A ‘wiring diagram’ for sink strength traits impacting wheat yield potential

Gustavo A. Slafer1,2,*, M. John Foulkes3,*, Matthew P. Reynolds4, Erik H. Murchie1,*, Elizabete Carmo-Silva5, Richard Flavell6, Jeff Gwyn6, Mark Sawkins6 and Simon Griffiths7

1 Department of Crop and Forest Sciences, University of Lleida–AGROTECNIO-CERCA Center, Av. R. Roure 191, 25198 Lleida, Spain
2 ICREA (Catalonian Institution for Research and Advanced Studies), Barcelona, Spain
3 Plant and Crop Sciences, School of Biosciences, University of Nottingham, Leicestershire LE12 5RD, UK
4 International Maize and Wheat Improvement Center (CIMMYT), Km. 45, Carretera Mexico, El Batan, Texcoco, Mexico
5 Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK
6 International Wheat Yield Partnership, 1500 Research Parkway, College Station, TX 77843, USA
7 John Innes Centre, Norwich Research Park, Colney Ln, Norwich NR4 7UH, UK

* These authors contributed equally to this work.

© The Author(s) 2022. Published by Oxford University Press on behalf of the Society for Experimental Biology. This is an Open Access article distributed under the terms of the Creative Commons Attribution License (https://creativecommons.org/licenses/by/4.0/), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.
Introduction

The concept of a physiological sink refers to organs which are net ‘receivers’ of photosynthate and other metabolites that are then either consumed by the organ for its own metabolism or stored (to be used later by other sinks). Identifying appropriate traits responsible for improving sink strength is one of the current bottlenecks to further increases in yield potential (Reynolds et al., 2021). In this context, we mostly limit the concept to the reproductive sinks, and consider sink strength as the collective capacity of grains to accumulate dry matter as defined by the number of grains set per unit area and their potential weight. Although this review is sink oriented, it is necessary to appreciate the crop’s photoassimilate supply (source strength, considered specifically in the companion paper; Murchie et al., 2023), which provides energy and molecules for constructing sinks, and also the interactions between source and sink. Briefly (for more detailed consideration, please see the discussion offered in Sláfer et al., 2021; Reynolds et al., 2022), although yield is being formed throughout the whole crop cycle (Sláfer and Rawson, 1994), the different phases have more or less relevance, depending on both their sensitivity to environmental factors and the consequences of that sensitivity on yield. Most frequently, yield is limited by sink strength during the effective period of grain filling, and source limited from the terminal spikelet initiation up to the onset of grain filling (Fig. 1). For instance, in a recent study by Dreisser et al. (2022) subjecting wheat plants to changes in resources (CO₂) and signals (red:far red ratio) during different phases, it was demonstrated that yield responses were concentrated around treatments applied when sink strength is built up, while changes during grain filling were far less effective (as sink strength has already been set and there is no source limitation to filling the grains). This reinforces, with a new approach, what has been the most frequent scenario in the literature (e.g. see reviews by Sláfer, 2003; Fischer, 2011; Foulkes et al., 2011; Reynolds et al., 2021, 2022; and a wealth of references quoted therein), and extends the knowledge on the effects of resources on signals, in agreement with what was found when wheat was subject to the contrasting effects of poorer light quality (Ugarte et al., 2010) and longer photoperiods (Gonzalez et al., 2003, 2005; Ferrante et al., 2020).

During the period from terminal spikelet to slightly after anthesis, the number of grains per unit land area is set mainly through tiller mortality, floret primordia death, and grain abortion from anthesis to the watery ripe grain stage; potential grain size is established from booting to the watery ripe stage (Fig. 1; and see also Sláfer et al., 2021). Crop growth before the terminal spikelet is less critical for yield determination provided crop growth is maximized from the terminal spikelet onwards (an empiric proof of concept for this is that plant densities optimizing yield potential are far lower than those maximizing biomass in early stages).

The interacting processes that determine yield potential are complex (Fig. 1). To help visualize and analyse them, an interactive graphical representation—or set of ‘wiring diagrams’ (WDs), covering the most critical phases of crop development—has been developed (Reynolds et al., 2022). The present review provides additional WDs to aid understanding and further analysis in much greater detail. We focus here on traits and relationships that are relevant for sink strength determination and have divided them into four phenological phases, with a dedicated WD for each of them, delimited by the stages of onset of stem elongation (roughly coinciding with terminal spikelet), booting, anthesis, watery ripe, and physiological maturity (Fig. 1). In the first three phases, different processes that are responsible for the determination of the sink strength are considered, while in the last phase the factors defining whether the crop realizes the sink strength–determined yield are described (Fig. 1). A companion review (Murchie et al., 2023) presents WDs for stages of crop development responsible for source strength. Appreciation of the source–sink interactions outlined in both reviews is essential to understand the determination of grain yield because the separation of the full set of WD reviews into source and sink papers, primarily for the convenience of publication, can easily minimize the importance of the interactions between tissues and organs that occur at different times in crop development.

The ratio between aboveground source and sink organs at harvest is described as the harvest index (HI; grain dry matter/aboveground dry matter). A step change in HI underpinned the dramatic yield gains of the Green Revolution, even though biomass was not improved and thereby necessarily setting an upper limit on yield. [Although the introgression of semi-dwarfing alleles (which is the foundation of the Green Revolution) did not increase biomass, the increased tolerance to lodging allowed higher levels of N fertilization, which did indeed increase biomass noticeably, but through the adapted management, not through crop genetics.] Semi-dwarf wheats had higher HI than their tall counterparts by creating a higher reproductive sink strength due to a shift in the proportion of dry matter from vegetative stem tissue to juvenile spikes in the pre-anthesis phase. This shift stimulates more floret primordia to continue developing normally and become fully developed, presumably fertile, florets (Fig. 2) able to set grains, thereby illustrating how source–sink interactions determine yield potential in wheat.

Steady genetic gains in HI were associated with yield improvement in wheat until the late 1990s (Reynolds et al., 1999), and explained the success of wheat breeding across many countries with contrasting growing conditions (e.g. Austin et al., 1980; Siddique et al., 1989; Calderini et al., 1995; Shearman et al., 2005; Acreche et al., 2008; Sadras and Lawson, 2011; del Pozo et al., 2014; Flohr et al., 2018; Lo Valvo et al., 2018; Maekawa et al., 2020; Mondal et al., 2020). HI still shows significant genetic variation in modern wheat cultivars.
**Fig. 1.** Graphical time course of wheat phenology indicating key developmental stages (organs are not at the same scale and the relative duration of different phases varies depending on genotypes and environments), illustrating the appearance of the apex/spike, the timing of differentiation and growth of organs, and the degree of source or sink limitation for yield [from terminal spikelet stage to shortly after anthesis, source strength determines the grain sink strength (number of grains and their potential size), that then limits the potential accumulation of yield during the effective grain-filling period]. That is, pre-anthesis source strength influences yield because it determines sink strength during grain filling. This defines periods over which sink strength forms (in this study divided into three dedicated WDs, later shown in Figs 4, 5 and 8) and realized (during the effective period of grain filling, with a WD shown in Fig. 9) (see shaded boxes behind the schemes). Based on an original scheme from Slafer and Rawson (1994); and from Ochagavía et al. (2021) and Slafer et al. (2021). Reprinted with permission from Elsevier.
Sink strength and yield in wheat

The period of stem elongation, from terminal spikelet to anthesis (TS–An; embracing the growth of the juvenile spike in which florets are developing within spikelets), is critical for yield determination (Miralles et al., 2000; Slaf er et al., 2001; Reynolds et al., 2022). It is during this period that not only the number of grains per m² most strongly determined but also grain weight potential is, at least partly, set (Calderini et al., 2001). Grain number is far more responsive to changes in crop growth and development during this phase than in any of the others (e.g. Slaf er, 2003; Fischer, 2011, and references therein), in line with the idea that grain number is strongly influenced by photoassimilate supply before anthesis (Patrick and Colyvas, 2014; Reynolds et al., 2022). Increasing the allocation of dry matter to juvenile spikes (considering the population of spikes, i.e. heavier individual spikes or more spikes becoming fertile) results in increases in grain number by preventing the death of some labile floret primordia (Ferrante et al., 2013b, 2020; Dreccer et al., 2014; Guo et al., 2016). At the same time, the florets that continue to develop and become fertile actively grow, and the size attained by the carpels of these florets is an important

(Aisawi et al., 2015), indicating that breeders have not yet fixed this trait.

The genetic basis of assimilate partitioning among different plant organs is only partially understood, and shows significant interactions between environment and genetic background (Griffiths et al., 2015; Slaf er et al., 2015; Ferrante et al., 2017). Nonetheless, in recent studies of wheat yield potential, large genetic ranges for dry matter partitioning among plant organs have been reported and some promising leads have been identified (Slaf er et al., 2015; Rivera-Amado et al., 2019).

This variation represents significant untapped yield potential, especially given the generally negative association between HI and biomass seen in most sets of modern cultivars (Aisawi et al., 2015; Rivera-Amado et al., 2019; Sierra-Gonzalez et al., 2021). Through specific understanding of genetic and physiological mechanisms of increased HI, it should be possible to minimize the extent of this trade–off (Foulkes et al., 2011).

In the WDs in this review, as in the companion paper focusing on source strength (Murchie et al., 2023), numbered links have been developed for each of the specific ‘wires’ of the diagrams that correspond to different processes underlying sink strength. We have also commented on the genetic bases of these processes, when the established genetic bases were sufficiently soundly defined. The diagrams and evidence supporting them are necessarily ‘high level’ for the sake of clarity. Only in recent years have gene expression profiles and subcellular assays enriched knowledge of wheat traits. This review does not include these details, except in a few pertinent cases, because the aim has been to present a whole-crop picture.

To locate the focus in crop development of each section of text, the reader is referred to the chronological series of WDs (Figs 4, 5, 8, 9, which correspond to the phases indicated in Fig. 1). Each of the numbered wires in the figures is explained in the text. Some wires are active and important in more than one of the phases considered. In those cases, the description of that wire is provided only in the first phase where it is mentioned.

**WDs from the onset of stem elongation to anthesis**

Fig. 2. Schematic representation of how the introgression of semi-dwarfing alleles increased sink strength in wheat. The Rht-B1 and Rht-D1 genes (formerly known as Rht-1 and Rht-2) restricted the capacity of the stem to grow, allowing more assimilates to be allocated to the juvenile spike before anthesis (A) (Fischer and Stockman, 1986; Siddique et al., 1989; Slaf er and Andrade, 1993; Miralles et al., 1998). Floret development takes place in those juvenile spikes: many floret primordia are initiated and develop until a shortage of assimilates causes later initiated and weaker florets to die (e.g. Ferrante et al., 2013a; Dreccer et al., 2014). As semi-dwarf genotypes allocate more resources to the juvenile spike, more florets continue developing, thus reducing the rate of floret mortality and therefore increasing spike fertility (B) (e.g. Miralles et al., 1998). This is the mechanistic basis for the well-reported linear relationship between the number of grains and the spike dry weight at anthesis (C), and explains how semi-dwarf alleles of Rht-1 genes increased sink strength during grain filling and then increased the partitioning of aboveground biomass to yield, thereby resulting in a higher harvest index. This is a good empiric proof of concept of the model schematically represented in Fig. 1, where alleviation of restricted source strength for spike growth before anthesis increased yield through raising the level of sink strength.
component of the ultimate potential grain size after anthesis (Calderini et al., 2021; and many references quoted therein), because the ovary wall of the florets becomes the pericarp of the grain (Fig. 3).

We divided the TS–An period into two WDs. The first focuses on the onset of stem elongation to booting (Fig. 4), when florets are being initiated but no significant biomass investment has been made in ovary growth; and the second from booting to anthesis (Fig. 5), when floret mortality takes place, and floral organs of the surviving florets grow noticeably, determining the final number of fertile florets and the final size of their ovaries.

Grain set and determination of sink strength (major Link A, Figs 3, 4)

The physiology of grain set

In wheat, grain yield improvement has been highly associated with increased grain number per unit area (Canevara et al., 1994; Slasfer and Savin, 1994; Abbate et al., 1995; Sayre et al., 1997; Brancourt-Hulmel et al., 2003; Shearman et al., 2005; Miralles and Slasfer, 2007; Peltonen-Sainio et al., 2007). Current evidence suggests that sink strength during the grain-filling period (given by the number of grains and their potential size) remains a critical yield-limiting factor (Fischer, 1985, 2011; Beche et al., 2014; LoValvo et al., 2018). Grain number per unit area subsumes several components determined before anthesis: spikes per unit area, spikelets per spike, and grains per spikelet (see fig. 2 in Reynolds et al., 2022). Since these components are subject to interaction with environmental conditions affecting tiller and/or floret production and survival and are determined by highly polygenic systems, grain number has a relatively low heritability (Sadrás and Slasfer, 2012). The period from onset of stem extension to anthesis is very important for the determination of grain number. It is generally accepted that the most critical stage covers the phase from late booting to anthesis (Slasfer et al., 1999). Indeed, experiments impairing crop growth at different stages of crop development have shown that affecting crop growth before the onset of stem elongation, at the time of spikelet initiation and tillering, does not affect grain number per m², whilst doing so during the stem elongation phase (during which tiller mortality and floret development within spikelets occur) has a dramatic consequence on grains per m² (Fischer, 1985, and a plethora of studies confirming the same in a range of countries, and genotypes; e.g. Savin and Slasfer, 1991; Abbate et al., 1995; Dreccer et al., 2000; Demontes-Meynard and Jeuffroy, 2004; Ugarte et al., 2007; Prasad and Djanaguiraman, 2014). Greater spike growth during this phase is strongly associated with higher grain number through increased floret survival (Calderini et al., 1997; Fischer, 2007).

Grain growth of modern wheat cultivars is in general not strongly limited by the source [including actual canopy photosynthesis as well as remobilization of water-soluble carbohydrates (WSCs) during grain filling (Dreccer et al., 1997; Borrás et al., 2004; Calderini et al., 2006)], although co-limitation by source may occur in some cases (Shearman et al., 2005; Acche and Slasfer, 2009; Aisawi et al., 2015) (see link B within the WDs for the phases from anthesis to maturity below). For example, photosynthesis during the post-anthesis period (at both leaf and canopy levels) seems to be responsive to increases in grain number, via source/sink manipulation treatments imposed around anthesis, as well as to genetic effects that increase grain number, even in modern cultivars with high grain numbers (e.g. Reynolds et al., 2001, 2005; Acche and Slasfer, 2009).

The genetics of grain set

The purpose of the genetic narrative that follows is to highlight those studies which have identified the underlying genetic basis of grain number traits likely to deliver benefit to a modern breeding programme targeting high yield potential environments. Far fewer quantitative trait loci (QTLs) and marker trait associations (MTAs) are described for grains per unit area or its components than for grain size. This is not because there are fewer genes involved in the control of grain number. In fact, there are almost certainly more (Wang et al., 2017), but many are of small genetic effect and subject to strong environmental interactions, and are therefore less likely to be detected in QTL analyses. They also result in low heritability (e.g. Sadrás and Slasfer, 2012).

Despite these challenges, there are good genetic routes that can complement phenotypic selection conducted by wheat breeders. For the complex reshuffling of small effect alleles, genomic selection shows great promise (Lozada et al., 2019), while alleles with large effects are amenable to direct selection.

---

**Fig. 3.** Changes in floret development from terminal spikelet to anthesis and in grain development from then to maturity (images not to scale). The ovary that becomes the pericarp is indicated. For reference, the anthers (a), stigma (s), and embryo (e) are also indicated. Reprinted from Ochagavía et al., 2021. Copyright (2021), with permission from Elsevier.
Sink strength and yield in wheat

and positional cloning. There are few genes/QTLs that have been found to be robust and validated, ideally using near-isogenic lines (NILs). These include—though are not limited to—GNI-A1, Rht-B1 and -D1, and TaAPO-A1 (Box 1; Table 1). The favourable alleles of these four genes are present at very high frequencies in elite wheat breeding pools. This is perhaps unsurprising as selection pressure for yield has been high, and with yield tightly linked to grain number, selection would have
fixed these factors. There is unlikely, therefore, to be much scope for improved deployment of these alleles. However, the fact that the genes and causative polymorphisms are cloned opens up avenues to explore some of the molecular and biochemical pathways underlying grain number determination, many of which will be responsible for the relationships described below. These pathways are good targets for the study, manipulation, and deployment of induced and natural variation for increased grain number. In addition to the above-mentioned genes directly affecting grain number, phenology genes, mainly vernalization...
Box 1. Genetic effects with consistent effect on grain number and its components

The following highlights three genetic effects found to control overall grain number per unit area and the components of grain number.

*GNI-1A* on chromosome 2AL. Sakuma et al. (2018) identified a homeodomain leucine zipper class I (HD-Zip I) transcription factor, the expression of which was highest in the distal floret primordia of the spikelet and in parts of the rachilla. The authors demonstrated that the probable mode of action is to inhibit rachilla growth and development. In tetraploid wheat, reduced function mutations resulted in increased grain set per spikelet, grain number, and yield. The authors stated that the level of *GNI-1* expression had decreased during the domestication of wheat, thus enabling grain number increases.

*Rht-1* with reduced height alleles, *Rht-B1b* and *Rht-D1b*, are the basis of a well-known story (e.g. Hedden, 2003) in which a gain-of-function mutation arose from a premature stop codon which effectively removed the DELLA domain of GRAS proteins on chromosomes 4B and 4D, respectively, resulting in a semi-dwarf phenotype (Peng et al., 1999) together with increased grain number per unit area. For this reason, semi-dwarf alleles of *Rht-B1b* and *Rht-D1b* have been deployed in most of the world’s irrigated spring wheat and winter wheat varieties (and in many rainfed areas as well). The hypothesis suggested for the molecular function of the semi-dwarfing alleles *Rht-D1b* and *Rht-B1b* was that a methionine that occurs after the N-terminus premature stop codon acted as a new site for translational initiation so that a new shorter peptide carrying the growth-inhibiting GRAS domain was no longer subject to regulation by GA. However, the presence of these N-terminal premature stop codon acted as a new site for translational initiation so that a new shorter peptide carrying the growth-inhibiting GRAS domain was no longer subject to regulation by GA. However, Van De Velde et al., 2021). This recent study also showed that re-initiation occurs in the stem to reduce height, but not in the aleurone layer of wheat seeds where this type of GA insensitivity would cause excessive seed dormancy. These very specific changes in the developmental profile required for a desirable agronomic outcome go some way to illustrate why many dwarfing genes do not produce as desirable an agronomic phenotype as *Rht-1*.

*TaAPO-A1* is the wheat orthologue of Aberrant Panicle Organization in rice (Kuzay et al., 2019, 2022; Muqaddasi et al., 2019) on chromosome 7A in wheat. A mutation in the F-box domain defines two common alleles in modern global bread wheat which are strongly associated with spikelet number. Association with grain yield is weak, which probably reflects the physiological constraints on achieving increased grain number via spikelet number.

Wang et al. (2017) identified several transcription factors that appeared to affect spikelet and floret number. When a subset of three transcription factors was overexpressed as single transgenes, strong correlations were found between their expression and spikelet number, floret number, and seed number per spike, suggesting that the expression of single transcription factor genes can influence spike development and photoperiod-sensitivity genes (*Vrn-1* and *Ppd-1*, respectively), and a number of different genes acknowledged collectively as earliness per se genes (*Eps*), also ultimately affect grain number significantly (Box 2; Table 1).

**Main traits and relationships determining sink strength before anthesis**

**Crop growth and partitioning of assimilates between organs**

It has been hypothesized that increasing the relative duration of the TS–An phase would improve grain number by allowing more time for spike biomass accumulation during this critical period, and thereby increasing floret growth at anthesis (Link 1; Fig. 4). This strategy may also lead to increased grain number for a particular level of floret formation by deploying more spike biosynthetic capacity to promote grain set (thereby increasing fruiting efficiency (FE); number of grains per unit spike dry weight at anthesis) (Slafer et al., 2001; Miralles and Slafer, 2007; Guo and Schnurbusch, 2015; Pérez-Gianmarco et al., 2019).

This strategy has also been suggested from modelling exercises (e.g. Sylvester-Bradley et al., 2012). In some field comparisons of varying genotypes, extended duration of this critical phase was related to yield, albeit only weakly (e.g. Gonzalez et al., 2011a; Basavaraddi et al., 2021d; see also Wang et al., 2017), while in others this trait was beneficial in favourable environments (Botwright Acuña et al., 2019). The diversity of results may be due to the cultivars differing not only in the duration of this phase but also in many other traits that affect grain number and yield.

Variability in the duration of this phase independently (at least partially) of total duration of time to anthesis has been reported among elite material (Whitechurch et al., 2007; García et al., 2011; Borras-Gelonch et al., 2012; Botwright Acuña et al., 2019; Basavaraddi et al., 2021a), and seems to be selectable in breeding (Botwright Acuña et al., 2019). Furthermore, specific QTLs for the duration of this phase have been identified (e.g. Borras-Gelonch et al., 2012). An important exercise will be to analyse the location of genes underlying these QTLs where the expression levels correlate with the duration of spike development (Wang et al., 2017).
| Trait–trait | Reference | Main finding in relation to WD | Gene(s) | Chromosome | Validation |
|-------------|-----------|-------------------------------|---------|------------|------------|
| Grain set×yield | Sakuma et al. (2019) | This gene is an HD-Zip I transcription factor which is expressed most abundantly in the most distal floret primordia where the authors suggest it inhibits growth. Reduced function mutants produce more fertile florets. | GN1-1A | 2A | Tilling, RNAi |
| Peng et al. (1999) | Rht-D1b dwarfing alleles increase grain number. | Rht-1 | 4B and 4D | NIL, transgenic |
| Muqaddasi et al. (2019); Kuzay et al. (2019, 2022) | Both studies showed that the wheat homologue of the rice gene Aberrant panicle organization 1 (APO-1) controls spikelet number in bread wheat. | TaAPO-A1/ WAPO1 QTL | 7A | GWAS |
| Griffiths et al. (2009) | Meta QTL analysis identified a number of Earliness per se QTLs, some of which were later shown to also effect grain number. | Eps-D1/ TaELF3D1 | 1D | GWAS |
| Sukumaran et al. (2016) | This work showed that a major Earliness per se gene (EPS-D1) identified in the UK was also important in CIMMYT germplasm and these phenology effects were later shown to influence grain number. | TaAPO-A1/ WAPO1 QTL | Multiple | Meta QTL |
| Alvarez et al. (2016); Zikhali et al. (2016) | These studies showed that EPS-D1 corresponded to ELF3 which is a component of the circadian clock. | EpsD1/ TaELF3D and EpsAm1 (candidate) | 1D and 1A | NIL, fine map |
| Martinez et al. (2021) | A yield QTL identified in the Avalon×Cadenza population and validated using NILs was mapped at higher genetic resolution and shown to co-localize with heading date effects for which the best gene candidate was TaFT2. | TaFT2 | Group 3 | Transgenic |
| Shaw et al. (2019) | This work supports an important role for FT2 in grain number determination, with transgenic manipulation of the gene producing changes in various fertility traits. | TaFT2 | 3A | NIL and population studies |
| Glenn et al. (2022) | A single amino acid substitution was associated with significant increases in grain number per spike in bread and pasta wheat. | TaFT2 | 6A | NIL (later studies) |
| Grain size×yield | Snape et al. (2007) | The identification of a major QTL for grain size underwent intensive subsequent study. | QTL | 6A | NIL |
| Farre et al. (2016); Huang et al. (2015) | Grain size QTL validated in the Avalon×Cadenza NIL library. A robust set of QTLs identified in Chinese germplasm for grain size were validated in NILs showing that marker-assisted selection for this trait is effective and relatively facile. | NIL effects | 2A, 5A, 6A | NIL |
| Guan et al. (2019); Calderini et al. (2021) | As above. Overexpression of an α-expansin in early developing wheat seeds leads to a significant increase in grain size without a negative effect on grain number, resulting in a yield boost under field conditions. | QTL Expansin | 4A | NIL |
| Glenn et al. (2022) | Probably the most intensively studied grain size QTL in wheat. | TaGW2-A1 QTL | 6A | NIL, tilling |
| Simmonds et al. (2014); Borras-Gelonch et al. (2012) | Independent genetic control of phenology stages shows that, if it is beneficial to allocate more time to the TS–An phase, the genetic variation to do this is available. | Nil GWAS | Multiple QTLs | None |
| Guo et al. (2016) | Detailed glasshouse study using GWAS to map genes controlling phenology phases. | MTA | Multiple | None |
| Peng et al. (1999) | Rht-1 was cloned and shown to be a DELLLA domain growth inhibitor. The wild-type protein (full length) is degraded when GA levels increase so that growth is no longer supressed. This sensitivity is removed in the semi-dwarf plants so that growth repression (stem extension) is constitutively expressed so more assimilate can be directed towards the spike. | Rht-1 | Homoeologous loci on group 4 chromosomes. | NIL, transgenic |
| Trait–trait             | Reference                      | Main finding in relation to WD                                                                 | Gene(s) | Chromosome | Validation     |
|------------------------|--------------------------------|-----------------------------------------------------------------------------------------------|---------|-------------|----------------|
| Spike partition×spike growth | Abeledo et al. (2019)          | This study shows that when the trouble is taken to collect these phenotypes, QTLs are detected, in this case for spike dry weight at anthesis. | QTL     |             |                |
|                        | Rebetzke et al. (2011)         | Rht13 is an NBS-LRR class of gene with the Rht13b allele autoactivated to reduce height to a similar extent to Rht1 semi-dwarfing alleles and, like those alleles, can also act to increase grain yield through grain number. |         | Rht13       | 7B, NIL, till   |
|                        | Cui et al. (2011); Zhang et al. (2017); Abeledo et al. (2019) | Physiological studies show that even when optimal height is achieved in wheat, further fine-tuning is possible by reducing the length of specific internodes. These studies show that QTLs can be identified for internode specific length variation. | QTL     | Multiple QTLs | NIL            |
|                        | Miralles and Säfer (1995); Flintham et al. (1997) | Both studies use NILs in very diverse backgrounds to show that genetic variation at the Rht1 locus reduces height, increases harvest index, and increases grain yield by increasing grain number. |         | Rht-1       | See above, NIL  |
|                        | Tang et al. (2021)             | This work shows that Rht18 can confer the same advantages as Rht1 without some of the negative effects such as reduced coleoptile length. |         | Rht18       | (major gene not cloned) |
| Fruiting efficiency×grain set | Pretini et al. (2020b)        | In a doubled haploid population (Baguette 19×BIOINTA 2002) increasing alleles for a fertile floret efficiency QTL acted through increased grain set. | QTL     | 5A          | F2              |
|                        | Prieto et al. (2020)           | This shows how Earliness per se genes alter seed number by influencing floret survival, but the direction of effect is temperature dependent, so maximizing grain number via phenology is a genetic balancing act that depends on environmental factors. |         | ELF3 and FT2 | (candidates)    |
|                        | Giunta et al. (2018)           | Fruiting efficiency QTLs were identified and their relationship to phenology dissected. | QTL     | Multiple    | None            |
|                        | Basavaraddi et al. (2021b, c)  | Both QTLs affected the spike fertility by altering the rate of floret development and mortality. | QTL     | 2B and 7D   | NIL             |
|                        | Sang et al. (2010)             | No publications could be found for QTLs for variation in spike vasculature, but Sang et al. did find QTLs for small and large vascular bundles of the peduncle. | QTL     | Multiple    | None            |
|                        | Brinton et al. (2017)          | A robust QTL controlling a 7% increase in grain weight shown to be due to increased pericarp cell length. | QTL     | 5A          | NIL             |
|                        | Chapman et al. (2021)          | Independent EMS-induced mutants expressing delayed senescence and increased grain yield by extended grain fill were shown to have undergone amino acid changes in subdomain 4 of the NAC domain of NAM1. |         | NAM-A1 and NAM-D1 | 6A and 6D, Major gene, till, NIL |
|                        | Bednarek et al. (2012)         | Cell number has been shown to underlie single gene effects on grain size, as in this study. |         | TaGW2       | Group 6, RNAi   |
|                        | Guo et al. (2022)              | TaCYP78A5 participates in auxin synthesis pathway and promotes auxin accumulation and cell wall remodelling in ovary. Localized overexpression of TaCYP78A5 in ovary results in delayed flowering and prolonged proliferation of maternal integument cells, which promote grain enlargement. |         | TaCYP78A5    | Transgenic      |
### Table 1. Continued

| Trait–trait                  | Reference                        | Main finding in relation to WD                                                                 | Gene(s)          | Chromosome | Validation      |
|------------------------------|----------------------------------|------------------------------------------------------------------------------------------------|------------------|------------|-----------------|
| Sink strength×source strength| Mason et al. (2013)              | Source and sink strength are captured in many studies as biomass components at harvest. Here a Halberd×Karl92 population was used to show the co-localization of grain yield and biomass QTL. | QTL              | 3B         | None            |
| Protein/starch synthesis×grain weight realization | Uauy et al. (2006)              | Grain yield and protein concentration are negatively correlated but yield can be increased without decreasing protein if genes controlling grain protein difference (GPD) are exploited. In this work it was shown that NAM-B1 variants can increase grain protein without decreasing grain yield. | NAM-B1/Gpc-B1    | 6B         | NIL, transgenic |
| Duration of grain fill×grain weight realization | Chapman et al. (2021)           | Independent EMS-induced mutants expressing delayed senescence and increased grain yield by extended grain fill were shown to have undergone amino acid changes in subdomain 4 of the NAC domain of NAM1. | NAM-A1 and NAM-D1 | 6A and 6D | Major gene, tilling, NIL |
| Source strength×grain weight realization | Chapman et al. (2021)           | Source strength was increased through delayed senescence.                                                                 | NAM-B1           | 6B         | NIL, fine map, transgenic |
| Source strength×protein/starch synthesis | Uauy et al. (2006)              | This study showed that a NAC transcription factor was a major regulator of senescence in wheat.                                                                 | NAM-B1           | 6B         | NIL, fine map, transgenic |
| Carbohydrate storage and remobilization×starch synthesis | Chapman et al. (2021)           | Independent EMS-induced mutants expressing delayed senescence and increased grain yield by extended grain fill were shown to have undergone amino acid changes in subdomain 4 of the NAC domain of NAM1. | NAM-A1 and NAM-D1 | 6A and 6D | Major gene, tilling, NIL |
| Protein synthesis×starch synthesis | Yang et al. (2007)              | Several studies had identified QTLs for stem soluble carbohydrate reserves and, as in this case, the remobilization efficiency of those reserves (RESWC) and effect on yield. | QTL              | 1A, 3B, 7A | None            |
|                             | Numerous                        | The strong negative correlation between yield and protein content means that almost all yield QTLs correspond to an opposite effect for protein. |                  |            |                 |

For well-studied traits with high heritability, studies in which causative genes have been identified are prioritized. When most evidence is at the level of QTL studies or genome-wide association studies (GWAS), the support of independent validation using unrelated populations and/or NILs is used to help prioritize studies for inclusion. In several cases, the only level of genetic evidence (if any) is based on QTL studies without further validation. Priority is also given to studies in which the wider deployment of beneficial alleles is most likely to lead to progress in modern breeding programmes. In cases where no publications were found in spite of best efforts, this is stated. In all but a few cases, these studies are based on yield measured in field experiments with wheat grown in replicated plots.
Box 2. Phenology genes modifying grain number

There is an increasing body of evidence suggesting a role for phenology genes in increasing grain number and yield. The small number of genes shown to have a reasonably direct and consistent positive effect on grain number in wheat and also in rice, maize, and barley reveals something about the genetic control of grain set. Grain set is a highly plastic process, and the maximization of grain set is tightly linked with the adaptation of a crop to the environment in which it is growing. That is why the very first breeding activity undertaken when a new crop is incorporated in a region is adjusting the time to anthesis and, when optimized, other traits can then be improved. This is because optimizing the time to anthesis is critical for maximizing reproductive output (Fig. B1). In the WDs, this is represented by the boxes at the bottom of the diagram: phenology, total crop cycle, time of anthesis, and terminal spikelet to anthesis.

Fig. B1. Schematic representation of changes in harvest index associated with time to anthesis for a range of cultivars varying constitutively in their partitioning patterns (e.g. from very old to modern cultivars). The scheme illustrates why adaptation via adjusting time to anthesis is critical to maximize reproductive output: earlier or later than optimum times to anthesis penalize sink strength through damage from frost or heat, respectively. The most important genetic factors controlling time to anthesis are categorized as earliness per se, vernalization, and photoperiod sensitivity (Eps, Vrn, and Ppd).

The genetics of phenology in wheat are relatively well understood. The genes controlling winter/spring growth habit (Vrn-1, expressed more highly in the young spike after vernalization, Li et al., 2018) and photoperiod response (Ppd-1, expressed highly when spikelets are differentiated, Li et al., 2018), which are responsible for coarse-tuning time to anthesis, are well described elsewhere (Snape et al., 2001; Cockram et al., 2007; Bentley et al., 2013; Bloomfield et al., 2018; Hyles et al., 2020) and are often completely fixed in breeders’ gene pools that target a specific environment. Changing these environmental responses indeed affects grain number, but in the wrong direction when elite germplasm is already well adapted. However, QTLs with smaller effects on phenology are always present, even within the most mature breeding programmes. These are collectively recognized as Eps, earliness per se, genes and are critical for fine-tuning time to anthesis as well as for the duration of particular subphases composing time to anthesis (Appendino and Slafer, 2003; Lewis et al., 2008; Alvarez et al., 2016; Ochagavía et al., 2018; Basavaraddi et al., 2021b, c). This suggests that disruptive selection generates different combinations of phenology alleles to maintain and enhance genetic gain. The importance of phenology in the WD presentation is reflected by the compartmentation of the WDs into phenology subphases: stem extension; booting; anthesis; watery ripe; and maturity (Figs 4, 5, 8, 9). Five links in this review (Links 1, 13, 14, 29, and 34) relate to wires connected to these phenology phases.

Examples of relationships between genes and phenology are provided by QTLs on chromosomes 1D and 3A which were first identified as heading date QTLs in several UK and CIMMYT wheat populations (Griffiths et al., 2009; Sukumaran et al., 2016). Near isogenic lines (NILs) were developed, validating the heading date QTLs and resulting in a significant grain number effect in both cases. More detailed physiological dissection (Ochagavía et al., 2017) demonstrated that this grain number increase was due to increased floret survival. The 1D QTL effect was shown to be controlled by Ta-ELF3 (Alvarez et al., 2016; Zikhali et al., 2016). For the QTL on chromosome 3A, fine-mapping of the phenology and grain number effect suggested that the most likely candidate was FT2 (Martinez et al., 2021). FT2 has been further implicated in grain number in transgenic studies (Shaw et al., 2019) and diagnostic haplotypes proposed (Glenn et al., 2021).
Improved photosynthesis during the stem elongation phase (see Murchie et al., 2023) would result in improved growth of the juvenile spikes per unit land area (Link 2; Fig. 4). Maintaining spike partitioning could be achieved, for example, by avoiding tiller mortality and/or by increasing growth of the individual spikes. Proof of concept experiments have been conducted where the provision of resources affecting crop growth has been manipulated. For instance, the yield response to CO₂ enrichment in FACE (free-air CO₂ enrichment) experiments is consistently related more to improvements in grain number than to improvements in average grain weight (e.g. Ainsworth and Long, 2005; Sun et al., 2009; Fitzgerald et al., 2016), which is compatible with the idea that the yield advantage arises from the increased crop growth during the TS–An critical period for grain number determination. Another proof of concept can be found in a study combining an extensive range of nitrogen (N) doses and timings of application. Yield increases were always related to increases in grain number and spike dry weight at anthesis, but the response was similar for crops fertilized from early in the season or from the onset of stem elongation, implying that growth during TS–An rather than simply total biomass at anthesis or maturity was the critical aspect determining yield responses to fertilization (Fischer, 1993; Fischer et al., 1993; Dreckcer et al., 2000). Proof of concept is also provided by genotypic effects. It was demonstrated in a segregating population that QTLs for crop growth rate during the critical period of TS–An could be detected and that the genotypic differences in this rate explained most of those in spike growth and spike dry weight at anthesis (Abeledo et al., 2019). Similar results had also been reported earlier for a different population grown in two contrasting environments (Garcia et al., 2014). Finally, in another proof of concept research, genotypes possessing erect canopies that increase RUE and biomass, discussed in the companion paper (Murchie et al., 2023), increase yield through increasing grain number (Richards et al., 2019).

Increased grain growth requires increased allocation of assimilates to the spikes at anthesis (spike partitioning index; SPI; the ratio between spike and aboveground dry mass at anthesis: Link 3; Fig. 4) as was achieved by the gibberellin (GA)-insensitive semi-dwarf alleles (Miralles and Slafer, 1995; Flintham et al., 1997; Peng et al., 1999) and independent QTLs such as those described by Abeledo et al. (2019). Assimilates partitioned to the spike determine the proportion of floret primordia that survive to become competent florets at anthesis (Fischer, 1985; Miralles et al., 1998) and later grains. There is a negative association between spike and stem partitioning of assimilates because rapid growth of stem and spike coincides during stem elongation (Figs 1, 2), especially from booting to anthesis. Beyond GA-insensitive Rht-B1b and Rht-D1b genes, other dwarfing genes such as Rht13 (Rebetzke et al., 2011) or Rht18 (Tang et al., 2021) have been shown to increase grain yield, and others such as Rht8 may also increase yield but only under particular environmental conditions (Kowalski et al., 2016). These results support the general hypothesis that reductions in stem growth can favour increased metabolite flow to spikes, florets, and grains.

As plant height is a critical determinant of yield (Richards, 1992; Miralles and Slafer, 1995; Flintham et al., 1997; Lopes et al., 2018), it would have been optimized and fixed in wheat traditional growing regions, and further increases in spike growth would require the identification of sources of variation favouring partitioning of assimilates towards the juvenile spike independent of further reductions in plant height. Alternatively, reductions would be limited to small, specific stem internodes to favour spike growth (Link 4; Fig. 4) as proposed by Rivera-Amado et al. (2019), when the elite materials are taller than the lower limit of optimal plant height (Richards, 1992; Miralles and Slafer, 1995). Such alternatives were recently demonstrated with CIMMYT elite wheats that showed variation for an enhanced SPI related to increased spike growth before anthesis (Rivera-Amado et al., 2019). In this collection of 26 spring wheats, stem–internode lengths (for the peduncle, internode 2, and internode 3) were measured as proxies for stem–internode dry matter at GS65 + 7 d and strong negative associations between lengths for internodes 2 and 3 and spike growth (which occurs simultaneously) were observed. Sierra-Gonzalez et al. (2021) similarly observed in a panel of 150 CIMMYT spring wheat genotypes that stem–internode 3 length was negatively associated with spike partitioning index and grain number per unit area, supporting reducing the length of internode 3 as a strategy to increase spike partitioning and grains per unit area whilst maintaining lamina partitioning and lamina growth (Link 5; Fig. 4). Several studies have identified QTLs which control height by a disproportionate reduction in the length of specific internodes (e.g. Cui et al., 2011; Zhang et al., 2017). However, these studies did not include the measurement of SPI or grain yield.

Spike photosynthesis also plays an important role as a source of photoassimilates during grain filling, not only under drought, but also under optimal agronomical conditions (Araus et al., 1993; Tambussi et al., 2005, 2007; Maydup et al., 2010; Sanchez-Bragado et al., 2014a; Link 6; Fig. 5). Therefore, plant development profiles that favour spike growth in the pre-anthesis phase will also increase post-anthesis source strength through enhanced spike photosynthesis, helping to maintain optimum source–sink dynamics in modern cultivars.

All hypotheses and models incorporating transfer of source photoassimilates to the sink to achieve high sink growth activity must consider not only the rates of photosynthate generated and the diverse ways it is used in source materials, including storage, but also the efficiency of transport to sink tissue. There is now a general understanding of, for example, sucrose transport from leaves and stems to sink tissue that has been gained over the past 10 years in monocots, especially through molecular genetic studies on rice. The many transporters involved, their locations, and the energy requirements to move sugars in and out of vacuoles, through the plasmem and into sink cells, will have a large effect on the overall ability of
sink cells, tissues, and organs to grow and contribute to grain yield. Such systems may be rate limiting for yield (Braun et al., 2014; White et al., 2016). This hypothesis is supported by research on transgenic wheat plants expressing high levels of the AVP1 H+-PPase transporter gene from Arabidopsis (Regmi et al., 2020). The transgenes in these plants, constitutively expressed under the control of a maize ubiquitin promoter in the spring wheat cultivar Bobwhite L. stimulated augmented the presence of H+-PPase in the collection phloem and higher rates of carbon transfer into developing grains and higher yields, with higher numbers of grains per spike, in both greenhouse and field assays. The plants also showed enhanced carbon partitioning between shoots and roots. Further evidence of the importance of transfer of source photoasimilates to the sink is provided by studies where overexpression of the barley sucrose transporter, HvSUT1, under the control of an endosperm-specific promoter, enhanced sucrose flux into wheat grains. This resulted in elevated grain biomass and grain Zn and Fe content of transgenic winter wheat lines in field micro-plots (Saalbach et al., 2014) and grain protein content in greenhouse and field conditions compared with the wild-type cv. Certo (Weichert et al., 2010). Interestingly, CO2 fertilization negated these phenotypic responses in the transgenic lines, pointing to upstream factors regulating sucrose import into, or maternal transport within, developing grains (Weichert et al., 2017).

Transport of amino acids, metal ions, and other molecules is also vital for high yields. Transport of amino acids is dependent on supplies and storage of N compounds that late in the plant life cycle can be limiting. In addition, sucrose and nitrate are signalling molecules (e.g. Krouk et al., 2010; Tognetti et al., 2013; Lastdrager et al., 2014), and so the efficiency of these signalling effects may also contribute to the efficiencies of source to sink transfer of assimilates and essential metabolites. Finally, spike growth may be enhanced by manipulating the trehalose-6-phosphate (T6P) signalling system (Paul et al., 2020). Genetic and chemical intervention approaches have been used to modify the T6P pathway and improve performance of wheat (Paul et al., 2018), and this aspect of sugar utilization can contribute to enhanced partitioning of sucrose into spikes.

**Floret development and fruiting efficiency**

Yield increases due to environmental effects, such as N fertilization, are related to changes in spike dry weight at anthesis (e.g. Fischer, 1985, 1993; Prusty et al., 2004; Slafer et al., 2022) as a consequence of more floret primordia becoming fertile florets (Ferrante et al., 2020), supporting the proposed hypothesis that floret developmental rates reflect the resources allocated to the growing juvenile spikes (Ferrante et al., 2013a; Dreccer et al., 2014). Indeed, floret primordia mortality seems to be triggered by the trophic relationships associated with the initiation of the active growth of the juvenile spikes (González et al., 2011b; Ferrante et al., 2013b). Also, the relationship between number of grains set (or the number of fertile florets at anthesis) and spike dry weight at anthesis (Link 7, Fig. 5) is maintained during genetic improvement (e.g. Brookings and Kirby, 1981; Fischer and Stockman, 1980; Acreche et al., 2008). Much of the genetic gain obtained to date is due to the improvement of the growth of juvenile spikes, in large part due to the introgression of the Rth genes as described above (e.g. Siddique et al., 1989; Slafer and Andrade, 1993). However, not all genotypes translate resources transferred to the growing juvenile spike into grains with the same efficiency (Slafer et al., 2015, 2022). Fruiting efficiency is a key trait which reflects this (Link 8, Fig. 5). Fruiting efficiency (i.e. the efficiency for using dry matter allocated to the juvenile spike before anthesis to set a certain number of grains, determined as the number of grains per unit spike dry weight at anthesis; Slafer et al., 2015), is a measure of the outcome of processes related to floret development pre-anthesis (Fig. 5), as well as grain abortion post-anthesis (Fig. 8). There is genetic variability in fruiting efficiency among modern wheat cultivars that correlates well with grains per unit area (González et al., 2011a; Elia et al.,

Fig. 6. Dynamics of development of individual florets within spikelets, considering proximal florets (say the 2–3 florets most proximal to the rachis; FP), intermediate florets that are labile florets, depend on the G×E conditions, and may progress to produce a fertile floret or die (say florets 3–5, depending on the specific spikelet; FL), and distal florets (say florets 5–6 or more distal, that never produce fertile florets; FD). The scheme illustrates that when the period of floret development, from the onset of floret development (OFD) to anthesis (An) is extended (dashed lines), the longer period available for each floret to develop allows some labile florets to keep developing normally and to produce fertile florets instead of dying. Curved black lines represent the dynamics of the number of living floret primordia. The mark on the axis of floret score indicates when a floret primordium reaches the stage of fertile floret.
Effective grain filling of cultivars (Slafer and Andrade, 1993) but also within modern cultivars (González-Navarro et al., 2016; Rivera-Amado et al., 2019; Slafer et al., 2022) with QTLs and identified MTAs (e.g. Gerard et al., 2019).

Improvements in fruiting efficiency may arise from an accelerated rate of floret development and improved partitioning of spike assimilates between the main body of the spike and its developing florets (Link 9, Fig. 5). In fact, both might be linked because increasing the allocation of resources to spikes increases the rate of floret development (Ferrante et al., 2013a; Dreccer et al., 2014). Genetic variation in the rate of floret development in the absence of variation in spike growth seems possible (Ferrante et al., 2020) where a difference in floret development is due to improved intra-spike assimilate partitioning favouring florets over the structural tissues of the spike (Foulkes et al., 2011; Slafer et al., 2015; Rivera-Amado et al., 2019). Indeed, variation in intra-spike partitioning, with a concomitant increase in biomass occurring in developing florets instead of structural components of the spike (rachis, glumes, and so on), has been shown not only between old and modern cultivars (Slafer and Andrade, 1993) but also within modern germplasm (Abbate et al., 1998; García et al., 2014). However, there are uncertainties about the potential for manipulating this partitioning effect within the juvenile spike as the physiology of this partitioning has not been studied in great detail (Fischer, 2007) and assessments of potential drawbacks require more data and further analysis (Foulkes and Reynolds, 2015). There is also evidence that genetic variation in fruiting efficiency is influenced by levels of spike hormones (see later). Several QTLs (although not yet validated) for fruiting efficiency have been reported (e.g. Giunta et al., 2018), and should be useful for breeding because the trait is heritable, exhibits transgressive segregation (Martino et al., 2015), and responds to selection (Pedro et al., 2012; Alonso et al., 2018). During the anthesis to watery ripe period, influences on fruiting efficiency may also result from grain abortion (i.e. failure of fertile florets to set grains; see later).

There may exist a trade-off between fruiting efficiency and spike dry matter (Link 10, Fig. 5), as reported in independent studies (e.g. Dreccer et al., 2009; Lázaro and Abbate, 2012), particularly when differences in grains per m² are small (Slafer et al., 2022). However, many cultivars having both high fruiting efficiency and high spike weight at anthesis have been identified (Bustos et al., 2013; García et al., 2014; Elia et al., 2016; Ferrante et al., 2017). This suggests there is no feedback regulation between these traits, and it is possible (and likely) to achieve an increase in one with no compensating responses from the other. Nonetheless, in breeding for improved fruiting efficiency, breeders should be alert to any trade-off with spike dry weight at anthesis and should select against it in the progeny being selected.

Floret initiation during the phase from the onset of stem elongation to booting is only marginally responsive to spike growth. Therefore, genotypes differing strongly in the allocation of resources to spike growth and then spike fertility do not differ in the maximum number of viable floret primordia just prior to booting (e.g. NILs for Rht genes have clear differences in spike fertility but similar maximum numbers of florets initiated; Miralles et al., 1998). Thus, environmental factors affecting growth before booting barely affect the number of primordia initiated (Ferrante et al., 2013a). During the following period, from booting to anthesis, floret development is highly responsive to spike growth, or vice versa (Link 11, Fig. 5). Most proximal florets normally develop to produce a fertile floret, while distal floret primordia always die before becoming a fertile floret (e.g. Ferrante et al., 2020), probably because they have a rather delayed onset of development (Backhaus et al., 2022). Labile florets in intermediate positions of the spikelets either progress towards producing fertile florets or die, which is critical in determination of overall spike fertility. The potential of each of these intermediate floret primordia to progress through normal development and become a fertile floret, or alternatively abort, depends on the influx of resources to the growing juvenile spike. This has been demonstrated by altering the dynamics of spike growth using environmental interventions (Ferrante et al., 2013a) as well as studying genetic variants (Miralles et al., 1998; González et al., 2011b) including NILs for cloned QTLs (Prieto et al., 2020).

It has been postulated that, during the evolution of the wild grass ancestors, natural selection favoured the production of a very large number of floret primordia, regardless of the conditions, whose development is dependent on the subsequent

![Diagram of grain volume and weight phases](image-url)

**Fig. 7.** Schematic representation of the dynamics of grain volume and weight from anthesis to maturity (weight of pericarp and endosperm are shown in dotted lines). The stages of anthesis (An), watery ripe grain (WR), and physiological maturity (PM) as well as the duration of the lag phase and the effective grain-filling period are indicated underneath the abscissa. Changes in grain volume and colour from anthesis to maturity are illustrated on top. During the lag phase, non-aborting grains develop actively, producing the endosperm cells, and actively take up water which drives a large increase in volume. Grain volume is maximized first (establishing a likely upper threshold for grain size and, from then on, during the effective grain-filling period, assimilates are actively loaded into the grains and the actual grain weight is finally realized.)
availability of resources (Sadras and Slafer, 2012). Genetic strategies to test and exploit this hypothesis include reducing the duration of the TS to the initiation of booting phase while increasing the duration of booting to anthesis. Although several studies on the timing and duration of these phases have been published (e.g. Guo et al., 2018), limited evidence for the effects of the specific reduction of the duration of this phase on spike growth and floret development is available.

There may be a trade-off between floret development and grain abortion (Link 12, Fig. 5). Ovary size at anthesis is associated with both floret survival (pre-anthesis) and grain abortion (post-anthesis), providing a connection between these two traits (see later). Thus, assimilates available to distal florets may play a critical role in regulating both floret survival and grain setting (Ferrante et al., 2020).

Timing of anthesis directly affects sink strength (Link 13, Fig. 5) because it influences the period of floret development and so the ambient temperature experienced by those florets. Suboptimal temperatures immediately before anthesis reduce fruiting efficiency, when anthesis is earlier (low-temperature damage to floral organs) or later (heat effects on floret fertility) than optimum for each particular environment. High temperatures > 31 °C can lead to sterility through floret abortion and/or reduction of pollen tube development, and increases of pollen mortality in wheat (Prasad and Djanaguiraman, 2014). A one pot temperature transfer study showed the ‘double dip’ effect of high temperature at phases that might correspond to meiosis and microsporogenesis (Barber et al., 2017). There are also effects of low temperatures, with meiosis at the early booting stage identified as the most sensitive period (Thakur et al., 2010; Ji et al., 2017). In the UK and France, cold and wet weather during floral development in the wheat variety ‘Moulin’ caused significant sterility and a reduction in grain yield of > 70% (Law, 1999) due to low temperatures at meiosis. It was suggested that Moulin might carry specific alleles from diverse sources that made it more sensitive to cold weather during meiosis. The meiotic recombination gene Dmc1 on wheat chromosome 5D has been identified as a candidate for the maintenance of normal chromosome synopsis and crossover at low and possibly high temperatures (Draeger et al., 2020). Meiosis is preceded by a long pre-meiotic cell cycle where many epigenetic events take place. This phase may be very sensitive to temperature and other stresses that can lead to floret abortion. An examination of the portfolio of genes highly expressed during these phases revealed that those which confer stress tolerance are especially active during the double ridge phase (Li et al., 2018), indicating that spike development is inherently stressful, particularly due to poor supply of nutrients.

Given that anthesis date is usually the first trait optimized in breeding programmes, any lengthening of the duration of the critical phase for grain number determination (TS–An) would further indirectly increase the number of florets that develop normally through increasing the growth accumulated in that phase (see above; Link 1, Fig. 5). There may also be a direct effect: if the onset of floret development is not proportionally delayed, there would be additional time for the development of individual florets, allowing some labile florets to develop into fertile florets instead of stopping their development and dying (Link 14, Fig. 5). As floret initiation is far less responsive to genetic and environmental factors than floret mortality (Sadras and Slafer, 2012) during the period of booting to anthesis (when floret mortality takes place), extending the duration of the phase provides more time for floret development, thereby increasing the number of florets that develop normally (Fig. 6).

Extension of the floret development period does not affect the progress of the most robust primordia (e.g. florets most proximal to the rachis) but increases the chance of labile floret survival (e.g. the fourth or even fifth floret position in central spikelets and florets 2–3 of more basal and apical spikelets). These labile florets would stop developing in other circumstances (contributing to floret mortality) but, provided with an extended period of development, can progress to fertile florets instead of dying before anthesis (González-Navarro et al., 2015; Prieto et al., 2018; Perez-Gianmarco et al., 2019).

In summary, the likely effect of a longer duration of stem elongation would function more through floret survival than simply floret initiation (e.g. González-Navarro et al., 2005; Guo et al., 2016; Fig. 6), thereby principally affecting fruiting efficiency; and would be more relevant during the phase from booting to anthesis rather than TS to booting. Empirical support for this was reported by Wang et al. (2017) in demonstrating that expression levels of single genes can lead to more florets and a longer duration of spike development and by González-Navarro et al. (2015) who demonstrated that fruiting efficiency showed a positive trend with the duration of stem elongation. A boundary function suggested that the length of this phase may impose a threshold for fruiting efficiency and grain number, and that maximum fruiting efficiency may require both generation of many florets and a relatively long stem elongation phase, as illustrated by manipulating daylength in the field to make the period from TS to anthesis longer or shorter, affecting floret development (Gonzalez et al., 2003, 2005; Serrago et al., 2008).

Hormones and vascular architecture

There is increasing evidence that variation in fruiting efficiency is regulated by plant growth regulators during the rapid spike growth phase from booting to anthesis (Link 15, Fig. 5). Auxin and cytokinin (CK) are key regulators during meristem formation, and their interactions regulate meristem differentiation and function. CKs stimulate cell division and nucleic acid metabolism, and are known to be associated with grain number in wheat (Sakai, 2006). Higher CK signalling levels occur before the double ridge phase which helps retain meristem activity, while high auxin activity is
up-regulated from the double ridge stage, most probably contributing to the generation of new axillary meristems (Li et al., 2018). However, there is a negative correlation between auxin concentration and the number of fertile florets at the abortion stage. Adding exogenous 6-benzylaminopurine (6-BA, a synthetic CK) during the abortion stage increased the CK level, reduced the auxin level, decreased the number of floret abortions, and increased spike dry weight (Li et al., 2019). Thus, increasing CK levels in spikes during the floret abortion phase results in increased grain number, for example, by decreasing cytokinin oxidase activity that catalyses the degradation of CK (Bartrina et al., 2011; Zhang et al., 2011). CK levels are regulated by a balance between biosynthesis [e.g. isopentenyl pyrophosphate transferase (IPT)] and degradation [e.g. cytokinin oxidase/dehydrogenase, CKX] enzymes. The grain sink strength of the spike meristem could therefore be enhanced by altering CK homeostasis through the up-regulation or down-regulation of these enzymes, respectively, to coordinate growth and floret fertility (Li et al., 2019). While there has been speculation on a possible trade-off between fruiting efficiency and spike dry weight at anthesis (see above; Link 10, Fig. 5), manipulating spike hormones may offer breeders one avenue for simultaneously raising both.

Hanif and Langer (1972) showed that floret fertility is dependent on spike vascular architecture (Link 16, Fig. 5). Therefore, improved knowledge of vascular bundle development and connectivity is required to better understand floret survival in wheat. There is evidence for branching of the main vascular bundles in the spike rachis (Kirby and Rymer, 1974; Whingwiri et al., 1981; Wolde et al., 2019), but it is not yet clear how the assimilates are allocated to each of the branch units—the spikelets. It has been suggested that florets closer to the rachis node (i.e. the basal three florets in the spikelets) are directly supplied by the principal vascular bundles of the rachilla, while the distal florets lack a direct connection to the vascular bundle (Hanif and Langer, 1972) and therefore might not have an equal chance of accessing assimilates from the source. Wolde et al. (2019) postulated that the vascular structure in the wheat spikelet might relate to the wide conduits assigned at the base of the spikelet feeding the narrower conduits of the distal florets. In summary, if florets are formed normally with a good potential for viability, the flow of assimilate may be too limiting to support all rapidly growing florets because of features of the spike vascular architecture.

The number and arrangement of each spikelet on the spike are under strong hormonal control (McSteen, 2009; Pour-sarebani et al., 2015; Dixon et al., 2018). However, relatively little is known on the role of plant hormones in regulating the development of the spike vascular architecture (Link 17, Fig. 5), especially the main conducting elements (i.e. the sieve tube elements) and their architectural configurations in the spikelet/floret. There is evidence that the PIN-FORMED1 (PIN1) efflux carrier concentrates auxin into local maxima in the epidermis, which position incipient leaf or floral primordia in angiosperms. In Brachypodium distachyon, transgenes for the duplicate PIN1 clade members PIN1a and PIN1b were shown to stimulate the transport of auxin from these maxima into internal tissues along emergent paths that pattern leaf and stem vasculature (O’Connor et al., 2014). Therefore, the PIN1 genes may have a role in determining the paths that pattern spike vasculature. Genes controlling wheat spike architecture and spikelet arrangement have already been reported (Boden et al., 2015; Dixon et al., 2018; Wolde et al., 2019), but to date no genes determining spike vascular architecture have been identified. In summary, the elucidation of spike vascular architecture and its genetic regulation is at an early stage and requires more study.

Ovary size and grain weight potential
As discussed above (Link 12, Fig. 5), a possible mechanism for increasing fruiting efficiency would be reduction of the resource threshold required for floret development (Slafer et al., 2015). This would permit a larger proportion of initiated florets to survive, but these would all be reduced in size (Drecker et al., 2009). This would not be ideal as the improvements in fruiting efficiency would come at the cost of compensatory reductions in grain weight (Link 18, Fig. 5). Thus, this avenue for improving fruiting efficiency would probably be inefficient in improving yield (Ferrante et al., 2015).

The connection between ovary size and final grain weight is based on the fact that potential grain weight is related to the size of the ovary (Calderini et al., 2001; Hasan et al., 2011; Xie et al., 2015; Reale et al., 2017). This relationship has been demonstrated regardless of the source of variation, that could be either genotypic (Calderini and Reynolds, 2000; Yu et al., 2015; Simmonds et al., 2016) or environmental (Wardlaw, 1994; Calderini et al., 1999; Ugarte et al., 2007). Because the ovary wall becomes the pericarp of the grain, the size of the ovary determines the upper limit for grain growth (i.e. grain weight potential; Link 19, Fig. 5). Thus, the final size of the grains would appear to be regulated by maternal tissues, because grain weight potential is a critical determinant of final grain weight (Link 20, Fig. 5).

Final grain weight is the result of a balance between potential size of the grains and the capacity of the crop to realize this potential during the effective period of grain filling. As the capacity of the source to fill the grains seems to be in excess of the demands of the growing grains (see also below), grains normally grow as much as they can; that is, they mostly do not respond to manipulations of source strength per growing grain from the onset of the effective period of grain filling. This significantly reduces their plasticity (compared with that of grain number; Sadras, 2007; Slafer et al., 2014) and is a major cause for the much higher heritability of final grain weight compared with any other yield component (Sadras and Slafer, 2012). The final grain weight then depends on the capacity of the grains themselves
to grow, an attribute that is genotypically determined by the potential size of the grains and environmentally regulated by factors affecting the capacity of the grains to fulfil that potential (e.g. high temperatures during the effective period of grain filling reduce grain weight by directly affecting their capacity to grow, in addition to any effects they may also have on leaf senescence). The potential grain weight is determined prior to the onset of the effective grain filling (Calderini et al., 2001; Fahy et al., 2018; Xie et al., 2015) by the size of the ovary determined during booting to anthesis (Link 19, Fig. 5), and the number of endosperm cells and maximum water content determined during anthesis to watery ripe (see below).

These latter two inter-related traits (number of endosperm cells and maximum water content) are likely to be pre-determined by the ovary size (Link 21, Fig. 5). There is evidence showing a positive relationship of grain weight potential to either ovary size (Singh and Jenner, 1982; Calderini et al., 1999; Hasan et al., 2011), number of endosperm cells (Brocklehurst, 1977; Gleadow et al., 1982), or maximum water content (Saini and Westgate, 1999; Pepler et al., 2006; Hasan et al., 2011). For all three traits, the independent variables reflect the sink capacity of each single grain: the ovary wall becomes the pericarp of the grain, the endosperm cells are the units where starch will be stored, and the maximum water content provides a reference to the volume of the grain. Furthermore, when analysed together, ovary size, water accumulation, and grain dimensions are probably controlled by the same QTLs (Xie et al., 2015).

Ovary size at anthesis represents a possible predictor for grain setting (Guo et al., 2016) and is naturally related to the allocation of resources to the spike (Link 22, Fig. 5). In the field, spike dry weight was positively associated with ovary size for 30 European winter wheat genotypes (Guo et al., 2016), probably due to a longer duration of pre-anthesis phases (see above). Ovary size has been reported to have high heritability (Komaki and Tsunewaki, 1981; Guo et al., 2015), and QTLs for grain size, validated for their effects on grain yield, have been identified (Simmonds et al., 2014).

**WDs from anthesis to maturity**

As discussed above and in a previous paper (Reynolds et al., 2022), it is mainly during the pre-anthesis period when yield potential is determined. During the post-anthesis period, potential yield is finalized and actual yield is achieved from this potential through the process of grain weight realization.

‘Grain filling’ comprises two subphases that contribute differently to yield (Fig. 7). The first occurs during ~7–10 d (depending on temperature) from anthesis to the stage of watery ripe grain, when potential yield is finally established, thereby determining sink strength during the effective period of grain filling. In the embryo, this period is marked by the establishment of the new genotype following fertilization, during which many epigenetic events establish the potential gene expression profiles in the embryo and at later developmental stages.

During this first period, both the final number of grains and their final potential size are established through (i) the level of abortion determined by the proportion of fertile florets setting grains that grow normally afterwards, and (ii) the final volume of the grains to be subsequently filled with assimilates (Fig. 7). During this period, overall development is very active, with multiplication of endosperm cells, but there is virtually no growth of the grains (in terms of dry matter gain). This period is commonly known as the ‘lag phase’, referring to the delay before initiation of dry matter gain. The second subphase is significantly longer (~25–50 d, depending on temperature) and known as the effective period of grain filling (Fig. 7). The completion of the effective grain-filling phase defines the physiological maturity of the crop.

As in the pre-anthesis WD, the period from anthesis to maturity is divided into two WDs to provide a detailed description of key traits. The first focuses on traits determining sink strength from anthesis to watery ripe (Fig. 8). The second focuses on the effective grain-filling period from watery ripe to maturity (Fig. 9).

**The relevance of grain weight to determination of harvest index and yield (major Link B, Fig. 8)**

Relevance of grain size in wheat

Final grain size is one of the two major yield components (Slafer et al., 2014) and is therefore a critical factor to consider when attempting to improve yield, particularly as it has a relatively high heritability (significantly higher than the number of grains set by the crop; e.g. Egli, 1981; Kuchel et al., 2007; Sadras and Slafer, 2012), and several genetic factors have already been identified that could be exploited (see below).

Conversely, grain size is a rather conservative trait exhibiting far less variation than grain number (e.g. Peltonen-Sainio et al., 2007; Sadras, 2007) and there are evolutionary reasons (also exploited in breeding) why grain size is less plastic than grain number (Sadras and Slafer, 2012). As such, the expected magnitude of yield improvement that might be envisaged through selecting for larger grains would probably be modest. An indirect proof of concept for this is that wheat breeding has more frequently made yield advances by improving grain number (despite the expected difficulties with the low heritability of grain number, as already described in Link A; although exceptions can be identified (e.g. Aisawi et al., 2013)). In addition, breeders have usually sought greater homogeneity in the weights of individual grains in seed lots (Finch-Savage and Bassel, 2016), because when grains undergo industrial processes such as milling, high variability in weight adversely affects the nutritional and processing quality of the end-products.
A factor that partly explains the low plasticity of grain size is the lack of source restrictions (considering together post-anthesis photosynthesis and remobilization of pre-anthesis stored reserves) to fill the grains (see also Links 30 and 31, Fig. 9). However, as past breeding has consistently exploited this avenue through increasing grain number, current elite material might be exhibiting an incipient co-limitation from both source and sink strengths (e.g. Shearman et al., 2005; Acreche and Slafer, 2009; Aisawi et al., 2015), although, even in these cases of incipient ‘co-limitation’, yield is far more sink limited.
than source limited during grain filling. Thus, the relevance of grain size may increase in future breeding efforts to raise yield potential. While this restriction in variability for grain size is linked directly to effective grain growth, final grain size also depends on the potential size of the grains. Therefore, achieving positive impacts on yield by improving grain size through increasing grain weight potential may be possible (see details and references in Link 20). However, this would only be effective if potential trade-offs between the generation of grain number and potential grain weight are recognized and
avoided (see Links 18 and 22), for instance, through the selection of germplasm with higher grain weight potential (and normally higher final grain size) achieved without sacrificing grain number (see discussion on this trade-off in Slafer et al., 2015). The fact that empirical evidence shows that it is possible, in some lines, to combine high grain number with larger grains (e.g. Bustos et al., 2013; Calderini et al., 2021) is encouraging.

**Genetic variation for grain size in wheat**

There is a rich body of literature describing the genetic architecture of this trait and the molecular genetics underpinning wheat grain development, probably due to the high heritability of grain size. It is generally the case that QTLs for grain size are not accompanied by QTLs with positive effects for yield. Indeed, alleles responsible for increasing grain size usually co-locate with QTLs for decreased grain number per unit area, reflecting the physiological trade-off already described (e.g. Zhai et al., 2018). Due to the unbalanced nature of this trade-off, in the direction of grain number, there is quite often a significant yield penalty that accompanies increasing grain size. Therefore, the challenge for future yield improvement is to devise strategies that will enhance the scope for potential grain weight to respond to availability of assimilates without unduly enhancing the risk of incomplete grain filling.

It will be important for such work to be underpinned by genetic analysis, and it is encouraging that, for a range of different wheat crosses, several QTLs and MTAs controlling grain yield have been discovered that influence individual grain weight without pleiotropic effects on grain number (Snape et al., 2007; Calderini et al., 2021). A detailed review of the genetics and development of the wheat grain is given in Brinton et al. (2018). Here we focus on variants for grain size that appear to minimize the trade-off and so show promise for the improvement of grain yield within current breeding programmes that target high yield potential environments. This also means that these effects need to have been validated beyond their initial description as QTLs, MTAs, or induced variants (Table 1). It should be emphasized that grain size is important beyond grain yield. The manipulation of grain size also influences early plant establishment, specific weight, milling efficiency, and market preference. Our criteria for further description should not be taken to mean that the genetic effects not described in detail here are unimportant.

Robust and NIL-validated grain size effects have been described on wheat chromosomes 2A (Farre et al., 2016), 2D (Huang et al., 2015), 4A (Guan et al., 2019), 4B (Huang et al., 2015), 5A (Farre et al., 2016; Huang et al., 2015), and 6A (Simmonds et al., 2014; Farre et al., 2016). Of these, it is only the QTL on chromosome 6A which has been shown to have a consistent beneficial effect on grain yield. This QTL was first identified in multiple UK elite winter wheat populations (Snape et al., 2007; Ma et al., 2015) and then validated (Simmonds et al., 2014; Farre et al., 2016). Candidate genes for this QTL have been studied in some detail, in particular the wheat orthologue of GW2 from rice. Su et al. (2011) and Zhang et al. (2013) both identified significant associations of TaGW2 alleles with grain size. Simmonds et al. (2016) used tilling populations to identify a G to A transition in the splice acceptor site of exon 5 of TaGW2-A1 which leads to mis-splicing of the mRNA transcript and larger grains. These results increase our knowledge of the genetics of grain size, but some uncertainty remains as to whether TaGW2 and these associated alleles really underlie the 6A QTL for grain size and yield effects. The first two studies show association of opposite alleles with the increasing effect, and the rate of recombination on chromosome 6A is so low that most of the genes mapped on it are present in very few haplotypes. This would suggest that TaGW2 is a negative regulator of grain size in wheat, similar to the function in rice, but is probably not the same as the yield-increasing effect identified by Simmonds et al. (2014). It is most likely that the expansive 6A haplotypes carry multiple genes that influence different yield components (Sukumaran et al., 2018; Brinton et al., 2020).

**Main traits and relationships determining sink strength after anthesis**

**Grain abortion**

Grain number depends principally on the number of fertile florets that are pollinated but also on the proportion of grains which abort before starting their active growth. The latter process takes place in the ‘lag phase’ of ~7–10 d after anthesis (the period from then to watery ripe grains). After anthesis and pollination have occurred and before grains start to grow, there is a critical process of grain set responsible for the proportion of fertile florets effectively becoming growing grains. This is when the maternal and paternal sets of chromosomes undergo epigenetic changes and embryo development is initiated. Although in elite germplasm, including modern cultivars, most fertile florets successfully develop a grain, a variable number of grains abort before they start growing (abortion ranging in modern cultivars under non-stressed field conditions from virtually zero to ~40%; Siddique et al., 1989; González et al., 2003; Elía et al., 2016; Guo et al., 2016). This process seems to be sensitive to environmental and genetic stresses (e.g. Savin and Slafer, 1991; Hays et al., 2007). For example, high temperatures (Prasad and Djanaguiraman, 2014) and lack of N availability (Ferrante et al., 2013a) can increase grain abortion. Guo et al. (2016) demonstrated a large genetic variation in grain set in both field and glasshouse conditions and across all spikelet positions studied, although the trait also displayed moderate levels of heritability. More recently it was established that grain set was a relevant component of genetic variation in fruiting efficiency (Pretini et al., 2020a). Thus, grain abortion is a component of fruiting efficiency (Link 23, Fig. 8), and improvements in the latter could be achieved through reducing grain abortion.
One possible avenue to reduce grain abortion would be to select against florets of very small size, as small florets probably produce abortive grains (Link 24, Fig. 8). Fertile florets vary greatly in size, depending on their position in the spikelet and the size and shape of the spikelet in the spike and the chronological order of the spike-bearing tiller. Allowing more floret primordia to become fertile florets without proportional increases in availability of resources for floret growth would increase the proportion of fertile florets that are small. This occurs normally with the most distal florets becoming fertile. Empirical data show that the size of the ovaries at anthesis could be used as a predictor for the probability of grain setting (Guo et al., 2015). Guo et al. (2016), comparing contrasting genotypes for the size of the ovaries of the fourth floret from the rachis (a distal floret), reported that smaller ovaries led to increasing probabilities of grain abortion. This reinforces the hypothesis that for fruiting efficiency to be a relevant trait for yield improvement, it should not be achieved at the expense of having smaller florets but instead by increasing intra-spike partitioning favouring floret growth. Empirical evidence supports the fact that genotypic differences in fruiting efficiency could be independent of concomitant differences in ovary size (Elia et al., 2016).

Grain abortion may also be affected by spike hormones (Link 25, Fig. 8). It has been observed that excessive ethylene production results in wheat grain abortion under high temperature stress (Hays et al., 2007), suggesting that grain accumulation of ethylene may be a trait to target. Similarly, a negative association was observed at high temperatures in the field between spike dry weight at anthesis and ethylene production in a genome-wide association study population, and the genetic basis underlying this trait was suggested (Valluru et al., 2017). High ethylene levels can reduce grain yields in maize by accelerating embryo and grain abortion, thereby reducing sink size (Shi et al., 2015). In addition, there is a clear indication that accumulation of abscisic acid (ABA) in developing grains of maize can result in grain abortion (Wang et al., 2002). In addition, CKs during the grain abortion phase have been identified as playing a potentially relevant role in increasing sink strength (Zalewski et al., 2010; Li et al., 2019). In summary, pinpointing the plant hormone signals underlying grain abortion and their genetic control in wheat may allow the development of genotypes with a less conservative strategy for determination of grain number.

It also seems likely that grain abortion may be influenced by the spike vascular architecture (Link 26, Fig. 8), especially for the distal florets which are too small to avoid abortion after pollination (see above; Link 23, Fig. 8), but more needs to be known about this. The vascular system of the spike is sufficiently different from the pattern encountered in vegetative nodes to warrant unique study (O’Brien et al., 1985). The basal three florets in the spikelets appear to be directly supplied by the principal vascular bundles of the rachilla, while the distal florets may lack a direct connection to the vascular bundle (Hanif and Langer, 1972; O’Brien et al., 1985). Thus, mechanical modifications to improve the vascular connectivity of the bundles supplying the distal florets might increase assimilate translocation and reduce grain abortion. However, little is presently known about how sieve tube elements in the bundles are distributed in wheat spikelets and how a single sieve tube bifurcates at each junction of the branches. Therefore, further study of the phloem anatomy and structure in wheat spikelets to develop a mechanistic working model using the appropriate genetic material is important to exploit this potential avenue to reducing grain abortion (Wolde and Schnurbusch, 2019).

**Grain weight potential**

Grain weight potential, together with the number of grains set, is the final component determining sink strength during grain filling. Grain weight potential is initially determined through attributes related to the size of the ovary (see above) and complemented by the number of endosperm cells that are produced in each of the grains (Link 27, Fig. 8). Endosperm formation is initiated by very rapid DNA synthesis without cell division to produce a coenocytic bag. The number of rounds of DNA replication influences the number of endosperm cells and hence grain weight potential. The endosperm consists of cells with widely differing shapes and sizes, with large numbers of small, regularly shaped cells beneath the aleurone layer and small tubes of large, isodiametric cells in the central parts of the tissue (MacMasters et al., 1971). Despite this variety of cell types, the final endosperm cell number is related to final grain weight, as it is in these cells that starch (by far the largest component of grain dry matter; Stone and Savin, 1999; Shewry, 2009) is stored. Endosperm DNA content and cell number are both positively associated with mature grain weight among a range of genotypes. However, not all of the variation in grain weight can be attributed to variation in cell number because of differences in mean dry weight per endosperm cell (Chojecki et al., 1986). Genetic variation exists for the rates of increase of DNA and cell number which are related to final grain weight (Bennett et al., 1975).

The switch from mitotic division to endoreduplication is associated with decreases in mitotic CKDs (cyclin-dependent kinases; protein kinases regulating the cell cycle) and increases in S phase CDKs (Sabelli and Larkins, 2009). If endoreduplication boosts the number of cells to drive rapid carbohydrate and protein synthesis, then the numbers of rounds of endoreduplication is relevant to define potential grain size. Zeatin is high in early endosperm formation when cell division and the mitotic index are high (1–3 d), while indole acetic acid (IAA) is boosted later when endoreduplication occurs. Endosperm filling has been thought to be determined by the rate of transport of sugars (and N) into endosperms, and the energy available for biosynthesis. This appears to be rate limiting per endosperm because if florets are removed then the remaining endosperm/grains become larger (Calderini and Reynolds, 2000). However, Calderini et al. (2021) recently illustrated
Grain weight realization

Grain weight realization is related to the rate and duration of grain growth. Genetic variation exists for both processes, and positive relationships are reported between final grain weight and each of these two components (most commonly the rate of grain filling; e.g. Calderini and Reynolds, 2000; Charmet et al., 2005; Xie et al., 2015). However, as the availability of assimilates (actual photosynthesis plus available reserves) seems to be in excess of the sink capacity to store them during the effective period of grain filling (e.g. Borras et al., 2004; Reynolds et al., 2005; Cartelle et al., 2006; Serrago et al., 2013; Borrill et al., 2015; as discussed in the previous paper; see fig. 1 in Reynolds et al., 2022), the relationship between grain filling and final grain weight is less relevant than that between potential and actual grain weight. Clearly, grain weight realization will always be tightly linked to final grain weight (Link 31, Fig. 9), but this realization depends more on the capacity of the grains to grow than on the availability of assimilates. Thus, despite the high correlation, the link is not considered as having the highest relevance, at least under optimal growing conditions. This is borne out by the fact that considerable amounts of WSCs often remain in the stem when measured at physiological maturity (Foulkes et al., 2002; Serrago et al., 2013). Under a given temperature regime, genetic variation in the duration of grain filling is smaller than in the rate of grain growth (e.g. Sofield et al., 1977; Duguid and Brülé-Babel, 1994); therefore, only small improvements in final grain weight might be achieved in yield by lengthening the duration of grain filling (Link 32, Fig. 9). The effect of high temperatures on reducing grain weight, however, is more related to duration than rate of grain filling (Sofield et al., 1977; Wiegand and Cuellar, 1981).

Finally, when grain weight potential is fixed, the sink strength of the crop during the effective period of grain filling (from watery ripe to physiological maturity) is established. This level of sink strength established by the crop may influence the levels of canopy photosynthesis during grain filling (Link 30, Fig. 9). Although in theory yield potential of wheat would be determined by photosynthesis over the entire growing season, it may be that photosynthesis influences yield increases only during periods of crop growth that are source limited (see conclusions in Reynolds et al., 2005; and the paper introducing the concept of the WD; Reynolds et al., 2022). There have been reports, among contrasting genotypes, associating post-anthesis canopy (including spike) photosynthesis with yield when comparing modern/semi-dwarf and old/tall genotypes (e.g. Calderini et al., 1997; Miralles and Slafer; 1997; Reynolds et al., 2005, 2001). Intuitively it may be interpreted that the improved photosynthetic rates resulted in the yield improvements. However, evidence suggests otherwise. Improved sink strength results in increases in photosynthesis and RUE during the effective period of grain filling, and leaf, spike, and canopy photosynthesis was down-regulated from watery ripe to maturity when there is insufficient sink strength (e.g. Acree and Slafer, 2009; Serrago et al., 2013). This conclusion, from experiments manipulating source–sink balances, is in line with the evidence coming from increasing sink strength genetically (e.g. Calderini et al., 1997; Miralles and Slafer, 1997), and was further proven when strategic crosses done in a realistic breeding context demonstrated that increasing sink strength boosts RUE (Reynolds et al., 2017).
is also a major contributor of assimilates filling the grains (Tam-bussi et al., 2007; Maydup et al., 2010). By using different tech-
niques, it has been shown that in general most of the assimilates
used to fill the grains effectively come from the actual leaf (and
particularly the flag leaf) and spike photosynthesis (Sanchez-
Bragado et al., 2014b, 2016) (Link 33, Fig. 9). There is evi-
dence that breeding has improved post-anthesis photosynthesis
and RUE (Calderini et al., 1997; Molero and Reynolds, 2020),
and recently Molero and Reynolds (2020) demonstrated that
spike photosynthesis is a heritable trait. However, some redu-
dancy may exist between particular organs if their photosyn-
thetic contribution is replaced by other sources, including the
remobilization of reserves stored in the stems before the onset
of grain filling. Further, improving leaf/spike photosynthesis
during the effective period of grain filling would probably pro-
duce gains in yield, only in cases where grain filling was source
limited, a situation that is not common, particularly for poten-
tial yielding conditions (see other links in this paper, as well as
discussion on spike photosynthesis in the companion paper by
Murchie et al., 2023). It follows that in some cases photosyn-
thetic activity during grain filling may be a consequence rather
than a cause of increased yield (e.g. Calderini et al., 1997).

Although not the most common situation, there is never-
theless evidence in modern wheat cultivars of some source
limitation during grain filling under optimal conditions. In
this situation, grain growth is co-limited during grain filling,
as sink capacity is limited during early grain filling and source
capacity is limited at later stages of grain filling (Acreche and
Slafer, 2009). The stay-green trait and extended duration of
grain filling (Link 34, Fig. 9) may be associated with yield
gains in these situations. Genetic variation for functional stay-
green—delayed senescence associated with extended photo-
synthesis (Thomas and Howarth, 2000)—has been reported in
bread wheat (Christopher et al., 2008; Kumar et al., 2010; Gaju
et al., 2011; Derkx et al., 2012), and remote sensing has been
used to phenotype such genetic variation (Lopes and Reyn-
olds, 2012). Bogard et al. (2011) reported that the timing of flag
leaf senescence was associated with a QTL for flowering date
in a winter wheat Toisondor×CF9107 doubled haploid (DH)
population in field experiments in France and the UK. Kumar
et al. (2010) reported QTLs for a stay-green trait under field
conditions in Indian wheat lines using a recombinant inbred
population from a cross between ‘Chirya 3’ and ‘Sonalka’, with
the QTLs accounting for up to 39% of phenotypic variation. In
addition, Christopher et al. (2016) identified variation in a
SeriM82×Hartog DH population of wheat for specific stay-
green traits, combinations of traits, and/or molecular markers
related to the traits which were associated with higher yield in
both well-watered and water-limited conditions.

As leaves senesce, proteins including Rubisco are degraded
and N is remobilized to the grain, resulting in a reduction in
photosynthetic capacity (e.g. Feller et al., 2008). Therefore,
delayed remobilization of N to grains for protein synthesis is as-
associated with stay-green (Link 35, Fig. 9). Genetic improvement
in stay-green traits has been specifically associated with lower
post-anthesis N remobilization (Gaju et al., 2011; Derkx et al.,
2012; Hawkesford, 2014) and/or increased post-anthesis N
uptake (Bogard et al., 2011; Gaju et al., 2014). A transcrip-
tion factor (NAM-B1) accelerates senescence and increases N
remobilization from leaves to grains in wheat (Uauy et al.,
2006). Therefore, a better understanding of the mechanisms
determining post-anthesis N remobilization and senescence
may offer scope to increase grain yield and/or grain protein
content in wheat cultivars in these cases of co-limitation of
growth during grain filling.

Stem carbohydrate and its remobilization

The relative contribution of stem carbohydrate remobilization
(Link 36, Fig. 9) to grain yield varies widely depending on the
environmental conditions and cultivar (Blum, 1998; Foulkes
et al., 2002; Ruuska et al., 2006). In general, a reduction in
current assimilation under post-anthesis drought will induce
greater stem reserve mobilization, and utilization by the grain
(Palta et al., 1994; Saint Pierre et al., 2010). However, there is
also evidence for significant deposition of stem WSC reserves
in grains contributing between 10% and 34% grain yield in the
absence of post-anthesis stress in wheat (Gebbink and Schny-
der, 1999; Gebbing et al., 1999; Foulkes et al., 2002). The results
of Shearman et al. (2005) and Saint Pierre et al. (2010) confirm
the potential importance of stem WSC for grain yield potential
even under favourable post-anthesis conditions.

In wheat, stem WSCs are composed mainly of fructans
(Ruuska et al., 2006) which are polymers of fructose. The
breakdown of fructans supports the growing grains: fructan
exohydrolase 1-FEHw3 mapping on chromosome 6B is a
useful marker for fructose breakdown (Zhang et al., 2008).
Indeed, this gene is a major factor determining genotypic var-
ation in WSC remobilization in wheat (Zhang et al., 2015).
Khoshro et al. (2014) identified that the wheat cultivar Zagros,
possessing enhanced capability for fructan storage and higher
mobilization efficiency; had a higher gene expression level of
1-SST, 6-SFT, 1-FEHw3, as well as 6-FEH genes. Expression
of 1FEHw3 and 6-FEH increased during carbon remobiliza-
tion in this cultivar, suggesting that both genes are necessary
for an efficient degradation and translocation of stem fructans.
The mRNA levels of two fructan synthetic enzymes (1-SST
and 6-SFT) in the stem were positively correlated with stem
WSC concentrations, while the mRNA levels of enzymes
involved in fructan hydrolysis (INV, 1-FEHw3, and 6-FEH)
were inversely correlated with WSC concentration. Carbon as-
similate availability through stem carbohydrate remobilization
should prolong starch synthesis and/or grain growth, therefore
enhancing grain weight realization by extending the duration
of grain growth.

Grain filling commences 5–10 d after anthesis and continues
over the last 25–50 d until the grain ripens. The accumula-
tion of structural proteins (albumin, globulin, and the amphi-
philic fraction) occurs up to 25 d after anthesis followed by
the storage proteins (gliadin and glutenin fraction) when cell division has ceased (Stone and Nicolas, 1996). The initial accumulation of structural proteins is considered sink regulated, whereas the supply of storage proteins is considered source limited (Martre et al., 2003). The genotype–environment interaction modifies total grain N, through source limitation (Martre et al., 2003). The relationship between grain protein and starch synthesis (Link 37, Fig. 9) is influenced by the concentration of sucrose and glutamine and their ratio in the grain, as affected by the key enzymes sucrose synthase and glutamine synthetase, respectively (Zhou et al., 2006). Since starch and protein deposition in the endosperm of wheat are controlled by separate mechanisms, starch yield and protein yield should therefore be selected as independent traits in breeding.

It has been suggested that grain weight realization might be affected by spike vascular architecture (Link 38; Fig. 9). It is presently unclear whether the provision of sucrose to the grain during the watery ripe to physiological maturity stage is limited by transport system activities and/or spike vascular connections of the grains to the plant, thereby affecting grain weight realization. Under normal conditions, starch synthesis in the developing grain appears not to be restricted by a lack of carbohydrate precursor, as described above. Further studies are required to study the dynamics of grain filling, development of spike vascular tissue, and the rate of dry matter accumulation, in relation to the anatomy and activities of the phloem transport systems. In addition to vascular architecture, it has also been hypothesized that improvements in phloem loading may be useful for enhancing assimilate supply to growing grains (Braun et al., 2014; White et al., 2016), but extensive evidence for this is so far available only from model plants. However, Regmi et al. (2020) demonstrated that increasing a specific H+-PPase transporter activity via transgenesis led to increased transfer of carbon into wheat grains.

Concluding remarks

The diagrams presented here and in the companion paper (Murchie et al., 2023) represent—as far as we are aware—the most up-to-date (albeit high level) understanding of the interactions among yield potential traits that has been documented in wheat and based on evidence gathered mostly under agriculturally relevant growing conditions. While presenting the platform organized around WDs as a potential workspace for breeders and other crop scientists, the authors recognize that the details of the WDs and table of genetic information will need updating regularly as knowledge accumulates about trait and gene interactions, and as new traits and their genetic basis are discovered (Reynolds et al., 2022). This is perhaps especially so at the molecular frontier, as such techniques become increasingly applied to tissues from plants grown in realistic crop environments. Such outputs, along with high throughput and precision phenotyping data, measured directly on field-grown plots, and perhaps with the aid of artificial intelligence (AI), will help build new dynamic models of trait and gene interactions in wheat and other field crops.

Acknowledgements

We gratefully acknowledge the constructive criticism and suggestions generously offered by Richard Richards (CSIRO, Australia), Yann Manes (Syngenta, France), and Jacques Le Gouis (INRAe, France) on an early version of this work. The authors acknowledge the role IWYP played in identifying the need for a tool to drive crop research and physiological breeding.

Author contributions

GAS, MJE, MPR, and SG: conceptualization (after discussions involving all co-authors over several meetings); GAS: visualization; GAS, MJE, and SG: writing different parts of the original draft; GAS, MJE, MPR, EHM, ECS, RF, JG, MS, and SG: review and editing different versions

Conflict of interest

The authors declare that there is no conflict of interest.

Funding

Research of the authors on physiology and genetics of wheat yield potential has been funded by many different sources over the years. Most recent grants include the International Wheat Yield Partnership (IWYP) projects funded by the Biotechnology and Biological Research Council of the UK (e.g. IWYP48 BB/N021061/1, IWYP64 BB/ N020871/2, IWYP163 BB/S005072/1, and IWYP25FP), National Institute of Food and Agriculture of the USA (IWYP700 NIFA 2017-67007-25929), as well as projects funded by other donors (State Research Agency of Spain: AGL2015-69595-R, and RTI2018-096213-B-100).

References

Abbate PE, Andrade FH, Culot JP. 1995. The effects of radiation and nitrogen on number of grains in wheat. Journal of Agricultural Science 124, 351–360.

Abbate PE, Andrade FH, Lázaro L, Bariffi JH, Berardocco HG, Inza VH, Marturano F. 1998. Grain yield increase in recent Argentine wheat cultivars. Crop Science 38, 1203–1209.

Abeledo LG, Prado SA, Puhl LE, Zhou Y, Costa JM, Miralles DJ. 2019. Phenotypic and genetic analysis to identify secondary physiological traits for improving grain yield in wheat considering anthesis time variability. Euphytica 215, 171.

Acreche M, Briçeno-Félix G, Martin 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. 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.

Ainsworth E, Long S. 2005. What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of
photosynthesis, canopy properties and plant production to rising CO₂. New Phytologist 165, 351–372.

Aisawi KAB, Reynolds MP, Singh RP, Foulkes MJ. 2015. The physiological basis of the genetic progress in yield potential of CIMMYT spring wheat cultivars from 1966 to 2009. Crop Science 55, 1749–1764.

Alonso MP, Mirabella NE, Panojo JS, Cendoya MG, Pontaroli AC. 2018. Selection for high spike fertility index increases genetic progress in grain yield and stability in bread wheat. Euphytica 214, 112.

Alvarez MA, Tranquilli G, Lewis S, Kippes N, Dubcovsky J. 2016. Genetic and physical mapping of the Earliness per se locus Eps-Am1 1 in Triticum monococcum identifies EARLY FLOWERING 3 (ELF3) as a candidate gene. Functional & Integrative Genomics 16, 365–382.

Appendino ML, Slafer GA. 2003. Earliness per se and its dependence upon temperature in diploid wheat lines differing in the major gene Eps-Am1. Journal of Agricultural Science 141, 149–154.

Araus JL, Brown HR, Febrero A, Bot J, Serret MD. 2012. Down-regulation of the TaGW2 gene regulates the activity of reproductive meristems, flower organ size, ovule formation, and thus seed yield in Arabidopsis thaliana. The Plant Cell 23, 69–80.

Basavaraddi PA, Savin R, Bencivenga S, Griffiths S, Slafer GA. 2021b. Wheat developmental traits as affected by the interaction between Eps-7D and temperature under contrasting photoperiods with insensitive Ppd-D1 background. Plants 10, 547.

Basavaraddi PA, Savin R, Bencivenga S, Griffiths S, Slafer GA. 2021c. Phenology and floret development as affected by the interaction between Eps-7D and Ppd-D1. Plants 10, 533.

Basavaraddi PA, Savin R, Sukumaran S, Reynolds MP, Griffiths S, Slafer GA. 2021d. Genotypic differences in wheat yield determinants within a NAM population based on elite parents. European Journal of Agronomy 123, 126223.

Bogard M, Jourdan M, Allard V, et al. 2011. Anthesis date mainly explained correlations between post-anthesis leaf senescence, grain yield, and grain protein concentration in a winter wheat population segregating for flowering time QTLs. Journal of Experimental Botany 62, 3621–3636.

Borrás 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.

Borrás-Gelonch G, Rebetzke GJ, Richards RA, Romagosa I. 2012. Genetic control of duration of pre-anthesis phases in wheat (Triticum aestivum L.) and relationships to leaf appearance, tillering, and dry matter accumulation. Journal of Experimental Botany 63, 69–89.

Borrill P, Fahy B, Smith AM, Uauy C. 2015. Wheat grain filling is limited by grain filling capacity rather than the duration of flag leaf photosynthesis: a case study using NAM RNAi plants. PLOS One 10, e0154947.

Brancourt-Hulmel M, Doussinault G, Lecomte C, Bérard P, Le Buaneck 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.

Braun DM, Wang L, Ruan YL. 2014. Understanding and manipulating sucrose phloem loading, unloading, metabolism, and signaling to enhance crop yield and food security. Journal of Experimental Botany 65, 1713–1735.

Brinton J, Ramirez-Gonzalez RH, Simmonds J, et al. 2020. A haplotype-lead approach to increase the precision of wheat breeding. Communications Biology 3, 712.

Brinton J, Simmonds J, Minter F, Leverington-Waite M, Snape J, Uauy C. 2017. Increased pericarp cell length underlies a major quantitative trait locus for grain weight in hexaploid wheat. New Phytologist 215, 1026–1038.

Brinton J, Simmonds J, Uauy C. 2018. Ubiquitin-related genes are differentially expressed in isogenic lines contrasting for pericarp cell size and grain weight in hexaploid wheat. BMC Plant Biology 18, 22.

Brinton J, Uauy C. 2019. A reductionist approach to dissecting grain weight and yield in wheat. Journal of Integrative Plant Biology 61, 337–358.

Brocklehurst PA. 1977. Factors controlling grain weight in wheat. Nature 266, 348–349.

Brooking IR, Kirby EJM. 1981. Interrelationship between stem and ear development in winter wheat: the effects of a Norin 10 dwarfing gene, Gai/ Rht12. Journal of Agricultural Science 97, 373–381.

Bustos DV, Hasan AK, Reynolds MP, Calderini DF. 2013. Combining high grain number and weight through a DH-population to improve grain yield potential of wheat in high-yielding environments. Field Crops Research 145, 106–115.

Calderini DF, Abeledo LG, Savin R, Slafer GA. 1999. Effect of temperature and carpel size during pre-anthesis on potential grain weight in wheat. Journal of Agricultural Science 132, 453–459.

Calderini DF, Castillo FM, Arenas MA, et al. 2021. Overcoming the trade-off between grain weight and number in wheat by the ectopic expression of expansin in developing seeds leads to increased yield potential. New Phytologist 230, 629–640.

Calderini DF, Drecrer MF, Slafer GA. 1995. Genetic improvement in wheat yield and associated traits. A re-examination of previous results and the latest trends. Plant Breeding 114, 108–112.

Calderini DF, Drecrer MF, Slafer GA. 1997. Consequences of breeding on biomass, 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, Slofer GA. 2006. Source–sink effects on grain weight of bread wheat, durum wheat, and triticale at different locations. Australian Journal of Agricultural Research 57, 227–233.

Calderini DF, Savin R, Abeledo LG, Calderini MP, Slofer GA. 2001. The importance of the immediately preceding anthesis period for grain weight determination in wheat. Euphytica 119, 199–204.

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.

Cartelle J, Pedró A, Savin R, Slofer GA. 2006. Grain weight responses to post-anthesis spikelet-trimming in an old and a modern wheat under Mediterranean conditions. European Journal of Agronomy 25, 365–371.

Chapman EA, Orford S, Lago J, Griffis S. 2021. Delaying or delaying identification of novel NAM-1 alleles which delay senescence to extend wheat grain fill duration. Journal of Experimental Botany 72, 7710–7729.

Charmet G, Robert N, Braniard G, Linossier L, Martre P, Tribol E. 2005. Genetic analysis of dry matter and nitrogen accumulation and protein composition in wheat kernels. Theoretical and Applied Genetics 111, 540–550.

Chojecki AJ, Bayliss MW, Gale MD. 1986. Cell production and DNA accumulation in the wheat endosperm, and their association with grain weight. Annals of Botany 58, 809–817.

Christopher JT, Christopher MJ, Borrell AK, Fletcher S, Chenu K. 2016. Stay-green traits to improve wheat adaptation in water-limited environments. Journal of Experimental Botany 67, 5159–5172.

Christopher JT, Manschadi AM, Hammer GL, Borrell AK. 2008. Developmental and physiological traits associated with high yield and stay-green phenotype in wheat. Crop and Pasture Science 59, 354–364.

Cui F, Li J, Ding A, et al. 2011. Conditional QTL mapping for plant height with respect to the length of the spike and internode in two mapping populations of wheat. Theoretical and Applied Genetics 122, 1517–1536.

del Pozo A, Matus I, Serret MD, Araus JL. 2014. Agronomic and physiological traits associated with breeding advances of wheat under high-productive Mediterranean conditions. The case of Chile. Environmental and Experimental Botany 103, 180–189.

Demontes-Meynard S, Jeffreys MH. 2004. Effects of nitrogen and radiation on dry matter and nitrogen accumulation in the spike of winter wheat. Field Crops Research 87, 221–233.

Derx AP, Orford S, Griffis S, Foulkes MJ, Hawkesford MJ. 2012. Identification of differentially senescing mutants of wheat and impacts on yield, biomass and nitrogen partitioning. Journal of Integrative Plant Biology 54, 555–566.

Dixon LE, Greenwood JR, Bencivenga S, Zhang P, Cockram J, Mellers G, Ramm K, Cavanagh C, Swain SM, Boden SA. 2018. TECOSINTE BRANCHED1 regulates inflorescence architecture and development in bread wheat (Triticum aestivum). The Plant Cell 30, 563–581.

Draeger T, Azahara CM, Alabdullah AK, Pendle A, Rey MD, Shaw P, Moore G. 2020. Dmc1 is a candidate for temperature tolerance during wheat meiosis. Theoretical and Applied Genetics 133, 809–828.

Dreccer MF, Grashoff C, Rabbinge R. 1997. Source–sink ratio in barley (Hordeum vulgare, L.) during grain filling: effects on senescence and grain protein concentration. Field Crop Research 49, 269–277.

Dreccer MF, Schapendonk AHCM, Slofer GA, Rabbinge R. 2000. Comparative response of wheat and oilseed rape to nitrogen supply: absorption and utilitarian efficiency of radiation and nitrogen during the reproductive stages determining yield. Plant and Soil 220, 189–205.

Dreccer MF, Van Herwaarden AF, Chapman SC. 2009. Grain number and grain weight in wheat lines contrasting for stem water soluble carbohydrate concentration. Field Crops Research 112, 43–54.
Fischer RA, Stockman YM. 1986. Increased kernel number in Norin 10-derived dwarf wheat: evaluation of the cause. Australian Journal of Plant Physiology 13, 767–784.

Fitzgerald GJ, Tausz M, O’Leary G, et al. 2016. Elevated atmospheric [CO₂] can dramatically increase wheat yields in semi-arid environments and buffer against heat waves. Global Change Biology 22, 2269–2284.

Flintham JE, Borner A, Worland AJ, Gale MD. 1997. Optimizing wheat grain yield: effects of Rht (gibberellin-insensitive) dwarving genes. Journal of Agricultural Science 128, 11–25.

Flohr BM, Hunt JR, Kirkegaard JA, Evans JR, Swan A, Rheinheimer B. 2018. Genetic gains in NSW wheat cultivars from 1901 to 2014 as revealed from synchronous flowering during the optimum period. European Journal of Agronomy 98, 1–13.

Ford BA, Foo E, Sharwood R, et al. 2018. Rht18 semidwarfism in wheat is due to increased GA 2-oxidaseA9 expression and reduced GA content. Plant Physiology 177, 168–180.

Foulkes MJ, Reynolds MP. 2015. Breeding challenge: improving yield potential. In: Sadras VO, Caldeni DF, eds. Crop physiology applications for genetic improvement and agronomy, 2nd edn. Amsterdam: Elsevier, 397–421.

Foulkes MJ, Scott RKK, Sylvester-Bradley R. 2002. The ability of wheat cultivars to withstand drought in UK conditions: formation of grain yield. Journal of Agricultural Science 138, 153–169.

Foulkes MJ, Slafer GA, Davies WJ, Berry PM, Sylvester-Bradley R, Martre P, Caldeni DF, Griffiths S, Reynolds MP. 2011. Raising yield potential of wheat. Ill. Optimizing partitioning to grain while maintaining lodging resistance. Journal of Experimental Botany 62, 469–486.

Gaju O, Allard V, Martre P, et al. 2011. Identification of traits to improve the nitrogen-use efficiency of wheat genotypes. Field Crops Research 123, 139–152.

Gaju O, Allard V, Martre P, Le Gouis J, Moreau D, Bogard M, Hubbart S, Foulkes MJ. 2014. Nitrogen partitioning and remobilization in relation to leaf senescence, grain yield and grain N concentration in wheat cultivars. Field Crops Research 155, 213–223.

García GA, Serrano RA, Appendino ML, Lombardo LA, Vanzetti LS, Huelgara M, Miralles DJ. 2011. Variability of duration of pre-anthesis phases as a strategy for increasing wheat grain yield. Field Crops Research 124, 408–416.

García GA, Serrano RA, González FG, Slafer GA, Reynolds MP, Miralles DJ. 2014. Wheat grain number: identification of favourable physiological traits in an elite doubled-haploid population. Field Crops Research 168, 126–134.

Gebing T, Schnyder H. 1999. Pre-anthesis reserve utilization for protein and carbohydrate synthesis in grains of wheat. Plant Physiology 121, 871–878.

Gebing T, Schnyder H, Kühältbauch W. 1999. The utilization of pre-anthesis reserves in grain filling of wheat. Assessment by steady-state 13CO₂/12CO₂ labelling. Plant, Cell & Environment 22, 851–858.

Gerard GS, Alqudah A, Lohwasser U, Börner A, Simón MA. 2019. Uncovering the genetic architecture of fruiting efficiency in bread wheat: a viable alternative to increase yield potential. Crop Science 59, 1853–1869.

Giunta F, De Vito P, Mastrangelo AM, Sanna G, Motzo R. 2018. Environmental and genetic variation for yield-related traits of durum wheat as affected by development. Frontiers in Plant Science 9, 1256.

Gleadrow RM, Dalling MJ, Halloran GM. 1982. Variation in endosperm characteristics and nitrogen content in six wheat lines. Australian Journal of Plant Physiology 9, 539–551.

Glenn P, Zhang J, Brown-Guedira G, DeWitt N, Cook JP, Li K, Akhunov E, Dubcovsky J. 2022. Identification and characterization of a natural polymorphism in FT-A2 associated with increased number of grains per spike in wheat. Theoretical and Applied Genetics 135, 679–692.

González FG, Miralles DJ, Slafer GA. 2011b. Wheat floret survival as related to pre-anthesis spike growth. Journal of Experimental Botany 62, 4889–4901.

González FG, Slafer GA, Miralles DJ. 2003. Grain and floret number in response to photoperiod during stem elongation in fully and slightly vernalized wheats. Field Crops Research 81, 17–27.

González FG, Slafer GA, Miralles DJ. 2005. Floret development and survival in wheat plants exposed to contrasting photoperiod and radiation environments during stem elongation. Functional Plant Biology 32, 189–197.

González FG, Terrile II, Falcón MO. 2011a. Spike fertility and duration of stem elongation as promising traits to improve potential grain number (and yield): variation in modern Argentinean wheats. Crop Science 51, 1693–1702.

González-Navarro OE, Griffiths S, Molero G, Reynolds MP, Slafer GA. 2015. Dynamics of floret development determining differences in spike fertility in an elite population of wheat. Field Crops Research 172, 21–31.

González-Navarro OE, Griffiths S, Molero G, Reynolds MP, Slafer GA. 2016. Variation in developmental patterns among elite wheat lines and relationships with yield, yield components and spike fertility. Field Crops Research 196, 294–304.

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.

Griffiths S, Wingen L, Pietragalla J, et al. 2015. Genetic dissection of grain size and grain number trade-offs in CIMMYT wheat germplasm. PLoS One 10, e0118847.

Guan P, Di N, Mu Q, et al. 2019. Use of near-isogenic lines to precisely map and validate a major QTL for grain weight on chromosome 4A-L in bread wheat (Triticum aestivum L.). Theoretical and Applied Genetics 132, 2367–2379.

Guo L, Ma M, Wu L, et al. 2022. Modified expression of TaCYP78A5 enhances grain weight with yield potential by accumulating auxin in wheat (Triticum aestivum L.). Plant Biotechnology Journal 20, 168–182.

Guo Z, Chen D, Röder MS, Canal MW, Schnurbusch T. 2015. Genetic dissection of pre-anthesis sub-phase durations during the reproductive spike development of wheat. The Plant Journal 95, 909–918.

Guo Z, Chen D, Schnurbusch T. 2015. Variance components, heritability and correlation analysis of anther and ovary size during the floral development of bread wheat. Journal of Experimental Botany 66, 3099–3111.

Guo Z, Schnurbusch T. 2015. Variation of floret fertility in hexaploid wheat revealed by tiller removal. Journal of Experimental Botany 66, 5945–5958.

Guo Z, Slafer GA, Schnurbusch T. 2016. Genotypic variation in spike fertility traits and ovary size as determinants of floret and grain survival rate in wheat. Journal of Experimental Botany 67, 4221–4230.

Hanif M, Langer RHM. 1972. The vascular system of the spikelet in wheat (Triticum aestivum). Annals of Botany 36, 721–727.

Hasan AK, Herrera J, Lizana C, Caldeni DF. 2011. Carpel weight: grain length and stabilized grain water content are physiological drivers of grain weight determination of wheat. Field Crops Research 123, 241–247.

Hawkesford MJ. 2014. Reducing the reliance on nitrogen fertilizer for wheat production. Journal of Cereal Science 59, 276–283.

Hays DB, Do JH, Mason RE, Morgan G, Finlayson SA. 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.

Huang Y, Kong Z, Wu X, Cheng R, Yu D, Ma Z. 2015. Characterization of three wheat grain weight QTLs that differentially affect kernel dimensions. Theoretical and Applied Genetics 129, 2437–2448.

Hyles J, Bloomfield MT, Hunt JR, Trethowan RM, Trevaskis B. 2020. Phenology and related traits for wheat adaptation. Hereditas 125, 417–430.

Ji H, Xiao L, Xia Y, Song H, Liu B, Tang L, Cao W, Zhu Y, Liu L. 2017. Effects of jointing and booting low temperature stresses on grain yield and yield components in wheat. Agricultural and Forest Meteorology 243, 33–42.

Kaur V, Behl R, Singh S, Madaan S. 2011. Endosperm and pericarp size in wheat (Triticum aestivum L.) grains developed under high temperature and drought stress conditions. Cereal Research Communications 39, 515–524.

Khoshro HH, Talaee A, Bihamta MR, Shabzadi M, Abbasi A, Ramezanpour SS. 2014. Expression analysis of the genes involved in accumulation and remobilization of assimilates in wheat stem under terminal drought stress. Plant Growth Regulation 74, 165–176.
Breeding pare breeding strategies in elite Western European bread wheat. Molecular
Using the UK reference population Avalon×Cadenza as a platform to com-
indirect selection for grain yield using spectral reflectance indices from high-
Argentine bread wheat varieties released between 1918 and 2011: changes
2018. Genetic progress in
LoValvo PJL, Miralles DJ, Serrago RA.
2012. Stay-green in spring wheat can be deter-
setting in winter wheat. Agronomy
9
63
565–573.
Kino RI, Pellny TK, Mitchell RAC, Gonzalez-Uriarte A, Tosi P. 2020. High post-anthesis temperature effects on bread wheat (Triticum aestivum L.) grain transcriptome during early grain-filling. BMC Plant Biology 20, 170.
Kirby EJM, Rymer JL. 1974. Development of the vascular system in the ear of barley. Annals of Botany 38, 565–573.
Komaki MK, Tsunewaki K. 1981. Genetical studies on the difference of anther length among common wheat cultivars. Euphytica 30, 45–53.
Kowalski AM, Gooding M, Ferrante A, Slafer GA, Orford S, Gasperini D, Griffiths S. 2016. Agronomic assessment of the wheat semi-dwarfing gene Ppd-D1 in contrasting nitrogen treatments and water regimes. Field Crops Research 191, 150–160.
Krouk G, Crawford NM, Coruzzi GM, Tsay Y. 2010. Nitrate signaling: adaptation to fluctuating environments. Current Opinion in Plant Biology 13, 266–273.
Kuchel H, Williams KJ, Langridge P, Eagles HA, Jefferies SP. 2007. Genetic dissection of grain yield in bread wheat. I. QTL analysis. Theoretical and Applied Genetics 115, 1029–1041.
Kumar U, Joshi AK, Kumari M, Paliwal R, Kumar S, Röder MS. 2010. Identification of QTLs for stay green trait in wheat (Triticum aestivum L.) in the ‘Chirya 3’ × ‘Sonalka’ population. Euphycita 174, 437–445.
Kuzay S, Lin H, Li C, Chen S, Woods DP, Zhang J, Lan T, von Korff M, Dubcovsky J. 2022. WAPO-A1 is the causal gene of the 7AL QTL for spikelet number per spike in wheat. PLoS Genetics 18, e1009747.
Kuzay S, Xu Y, Zhang J, et al. 2019. Identification of a candidate gene for a QTL for spikelet number per spike on wheat chromosome arm 7AL by high-resolution genetic mapping. Theoretical and Applied Genetics 132, 2705–2689.
Lastdrager J, Hanson J, Smeekens S. 2014. Sugar signals and the control of plant growth and development. Journal of Experimental Botany 65, 799–807.
Law CN. 1999. Sterility in winter wheat: review of occurrence in different varieties and possible causes. Research Review 44. London: Home-Grown Cereals Authority.
Lázaro L, Abbate PE. 2012. Cultivar effects on relationship between grain number and photothermal quotient or spike dry weight in wheat. Journal of Agricultural Science 150, 442–459.
Lewis S, Faricelli ME, Appendino ML, Valárík M, Dubcovsky J. 2008. The chromosome region including the Earliness per se locus Eps-A M1 affects the duration of early developmental phases and spikelet number in diploid wheat. Journal of Experimental Botany 59, 3595–3607.
Li Y, Fu X, Zhao M, Zhang W, Li B, An D, Li J, Zhang A, Liu R, Liu X. 2018. A genome-wide view of transcriptome dynamics during early spike development in bread wheat. Scientific Reports 8, 15538.
Li S, Song M, Duan J, Yang J, Zhu Y, Zhou S. 2019. Regulation of spraying 6-BA in the late jointing stage on the fertile floret development and grain setting in winter wheat. Agronomy 9, 546.
Lopes MS, Reynolds MP. 2012. Stay-green in spring wheat can be deter-
minded by spectral reflectance measurements (normalized difference vege-
tation index) independently from phenology. Journal of Experimental Botany 63, 3789–3798.
Lopes MS, Royo C, Alvaro F, Sanchez-Garcia M, Ozer E, Ozdemir F, Karaman M, Roustaii M, Jalal-Kamali MR, Pequeno D. 2018. Optimizing winter wheat resilience to climate change in rain fed crop systems of Turkey and Iran. Frontiers in Plant Science 9, 563.
LoValvo PJL, Miralles DJ, Serrago RA. 2018. Genetic progress in Argentine bread wheat varieties released between 1918 and 2011: changes in physiological and numerical yield components. Field Crops Research 221, 314–321.
Lozada DN, Godoy JV, Ward BP, Carter AH. 2019. Genomic prediction and indirect selection for grain yield using spectral reflectance indices from high-
throughput phenotyping. International Journal of Molecular Science 21, 165.
Ma J, Wingen LU, Orford S, Fenwick P, Wang J, Griffiths S. 2015. Using the UK reference population Avalon×Cadenza as a platform to com-
pare breeding strategies in elite Western European bread wheat. Molecular Breeding 35, 70.
MacMasters MM, Hinton JJC, Bradbury D. 1971. Microscopic structure and composition of wheat kernel. In: Pomeranz Y, ed. Wheat chemistry and technology. St. Paul, MN: American Association of Cereal Chemists, 51–113.
Maeoka RE, Sadras VO, Ciampitti IA, Diaz DR, Fritz AK, Lolilato RP. 2020. Changes in the phenotype of winter wheat varieties released be-
tween 1920 and 2016 in response to in-furrow fertilizer: biomass alloca-
tion, yield, and grain protein concentration. Frontiers in Plant Science 10, 1786.
Martinez AF, Lister C, Freeman S, Ma J, Berry S, Wingen L, Griffiths S. 2021. Resolving a QTL complex for height, heading, and grain yield on chromosome 3A in bread wheat. Journal of Experimental Botany 72, 2965–2978.
Martino DL, Abbate PE, Cendoya MG, Gutheim F, Mirabella NE, Pontaroli AC. 2015. Wheat spike fertility: inheritance and relationship with spike yield components in early generations. Plant Breeding 134, 264–270.
Martre P, Porter JR, Jamieson PD, Triboi E. 2003. Modeling grain ni-
trogen accumulation and protein composition to understand the sink/ source regulations of nitrogen remobilization for wheat. Plant Physiology 133, 1959–1967.
Mason RE, Hays DB, Mondal S, Ibrham AMH, Basnet BR. 2013. QTL for yield, yield components and canopy temperature depression in wheat under late sown field conditions. Euphytica 194, 243–259.
Maydup ML, Antonietta M, Guiamet JJ, Graciano C, López JR, Tambussi EA. 2010. The contribution of ear photosynthesis to grain filling in bread wheat (Triticum aestivum L.). Field Crops Research 119, 48–58.
McSteen P. 2009. Hormonal regulation of branching in grasses. Plant Physiology 146, 46–55.
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, 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. 1995. Yield, biomass and yield components in dwarf, semidwarf and tall isogenic lines of spring wheat under recom-
manded and late sowing 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 145, 139–149.
Molero G, Reynolds MP. 2020. Spike photosynthesis measured at high throughput indicates genetic variation independent of flag leaf photosyn-
sis. Field Crops Research 255, 107866.
Mondal S, Dutta S, Crespo-Herrera L, Huerta-Espino J, Braun HJ, Singh RP. 2020. Fifty years of semi-dwarf spring wheat breeding at CIMMYT: grain yield progress in optimum, drought and heat stress environments. Field Crops Research 250, 107757.
Muqaddasi QH, Brassac J, Koppolu R, et al. 2019. TaAPO-A1, an ortholog of rice ABERANT PANICLE ORGANIZATION 1, is associated with total spikelet number per spike in elite European hexaploid winter wheat (Triticum aestivum L.) varieties, Scientific Reports 9, 13853.
Murchie E, Acevedo-Siaca L, McAusland L, et al. 2023. A ‘wiring dia-
gram’ for source strength traits impacting wheat yield potential. Journal of Experimental Botany 74, 72–90.
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.
O’Brien TP, Sammut ME, Lee JWM, Smart MG. 1985. The vascular system of the wheat spikelet. Australian Journal of Plant Physiology 12, 487–512.
O’Connor DL, Runions A, Sluis A, Bragg J, Vogel JP, Prusinkiewicz P, Hake S. 2014. A division in PIN-mediated auxin patterning during organ initiation in grasses. PLoS Computational Biology 10, e1003447.
Ochagavia H, Prieto P, Savin R, Griffiths S, Slafer GA. 2017. Duration of developmental phases, and dynamics of leaf appearance and tillering, as
affected by source and doses of photoperiod insensitivity alleles in wheat under field conditions. Field Crops Research 214, 45–55.

Ochagavia H, Prieto P, Savin R, Griffiths S, Slaffer GA. 2018. Earliness per se effects on developmental traits in hexaploid wheat grown under field conditions. European Journal of Agronomy 99, 214–223.

Ochagavia H, Prieto P, Savin R, Slaffer GA. 2021. Developmental patterns and rates of organogenesis across modern and well-adapted wheat cultivars. European Journal of Agronomy 126, 126280.

Palta JA, Kobata T, Turner NC, Fillery IR. 1994. Remobilization of carbon and nitrogen in wheat as influenced by postanthesis water deficits. Crop Science 34, 118–124.

Patrick JW, Colvias K. 2014. Crop yield components—photoassimilate supply- or utilization limited-organ development? Functional Plant Biology 41, 893–913.

Paul MJ, Gonzalez-Urriarte A, Griffiths CA, Hassani-Pak K. 2018. The role of trehalose 6-phosphate in crop yield and resilience. Plant Physiology 177, 12–23.

Paul MJ, Watson A, Griffiths CA. 2020. Trehalose 6-phosphate signalling and impact on crop yield. Biochemical Society Transactions 48, 2127–2137.

Pedro A, Savin R, Parry MAJ, Slaffer GA. 2012. Selection for high grain number per unit stem length through four generations from mutants in a durum wheat population to increase yields of individual plants and crops. Field Crops Research 129, 59–70.

Peltosen-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.

Peng J, Richards DE, Hartley NM, et al. 1999. ‘Green revolution’ genes encode mutant gibberellin response modifiers. Nature 400, 256–261.

Pepler S, Gooding MJ, Ellis RH. 2006. Modelling simultaneously water content and dry matter dynamics of wheat grains. Field Crops Research 95, 49–63.

Pérez-Giannmarco Tl, Slaffer GA, González FG. 2019. Photoperiod-sensitivity genes (Ppd-1) shape floret development in wheat. Journal of Experimental Botany 70, 1339–1348.

Poursarebani N, Seidensticker T, Koppolu R, et al. 2015. The genetic basis of composite spike form in barley and ‘miracle-wheat’. Genetics 201, 155–165.

Prasad PVV, Djanaguiraman M. 2014. Response of floret fertility and individual grain weight of wheat to high temperature stress, sensitive stages and thresholds for temperature and duration. Functional Plant Biology 41, 1261–1269.

Pretini N, Terrile II, Gazaba LN, Donaire GM, Arisnabarreta S, Vanzetti LS, González FG. 2020a. A comprehensive study of spike fruiting efficiency in wheat. Crop Science 60, 1541–1555.

Pretini N, Vanzetti LS, Terrile II, Börner A, Plieske J, Ganal M, Röder M, González FG. 2020b. Identification and validation of QTL for spike fertile floret and fruiting efficiencies in hexaploid wheat (Triticum aestivum L.). Theoretical and Applied Genetics 133, 2655–2671.

Prieto P, Ochagavia H, Griffiths S, Slaffer GA. 2020. Earliness per se × temperature interaction consequences on leaf, spikelet and floret development in wheat. Journal of Experimental Botany 71, 1956–1968.

Prieto P, Ochagavia H, Savin R, Griffiths S, Slaffer GA. 2018. Dynamics of floret initiation/death determining spike fertility in wheat as affected by Ppd genes under field conditions. Journal of Experimental Botany 69, 2633–2645.

Przystupa P, Savin R, Slaffer GA. 2004. Grain number and its relationship with dry matter, N and P in the spikes at heading in response to N+P fertilization in barley. Field Crop Research 90, 245–254.

Reale L, Rosati A, Tedeschi E, et al. 2017. Ovary size in wheat (Triticum aestivum L.) is related to cell number. Crop Science 57, 914–925.

Rebetzke GJ, Ellis MH, Bonnett DG, Condon AG, Falk D, Richards RA. 2011. The Rht13 dwarfing gene reduces peduncle length and plant height to increase grain number and yield of wheat. Field Crops Research 124, 323–331.

Regmi KC, Yogendra K, Farias JG, et al. 2020. Improved yield and photosynthate partitioning in AVP1 expressing wheat (Triticum aestivum) plants. Frontiers in Plant Science 11, 273.

Reynolds M, Atkin OK, Bennett M, et al. 2021. Addressing research bottlenecks to crop productivity. Trends in Plant Science 26, 607–630.

Reynolds MP, Calderini DF, Condon AG, Rajaram S. 2001. Physiological basis of yield gains in wheat associated with the LR19 translocation from Agropyron elongatum. Euphytica 119, 139–144.

Reynolds MP, Pask AJD, Hoppitt WJE, et al. 2017. Strategic crossing of biomass and harvest index—source and sink—achieves genetic gains in wheat. Euphytica 213, 257.

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 148, 39–49.

Reynolds MP, Rajaram S, Sayre KD. 1999. Physiological and genetic changes of irrigated wheat in the period and approaches for meeting projected global demand. Crop Science 39, 1611–1621.

Reynolds MP, Slaffer GA, Foulkes JM, et al. 2022. A wiring diagram to integrate physiological traits of wheat yield potential. Nature Food 3, 318–324.

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, Cavanagh CR, Riffkin P. 2019. Selection for erect canopy architecture can increase yield and biomass of spring wheat. Field Crops Research 244, 107649.

Rivera-Amado C, Trujillo-Negrellos E, Molero G, Reynolds MP, Sylvester-Bradley R, Foulkes MJ. 2019. Optimizing dry-matter partitioning for increased spike growth, grain number and harvest index in spring wheat. Field Crops Research 240, 154–167.

Ruuska SA, Rebetzke GJ, Van Herwaarden AF, Richards RA, Fettell NA, Tabe L, Jenkins CLD. 2006. Genotypic variation in water-soluble carbohydrate accumulation in wheat. Functional Plant Biology 33, 799–809.

Saalbach I, Mora-Ramirez I, Weichert N, et al. 2014. Increased grain yield and micronutrient concentration in transgenic winter wheat by ectopic expression of a barley sucrose transporter. Journal of Cereal Science 60, 75–81.

Sabeli PA, Larkins BA. 2009. The development of endosperm in grasses. Plant Physiology 149, 14–26.

Sadras VO. 2007. Evolutionary aspects of the trade-off between seed size and number in crops. Field Crops Research 100, 125–138.

Sadras VO, Lawson C. 2011. Genetic gain in yield and associated changes in phenotype, trait plasticity and competitive ability of South Australian wheat varieties released between 1958 and 2007. Crop and Pasture Science 62, 533–549.

Sadras VO, Slafer GA. 2007. Evolutionary aspects of the trade-off between seed size and number in crops. Field Crops Research 100, 125–138.

Sadras VO, Slafer GA. 2012. Environmental modulation of yield components in cereals: heritabilities reveal a hierarchy of phenotypic plasticities. Field Crops Research 127, 215–224.

Saini HS, Westgate ME. 1999. Reproductive development in grain crops during drought. Advances in Agronomy 68, 59–96.

Saint Pierre C, Trehowran R, Reynolds M. 2010. Stem solidity and its relationship to water-soluble carbohydrates: association with wheat yield under water deficit. Functional Plant Biology 37, 166–174.

Sakakihara H. 2006. Cytokinins: activity, biosynthesis and translocation. Annual Reviews of Plant Biology 57, 431–449.

Sakuma S, Golan G, Guo Z, et al. 2019. Unleashing floret fertility in wheat through the mutation of a homeobox gene. Proceedings of the National Academy of Sciences, USA 116, 5182–5187.

Sanchez-Bragado R, Elazab A, Zhou B, Serret MD, Bort J, Nieto-Taladriz MT, Araus JL. 2014a. Contribution of the ear and the flag leaf to grain filling in durum wheat inferred from the carbon isotope signature: genotypic and growing conditions effects. Journal of Integrative Plant Biology 56, 444–454.

Sanchez-Bragado R, Molero G, Reynolds MP, Araus JL. 2014b. Relative contribution of shoot and ear photosynthesis to grain filling in wheat under good agronomical conditions assessed by differential organ 813C. Journal of Experimental Botany 65, 5401–5413.
Sanchez-Bragado R, Molero G, Reynolds MP, Araus JL. 2016. Photosynthetic contribution of the ear to grain filling in wheat: a comparison of different methodologies for evaluation. Journal of Experimental Botany 67, 2787–2798.

Sang Y, Deng ZY, Zhao L, Zhang KP, Tian JC, Ye BX. 2010. QTLs for the vascular bundle system of the uppermost internode using a doubled haploid population of two elite Chinese wheat cultivars. Plant Breeding 129, 605–610.

Savin R, Slafer GA. 1991. Shading effects on the yield of an Argentinean wheat cultivar. Journal of Agricultural Science 116, 1–7.

Sayre KD, Rajaram S, Fischer RA. 1997. Yield potential progress in short bread wheats in northwest Mexico. Crop Science 37, 36–42.

Serrago RA, Alzueta I, Savin R, Slafer GA. 2013. Understanding grain yield responses to source–sink ratios during grain filling in wheat and barley under contrasting environments. Field Crops Research 150, 42–51.

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.

Shaw LM, Lyu B, Turner R, Li C, Chen F, Han X, Fu D, Dubcovsky J. 2019. FLOWERERING LOCUS T2 regulates spike development and fertility in temperate cereals. Journal of Experimental Botany 70, 193–204.

Shearman VJ, Sylvester-Bradley R, Scott RK, Foulkes MJ. 2005. Physiological processes associated with wheat yield progress in the UK. Crop Science 45, 175–185.

Shewry PR. 2009. Wheat. Journal of Experimental Botany 60, 1537–1553.

Shi J, Habben JE, Archibald RL, Drummond BJ, Chamberlin MA, Williams RW, Lafitte HR, Weers BP. 2015. Overexpression of ARGOS genes modifies plant sensitivity to ethylene, leading to improved drought tolerance in both Arabidopsis and maize. Plant Physiologist 169, 266–282.

Siddique KHM, Kirby EJM, Perry MW. 1989. Ear to 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.

Sierra-Gonzalez A, Molero G, Rivera-Amado C, Babar MA, Reynolds MP, Foulkes MJ. 2021. Exploring genetic diversity for grain partitioning traits to enhance yield in a high biomass spring wheat panel. Field Crops Research 280, 108797.

Simmonds J, Scott P, Briton J, Mestre TC, Bush M, del Blanco A, Dubcovsky J, Uauy C. 2016. A spike acceptor site mutation in TaGW2-A1 increases thousand grain weight in tetraploid and hexaploid wheat through wider and longer grained. Theoretical and Applied Genetics 129, 1099–1112.

Simmonds J, Scott P, Leverington-Waite M, Turner AS, Briton J, Korzn V, Snape J, Uauy C. 2014. Identification and independent validation of a stable yield and thousand grain weight QTL on chromosome 6A of hexaploid wheat (Triticum aestivum L.). BMC Plant Biology 14, 191.

Singh BK, Jenner CF. 1999. Grain quality and its physiological determinants. Crop Science 39, 785–797.

Snape JW, Butterworth K, Whitechurch E, Worland AJ. 2001. Waiting for fine times: genetics of flowering time in wheat. Euphytica 119, 185–190.

Snape JW, Foulkes MJ, Simmons J, Leverington M, Fish LJ, Wang Y, Ciavarrella M. 2007. Dissecting gene-environmental effects on wheat yields via QTL and physiological analysis. Euphytica 154, 401–408.

Sofield I, Evans LT, Cook MG, Wardlaw IF. 1977. Factors influencing the rate and duration of grain filling in wheat. Australian Journal of Plant Physiology 4, 785–797.

Stone PJ, Nicolas ME. 1996. Varietal differences in mature protein composition of wheat resulted from different rates of polymer accumulation during grain filling. Australian Journal of Plant Physiology 23, 727–737.

Stone PJ, Savin R. 1999. Grain quality and its physiological determinants. In: Satorre EH, Slafer GA, eds. Wheat: ecology and physiology of yield determination. New York: Food Product Press, 85–120.

Sun J, Yang L, Wang Y, Ort DR. 2009. FACE-ing the global change: opportunities for improvement in photosynthetic radiation use efficiency and crop yield. Plant Science 177, 511–522.

Sukumaran S, Lopes MS, Dreisigacker S, Dixon LE, Zikhal M, Griffiths S, Zheng B, Chapman S, Reynolds MP. 2016. Identification of earliness per se flowering time locus in spring wheat through a genome-wide association study. Crop Science 56, 2962–2972.

Sukumaran S, Lopes M, Dreisigacker S, Reynolds M. 2018. Genetic analysis of multi-environmental spring wheat trials identifies genomic regions for locus-specific trade-offs for grain weight and grain number. Theoretical and Applied Genetics 131, 985–999.

Sun J, Yang L, Wang Y, Ort DR. 2009. FACE-ing the global change: opportunities for improvement in photosynthetic radiation use efficiency and crop yield. Plant Science 177, 511–522.

Sylvestre-Bradley R, Riffkin P, O'Leary G. 2014. Identification and development of a stable yield and thousand grain weight QTL on chromosome 6A of hexaploid wheat (Triticum aestivum L.). Theoretical and Applied Genetics 122, 211–223.

Sukumaran S, Lopes MS, Dreisigacker S, Reynolds M. 2018. Genetic analysis of multi-environmental spring wheat trials identifies genomic regions for locus-specific trade-offs for grain weight and grain number. Theoretical and Applied Genetics 131, 985–999.

Tambussi EA, Bort J, Guiamet JJ, Nogués S, Araus JL. 2007. The photosynthetic role of ears in C3 cereals: metabolism, water use efficiency and contribution to grain yield. Critical Reviews in Plant Sciences 26, 1–16.

Tambussi EA, Nogués S, Araus JL. 2015. Ear of durum wheat under water stress: water relations and photosynthetic metabolism. Planta 221, 446–458.

Tang T, Botwright Acuña T, Spielmeyer W, Richards RA. 2021. Effect of gibberellin-sensitive Rht18 and gibberellin-insensitive Rht-D1b dwarfing genes on vegetative and reproductive growth in bread wheat. Journal of Experimental Botany 72, 445–458.

Thakur P, Kumar S, Malik JA, Berger JD, Nayyar H. 2010. Cold stress effects on reproductive development in grain crops: an overview. Environmental and Experimental Botany 67, 429–443.

Thomas H, Howarth CJ. 2020. Five ways to stay green. Journal of Experimental Botany 51, 329–337.

Tognetti JA, Pontis HG, Martinez-Noël GM. 2013. Sucrose signaling in plants: a world yet to be explored. Plant Signaling & Behavior 8, e23316.

Uauy C, Distelfeld A, Fahima T, Blechl A, Dubcovsky J. 2006. A NAC gene regulating senescence improves grain protein, zinc, and iron content in wheat. Science 314, 1298–1301.
Sink strength and yield in wheat | 71

Díaz-Vivancos E, Cuellar JA, Atienza-Tapia I, Rodríguez-Gutiérrez A, Galindo-Vázquez C, Ramírez-Ortiz C, et al. 2016. Sink strength determines partitioning and subsequent grain yield in bread wheat. Journal of Experimental Botany 67, 287–299.

Zalipska S, Czechowska E, Skrzypek R, Ratafia K, Mrozowska A. 2015. The impact of water stress on grain yield and yield components in two varieties of winter wheat with different Rht phenotype. Polish Journal of Crop Science 7, 195–202.

Zalipska S, Czechowska E, Skrzypek R, Ratafia K, Mrozowska A. 2015. The impact of water stress on grain yield and yield components in two varieties of winter wheat with different Rht phenotype. Polish Journal of Crop Science 7, 195–202.

Zalipska S, Czechowska E, Skrzypek R, Ratafia K, Mrozowska A. 2015. The impact of water stress on grain yield and yield components in two varieties of winter wheat with different Rht phenotype. Polish Journal of Crop Science 7, 195–202.

Zalipska S, Czechowska E, Skrzypek R, Ratafia K, Mrozowska A. 2015. The impact of water stress on grain yield and yield components in two varieties of winter wheat with different Rht phenotype. Polish Journal of Crop Science 7, 195–202.

Zalipska S, Czechowska E, Skrzypek R, Ratafia K, Mrozowska A. 2015. The impact of water stress on grain yield and yield components in two varieties of winter wheat with different Rht phenotype. Polish Journal of Crop Science 7, 195–202.

Zalipska S, Czechowska E, Skrzypek R, Ratafia K, Mrozowska A. 2015. The impact of water stress on grain yield and yield components in two varieties of winter wheat with different Rht phenotype. Polish Journal of Crop Science 7, 195–202.

Zalipska S, Czechowska E, Skrzypek R, Ratafia K, Mrozowska A. 2015. The impact of water stress on grain yield and yield components in two varieties of winter wheat with different Rht phenotype. Polish Journal of Crop Science 7, 195–202.

Zalipska S, Czechowska E, Skrzypek R, Ratafia K, Mrozowska A. 2015. The impact of water stress on grain yield and yield components in two varieties of winter wheat with different Rht phenotype. Polish Journal of Crop Science 7, 195–202.