kroon H, Visser EJW.** 2004. Canopy studies on ethylene-insensitive tobacco identify ethylene as a novel element in blue light and plant-plant signalling. *Plant Journal* **38**, 310–319.
- Porter JR, Jamieson PD, Wilson DR.** 1993. Comparison of the wheat simulation models AFRCWHEAT2, CERES-Wheat and SWHEAT for non-limiting conditions of crop growth. *Field Crops Research* **33**, 131–157.
- Reynolds M, Tuberosa R.** 2008. Translational research impacting on crop productivity in drought-prone environments. *Current Opinion in Plant Biology* **11**, 171–179.
- Reynolds MP, Bonnett D, Chapman S, Furbank R, Manes Y, Mather D, Parry M.** 2010. Raising yield potential of wheat: (I)

- overview of a consortium approach and breeding strategies. *Journal of Experimental Botany* [JEXBOT/2010/050930].
- Reynolds MP, Borlaug NE.** 2006. Impacts of breeding on international collaborative wheat improvement. *Journal of Agricultural Science, Cambridge* **144**, 3–17.
- Reynolds MP, Calderini DF, Condon AG.** 2001. Physiological basis of yield gains in wheat associated with the LR19 translocation from *Agropyron elongatum*. *Euphytica* **119**, 137–141.
- Reynolds MP, Dreccer F, Trethowan R.** 2007. Drought-adaptive traits derived from wheat wild relatives and landraces. *Journal of Experimental Botany* **58**, 177–186.
- Reynolds MP, Foulkes MJ, Slafer GA, Berry PM, Parry MAJ, Snape JW, Angus WJ.** 2009. Raising yield potential in wheat. *Journal of Experimental Botany* **60**, 1899–1918.
- Reynolds MP, Pellegrineschi A, Skovmand B.** 2005. Sink-limitation to yield and biomass: a summary of some investigations in spring wheat. *Annals of Applied Biology* **146**, 39–49.
- Reynolds MP, Rajaram S, Sayre KD.** 1999. Physiological and genetic changes of irrigated wheat in the post-green revolution period and approaches for meeting projected global demand. *Crop Science* **39**, 1611–1621.
- Ribas-Vargas G, de Silva J, Docherty A, Gaju O, Reynolds MP, Werner P, Dodds M, Sylvester-Bradley R, Mayes S, Foulkes MJ.** 2008. Raising wheat yields through novel genes for grain number. Proceedings of the 4th European Plant Science Organization Conference 2008. 'Plants for Life' 22–26 June 2008, Toulon (Côte d'Azur), France.
- Richards RA.** 1992. The effect of dwarfing genes in spring wheat in dry environments. I. Agronomic characteristics. *Australian Journal of Agricultural Research* **43**, 517–527.
- Richards RA.** 1996. Increasing the yield potential of wheat: manipulating sources and sinks. In: Reynolds MP, Rajaram S, McNab A, eds. *Increasing yield potential in wheat: breaking the barriers*. Mexico, DF: CIMMYT.
- Richards RA, Rebetzke GA, Condon AG, van Herwaarden AF.** 2002. Breeding opportunities for increasing the efficiency of water use and crop yield in temperate cereals. *Crop Science* **42**, 111–121.
- Riffkin P, Sylvester-Bradley R.** 2008. A wheat ideotype for the high rainfall zone of south-west Victoria. Australian Society of Agronomy Conference paper, <http://www.regional.org.au/au/asa/2008/concurrent/biotechnology/5646_riffkinp.htm> (last accessed 15 September 2010).
- Rijven AHGC, Banbury CA.** 1960. Role of the grain coat in wheat grain development. *Nature* **188**, 546–547.
- Rogers SO, Quatrano RS.** 1983. Morphological staging of wheat caryopsis development. *American Journal of Botany* **70**, 308–311.
- Royal Society.** 2009. *Reaping the benefits: science and the sustainable intensification of global agriculture* Royal Society Policy Document 11/09, The Royal Society, London, UK, 1–72.
- Ruuska SA, Rebetzke GJ, van Herwaarden AF, Richards RA, Fettell DN, Tabe L, Jenkins CLD.** 2006. Genotypic variation in water-soluble carbohydrate accumulation in wheat. *Functional Plant Biology* **33**, 799–809.
- Sadras VO.** 2007. Evolutionary aspects of the trade-off between seed size and the number in crops. *Field Crops Research* **100**, 125–138.
- Sadras VO, Denison RF.** 2009. Do plant parts compete for resources? An evolutionary viewpoint. *New Phytologist* **183**, 565–574.
- Saini HS, Westgate ME.** 2000. Reproductive development in grain crops during drought. *Advances in Agronomy* **68**, 59–96.
- Sayre KD, Rajaram S, Fischer RA.** 1997. Yield potential progress in short bread wheats in northwest Mexico. *Crop Science* **37**, 36–42.
- Schnyder H, Baum U.** 1992. Growth of the grain of wheat (*Triticum aestivum* L.). The relationship between water content and dry matter accumulation. *European Journal of Agronomy* **1**, 51–57.
- Schruff MC, Spielman M, Tiwari S, Adams S, Fenby N, Scott RJ.** 2006. The *AUXIN RESPONSE FACTOR 2* gene of Arabidopsis links auxin signalling, cell division, and the size of seeds and other organs. *Development* **133**, 251–261.
- Scott WR, Appleyard M, Fellowes G, Kirby EJM.** 1983. Effects of genotype and position in the ear on carpel and grain growth and mature grain weight of spring barley. *Journal of Agricultural Science, Cambridge* **100**, 383–391.
- Semenov MA, Shewry PR.** 2010. Modelling predicts that heat stress and not drought will limit wheat yield in Europe. *Nature Proceedings* <<http://hdl.handle.net/10101/npre.2010.4335.1>> (2010).
- Serrago RA, Miralles DJ, Slafer GA.** 2008. Floret fertility in wheat as affected by photoperiod during stem elongation and removal of spikelets at booting. *European Journal of Agronomy* **28**, 301–308.
- Shearman VJ.** 2001. Changes in the yield limiting processes associated with the yield improvement of wheat. PhD Thesis, University of Nottingham, UK, 238.
- Shearman VJ, Sylvester-Bradley R, Foulkes MJ.** 2005. Physiological processes associated with wheat yield progress in the UK. *Crop Science* **45**, 175–185.
- Siddique KHM, Kirby EJM, Perry MW.** 1989. Ear: stem ratio in old and modern wheat varieties; relationship with improvement in number of grains per ear and yield. *Field Crops Research* **21**, 59–78.
- Silva SA, de Carvalho FIF, Caetano VR, Oliveira AC, Coimbra JLM, Vasconcellos NJS, Lorencetti C.** 2000. Genetic basis of stay-green trait in bread wheat. *Journal of New Seeds* **2**, 55–68.
- Simmons SR, Crookston RK, Kurlle JE.** 1982. Growth of spring wheat kernels as influenced by reduced kernel number per spike and defoliation. *Crop Science* **22**, 983–988.
- Slafer GA.** 1996. Differences in phasic development rate amongst wheat cultivars independent of responses to photoperiod and vernalization. A viewpoint of the intrinsic earliness hypothesis. *Journal of Agricultural Science, Cambridge* **126**, 403–419.
- Slafer GA.** 2003. Genetic basis of yield as viewed from a crop physiologist's perspective. *Annals of Applied Biology* **142**, 117–128.
- Slafer GA, Abeledo LG, Miralles DJ, Gonzalez FG, Whitechurch EM.** 2001. Photoperiod sensitivity during stem elongation as an avenue to raise potential yield in wheat. *Euphytica* **119**, 191–197.

- Slafer GA, Andrade FH.** 1993. Physiological attributes related to the generation of grain yield in bread wheat cultivars released at different eras. *Field Crops Research* **31**, 351–367.
- Slafer GA, Araus JL, Richards RA.** 1999. Physiological traits that increase the yield potential of wheat. In: Satorre EH, Slafer GA, eds. *Wheat: ecology and physiology of yield determination*. New York: Food Products Press, 379–415.
- Slafer GA, Araus JL, Royo C, García del Moral LF.** 2005. Promising ecophysiological traits for genetic improvement of cereal yields in Mediterranean environments. *Annals of Applied Biology* **146**, 61–70.
- Slafer GA, Calderini DF.** 2005. Importance of breeding for further improving durum wheat yield. In: Royo C, Nachit MM, di Fonzo N, Araus JL, Pfeiffer WH, Slafer GA, eds. *Durum wheat breeding: current approaches and future strategies*. New York: Food Product Press, 22–41.
- Slafer GA, Kantolic AG, Appendino ML, Miralles DJ, Savin R.** 2009. Crop development: genetic control, environmental modulation and relevance for genetic improvement of crop yield. In: Sadras VO, Calderini DF, eds. *Crop physiology: applications for genetic improvement and agronomy*. The Netherlands: Elsevier, 277–308.
- Slafer GA, Savin R.** 1994. Grain mass change in a semi-dwarf and a standard height wheat cultivar under different sink-source relationships. *Field Crops Research* **37**, 39–49.
- Snape JW, Foulkes MJ, Simmonds J, Leverington M, Fish LJ, Wang Y, Ciavarella M.** 2007. Dissecting gene×environmental effects on wheat yields via QTL and physiological analysis. *Euphytica* **154**, 401–408.
- Song X-J, Huang W, Shi M, Zhu M-Z, Lin H-X.** 2007. A QTL for rice grain width and weight encodes a previously unknown RING-type E3 ubiquitin ligase. *Nature Genetics* **39**, 623–630.
- Spielmeyer W, Richards R.** 2004. Comparative mapping of wheat chromosome 1AS which contains the tiller inhibition gene (*tin*) with rice chromosome 5S. *Theoretical and Applied Genetics* **109**, 1303–1310.
- Stapper M, Fischer RA.** 1990. Genotype, sowing date and plant spacing influence on high-yielding, irrigated wheat in southern New South Wales. I. Phasic development, canopy growth and spike production. *Australian Journal of Agricultural Research* **41**, 997–1019.
- Sylvester-Bradley R, Berry PM, Blake J, Kindred D, Spink J, Bingham I, McVittie J, Foulkes MJ.** 2008. *The Wheat Growth Guide*, 2nd Edition. HGCA, London 1–30.
- Sylvester-Bradley R, Kindred DR.** 2009. Analysing nitrogen responses of cereals to prioritize routes to the improvement of nitrogen use efficiency. *Journal of Experimental Botany* **60**, 1939–1951.
- Sylvester-Bradley R, Riffkin PA.** 2008. Designing resource-efficient ideotypes for new cropping conditions: wheat in the UK and Australasia. *Aspects of Applied Biology* **88**, *Effects of Climate Change on Plants: Implications for Agriculture* 127–133.
- Sylvester-Bradley R, Scott RK, Stokes DT, Clare RW.** 1997. The significance of crop canopies for nitrogen nutrition. *Aspects of Applied Biology* **50**, *Optimising Cereal Inputs: Its Scientific Basis* 103–116.
- Tashiro T, Wardlaw IF.** 1990a. The effect of high temperature at different stages of ripening on grain set, grain weight and grain dimension I the semi-dwarf wheat “Banks”. *Annals of Botany* **65**, 51–61.
- Tashiro T, Wardlaw IF.** 1990b. The response to high temperature shock and humidity changes prior to and during the early stages of grain development in wheat. *Australian Journal of Plant Physiology* **17**, 551–561.
- Tuberosa R, Salvi S, Sanguineti MC, Landi P, Maccaferri M, Conti S.** 2002. Mapping QTLs regulating morpho-physiological traits and yield: case studies, shortcomings and perspectives in drought-stressed maize. *Annals of Botany* **89**, 941–963.
- Ugarte C, Calderini DF, Slafer GA.** 2007. Grain weight and grain number responsiveness to pre-anthesis temperature in wheat, barley and triticale. *Field Crops Research* **100**, 240–248.
- van Oosterom EJ, Borrell AK, Chapman SC, Broad IJ, Hammer GL.** 2010a. Functional dynamics of the nitrogen balance of sorghum: I. N demand of vegetative plant parts. *Field Crops Research* **115**, 19–28.
- van Oosterom EJ, Borrell AK, Chapman SC, Broad IJ, Hammer GL.** 2010b. Functional dynamics of the nitrogen balance of sorghum. II. Grain filling period. *Field Crops Research* **115**, 29–48.
- Verma V, Foulkes MJ, Caligari P, Sylvester-Bradley R, Snape J.** 2004. Mapping quantitative trait loci for flag leaf senescence as a yield determinant in winter wheat under optimal and drought-stressed environments. *Euphytica* **135**, 255–263.
- Wang Z, Mambelli S, Setter TL.** 2002. Abscisic acid catabolism in maize kernels in response to water deficit at early endosperm development. *Annals of Botany* **90**, 623–630.
- Whitechurch EM, Slafer GA, Miralles DJ.** 2007. Variability in the duration of stem elongation in wheat and barley. *Journal of Agronomy and Crop Science* **193**, 138–145.
- Wilkinson S, Davies WJ.** 2009. Ozone suppresses soil drying- and abscisic acid (ABA)-induced stomatal closure via an ethylene-dependent mechanism. *Plant Cell and Environment* **32**, 949–959.
- Yang J, Zhang J, Wang Z, Liu K, Wang P.** 2006. Post-anthesis development of inferior and superior spikelets in rice in relation to abscisic acid and ethylene. *Journal of Experimental Botany* **57**, 149–160.
- Yang JC, Zhang JH, Huang ZL, Wang ZQ, Zhu QS, Liu LJ.** 2002. Correlation of cytokinin levels in the endosperms and roots with cell number and cell division activity during endosperm development in rice. *Annals of Botany* **90**, 369–377.
- Yang Z, van Oosterom EJ, Jordan DR, Hammer GL.** 2009. Pre-anthesis ovary development determines genotypic differences in potential kernel weight in sorghum. *Journal of Experimental Botany* **60**, 1399–1408.
- Yano M, Kojima S, Takahashi Y, Lin H, Sasaki T.** 2001. Genetic control of flowering time in rice, a short-day plant. *Plant Physiology* **127**, 1425–1429.