

## ORIGINAL RESEARCH

## Fruiting efficiency: an alternative trait to further rise wheat yield

Gustavo A. Slafer<sup>1,2</sup>, Mónica Elia<sup>1</sup>, Roxana Savin<sup>1</sup>, Guillermo A. García<sup>3,4</sup>, Ignacio I. Terrile<sup>5</sup>, Ariel Ferrante<sup>6</sup>, Daniel J. Miralles<sup>3,4</sup> & Fernanda G. González<sup>4,5</sup>

<sup>1</sup>Department of Crop and Forest Sciences and AGROTECNIO (Center for Research in Agrotechnology), University of Lleida, Av. Rovira Roure 191, 25198 Lleida, Spain

<sup>2</sup>ICREA, Catalanian Institution for Research and Advanced Studies, Barcelona, Spain

<sup>3</sup>IFEVA and Department of Plant Production, Faculty of Agronomy, University of Buenos Aires, Av. San Martín 4453, C1417DSE Buenos Aires, Argentina

<sup>4</sup>CONICET (National Scientific and Technical Research Council), Buenos Aires, Argentina

<sup>5</sup>EEA Pergamino, INTA (National Institute for Agricultural Technology) Ruta 32 km 4.5, B2700WAA Pergamino, Buenos Aires, Argentina

<sup>6</sup>Queensland Alliance for Agriculture and Food Innovation (QAAFI), The University of Queensland, P.O. Box 102, Toowoomba, Queensland 4350, Australia

### Keywords

Floret development, grain number, partitioning, spike dry weight, *Triticum aestivum*, *Triticum durum*, yield component.

### Correspondence

Gustavo A. Slafer, Department of Crop and Forest Sciences and AGROTECNIO (Center for Research in Agrotechnology), University of Lleida, Av. Rovira Roure 191, 25198 Lleida, Spain. Tel: +34 973003659; Fax: +34 973702690; E-mail: slafer@pvcf.udl.cat

### Funding Information

The work on fruiting efficiency has been funded by grants from the "National Plan" of Research in Spain, grants AGL2009-11964 and AGL2012-35300 at the Crop Physiology Lab of the University of Lleida; National Agency of Scientific and Technical Promotion (PICT-2008-1039) and INTA (PNCER-1336) at CONICET and INTA Lab, and PICT RAICES 1368 and UBACyT G-076 competitive grants at the University of Buenos Aires.

Received: 21 February 2015; Revised: 19 April 2015; Accepted: 29 April 2015

Food and Energy Security 2015; 4(2): 92–109

doi: 10.1002/fes3.59

## Introduction

### Overall context

Wheat is critical for food security, as it is the crop most widely grown and is the primary source of protein for

### Abstract

Further improvements in wheat yields are critical, for which increases in grain number would be required. In the recent past, higher grain number was achieved through increased growth of the juvenile spikes before anthesis, due to the reduction in stem growth. As current cultivars have already an optimum height, alternatives must be identified for further increasing grain number. One of them is increasing fruiting efficiency (grains set per unit of spike dry weight at anthesis). Fruiting efficiency is the final outcome of the fate of floret development and differences in this trait within modern cultivars would be related to higher survival of floret primordia. Then there are two alternative physiological pathways to improve fruiting efficiency by allowing a normal development of most vulnerable floret primordia: an increased allocation of assimilates for the developing florets before anthesis, or reduced demand of the florets for maintaining their normal development. Both alternatives may be possible, and it might be critical to recognize which of them is the actual cause of differences in fruiting efficiency. When considering this trait in breeding we must be aware of potential trade-offs and therefore it must be avoided that increases in fruiting efficiency be constitutively related to decreases in either spike dry weight at anthesis or grain weight. In this review we described fruiting efficiency and its physiological bases, analyzing genetic variation and considering potential drawbacks that must be taken into account to avoid increases in fruiting efficiency being compensated by other traits.

the world population (Chand 2009; Braun et al. 2010). Genetic gains in wheat yield have been outstanding during the second half of the 20th century (Calderini et al. 1999; Foulkes and Reynolds 2015; and references quoted therein). This success has been instrumental for, roughly contributing 50% (Slafer and Andrade 1991) to the increases in

production, more than matching the increased demand produced by an unprecedented growth in world population (more than doubling in just half-century the population built up in the previous 2000 centuries, since the beginning of our species). Thus genetic gains were critical for the improved levels of food security in the last half century.

The population is still growing fast and, in addition, there is an on-going change in diet habits, both factors determining that the demand will further increase over the next decades. This time, the satisfaction of the increased demand must mainly come from yield improvement as the amount of land for agriculture will not increase, and may even decline (Albajes *et al.* 2013). It may be required that yield of wheat (and other major crops) be increased by at least 50% in the next few decades (Reynolds *et al.* 2009), which will depend on improving yield potential (Fischer and Edmeades 2010; Hall and Richards 2012). As crop management should be environmentally more sustainable in the future (Godfray 2011; Tilman *et al.* 2011), the contribution from genetic gains should be similar to that of the few decades following the Green Revolution. But, in the last 2 decades wheat yield grew less than the demand and in several regions showed signs of stagnation (Calderini and Slafer 1998; Brisson *et al.* 2010; Ray *et al.* 2012). Likewise, genetic gains reported for different countries for the last decades also seem to have been increasing less than required (Shearman *et al.* 2005; Acreche *et al.* 2008; Sadras and Lawson 2011; Lopes *et al.* 2012).

### How was yield improved in the past?

It seems reasonable to speculate that a better understanding of crop yield physiology would help to increase the current rates of genetic gains (Slafer 2003; Araus *et al.* 2008; Reynolds *et al.* 2012). Based on the model proposed long time ago by Fischer (1984), and well developed in a recent review (Fischer 2011), the diagram in Figure 1 shows that:

- Wheat yield is most commonly sink-limited during grain filling; which means that the amount of available assimilates (current photosynthesis plus remobilization of preanthesis reserves) are in excess to the demand of the growing grains (Borras *et al.* 2004; González *et al.* 2014), not only under high-yielding but also across a wide range of conditions (Pedro *et al.* 2011; Serrago *et al.* 2013). Thus, genotypic differences in yield are frequently strongly related to those in grain number (García *et al.* 2013; Slafer *et al.* 2014), as it is more plastic than grain weight (Sadras and Slafer 2012). But for a particular number of grains there is

variation in grain size which does also affect yield though not as primarily (in most conditions) as grain number (Slafer *et al.* 2014). In fact, genetic gains in wheat yield have been more related to improvements in the number than in the size of the grains (e.g., Canevara *et al.* 1994; Calderini *et al.* 1995; Sayre *et al.* 1997; Shearman *et al.* 2005; Acreche *et al.* 2008).

- Grain number, in turn, is strongly related to spike dry weight at anthesis; which is quite reasonable as: (1) wheat is a cleistogamous plant and therefore most fertile florets set grains and consequently grain number is related to the number of fertile florets; (2) final number of fertile florets depends on the developmental process of floret generation/degeneration; (3) this developmental process occurs in the growing spike before anthesis; and (4) is related to the availability of resources (González *et al.* 2011a; Ferrante *et al.* 2013b; Dreccer *et al.* 2014). Therefore, the final number of grains is source-limited during preanthesis and depends mechanistically on the growth of the juvenile spikes in which floret primordia are developing (Slafer *et al.* 2005) and, for particular levels of spike dry weight, on the efficiency with which the resources are used to set grains or fruiting efficiency<sup>1</sup> (González *et al.* 2011b; Ferrante *et al.* 2012; García *et al.* 2014). Therefore, breeding through the Green Revolution improved spike growth (and consequently spike dry weight at anthesis) bringing about a reduced rate of floret mortality increasing the number of fertile florets (e.g., Miralles *et al.* 1998).
- Spike growth during the preflowering period is the result of crop growth during that period and the proportion of that growth partitioned to the spikes. Virtually all papers analyzing these aspects in breeding during the second half of the 20th century agreed in that there were not trends to systematically and consistently modify growth of the crop whilst there was a consistent trend to increase partitioning of biomass to the reproductive organs (e.g., Siddique *et al.* 1989b; Slafer and Andrade 1993).

When considering how wheat breeding has successfully achieved large gains in the second half of the 20th century, it seems quite straightforward. The tremendous success of the Green Revolution was achieved through relatively simple (seen retrospectively) interventions in yield physiology (Fig. 1, open arrows on left panels and panels on the right). Although exceptional cases could eventually be found, the vast majority of studies of physiological attributes explaining genetic gains in wheat yield coincides in that breeding during the second half of the last century:

- Did not systematically affect biomass production of the crop (Austin *et al.* 1980, 1989; Perry and D'Antuono 1989;

Siddique et al. 1989a; Slafer and Andrade 1991; Sayre et al. 1997; Calderini et al. 1999), but increased the partitioning toward the developing juvenile spike due to genetic restrictions to stem growth (Siddique et al. 1989a,b; Slafer and Andrade 1993), so that during the stem elongation phase, the stem requirements for extension were reduced and partitioning to the spikes favoured,

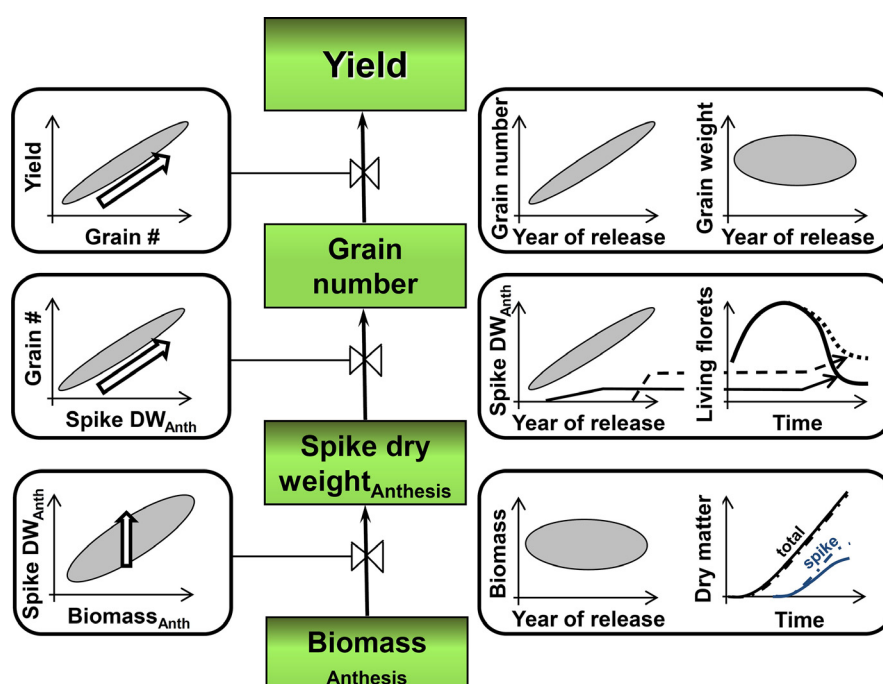
- Consequently, even with no trends to improve crop growth, spike dry weight at anthesis consistently increased whilst stem length was reduced from traditional to semi-dwarf plant stature; and the increased growth of the juvenile spikes brought about improvements in floret development increasing spike fertility (Miralles et al. 1998),
- As spike fertility increased, the number of grains set by the crop in modern cultivars improved compared to their predecessors and the increased postanthesis sink strength resulted in concomitant increases in yield (Sayre et al. 1997; Abbate et al. 1998; Calderini et al. 1999).

Consequently, when comparing cultivars released at different times from before to after the Green Revolution, or when comparing isogenic lines for dwarfism (Rht lines), it can be seen that modern cultivars (or semi-dwarfing lines) out-yield the older ones (or the tall lines)

due to having more grains associated with higher spike dry weight at anthesis (e.g., Fischer and Stockman 1980; Brooking and Kirby 1981; Siddique et al. 1989b; Slafer and Andrade 1993; Miralles et al. 1998; Acreche et al. 2008).

### The problem that fruiting efficiency could help to solve

Past breeding during the Green Revolution and the few decades following it was extremely successful. In the process plant type was modified optimizing its height and consequently current high-yielding cultivars possess a height that is within the optimum range to maximize yield (c. 0.7–1.0 m; Richards 1992; Miralles and Slafer 1995a, 1997; Flintham et al. 1997). This means that the main trait genetically manipulated to obtain remarkable genetic gains in yield cannot be further deployed: taller plants would have penalties due to poor partitioning, and higher risk of lodging; shorter plants would result in lower crop growth as radiation use efficiency would be reduced due to poor radiation distribution within the canopy (Miralles and Slafer 1995a). For future genetic gains to recover the pace that characterized breeding in the recent



**Figure 1.** Simplified conceptual model of the physiological components of yield in wheat (Fischer 1984, 2011; Slafer et al. 2005). On the left the most common relationships considering wide ranges in yield produced by genotypic or environmental factors are shown. The open arrows point out the main pathways used by breeding to produce genetic gains in yield during the second half of the 20th century. Panels on the right exemplify relationships most commonly found when the source of variation has been cultivars released at different years during the 20th century (when the abscissa is "time" it refers to the time from the onset of stem elongation to anthesis, and in these cases the solid and dashed lines stand for cultivars released before or after the Green Revolution, respectively). For more detail see Calderini et al. (1999) and Foulkes and Reynolds (2015).

past, alternative traits putatively related with grain number and yield, must be identified and exploited.

One avenue would be identifying sources of variation to increase crop photosynthesis, so that higher biomass at anthesis would result in more spike dry weight at anthesis bringing about more grains set and higher yields (Parry *et al.* 2011; Reynolds *et al.* 2012). Another alternative, not mutually exclusive with the previous one, could be to lengthen the duration of the spike growth period (or more broadly the duration of the stem elongation phase) so that for a constant rate of growth and level of partitioning, the longer the phase the higher the spike dry weight at anthesis (Slafer *et al.* 2001; Miralles and Slafer 2007; González *et al.* 2011b). Scaling up one step in Figure 1, there is another alternative which is to increase fruiting efficiency; that is the number of grains produced per unit of spike dry weight at anthesis. In other words, the efficiency with which the resources allocated to the spikes are used to produce a certain number of grains (Abbate *et al.* 1998, 2013; González *et al.* 2011b; Ferrante *et al.* 2012; Garcia *et al.* 2014).

## Objective

The aim of this paper is to review the state-of-the-art in wheat fruiting efficiency. For that purpose we (1) described the trait and its physiological bases, (2) revised to what degree fruiting efficiency has been deployed in past breeding, (3) reviewed the literature to quantify the degree of variation available for the trait, particularly within elite material including modern cultivars, and finally (4) considered potential drawbacks that must be taken into account to avoid increases in fruiting efficiency not resulting in yield gains by being compensated by other traits.

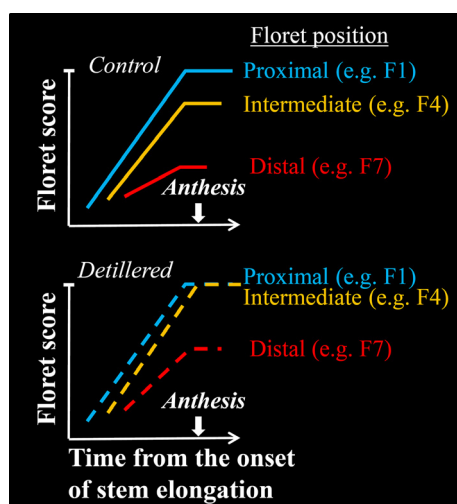
## Pathways to Increase Fruiting Efficiency

As indicated above, fruiting efficiency is estimated as the ratio between grain number (determined after grain set, normally at maturity) and spike dry weight at anthesis. It reflects the overall efficiency with which a certain amount of resources, allocated to the juvenile spike growing before anthesis, are used to set grains. Grains are the product of pollinated fertile florets, which in turn are the result of floret primordia development; which occurs within the spike (within the spikelets of the spike) precisely during the period when the juvenile spike grows before anthesis (Kirby 1988; González *et al.* 2011a; Slafer *et al.* 2015). It has been many times shown that floret primordia development is rather responsive to the availability of assimilates.

Studying the dynamics of floret development for contrasting availability of resources can illustrate the responsiveness of this developmental process. For instance, one of the treatments imposed by Ferrante *et al.* (2013a) consisted in detillering plants during stem elongation. Then, the fate of floret primordia in the main-shoot spikes of plants tillering freely (and then growing under competition with other spikes) was compared with the ones being detillered permanently (and then growing in the absence of the competition from other spikes). Detillering the plants did not affect the developmental patterns of the most proximal florets (which do develop to produce fertile florets in virtually any condition), but more vulnerable florets in less proximal positions within the spikelets (those that develop to produce fertile florets or die in the process, depending on the conditions; for example, florets 3, 4, and 5 from the rachis) developed more in the spikes of the detillered plants than in the spikes of the plants with free tillering (Fig. 2). This increased survival of the distal florets was associated with increased assimilate availability to the growth of the main stem spike in the detillered plants (Ferrante *et al.* 2013a).

This is the main reason why it has been widely documented that the number of grains is drastically sensitive to spike growth immediately before anthesis, and therefore it decreases sharply in response to shading during the period when spike growth takes place (Fischer 1985; Savin and Slafer 1991; Slafer *et al.* 1994; Abbate *et al.* 1997; Demotes-Mainard *et al.* 1999; Demotes-Mainard and Jeuffroy 2004), as well as to changes in duration of the spike growth phase as affected by manipulation of day-length in sensitive cultivars (Miralles *et al.* 2000; González *et al.* 2003, 2005b; Fischer 2007; Serrago *et al.* 2008). These responses are mostly related to the positive relationship between grain number and spike dry weight at anthesis, that also explains for instance grain number (and yield) responsiveness to nitrogen fertilization (Fischer 1993; Abbate *et al.* 1995; Demotes-Mainard *et al.* 1999; Demotes-Mainard and Jeuffroy 2001; Prystupa *et al.* 2004; Ferrante *et al.* 2010, 2012, 2013a) or to general environmental changes affecting yield (Marti and Slafer 2014), as well as to improvements in biomass partitioning to the juvenile spikes (as discussed above, explaining the main physiological reason for the Green Revolution). More recently, it has been also shown the mortality of floret primordia (the main component explaining the final number of fertile florets and grains) seems to be clearly dependent upon the availability of assimilates (González *et al.* 2011a; Ferrante *et al.* 2013b).

Fruiting efficiency is the final outcome of floret developmental rates (determining the number of floret primordia that reach the stage of fertile florets at anthesis) and the proportion of grain set per fertile floret (the opposite to grain abortion), per unit of spike weight

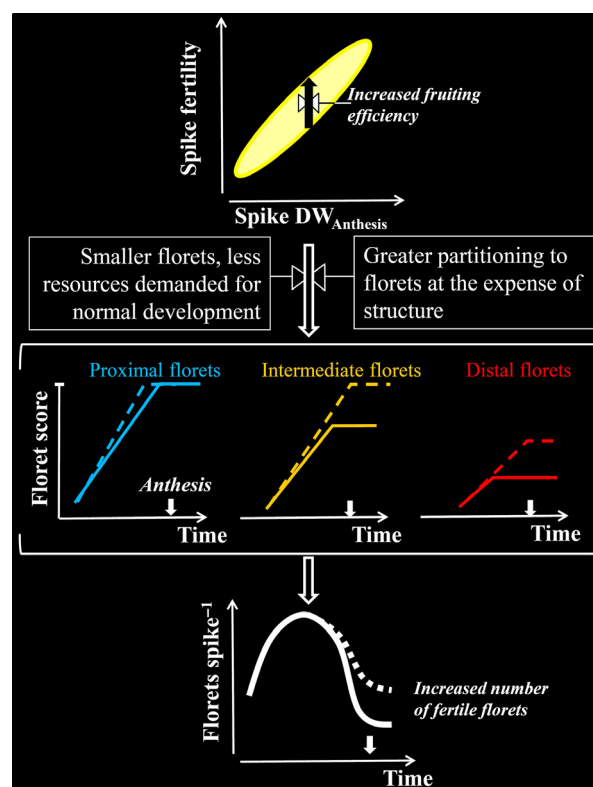


**Figure 2.** Schematic diagram highlighting changes in rate of development of florets at different positions within the spikelets (from the rachis, being F1 the most proximal) for main-shoot spikes of control or detillered plants (the spikes of the latter growing with more availability of resources). See details in Ferrante et al. (2013a).

(i.e., more efficient genotypes would show a higher survival of floret primordia, and/or a reduced level of grain abortion). As modern wheat cultivars show low grain abortion (Siddique et al. 1989a,b; González et al. 2003, 2005a), differences in fruiting efficiency in modern cultivars maybe likely related to higher survival of floret primordia.

Therefore, there are two alternative physiological pathways (Fig. 3) to improve fruiting efficiency, by allowing a normal development of most vulnerable floret primordia (those in more distal positions of the spikelets), through maintaining cell division in these florets and avoiding the initiation of autophagy<sup>2</sup> (Ghiglione et al. 2008). These are:

- An increased allocation of assimilates for the florets developing during spike growth before anthesis (for a particular level of spike growth). This would result in less investments in the structural pieces of the spike (rachis, glumes) in favour of an increased allocation to the growth of the florets, or
- A reduced demand of the florets for maintaining their normal development. If florets constitutively demand less assimilates for normal development, the proximal florets would leave more resources available for more distal florets which would maintain their growth and development normally for longer. Then, the intermediate florets would increase their likelihood to become fertile florets at anthesis (and to produce a grain). The most likely consequence of this would be that fertile florets at anthesis would be smaller in the genotype with higher fruiting efficiency.



**Figure 3.** Scheme presenting the two alternative physiological pathways that could bring about increases in fruiting efficiency (dashed lines), either by reducing the demands of individual florets or by increasing the spike dry matter partitioning towards florets. Proximal florets would be fertile in any case, but intermediate florets would increase their likelihood to become fertile florets and even distal florets which will not be fertile florets in any case would reach a higher level of development if fruiting efficiency is increased.

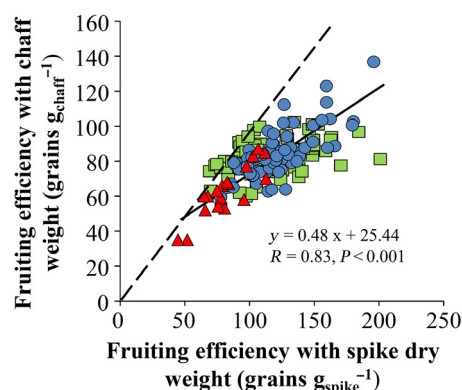
As in some studies differences in fruiting efficiency seemed associated with dry matter partitioning within the spike at anthesis (Slafer and Andrade 1993; Abbate et al. 1997), whilst in others such relationship was not identified (Abbate et al. 1998; Fischer 2007), both alternatives may be possible. It might be critical to recognize which of them is the actual cause of differences in fruiting efficiency as the potential trade-offs with grain weight are quite different (see later discussion on *Potential drawbacks*).

One inconvenience of fruiting efficiency is that it is a trait requiring the sampling and processing of samples at two different stages: spike dry weight must be determined at anthesis<sup>3</sup> and grain number when it has been fixed, at least 2–3 weeks later, most normally at maturity. To make this simpler, sometimes the dry weight of the chaff at maturity (structural parts of the spike after removing the grains) is used to provide an estimate of the dry weight of the spikes at anthesis (e.g., Abbate et al. 2013; Marti and Slafer 2014). For this to be accurate there should be



no growth in the nongrain parts of the spikes during grain filling. Although to the best of our knowledge reasons have not been understood, there are clear indications that chaff weight at maturity is consistently higher than spike dry weight at anthesis (or than the nongrain spike dry weight a week after anthesis). Fischer (2011) estimated this difference to be neither minor nor constant (chaff weight can be 20–50% greater), based on relatively old studies (Wall 1979; Fischer and Stockman 1980; Stockman *et al.* 1983) in which the focus was not genotypic variation in fruiting efficiency. Not many studies analyzed (or at least reported) genetic variation in spike dry weight at anthesis and chaff weight at maturity within high-yielding modern cultivars. The two of which we are aware of showed data that broadly confirmed that the estimated difference reported by Fischer (2011) was not an exception. In the papers by González *et al.* (2011b) and Abbate *et al.* (2013) chaff weight at maturity was, without a single exception, greater than spike dry weight at anthesis (averaging across genotypes and experiments a difference of 32 and 43%, respectively), with a substantial variation due to genotypes within each of the experiments; and there was a consistent trend to increase the magnitude of the underestimation with increases in fruiting efficiency as the slope was substantially lower than 1 (Fig. 4). Expanding further the analysis, when the variation was not restricted to modern cultivars but to a much larger population of double haploid lines (Garcia *et al.* 2014), the general pattern that using chaff at maturity does consistently underestimate fruiting efficiency (and the higher the efficiency the greater the magnitude of the overestimation) is further emphasized (Fig. 4). Thus, even though there was a significant positive relationship between both estimates, it seems clear that using chaff at maturity could provide only a rough proxy to fruiting efficiency.

In some cases it has been preferred to determine spike dry weight few days after anthesis to consider the period of grain set (during the lag-phase of grain filling; Loss *et al.*, 1989) as well. Although this is rather sensible, it has two major inconveniences. Firstly a huge amount of extra work is required to remove the tiny grains that might have already started to grow (otherwise the spike dry weight would be strongly overestimated and the overestimation would vary between genotypes (and environments) depending on the number of grains set and the potential size of the grains. Secondly, the estimated spike dry weight would include any eventual growth occurring during that extra week, which is naturally positive, but would exclude the weight contributed by the fertile florets to the spike dry weight at anthesis, which would be a drawback. All in all, we believe that it would be convenient to standardize the determination of fruiting efficiency using spike dry weight at anthesis.



**Figure 4.** Relationship between fruiting efficiency estimated with the chaff weight measured at maturity and estimated with spike dry weight at anthesis. Data adapted from Abbate *et al.* (2013, red triangles) and González *et al.* (2011b, blue circles) comparing modern cultivars. Solid line stands for the regression of the pooled data of these two sources, dashed line is the 1:1 ratio ( $y = x$ ). In addition, we added data adapted from Garcia *et al.* (2014) who analyzed variation among a mapping population with a much larger degree of variation than modern cultivars that broadly fall within the same cloud of data-points but with an even smaller slope; data from the study in which spike dry weight was measured at anthesis and values at chaff were unpublished).

## Contributions of Fruiting Efficiency to Wheat Breeding

### Was fruiting efficiency improved during past breeding?

Due to the dominating effect of reducing stem growth (semi-dwarfism), favoring the growth of the juvenile spike bringing about improvements in spike fertility and yield (see above), there have been only limited attempts to quantify the impact of past breeding on fruiting efficiency. In this section we revisited the very few cases in which this trait was analyzed in experiments comparing side-by-side cultivars released at different times (covering at least 20 years of breeding) under field conditions (Table 1).

Within the few cases available, there were no consistent trends: no increases in fruiting efficiency were observed at all in Argentina, there seemed to have been a clear positive trend in Spain; and the relationship was not significant but a positive trend might be inferred in the UK (Fig. 5). Grain number was increased in all the three countries analyzed, in Argentina the improvement in grain number was exclusively due to parallel increases in spike growth before anthesis (Slafer and Andrade 1993; González *et al.* 2003), while in Spain it was associated with spike growth before anthesis as well but also with fruiting efficiency of the cultivars (Acreche *et al.* 2008). In the UK (Shearman *et al.* 2005) increases in grain number were also consequence of increased

**Table 1.** Description of studies in which breeding impact on fruiting efficiency was estimated (or the data are available for the estimation). All experiments carried out under high-yielding conditions.

Location	Cultivar	Year of release	Grain number <sup>1</sup> (10 <sup>-3</sup> m <sup>-2</sup> )	Fruiting efficiency <sup>1</sup> (grains g <sub>spike</sub> <sup>-1</sup> )	Reference
Argentina, Buenos Aires	Klein Favorito	1920	12.7/20.8	122/130	Slafer and Andrade (1993)
	Eureka Ferrocarril Sur	1939	15.1/29.2	89/134	
	Buck Pucará	1980	22.8/37.4	118/114	
Argentina, Buenos Aires	Eureka Ferrocarril Sur	1939	13.6	128	González <i>et al.</i> (2003)
	Buck Manantial	1964	16.3	126	
	ProINTA Puntal	1994	19.5	139	
United Kingdom; Leicestershire	Maris Huntsman	1972	15.1	98	Shearman <i>et al.</i> (2005)
	Avalon	1980	19.1	91	
	Norman	1981	19.6	89	
	Galahad	1983	20.4	73	
	Riband	1989	19.1	102	
	Haven	1990	19.7	84	
	Brigadier	1993	23.91	128	
	Rialto	1995	19.5	92	
	Aragon 03	1940	9.7/16.1	68/79	Acreche <i>et al.</i> (2008)
Spain, Lleida	Pane 247	1950	11.8/18.1	74/93	
	Estrella	1963	17.7/21.2	116/108	
	Siete Cerros	1966	21.8/23.6	122/93	
	Anza	1971	22.4	105	
	Marius	1976	26.2	93	
	Soisson	1988	28.2	126	
	Isengrain	1998	26.1	100	

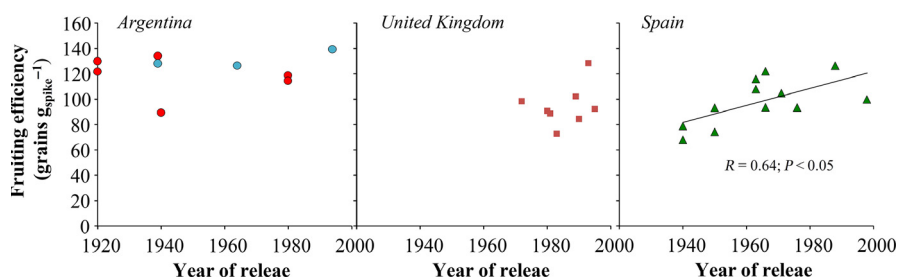
<sup>1</sup>When two figures were included they represent the values of two different growing seasons.

spike dry weight, although again there was a nonsignificant positive trend between grain number and fruiting efficiency for the cultivars released during the last three decades of the 20th century. In a much shorter period of analysis, Abbate *et al.* (1998) reported for cultivars released from 1984 to 1994 in Argentina that improvement of grain number was mostly associated with differences in fruiting efficiency.

### Potential usefulness of fruiting efficiency in future breeding

In the past, fruiting efficiency was not even considered as a possibility because huge gains could be obtained

relatively simply by selecting for reduced height (increasing partitioning to the spikes before anthesis and gaining in sink strength and yield, see above). In the future, it may be more relevant as a trait to consider, at least for identifying prospective parents for a cross designed to increase further yield potential. Selecting for fruiting efficiency would be much more difficult, unless trustworthy molecular markers are identified or high throughput tools could be developed. Abbate *et al.* (2013) have shown that selecting few individual spikes at maturity from a crop may produce sensible results reducing enormously the amount of work required for a more refined determination of fruiting efficiency. However, even measuring fruiting efficiency in few spikes would be a difficult task in realistic

**Figure 5.** Relationship between fruiting efficiency and the year of release of the cultivars for studies conducted in Argentina (left panel; Slafer and Andrade 1993; red circles; González *et al.* 2003, blue circles), UK (middle panel, Shearman *et al.* 2005), and Spain (right panel, Acreche *et al.* 2008).

breeding programs selecting thousands of plots per season.

In any case, there is an indication that if it were possible to identify proper markers (or to develop a high throughput screening method) it could be effective to select for fruiting efficiency. Pedro *et al.* (2012) have conducted an experimental selection procedure (selecting divergently for higher or lower fruiting efficiency) on segregating mutants (Fig. 6). These mutants were a TILLING population of durum wheat generated by Martin Parry's group at Rothamsted Research (RRes), UK (Parry *et al.* 2009). As determination of fruiting efficiency is destructive it would be impracticable in early generations when segregation is high and, therefore, the authors used the number of grains per unit stem length as a close proxy (see Pedro *et al.* 2012). The process started with a selection made on the M2 generation at RRes under glasshouse conditions and then continued for three further generations (M3, M4, and M5) under field conditions at the University of Lleida (UdL), although the M5 generation was grown and selected at RRes under glasshouse conditions as well. Finally the selected lines, already largely stabilized M6 populations, were grown in field plots at normal plant density at the UdL. Selection was systematically applied through successive generations (M2 to M5).

There was a positive response to selection through the entire process. At any single selecting generation the number of grains of the selected offspring evidenced response to the divergent selection, being the difference between the offspring selected for high or low fruiting efficiency enlarged throughout the generations (Fig. 6). In addition, these results were consistent, disregarding whether the performance of the offspring were analyzed under greenhouse or field conditions (Fig. 6, grain number in M5 plants). Finally in the M6 generation it was clear not only that lines selected for high fruiting efficiency produced more grains and higher yield than the sister lines selected for low fruiting efficiency, but also that the best lines from the population selected for high fruiting efficiency out-yielded (because they produced a higher number of grains) the controls in the field plot experiment (Fig. 6). Thus, selecting for a proxy of fruiting efficiency produced individual plants with enhanced reproductive output which did translate into the performance at the crop level of organization.

## Genetic Variation in Fruiting Efficiency Within elite Germplasm

It was shown (above) that when considering the physiological bases for yield gains in past breeding, fruiting efficiency was not consistently relevant: although there was genetic variation between cultivars released at different times, fruiting efficiency

was not regularly improved across studies (Fig. 5) during a period when improving partitioning of dry matter to the growing spikes was dominant (Calderini *et al.* 1999; Foulkes and Reynolds 2015). More relevant for future breeding is to count with genetic variation for this trait among modern, high-yielding genotypes (which are the elite material in most breeding programmes from which breeders attempt further pyramiding genes contributing to yield).

## Genetic variation among modern cultivars or advanced lines

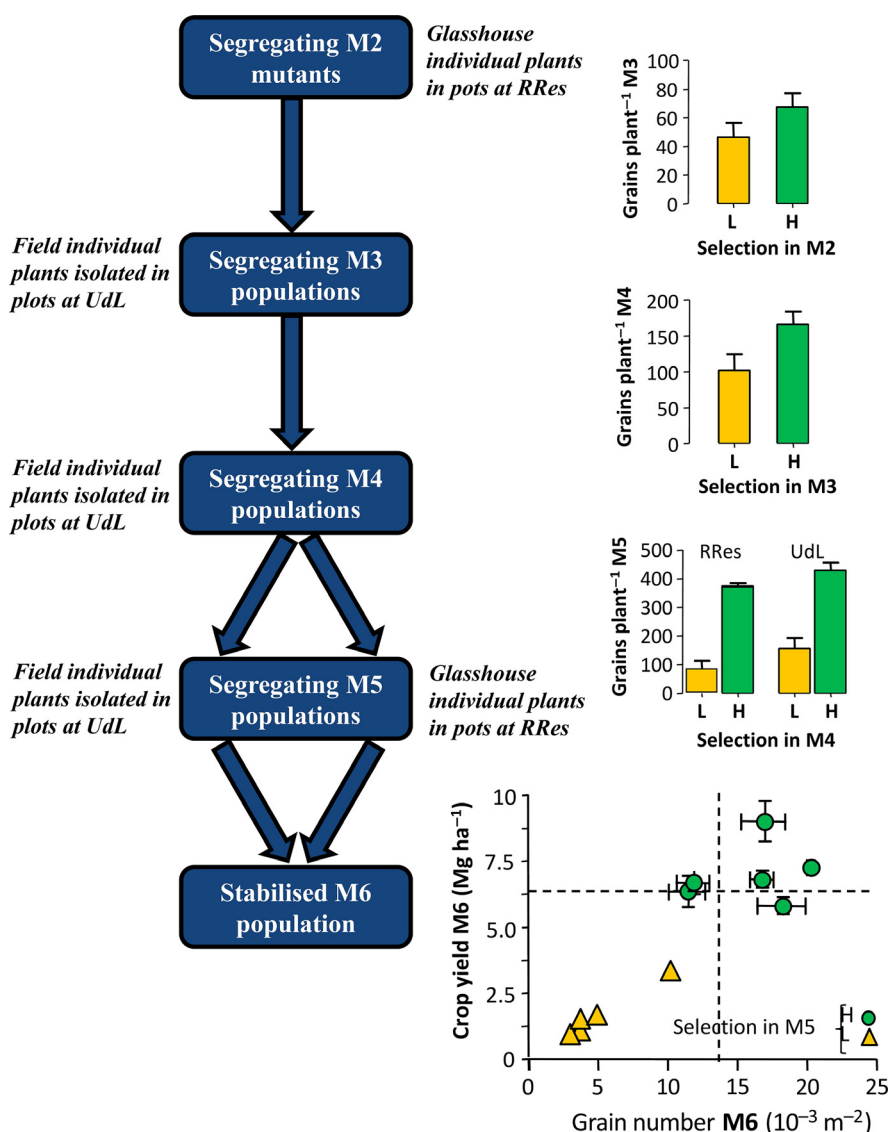
Again the number of studies reporting on fruiting efficiency for elite genotypes is rather scarce but the few published papers that we found showed a wide range of variability (Table 2). Differences among studies are expected as the actual values may depend on particular methodological details (e.g., how and when spike dry weight was measured). But what is really relevant is the consistently large degree of genotypic variation found within particular studies. It is clear that fruiting efficiency varies largely and, whenever different cultivars are compared a wide range of variation can be evidenced (Table 2).

In a paper that was just published, Mirabella *et al.* (2015) reported new results confirming wide variation in fruiting efficiency among modern cultivars and revealing that this variation was consistently larger than G×E interaction.

As genotypes within particular studies do differ in many other traits that may affect spike dry weight at anthesis, and then grain number determination, it would not be necessarily expected a strong correlation between grain number and fruiting efficiency in every single case. However, in the studies analyzed comparing modern cultivars or high-yielding lines there was in general a positive relationship: considering only the cases in which there were more than 10 genotypes compared (to have at least 8 degrees of freedom for the regression analysis) the relationship between grain number and fruiting efficiency was significantly positive in the studies published by Abbate *et al.* (2013); González *et al.* (2011b); Garcia *et al.* (2014) in the experiment carried out in Argentina; and Foulkes *et al.* (2011). The unique exception was the experiment conducted in Mexico by Garcia *et al.* (2014) in which a nonsignificant positive relationship was found.

Thus, in the cases analyzed not only was there substantial genetic variation among modern cultivars but also, unlike what occurs when comparing modern versus old cultivars, the differences among them in grain number tended to be due to their differences in fruiting efficiency; emphasizing the potential value of the trait for future breeding.





**Figure 6.** Diagram showing the selection process throughout the different seasons and conditions. At each generations plants were selected divergently for low (L) and high (H) fruiting efficiency and at each following generation there was a response of the number of grains per plant to the selection process (right bar plots). When lines selected were in the M6 generation (largely stabilized), a field plot experiment including the selected lines together with four commercial controls (dashed lines) was carried out. See details in Pedro et al. (2012).

### Relevance of fruiting efficiency in a population designed to increase grain number and yield

Beyond the degree of variation available in elite germplasm, further variation can be expected if the trait shows transgressive segregation (observation of extreme individual phenotypes which exceed parental phenotypic values in either a positive or negative direction; Rieseberg et al. 1999). Transgressive phenotypes can be produced when alleles at multiple loci present in parental lines (some of them reducing and others increasing the parental

phenotypic value) recombine in the segregating progeny (Bell and Travis 2005).

Phenotyping of wheat elite population, that is, population obtained by the cross of well-adapted and high-yielding parental lines, have reported positive transgressive segregation in traits related to phenology and tillering dynamics (Borràs Gelonch et al. 2012), in drought-adaptive traits (Olivares-Villegas et al. 2007), or in reserves and yield numerical components (Rebetzke et al. 2008; Rattey et al. 2009). Regarding fruiting efficiency, it has been recently phenotyped a doubled-haploid population derived from a cross between two high-yielding wheat cultivars with

**Table 2.** Genotypic variation (ranges) reported in the literature for grain number and fruiting efficiency in experiments in which different genotypes were compared side by side. Information is presented on whether fruiting efficiency was estimated with spike dry weight (including when and how) or chaff weight at maturity. Plant material type, number of genotypes, years of release (when it was mentioned) of these genotypes, country of evaluation, level of input in the experiment were also included.

Measurement used to estimate fruiting efficiency	Plant material	Number of genotypes	Year of release	Country	Input level	Grain number ( $10^{-3} \text{ m}^{-2}$ )	Fruiting efficiency (grains $\text{g}^{-1}$ )	Reference
Chaff at maturity	SW – CC	16	Not indicated	Argentina	High	11.2–24.6	35–87	Abbate <i>et al.</i> (2013)
	SW – CC	39	2000–2008	Argentina	High	15–29.7	59–137	González <i>et al.</i> (2011b)
Spike dry weight (SDW) at anthesis	SW – DH, CC	4	Not indicated	Chile	High	20.1–38.8	86–136	Bustos <i>et al.</i> (2013)
	DW – CC	4	1987–2002	Spain	High	27–30.9	80–115	Ferrante <i>et al.</i> (2012)
	DW – CC	4	1987–2003	Spain	Medium	18.5–21.3	64–90	Ferrante <i>et al.</i> (2012)
	SW – DH, CC	87	Not indicated	Argentina	High	11.5–28	69–201	García <i>et al.</i> (2014)
	SW – CC	39	2000–2008	Argentina	High	15–29.7	78–196	González <i>et al.</i> (2011b)
	DW – CC, RIL	6	Not indicated	Spain	High	12.6–16.8	64–84	Pedro <i>et al.</i> (2011)
	RIL	2	Not indicated	Australia	High	18.7–24.1	162–201	Dreccer <i>et al.</i> (2009)
SDW at 1 week after anthesis	SW – CC, DH, RIL, EL	30	Not indicated	Mexico	High	13.3–22.4	40–76	Foulkes <i>et al.</i> (2013)
	SW – DH	8	Not indicated	Mexico	High	16.4–26	44–75	Gaju <i>et al.</i> (2014)
	SW – DH, CC	107	Not indicated	Mexico	High	9.9–20	42–91	García <i>et al.</i> (2014)
	SW – CC, EL	6	Not indicated	Argentina	High	13.3–21.3	61–106	Abbate <i>et al.</i> (1998)
SDW at 1 week after anthesis (without grains)	SW – CC	16	Not indicated	Argentina	High	11.2–24.6	45–113	Abbate <i>et al.</i> (2013)
	SW – CC	4	1984–1994	Argentina	High	11.5–22.5	45–126	Lazaro and Abbate (2012)

SW, spring wheat; DW, durum wheat; CC, commercial cultivars; EL, experimental line; DH, doubled-haploid line; RIL, recombinant inbred line.

similar phenology but consistently differing in yield components: Bacanora (possessing high grain number) and Weebil (possessing heavy grains), under two different evaluation environments (García *et al.* 2014). It was reported that 20–34% (depending on the experiment) of the DH lines exhibited higher values of fruiting efficiency than Bacanora (the parent characterized by having high fruiting efficiency; García *et al.* 2014). Furthermore, focusing on top DH lines, simulating the selection carried out in a breeding program aimed to improve grain number, transgressive segregation was also evident (*i.e.*, lines with grain number increased by 25% over the parental mean had also higher fruiting efficiency, consistently across experiments; García *et al.* 2014). This suggests that crossing parents from the elite germplasm of high-yielding lines

of a breeding programme may be a valuable strategy to further increase grain number through the expression of transgressive variation in fruiting efficiency. In a paper that just became available, Martino *et al.* (2015) also found that fruiting efficiency exhibited transgressive segregation and would be reasonably heritable.

## Potential Drawbacks

As with any other potentially valuable trait, when considering the usefulness of fruiting efficiency to achieve yield gains through increasing grain number it must be considered whether it may cause important trade-offs with other yield determining components. The two most obvious trade-offs that must be analyzed are (1) that increases

in fruiting efficiency be not constitutively related to decreases in spike dry weight at anthesis (the other major determinant of grain number), resulting fruiting efficiency irrelevant to bring about actual increases in grain number; and (2) that increases in grain number produced by higher fruiting efficiency is not constitutively related to decreases in grain weight (the other major yield component), resulting fruiting efficiency irrelevant to bring about actual increases in yield.

### **Does high fruiting efficiency require low spike dry weights?**

The conceptual model proposed by Fischer (1984) includes the idea that fruiting efficiency and spike dry weight at anthesis are, at least partially, independent. The strong relationship between grain number and spike dry weight at anthesis when the variations were imposed either by genetic factors like introgressing semi-dwarfing genes (e.g., Fischer and Stockman 1980; Brooking and Kirby 1981; Miralles et al. 1998), management factors like nitrogen fertilization (e.g., Fischer 1993; Prystupa et al. 2004; Ferrante 2012), or artificial manipulations of the growing conditions like extending the photoperiod or shading the crops during stem elongation (e.g., Stockman et al. 1983; Savin and Slafer 1991; González et al. 2003, 2005a; Serrago et al. 2008) seem to support the idea that there would be no major trade-offs between these two components of grain number. However, studies directly analyzing trade-offs between fruiting efficiency and spike dry weight at anthesis are, once again, rather scarce.

From the few direct evidences reported in the literature, there are no evidences for a consistent conclusion. There are studies reporting negative relationship between these traits, supporting the idea of a likely trade-off (Dreccer et al. 2009; Ferrante et al. 2012; Lázaro and Abbate 2012); while in other cases there were no significant relationships, supporting the idea of independence (González et al. 2011b; Bustos et al. 2013; García et al. 2014). Thus, there are no evidences for postulating a constitutive, and therefore inexorable, trade-off between fruiting efficiency and spike dry weight at anthesis; and even in the cases in which such trade-off emerged, the cause is uncertain and the interpretation not possible at this stage of knowledge on the trait (Foulkes and Reynolds 2015).

Therefore, it is reinforced the idea that it may be possible to select for fruiting efficiency not necessarily expecting any trade-off in spike dry weight at anthesis. For instance, in the work by García et al. (2014) it was shown that high yield was associated with grain number due to higher fruiting efficiency, not compensated by reductions in spike dry weight, when the top yielding lines (which represent those that would have been selected in a

breeding program) were analyzed. Similarly, Pedro et al. (2012) showed that selecting divergently for (a proxy to) fruiting efficiency, after five generations there were two clear populations of either lower yielding with fewer grains or higher yielding with more grains than commercial controls used in the study.

### **Does high fruiting efficiency constitutively reduce the size of the grains?**

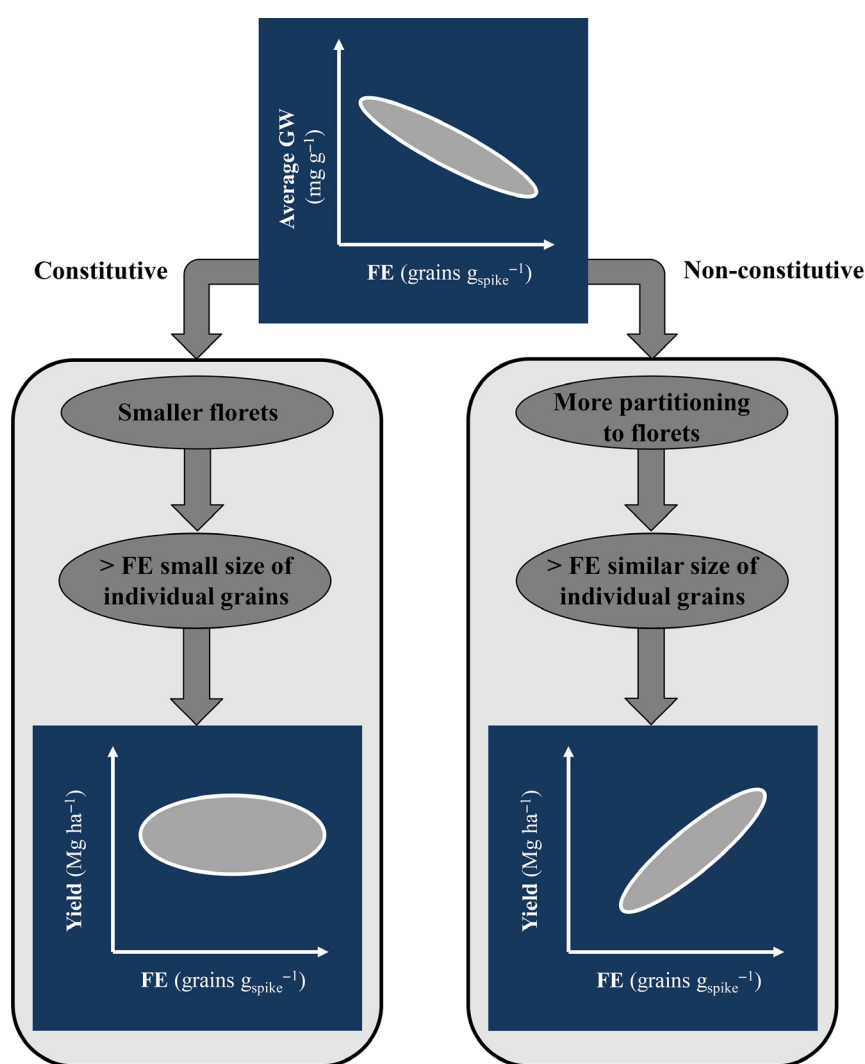
Increasing grain number via fruiting efficiency would result in low yield advantages if average grain weight is highly reduced due to a trade-off between fruiting efficiency and average grain weight. It seems likely to expect a negative relationship between the average weight of the grains and fruiting efficiency (Ferrante et al. 2012) although it is not necessarily so always (González et al. 2014). However, a negative relationship does not always represent a true compensation; this would depend upon the nature of the causes behind the negative relationship. For this analysis we will assume that the basis for the negative relationship would hardly be the increased competition for resources to maximize grain size as the availability of assimilates during the effective period of grain filling is most frequently enough to fill the grains (see above in section How was yield improved in the past?).

In this context, there are two alternative hypothetical causes for the negative relationship between average grain weight and fruiting efficiency, one representing a clear trade-off while in the other the trade-off is only apparent (Fig. 7). The mechanism behind the true trade-off would be that the cause of the increased fruiting efficiency would be a reduced demand of individual florets to develop normally and consequently the final size of the fertile florets would be smaller (i.e., the same amount of resources may sustain the normal growth or more, though smaller, florets). As final grain weight would be related, albeit not necessarily linearly, to the size of the florets (Calderini et al. 2001; Hasan et al. 2011) increasing fruiting efficiency would concomitantly reduce the size of all grains and consequently the average grain weight (Fig. 7, left side). Should this hypothesis reflect the reality, increasing fruiting efficiency would increase number of grains which would be of smaller potential size and consequently would not necessarily produce any yield gain. But the trade-off could be only apparent if the reason behind the increased fruiting efficiency would be independent of the size of the florets (and then potential size of the grains); which may require an improved partitioning of the resources within the juvenile spike toward the florets at the expense of the more-structural parts. Should this hypothesis be true, increasing fruiting efficiency would not affect the potential size of individual grains,

but as it would reduce the mortality of more distal florets and these florets have lower size potential than the proximal ones, it would increase the proportion of florets of smaller size potential (Miralles and Slafer 1995b; Acreche and Slafer 2006) and consequently the average size would be reduced but yield gains would be certain (Fig. 7, right side). In this case, fruiting efficiency could be used as a trustworthy selection criterion to further increase yield, if molecular markers were identified or high throughput tools were developed for making this possible in practice.

As far as we are aware there is only one paper reporting the relationship between potential grain weight (obtained after 50% trimming of the spike at the onset of grain

filling) and fruiting efficiency for cultivars differing in this last trait (González et al. 2014), in which it was not found a general negative relationship between potential grain weight and fruiting efficiency. Furthermore, in a rather comprehensive study comparing two cultivars contrasting in fruiting efficiency and average grain weight under 8 different environmental conditions (Ferrante et al. 2015), it was evident that the cultivar with consistently higher fruiting efficiency and lower average grain weight had grains at particular positions within the spike of very similar weight to those of the cultivar with consistently lower fruiting efficiency and higher average grain weight. It was clear in that case that the negative relationship would not be constitutive and there



**Figure 7.** Schematic representation of the two alternative hypotheses to explain the negative relationship between average grain weight and fruiting efficiency. Left: a constitutive reduction in floret size bringing about a trade-off between weight of each of the grains (not just the average weight of all grains) and fruiting efficiency resulting in no yield gain from increased fruiting efficiency. Right: a nonconstitutive alternative hypothesis in which the size of individual grains are not affected but the proportion of grains of smaller size potential is increased and then increasing fruiting efficiency does produce yield gain, even when the average grain weight is reduced. Adapted from Ferrante et al. (2015)

would be an apparent, not real, trade-off produced by the increased proportion of distal grains in the cultivar with high fruiting efficiency (Ferrante *et al.* 2015).

## Concluding Remarks

Alternative ways to further increase yield by breeding are urgently required to maintain current levels of food security. Fruiting efficiency is among the traits which could be exploited to achieve the needed gains in wheat yield. It has not been exploited consistently in past breeding and shows a wealth of genetic variation, particularly within the elite germplasm for breeding programmes. An empiric divergent selection exercise evidenced that it is likely to obtain yield gains through selecting for (a proxy to) fruiting efficiency. With the current understanding of the physiology of fruiting efficiency we can only characterize elite germplasm for breeders to be able to choose prospective parents when deciding their strategic crosses (in which case the characterization must consider the nature of the high fruiting efficiency to discard trade-offs). However, to be able to select for this trait in realistic breeding programmes molecular markers must be identified or high throughput phenotyping systems must be developed.

Finally, we focused this paper on wheat as it has been in this crop where this trait has been treated more explicitly. However, the concept is equally applicable to other cereals (and likely to any grain crop), as fruiting efficiency is an integral component to understand grain number determination through the general physiological model that establishing that grain number is related to growth during the “critical period for grain number determination” (e.g., for barley: Miralles *et al.* 2000; Prystupa *et al.* 2004; Arisnabarreta and Miralles 2010; maize: Otegui and Bonhomme 1998; Vega *et al.* 2001; Rattalino Edreira and Otegui 2012; and soybean: Jiang and Egli 1995; Kantolic and Slafer 2001, 2005; Egli 2010; Kantolic *et al.* 2013). Briefly, in all grain crops, due to evolutionary and breeding reasons, grain number is far more relevant than grain weight in determining yield (Sadras 2007) and grain number is far more dependent on floret survival than on floret initiation processes (Sadras and Slafer 2012). Therefore, in all grain crops grain number is related to growth in that critical period and genotypic differences in the efficiency of transforming that growth into grain number would likely be expected. Thus, what we exemplified in this paper for wheat is simply a general process linking reproductive biology and agronomic performance of crops that could likely be manipulated to further increase yield. However, comparisons among different species should be avoided as in this case differences in fruiting efficiency may be tightly related to constitutive differences in grain size among crops as shown by Gambín and Borrás (2010)

for a comprehensive comparison among widely different species; and by Marti and Slafer (2014) for a constitutive difference between durum and bread wheat.

## Acknowledgments

The work on fruiting efficiency has been funded by grants from the “National Plan” of Research in Spain, grants AGL2009-11964 and AGL2012-35300 at the Crop Physiology Lab of the University of Lleida; National Agency of Scientific and Technical Promotion (PICT-2008-1039) and INTA (PNCER-1336) at CONICET and INTA Lab, and PICT RAICES 1368 and UBACyT G-076 competitive grants at the University of Buenos Aires.

## Conflict of Interest

None declared.

## Notes

<sup>1</sup> This trait has been also termed “spike fertility index” (e.g. Fischer 2011; Foulkes *et al.* 2011; and references therein) but the term index in crop physiology usually refers to ratios of variables with similar units (like harvest index or leaf area index), while the term efficiency is used to reflect the translation of certain amount of resources into variables of agronomic interest (e.g. water or nitrogen use efficiency). Thus, the term fruiting efficiency has been increasingly employed to describe the efficiency with which resources allocated to the spikes translate to the generation of a certain number of grains (e.g. González *et al.* 2011a; Pedro *et al.* 2011; Ferrante *et al.* 2012; Reynolds *et al.* 2012; Bustos *et al.* 2013; González *et al.* 2014; Marti and Slafer 2014; Garcia *et al.* 2014; Foulkes and Reynolds 2015; Sadras and Calderini, 2015).

<sup>2</sup> a massive decrease in the expression of genes involved in cell proliferation, a decrease in soluble carbohydrate levels, and an increase in the expression of genes involved in programmed cell death; Ghiglione *et al.* 2008).

<sup>3</sup> In some cases it has been preferred to determine spike dry weight few days after anthesis to consider the period of grain set (during the lag-phase of grain filling; Loss *et al.*, 1989) as well. This is rather sensible but it has two major inconveniences. Firstly a huge amount of extra work is required to remove the tiny grains that might have already started to grow (otherwise the spike dry weight would be strongly overestimated and the overestimation would vary between genotypes (and environments) depending on the number of grains set and the potential size of the grains. Secondly, the estimated spike dry weight would include any eventual growth occurring



during that extra week, which is naturally positive, but would exclude the weight contributed by the fertile florets -as the small grains would have been removed- to the spike dry weight at anthesis, which would be a drawback. All in all, we believe that it would be convenient to standardize the determination of fruiting efficiency using spike dry weight at anthesis.

## References

- Abbate, P. E., F. H. Andrade, and J. P. Culot. 1995. The effects of radiation and nitrogen on number of grains in wheat. *J. Agric. Sci.* 124:351–360.
- Abbate, P. E., F. H. Andrade, J. P. Culot, and P. S. Bindraban. 1997. Grain yield in wheat: effects of radiation during spike growth period. *Field Crop Res.* 54:245–257.
- Abbate, P. E., F. H. Andrade, L. Lázaro, J. H. Bariffi, H. G. Berardocco, V. H. Inza, et al. 1998. Grain yield increase in recent argentine wheat cultivars. *Crop Sci.* 38:1203–1209.
- Abbate, P. E., A. C. Pontaroli, L. Lazaro, and F. Gutheim. 2013. A method of screening for spike fertility in wheat. *J. Agric. Sci.* 151:322–330.
- Acreche, M. M., G. Briceno-Felix, J. A. M. Sanchez, and G. A. Slafer. 2008. Physiological bases of genetic gains in Mediterranean bread wheat yield in Spain. *Eur. J. Agron.* 28:162–170.
- Acreche, M. M., and G. A. Slafer. 2006. Grain weight response to increases in number of grains in wheat in a Mediterranean area. *Field Crop Res.* 98:52–59.
- Albajes, R., C. Cantero-Martinez, T. Capell, P. Christou, A. Farre, J. Galceran, et al. 2013. Building bridges: an integrated strategy for sustainable food production throughout the value chain. *Mol. Breeding* 32:743–770.
- Araus, J. L., G. A. Slafer, C. Royo, and M. Dolores Serret. 2008. Breeding for yield potential and stress adaptation in cereals. *Crit. Rev. Plant Sci.* 27:377–412.
- Arisnabarreta, S., and D. J. Miralles. 2010. Nitrogen and radiation effects during the active spike-growth phase on floret development and biomass partitioning in 2- and 6-rowed barley isolines. *Crop Past. Sci.* 61:578–587.
- Austin, R. B., J. Bingham, R. D. Blackwell, L. T. Evans, M. A. Ford, C. L. Morgan, et al. 1980. Genetic improvements in winter-wheat yields since 1900 and associated physiological-changes. *J. Agric. Sci.* 94:675–689.
- Austin, R. B., M. A. Ford, and C. L. Morgan. 1989. Genetic-improvement in the yield of winter-wheat - a further evaluation. *J. Agric. Sci.* 112:295–301.
- Bell, M. A., and M. P. Travis. 2005. Hybridization, transgressive segregation, genetic covariation, and adaptive radiation. *Trends Ecol. Evol.* 20:358–361.
- Borrás, L., G. A. Slafer, and M. E. Otegui. 2004. Seed dry weight response to source-sink manipulations in wheat, maize and soybean: a quantitative reappraisal. *Field Crop Res.* 86:131–146.
- Borrás-Gelonch, G., G. J. Rebetzke, R. A. Richards, and I. Romagosa. 2012. Genetic control of duration of pre-anthesis phases in wheat (*Triticum aestivum* L.) and relationships to leaf appearance, tillering, and dry matter accumulation. *J. Exp. Bot.* 63:69–89.
- Braun, H.-J., G. Atlin, and T. Payne. 2010. Multi-location testing as a tool to identify plant response to global climate change. Pp. 115–138 in M. P. Reynolds, ed. *Climate change and crop production*. CABI, Wallingford, UK.
- Brisson, N., P. Gate, D. Gouache, G. Charmet, F.-X. Oury, and F. Huard. 2010. Why are wheat yields stagnating in Europe? A comprehensive data analysis for France. *Field Crop Res.* 119:201–212.
- Brooking, I. R., and E. J. M. Kirby. 1981. Interrelationships between stem and ear development in winter-wheat – the effects of a norin-10 dwarfing gene, *gai-Rht2*. *J. Agric. Sci.* 97:373–381.
- Bustos, D. V., A. K. Hasan, M. P. Reynolds, and D. F. Calderini. 2013. Combining high grain number and weight through a DH-population to improve grain yield potential of wheat in high-yielding environments. *Field Crop Res.* 145:106–115.
- Calderini, D. F., M. F. Dreccer, and G. A. Slafer. 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, D. F., M. P. Reynolds, and G. A. Slafer. 1999. Genetic gains in wheat yield and associated physiological changes during the twentieth century. Pp. 351–377 in E. H. Satorre and G. A. Slafer, eds. *Wheat: ecology and physiology of yield determination*. Food Products Press, New York.
- Calderini, D. F., R. Savin, L. G. Abeledo, M. P. Reynolds, and G. A. Slafer. 2001. The importance of the period immediately preceding anthesis for grain weight determination in wheat. *Euphytica* 119:199–204.
- Calderini, D. F., and G. A. Slafer. 1998. Changes in yield and yield stability in wheat during the 20th century. *Field Crop Res.* 57:335–347.
- Canevara, M., M. Romani, M. Corbellini, M. Perenzin, and B. Borghi. 1994. Evolutionary trends in morphological, physiological, agronomical and qualitative traits of *Triticum aestivum* L. cultivars bred in Italy since 1900. *Eur. J. Agron.* 3:175–185.
- Chand, R. 2009. Challenges to ensuring food security through wheat. *CAB Rev. Persp. Agricult. Vet. Sci. Nutr. Nat. Res.* 4:1–13.
- Demotes-Mainard, S., and M. H. Jeuffroy. 2001. Partitioning of dry matter and nitrogen to the spike throughout the spike growth period in wheat crops subjected to nitrogen deficiency. *Field Crop Res.* 70:153–165.

- Demotes-Mainard, S., and M. H. Jeuffroy. 2004. Effects of nitrogen and radiation on dry matter and nitrogen accumulation in the spike of winter wheat. *Field Crop Res.* 87:221–233.
- Demotes-Mainard, S., M. H. Jeuffroy, and S. Robin. 1999. Spike dry matter and nitrogen accumulation before anthesis in wheat as affected by nitrogen fertilizer: relationship to kernels per spike. *Field Crop Res.* 64:249–259.
- Dreccer, M. F., A. F. van Herwaarden, and S. C. Chapman. 2009. Grain number and grain weight in wheat lines contrasting for stem water soluble carbohydrate concentration. *Field Crop Res.* 112:43–54.
- Dreccer, M. F., K. B. Wockner, J. A. Palta, C. L. McIntyre, M. G. Borgognone, M. Bourgault, et al. 2014. More fertile florets and grains per spike can be achieved at higher temperature in wheat lines with high spike biomass and sugar content at booting. *Funct. Plant Biol.* 41:482–495.
- Egli, D. B. 2010. Soybean reproductive sink size and short-term reductions in photosynthesis during flowering and pod set. *Crop Sci.* 50:1971–1977.
- Ferrante, A., R. Savin, and G. A. Slafer. 2010. Floret development of durum wheat in response to nitrogen availability. *J. Exp. Bot.* 61:4351–4359.
- Ferrante, A., R. Savin, and G. A. Slafer. 2012. Differences in yield physiology between modern, well adapted durum wheat cultivars grown under contrasting conditions. *Field Crop Res.* 136:52–64.
- Ferrante, A., R. Savin, and G. A. Slafer. 2013a. Floret development and grain setting differences between modern durum wheats under contrasting nitrogen availability. *J. Exp. Bot.* 64:169–184.
- Ferrante, A., R. Savin, and G. A. Slafer. 2013b. Is floret primordia death triggered by floret development in durum wheat? *J. Exp. Bot.* 64:2859–2869.
- Ferrante, A., R. Savin, and G. A. Slafer. 2015. Relationship between fruiting efficiency and grain weight in durum wheat. *Field Crop Res.* 177:109–116.
- Fischer, R. A. 1984. Wheat. In: Smith, W. H., J., B. S. (Eds.), *Symposium on potential productivity of field crops under different environments* IRRI, Los Baños, Philippines pp.129–154 in 'Proc. Symp. on potential productivity of field crops under different environments, Sep. 1980'. IRRI, Los Baños.
- Fischer, R. A. 1985. Number of kernels in wheat crops and the influence of solar-radiation and temperature. *J. Agric. Sci.* 105:447–461.
- Fischer, R. A. 2007. Understanding the physiological basis of yield potential in wheat. *J. Agric. Sci.* 145:99–113.
- Fischer, R. A. 2011. Wheat physiology: a review of recent developments. *Crop Past. Sci.* 62:95–114.
- Fischer, R. A., and G. O. Edmeades. 2010. Breeding and cereal yield progress. *Crop Sci.* 50:S85–S98.
- Fischer, R. A., 1993. Irrigated spring wheat and timing and amount of nitrogen fertilizer. II. physiology of grain yield response *Field Crop Res.* 33:57–80.
- Fischer, R. A., and Y. M. Stockman. 1980. Kernel number per spike in wheat (*Triticum aestivum*) responses to preanthesis shading. *Aust. J. Plant Physiol.* 7:169–180.
- Flintham, J. E., A. Borner, A. J. Worland, and M. D. Gale. 1997. Optimizing wheat grain yield: effects of Rht (gibberellin-insensitive) dwarfing genes. *J. Agric. Sci.* 128:11–25.
- Foulkes, M. J., Rivera, C., Trujillo, E., Sylvester-Bradley, R., Slafer, G. A., Reynolds, M. P., 2013. Optimizing harvest index through increasing partitioning to spike growth and maximizing grain number. In: Reynolds, M., Braun, H. (Eds.), *3rd International Workshop of the Wheat Yield Consortium*. CIMMYT, Cd. Obregón, Mexico, pp. 26–31.
- Foulkes, M. J., and M. P. Reynolds. 2015. Breeding challenge: improving yield potential. Pp. 397–421 in V. O. Sadras and D. F. Calderini, eds. *Crop physiology applications for genetic improvement and agronomy*, 2nd edn. Elsevier, Amsterdam, The Netherlands.
- Foulkes, M. J., G. A. Slafer, W. J. Davies, P. M. Berry, R. Sylvester-Bradley, P. Martre, et al. 2011. Raising yield potential of wheat. III. Optimizing partitioning to grain while maintaining lodging resistance. *J. Exp. Bot.* 62:469–486.
- Gaju, O., M. P. Reynolds, D. L. Sparkes, S. Mayes, G. Ribas-Vargas, J. Crossa, et al. 2014. Relationships between physiological traits, grain number and yield potential in a wheat DH population of large spike phenotype. *Field Crop Res.* 164:126–135.
- Gambín, B. L., and L. Borrás. 2010. Resource distribution and the trade-off between seed number and seed weight: a comparison across crop species. *Anna. Appl. Biol.* 156:91–102.
- García, G. A., A. K. Hasan, L. E. Puhl, M. P. Reynolds, D. F. Calderini, and D. J. Miralles. 2013. Grain yield potential strategies in an elite wheat double-haploid population grown in contrasting environments. *Crop Sci.* 53:2577–2587.
- García, G. A., R. A. Serrago, F. G. González, G. A. Slafer, M. P. Reynolds, and D. J. Miralles. 2014. Wheat grain number: identification of favourable physiological traits in an elite doubled-haploid population. *Field Crop Res.* 168:126–134.
- Ghiglione, H. O., F. G. González, R. Serrago, S. B. Maldonado, C. Chilcott, J. A. Cura, et al. 2008. Autophagy regulated by day length determines the number of fertile florets in wheat. *Plant J.* 55:1010–1024.
- Godfray, H. C. J. 2011. Food for thought. *Proc. Natl Acad. Sci. U.S.A.* 108:19845–19846.
- González, F. G., M. L. Aldabe, I. I. Terrile, and D. P. Rondanini. 2014. Grain weight response to different

- postflowering source: sink ratios in modern high-yielding Argentinean wheats differing in spike fruiting efficiency. *Crop Sci.* 54:297–309.
- González, F. G., D. J. Miralles, and G. A. Slafer. 2011a. Wheat floret survival as related to pre-anthesis spike growth. *J. Exp. Bot.* 62:4889–4901.
- González, F. G., G. A. Slafer, and D. J. Miralles. 2003. Grain and floret number in response to photoperiod during stem elongation in fully and slightly vernalized wheats. *Field Crop Res.* 81:17–27.
- González, F. G., G. A. Slafer, and D. J. Miralles. 2005a. Floret development and survival in wheat plants exposed to contrasting photoperiod and radiation environments during stem elongation. *Funct. Plant Biol.* 32:189–197.
- González, F. G., G. A. Slafer, and D. J. Miralles. 2005b. Pre-anthesis development and number of fertile florets in wheat as affected by photoperiod sensitivity genes *Ppd-D1* and *Ppd-B1*. *Euphytica* 146:253–269.
- González, F. G., I. I. Terrile, and M. O. Falcon. 2011b. Spike fertility and duration of stem elongation as promising traits to improve potential grain number (and yield): variation in modern Argentinean wheats. *Crop Sci.* 51:1693–1702.
- Hall, A. J., and R. A. Richards. 2012. Prognosis for genetic improvement of yield potential and water-limited yield of major grain crops. *Field Crop Res.* 143:18–33.
- Hasan, A. K., J. Herrera, C. Lizana, and D. F. Calderini. 2011. Carpel weight, grain length and stabilized grain water content are physiological drivers of grain weight determination of wheat. *Field Crop Res.* 123:241–247.
- Jiang, H., and D. B. Egli. 1995. Soybean seed number and crop growth rate during flowering. *Agron. J.* 87:264–267.
- Kantolic, A. G., and G. A. Slafer. 2001. Photoperiod sensitivity after flowering and seed number determination in indeterminate soybean cultivars. *Field Crop Res.* 72:109–118.
- Kantolic, A. G., and G. A. Slafer. 2005. Reproductive development and yield components in indeterminate soybean as affected by post-flowering photoperiod. *Field Crop Res.* 93:212–222.
- Kantolic, A. G., G. E. Peralta, and G. A. Slafer. 2013. Seed number responses to extended photoperiod and shading during reproductive stages in indeterminate soybean. *Eur. J. Agron.* 51:91–100.
- Kirby, E. J. M. 1988. Analysis of leaf, stem and ear growth in wheat from terminal spikelet stage to anthesis. *Field Crop Res.* 18:127–140.
- Lazaro, L., and P. E. Abbate. 2012. Cultivar effects on relationship between grain number and photothermal quotient or spike dry weight in wheat. *J. Agric. Sci.* 150:442–459.
- Loss, S. P., Kirby, E. J. M., Siddique, K. H. M., Perry, M. W., 1989. Grain growth and development of old and modern Australian wheats. *Field Crops Res.* 21, 131–146.
- Lopes, M. S., M. P. Reynolds, Y. Manes, R. P. Singh, J. Crossa, and H. J. Braun. 2012. Genetic yield gains and changes in associated traits of CIMMYT spring bread wheat in a “historic” set representing 30 years of breeding. *Crop Sci.* 52:1123–1131.
- Marti, J., and G. A. Slafer. 2014. Bread and durum wheat yields under a wide range of environmental conditions. *Field Crop Res.* 156:258–271.
- Martino, D. L., P. E. Abbate, M. E. Cendoya, F. Gutheim, N. E. Mirabella, and A. C. Pontaroli. 2015. Wheat spike fertility: inheritance and relationship with spike yield components in early generations. *Plant Breeding*, in press.
- Mirabella, N. E., P. E. Abbate, I. A. Ramirez, and A. C. Pontaroli. 2015. Genetic variation for wheat spike fertility in cultivars and early breeding materials. *J. Agric. Sci.*, in press.
- Miralles, D. J., S. D. Katz, A. Colloca, and G. A. Slafer. 1998. Floret development in near isogenic wheat lines differing in plant height. *Field Crop Res.* 59:21–30.
- Miralles, D. J., R. A. Richards, and G. A. Slafer. 2000. Duration of the stem elongation period influences the number of fertile florets in wheat and barley. *Aust. J. Plant Physiol.* 27:931–940.
- Miralles, D. J., and G. A. Slafer. 1995a. Yield, biomass and yield components in dwarf, semi-dwarf and tall isogenic lines of spring wheat under recommended and late sowing dates. *Plant Breed.* 114:392–396.
- Miralles, D. J., and G. A. Slafer. 1995b. Individual grain weight responses to genetic reduction in culm length in wheat as affected by source-sink manipulations. *Field Crop Res.* 43:55–66.
- Miralles, D. J., and G. A. Slafer. 1997. Radiation interception and radiation use efficiency of near-isogenic wheat lines with different height. *Euphytica* 97:201–208.
- Miralles, D. J., and G. A. Slafer. 2007. Sink limitations to yield in wheat: how could it be reduced? *J. Agric. Sci.* 145:139–149.
- Olivares-Villegas, J. J., M. P. Reynolds, and G. K. McDonald. 2007. Drought-adaptive attributes in the Seri/Babax hexaploid wheat population. *Funct. Plant Biol.* 34:189–203.
- Otegui, M. E., and R. Bonhomme. 1998. Grain yield components in maize. *Field Crop Res.* 56:247–256.
- Parry, M. A. J., P. J. Madgwick, C. Bayon, K. Tearall, A. Hernandez-Lopez, M. Baudo, et al. 2009. Mutation discovery for crop improvement. *J. Exp. Bot.* 60:2817–2825.
- Parry, M. A. J., M. Reynolds, M. E. Salvucci, C. Raines, P. J. Andralojc, X.-G. Zhu, et al. 2011. Raising yield potential of wheat. II. Increasing photosynthetic capacity and efficiency. *J. Exp. Bot.* 62:453–467.
- Pedro, A., R. Savin, D. Z. Habash, and G. A. Slafer. 2011. Physiological attributes associated with yield and stability in selected lines of a durum wheat population. *Euphytica* 180:195–208.

- Pedro, A., R. Savin, M. A. J. Parry, and G. A. Slafer. 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 Crop Res.* 129:59–70.
- Perry, M. W., and M. F. D'Antuono. 1989. Yield improvement and associated characteristics of some Australian spring wheat cultivars introduced between 1860 and 1982. *Aust. J. Agric. Res.* 40:457–472.
- Prystupa, P., R. Savin, and G. A. Slafer. 2004. Grain number and its relationship with dry matter, N and P in the spikes at heading in response to N x P fertilization in barley. *Field Crop Res.* 90:245–254.
- Rattalino Edreira, J. I., and M. E. Otegui. 2012. Heat stress in temperate and tropical maize hybrids: Differences in crop growth, biomass partitioning and reserves use. *Field Crop Res.* 130:87–98.
- Rathey, A., R. Shorter, S. Chapman, F. Dreccer, and A. van Herwaarden. 2009. Variation for and relationships among biomass and grain yield component traits conferring improved yield and grain weight in an elite wheat population grown in variable yield environments. *Crop Past. Sci.* 60:717–729.
- Ray, D. K., N. Ramankutty, N. D. Mueller, P. C. West, and J. A. Foley. 2012. Recent patterns of crop yield growth and stagnation. *Nat. Commun.* 3:1–7.
- Rebetzke, G. J., A. F. van Herwaarden, C. Jenkins, M. Weiss, D. Lewis, S. Ruuska, et al. 2008. Quantitative trait loci for water-soluble carbohydrates and associations with agronomic traits in wheat. *Aust. J. Agric. Res.* 59:891–905.
- Reynolds, M., M. J. Foulkes, G. A. Slafer, P. Berry, M. A. J. Parry, J. W. Snape, et al. 2009. Raising yield potential in wheat. *J. Exp. Bot.* 60:1899–1918.
- Reynolds, M., J. Foulkes, R. Furbank, S. Griffiths, J. King, E. Murchie, et al. 2012. Achieving yield gains in wheat. *Plant Cell Environ.* 35:1799–1823.
- Richards, R. A. 1992. The effect of dwarfing genes in spring wheat in dry environments. I. Agronomic characteristics. *Aust. J. Agric. Res.* 43:517–527.
- Rieseberg, L. H., M. A. Archer, and R. K. Wayne. 1999. Transgressive segregation, adaptation and speciation. *Heredity* 83:363–372.
- Sadras, V. O. 2007. Evolutionary aspects of the trade-off between seed size and number in crops. *Field Crop Res.* 100:125–138.
- Sadras, V. O., and C. Lawson. 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 Past. Sci.* 62:533–549.
- Sadras, V. O., and G. A. Slafer. 2012. Environmental modulation of yield components in cereals: Heritabilities reveal a hierarchy of phenotypic plasticities. *Field Crop Res.* 127:215–224.
- Sadras, V. O., Calderini, D. F., 2015. Crop physiology: applications for breeding and agronomy. In: Sadras, V. O., Calderini, D. F. (Eds.), *Crop Physiology Applications for Genetic Improvement and Agronomy*. Second Edition. Elsevier, Amsterdam, The Netherlands, pp. 1–14.
- Savin, R., and G. A. Slafer. 1991. Shading effects on the yield of an Argentinean wheat cultivar. *J. Agric. Sci.* 116:1–7.
- Sayre, K. D., S. Rajaram, and R. A. Fischer. 1997. Yield potential progress in short bread wheat in Northwest Mexico. *Crop Sci.* 37:36–42.
- Serrago, R. A., I. Alzueta, R. Savin, and G. A. Slafer. 2013. Understanding grain yield responses to source-sink ratios during grain filling in wheat and barley under contrasting environments. *Field Crop Res.* 150:42–51.
- Serrago, R. A., D. J. Miralles, and G. A. Slafer. 2008. Floret fertility in wheat as affected by photoperiod during stem elongation and removal of spikelets at booting. *Eur. J. Agron.* 28:301–308.
- Shearman, V. J., R. Sylvester-Bradley, R. K. Scott, and M. J. Foulkes. 2005. Physiological processes associated with wheat yield progress in the UK. *Crop Sci.* 45:175–185.
- Siddique, K. H. M., E. J. M. Kirby, and M. W. Perry. 1989a. Ear stem ratio in old and modern wheat-varieties – relationship with improvement in number of grains per ear and yield. *Field Crop Res.* 21:59–78.
- Siddique, K. H. M., R. K. Belford, M. W. Perry, and D. Tennant. 1989b. Growth, development and light interception of old and modern wheat cultivars in a Mediterranean-type environment. *Aust. J. Agric. Res.* 40:473–487.
- Slafer, G. A. 2003. Genetic basis of yield as viewed from a crop physiologist's perspective. *Ann. Appl. Biol.* 142:117–128.
- Slafer, G. A., L. G. Abeledo, D. J. Miralles, F. G. González, and E. M. Whitechurch. 2001. Photoperiod sensitivity during stem elongation as an avenue to raise potential yield in wheat. *Euphytica* 119:191–197.
- Slafer, G. A., and F. H. Andrade. 1991. Changes in physiological attributes of the dry-matter economy of bread wheat (*triticum-aestivum*) through genetic-improvement of grain-yield potential at different regions of the world: a review. *Euphytica* 58:37–49.
- Slafer, G. A., and F. H. Andrade. 1993. Physiological attributes related to the generation of grain-yield in bread wheat cultivars released at different eras. *Field Crop Res.* 31:351–367.
- Slafer, G. A., J. L. Araus, C. Royo, and L. F. G. Del Moral. 2005. Promising eco-physiological traits for genetic improvement of cereal yields in Mediterranean environments. *Ann. Appl. Biol.* 146:61–70.
- Slafer, G. A., D. F. Calderini, D. J. Miralles, and M. F. Dreccer. 1994. Preanthesis shading effects on the number

- of grains of 3 bread wheat cultivars of different potential number of grains. *Field Crop Res.* 36:31–39.
- Slafer, G. A., A. G. Kantolic, M. L. Appendino, G. Tranquilli, D. J. Miralles, and R. Savin. 2015. Genetic and environmental effects on crop development determining adaptation and yield. Pp. 285–319 in V. O. Sadras and D. F. Calderini, eds. *Crop physiology applications for genetic improvement and agronomy*, 2nd edn.. Elsevier, Amsterdam, The Netherlands.
- Slafer, G. A., R. Savin, and V. O. Sadras. 2014. Coarse and fine regulation of wheat yield components in response to genotype and environment. *Field Crop Res.* 157:71–83.
- Stockman, Y. M., R. A. Fischer, and E. G. Brittain. 1983. Assimilate supply and floret development within the spike of wheat (*Triticum aestivum* L). *Aust. J. Plant Physiol.* 10:585–594.
- Tilman, D., C. Balzer, J. Hill, and B. L. Befort. 2011. Global food demand and the sustainable intensification of agriculture. *Proc. Natl Acad. Sci. U.S.A.* 108:20260–20264.
- Vega, C. R., F. Andrade, and V. Sadras. 2001. Reproductive partitioning and seed set efficiency in soybean, sunflower and maize. *Field Crop Res.* 72:163–175.
- Wall, P. C. 1979. An analysis of factors limiting grain numbers and yield of spring wheat in a low-latitude environment. Ph.D. thesis, University of Reading, UK.