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; Borras 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. Borras 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 HI should take account of the cropping system and/or rotational requirements, e.g. in cropping systems in which wheat is 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

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**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 (Hanoq 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 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.

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

<table>
<thead>
<tr>
<th>Crop component</th>
<th>Austin et al. (1980) (four most modern)ᵃ</th>
<th>Austin (1980) theoretical max. HIᵇ</th>
<th>HI theoretical max. calc. 1ᶜ</th>
<th>HI theoretical max. calc. 2ᵈ</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>g m⁻² %</td>
<td>g m⁻² %</td>
<td>g m⁻² %</td>
<td>g m⁻² %</td>
</tr>
<tr>
<td>Grain</td>
<td>707 49</td>
<td>896 62</td>
<td>992 63</td>
<td>1007 64</td>
</tr>
<tr>
<td>Chaff</td>
<td>143 10</td>
<td>181 13</td>
<td>193 12</td>
<td>177 11</td>
</tr>
<tr>
<td>Leaf lamina</td>
<td>139 10</td>
<td>139 10</td>
<td>153 10</td>
<td>153 10</td>
</tr>
<tr>
<td>Stem + sheath</td>
<td>453 31</td>
<td>226 15</td>
<td>249 15</td>
<td>249 15</td>
</tr>
<tr>
<td>AGDM</td>
<td>1442 –</td>
<td>1441 –</td>
<td>1586 –</td>
<td>1586 –</td>
</tr>
</tbody>
</table>

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.
of soil) is often below a critical threshold for potential water and nitrate capture of ~1 cm cm⁻³ (Barraclough et al., 1989; Gregory and Brown, 1989) at lower depths in the rooting profile (Ford et al., 2006; Reynolds et al., 2007; 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

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JM Foulkes (unpublished)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

SW, spring wheat; WSC, water-soluble carbohydrate in stem and leaf sheath; WW, winter wheat. *P<0.05; **P<0.01; ***P<0.001.
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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 (Spelmeyer 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 might 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 the 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 Slaf er, 1995a; Acreche and Slaf er, 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; Slaf er 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 syncitial 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; Cantagallos 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°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 preflowering 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 (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
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 photosynthesis, 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.

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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


