

Chapter 10

Challenges and Opportunities for Further Improvements in Wheat Yield

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Wheat is one of the most critical food crops. Globally wheat yield has been growing slower than wheat demand. Further improvements in yield are required. Due to environmental concerns, much of these improvements must come from genetic gains. As wheat yield potential is expressed across a wide range of environments, breeding cultivars of higher-yield potential than that of most modern cultivars is critical. The challenge is that the main physiological avenues for improving yield in the future must be different than that on which past breeding (including the “green revolution”) was based. Major improvements in yield potential were achieved by increased harvest index based on plant height reduction, but any further reductions in plant height would bring about yield penalties rather than gains. In this paper I will discuss alternative opportunities for future improvements beyond modifications in height or partitioning of dry matter.

Introduction

Wheat is likely our most critical crop. It was central to the beginning of agriculture (*e.g.* Harlan, 1981; Araus *et al.*, 2001), which in turn produced one of the most revolutionary changes in history shaping the future development of our societies (Araus *et al.*, 2003); and it continues to be our most largely grown crop (wheat is grown over roughly one sixth of the total arable land in the world) as well as our main source of protein (Slafer and Satorre, 1999). During the 20th century, wheat production has almost constantly increased, first from major increases in growing area (up to approximately the 1950s), followed by a dramatic increase in yields from then to the 1990s (*e.g.* Calderini and Slafer, 1998), associated with genetic and agronomic improvements in yield (Slafer and Andrade, 1991; Calderini *et al.*, 1999; Evenson and Gollin, 2003; Reynolds and Borlaug, 2006).

However, since the 1990s global wheat yield has been growing slower than wheat demand. Even worse, the predictions are that global demand for wheat (Rosegrant and Cline, 2003) will increase at a faster rate than the genetic gains that have been achieved lately (Calderini *et al.*, 1999; Denison *et al.*, 2003; Fischer, 2007). In this context, there seems to be little doubt that further improvements in yield are required. Due to environmental concerns, much of these improvements must come from genetic gains (Araus *et al.*, 2007; Reynolds *et al.*, 2009). As genetic gains must be increased with a crop that already possess a high yield potential, which implies the process will be more difficult than in the past (Slafer *et al.*, 1994), and breeding under high-yielding conditions seems far less complex than under stressful environments (R. Richards, 1996a; Araus *et al.*, 2002), the chances are that attempting to increase wheat yield potential would be the most promising alternative to face the future demand. But breeding to further raise yield potential would only be useful if it brings about improvements in yield under environmental constraints (Slafer *et al.*, 1999; Araus *et al.*, 2002).

Can we breed for yield potential with benefits in realistic growing conditions?

As discussed recently (Slafer and Araus, 2007) there is a debate in the literature on whether it might be more beneficial to breed for yield potential or for tolerance to stressful conditions, with examples supporting both views available in the literature. As discussed in that paper, it seems fair to assume that, with the likely exception of environments characterised by very severe stresses, with yields lower than 1-2 Mg ha⁻¹ (in which higher yield potential does not translate into higher actual yields; *e.g.* Ceccarelli and Grando, 1996), selecting for higher yield potential would result in concomitant improvements in adaptation to stress (Richards, 2000; Araus *et al.*, 2002; Slafer *et al.*, 2005), including environments affected by water deficit (Trethowan *et al.*, 2002), high temperatures (Reynolds *et al.*, 1998), and salinity (Richards, 1995; Isla *et al.*, 2003).

Empirical evidence supporting that increased yield potential would concomitantly increase yield in a wide range of conditions is that modern cultivars largely selected under high-yielding conditions are widely adopted by farmers whose crops are grown under more stressful conditions. This might well be the basis for the frequently found parallelism between potential and farmers' average yields over the years (Evans, 1993; Abeledo *et al.*, 2003a; Slafer and Calderini, 2005). Documenting experimentally the association between yield potential and yield under stressful conditions, Calderini and

Slafer (1999) showed that modern wheats over-yielded their predecessors throughout a wide range of environmental conditions (see also Ortiz Monasterio *et al.*, 1997; Abeledo *et al.*, 2003b; Tambussi *et al.*, 2004).

As wheat yield potential is expressed across a wide range of environments, breeding cultivars of higher-yield potential than that of most modern cultivars is critical. Although genetic gains under potential conditions are more likely than under stress, it is nothing but simple: to achieve the rates of gains required in the future, I believe that further improvements need the integration of new tools and strategies to complement traditional breeding approaches.

Major advances achieved in the field of molecular biology are no doubt of enormous importance for breeding for relatively simple traits. The success of GMO cultivars in countries with no major restrictions to their cultivation speaks for itself. However, when it comes to complex traits, heavily dependent on the interactions within the genetic background and with the environment, the powerfulness of biotechnological tools is strongly restricted. Empirical evidence of the difficulties is that whilst the literature is full of papers reporting quantitative trait *loci* (QTLs) for yield in wheat, there are no examples of breeding programmes introgressing those QTLs and ending up with a consistent yield gain (Slafer, 2003); in fact examples of ending up with yield penalties can be found, as reviewed by Slafer *et al.* (2005).

Molecular biology would only become a strong contributor to the actual breeding for complex traits such as potential yield when they acquire capabilities to manipulate predictably complex traits (Goodman, 2004). One way in which this predictability may increase is by using crop physiological knowledge, to identify relatively simple traits putatively associated with yield potential. We need an improved crop-physiological knowledge of which relatively simple traits may be putatively associated with yield under a wide range of conditions (Slafer, 2003).

What physiological traits may be useful in future improvements of wheat yield potential?

The challenge is that the main physiological avenues for improving yield in the future must be different from those on which past breeding (including the “green revolution”) was based. Major improvements in yield potential were achieved by increased harvest index based on plant height reduction (Calderini *et al.*, 1999 and several references quoted therein), but any further reductions in plant height would bring about yield penalties rather than gains (Richards, 1992; Miralles and Slafer, 1995; Flintham *et al.*, 1997).

Determination of yield potential

To identify physiological traits that may be useful in future improvements of wheat yield potential, we must first understand the determination of yield potential. Although there are different approaches to understand yield in terms of relatively simpler traits, since the pioneer work by Fischer (1985), it has been popularly recognised that although yield components are formed throughout the whole growing season (Slafer and Rawson, 1994), wheat yield is predominantly determined during a relatively short period from about four weeks before to one week after anthesis, mostly the period of stem elongation (Fischer and Stockman, 1980; Thorne and Wood, 1987; Savin and Slafer, 1991; Slafer

et al., 1994; Miralles *et al.*, 1998; Wang *et al.*, 2003; Demotes-Mainard and Jeuffroy, 2004; González *et al.*, 2005a; Fischer, 2008), when the number of fertile florets, and then grains, of the crop is largely determined (*e.g.* Kirby, 1988; Siddique *et al.*, 1989; Slafer and Andrade, 1993; Miralles and Slafer, 2007).

This is so because the number of grains per unit land area of the crop is a clear determinant of yield, as wheat grains hardly compete strongly for assimilates during grain filling (Borrás *et al.*, 2004; Bingham *et al.*, 2007) and any negative relationship between grains per m² and average grain weight seems to be independent of a strong competition for assimilates (Acreche and Slafer, 2006). This means that, in most conditions, the capacity of the crop canopy to provide assimilates to the growing grains is more or less adequate to allow grain filling (Savin and Slafer, 1991; Richards, 1996b; Reynolds *et al.*, 2004), and consequently average grain weight is far less variable than grain number (Slafer *et al.*, 2006; Peltonen-Sainio *et al.*, 2007) as due to evolutionary causes, the reproductive fitness of the crop is expressed in terms of the number of offspring it produces (Sadras, 2007).

It can be concluded that to further raise yield potential we must somehow increase the number of grains per m², which is strongly related to the growth of the spikes during the last half of stem elongation (Slafer *et al.*, 2005). This is so critical that actual gains achieved in the past in virtually any environmental condition in which the breeding programme was developed, including the green revolution, were almost entirely related to increases in the partitioning of dry matter to the spikes during stem elongation (Siddique *et al.*, 1989; Slafer and Andrade, 1993). To further raise the dry weight of the spikes at anthesis, as a way to improve the number of grains per unit land area of the crop, the opportunities from additional gains in spike-stem partitioning seem limited (Slafer *et al.*, 1999). Alternatives must be focused on improving growth during this critical pre-anthesis period in which wheat yield, oppositely to what occurs during grain filling, is strongly limited by the strength of the source (Slafer and Savin, 2006). Evidence of such limitation may be found in experiments in which yield is promoted by means of N fertilisation in which the driving force for increasing yield has been the improved growth during the stem elongation phase and the concomitant increase in spike dry weight at anthesis and number of grains per m² (*e.g.* Fischer, 1993; Prystupa *et al.*, 2004). As recently revised in depth (Araus *et al.*, 2008; Reynolds *et al.*, 2009), there are two alternative ways to genetically improve growth during the critical period of stem elongation: increasing crop growth rate, or lengthening the duration of that phase. For a full treatment of these alternatives please see the quoted references. I will only recapitulate briefly here some the main concepts behind these two alternatives.

Opportunities to improve crop growth rate

Crop growth is the product of radiation interception and radiation use efficiency (Sinclair and Muchow, 1999). As well managed crops fully intercept the incoming radiation during the critical period, the opportunity is restricted to particular conditions (such as those of Nordic growing areas) in which radiation interception is not maximised in well managed modern cultivars. In these conditions advantages of improving early vigour (*e.g.* Richards, 1996a) may be capitalised in improvements in radiation interception during the stem elongation phase. Early vigour has been dissected and found related to a number of seedling characteristics (Liang and Richards, 1994; López-Castañeda and Richards, 1994; López-Castañeda *et al.*, 1995). Fortunately for those regions in which this may be an important source of improvements in growth, substantial

variation in traits associated with early vigour has been documented (e.g. Rebetzke *et al.*, 1996).

In all other cases the alternative to improve crop growth rate during stem elongation would be restricted to improvements in radiation use efficiency. This depends on improving either the arrangement of the canopy structures so that the light is more evenly distributed and then used more efficiently or the photosynthetic capacity of the leaves and spikes. Although the former is unquestionably true, most modern, high-yielding cultivars already possess an erect canopy, which makes the possibilities for further raising radiation use efficiency difficult from altering the canopy structure in the near future. This leaves the actual possibility to improve radiation use efficiency into finding ways of improving the photosynthetic capacity of the leaves and spikes.

Rubisco, the enzyme involved in the photosynthetic capacity of wheat (and other C3 crops), is naturally the first alternative to attempt achieving genetic gains in radiation use efficiency (Reynolds *et al.*, 2009). One alternative would be through engineering Rubisco so that it becomes more active as a carboxylase and less active as an oxygenase (the latter responsible of the “waste” of energy involved in photorespiration, that reduces the photosynthetic activity). There is a large degree of variation for relative specificity for CO₂ among sources of Rubisco (e.g. Delgado *et al.*, 1995; Galmés *et al.*, 2005), that could be exploited (Parry *et al.*, 2007). Another alternative is attempting to introduce pump mechanisms in order to increase noticeably the concentration of CO₂ in the carboxylation site, thus empirically reducing photorespiration by competition (e.g. Leegood, 2002).

Opportunities to lengthen the stem elongation phase

The other hypothetical alternative to improve growth during the critical period of stem elongation would be lengthening the stem elongation phase (Slafer *et al.*, 2001; Slafer *et al.*, 2005; Miralles and Slafer, 2007). The rationale is that if making this phase longer does not affect the daily radiation use efficiency, the accumulated growth during stem elongation would increase proportionally to the extension of the phase. As photoperiodic responses of the length of different phases seem to differ depending on the genotype (Slafer and Rawson, 1996) and different combinations of timing to onset of stem elongation for similar time to anthesis may be found in detailed screenings of cereals (Whitechurch *et al.*, 2007), it seems possible to explore this alternative (Slafer *et al.*, 2009).

Evidence that increases in grain number would be feasible if we were able to genetically manipulate sensitivity to photoperiod during stem elongation can be found in experiments in which the duration of stem elongation has been artificially extended for particular genotypes. For instance by exposing the crop to different photoperiods only during the stem elongation phase, we were able to raise the number of grains that the plants produced (Miralles *et al.*, 2000; González *et al.*, 2003, 2005b; Serrago *et al.*, 2008; Borràs *et al.*, 2009).

The existence of healthy genetic variation is a requirement for considering a trait in breeding. But it would be extremely useful to identify proper genetic bases for this trait if the breeding process is to maximise its efficiency. Although we analysed experimentally the opportunity of increasing grain number through sensitivity to photoperiod, another alternative might be the selection for differences in earliness *per se* of the stem elongation phase. The fact that the stem elongation phase is sensitive to photoperiod and that there is genetic variation for that sensitivity has been evidenced several times (Slafer and

Rawson, 1994; 1997, Miralles and Richards, 2000; González *et al.*, 2002); whilst differences in earliness per se for this particular phase have not been explored widely, chances are that they exist (Slafer, 1996).

To the best of my knowledge, so far there have been studies aimed to identify genetic bases of photoperiod sensitivity during stem elongation. Attempts so far consisted of comparative of performance of recombinant inbred lines or isogenic lines for major Ppd alleles. As reviewed by González *et al.* (2005c) these approaches have mostly failed in identifying reliable genetic bases for the specific sensitivity to photoperiod in the stem elongation phase. Alternative approaches, including the analysis of genes that are up- or down-regulated when the wheat plants respond to the exposure to different photoperiods exclusively during the stem elongation phase (*e.g.* Ghiglione *et al.*, 2008) and the behaviour of mapping populations (Borràs *et al.*, 2009) are undergoing.

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