

CHAPTER 12

PHYSIOLOGICAL TRAITS FOR IMPROVING WHEAT YIELD UNDER A WIDE RANGE OF CONDITIONS

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Abstract. A better understanding of relatively simple crop-physiological attributes that determine yield in a wide range of conditions may be instrumental for assisting future breeding. Physiological traits may be selected either directly or through the use of molecular-biology tools. Physiological and breeding literature frequently distinguishes between yield under potential, stress-free conditions and under the pressure of stress, mostly abiotic. Although the rationale behind the idea that the different physiological attributes contribute to yield under these contrasting conditions may be sound, in practice there is a large body of evidence pointing out the other way around. For instance, genotypes with physiological attributes conferring higher yield potential usually also perform better under stress conditions, at least when excluding extremely severe environments. As breeders normally need to release improved cultivars to be grown in different sites throughout several seasons and subjected to a wide range of management decisions, identifying physiological traits that may confer simultaneously high yield potential and constitutive tolerance to stress would be critical. These traits must allow the plants to capture more resources or to use them more efficiently. A well-known attribute conferring high yield potential and widely studied physiologically has been semi-dwarfism. Semi-dwarf cultivars normally yield better than tall ones in a wide range of stressful conditions (at least if seedling emergence is not a major inconvenience). This is because reducing height to a certain level does not alter the ability of the crop to capture resources, whilst improving markedly the efficiency with which the resources are used to produce yield. This trait is not further useful as modern cultivars possess already a stature within the ranges optimizing yield. Two other traits that may also be associated with improved performance in a wide range of conditions may be the discrimination against ^{13}C ($\Delta^{13}\text{C}$) and a lengthened stem elongation phase at the expense of previous phases. Although more research is needed before conclusions may be robust, physiological evidence supports the hypothesis that increasing $\Delta^{13}\text{C}$ and lengthening the stem elongation phase would result in an improved performance over a range of environmental conditions.

INTRODUCTION

Brief description of the context

Wheat breeding for improved productivity has been noticeably successful during the second half of the 20th century (e.g., Calderini et al. 1999). In the future, breeding efficiency has to be increased in order to meet the constantly increasing demand of a still rapidly increasing population whilst facing a reduction, or at least a lack of expansion, of arable land if environmental sustainability is to be achieved (Reynolds et al. 1999; Cassman et al. 2003; Slafer et al. 2005). Thus, breeding to raise both yield potential and yield further under environmental constraints through improved adaptiveness will be of paramount importance (Slafer et al. 1999; Araus et al. 2002).

Do we need to breed for yield potential and adaptiveness separately?

There has been an active debate in literature whether to breed primarily for yield potential or for improved yield under the stressful environments that prevail in most wheat-growing areas worldwide. One can find examples of both views: (i) improving yield potential constitutively improves yield under stress conditions; and (ii) breeding for yield potential produces lines of poorer behaviour than landraces or lines selected for better performance under stress conditions.

Although recognizing that exceptions can doubtlessly be found, we believe that there is some agreement in literature on wheat and barley on:

- a. Selecting for high yield potential does not necessarily bring about improved performance (Ceccarelli and Grando 1996; Slafer and Araus 1998), and should not be advised¹ for severely stressful environments, for instance, those with yields consistently below 1.5–2.0 Mg ha⁻¹.
- b. Selecting for a higher yield potential in all other environments – from relatively harsh (e.g., yields ranging from 2.0 to 4.0 Mg ha⁻¹), through stressed (e.g., 4.0–6.0 Mg ha⁻¹) or mildly stressed (e.g., 6.0–8.0 Mg ha⁻¹), to unstressed conditions (yields > 8.0 Mg ha⁻¹) – will usually result in cultivars with constitutively improved adaptation to stress (i.e. performing in the stressed environment equally to, or better than, cultivars selected for performance in the prevalent environment, Slafer et al. 2005).

Thus, in most growing regions improved performance might be achieved by selecting for higher yield potential (i.e., selection under favourable conditions would even result in improved yields in less favourable environments, Richards 2000; Araus et al. 2002). There is clear empirical evidence supporting this generalized statement. Re-analysing data from studies conducted in different countries, Calderini and Slafer (1999) showed that modern wheats consistently yield more than their predecessors throughout a wide range of environmental conditions, a fact also recently shown from the comparison of yields of a modern and an older barley cultivar grown across a wide range of Mediterranean conditions (Tambussi et al. 2005). Other supporting evidence is provided by the parallelism in increase over the years in potential yield and in actual yields obtained by farmers (Evans 1993;

Abeledo et al. 2003; Slafer and Calderini 2005), which may mean that actual yields do not increase unless the genetic yield potential is improved.

The fact that we may trust that selecting for higher yield potential may bring about improved performance under a wide range of environmental conditions (though perhaps excluding extremely severe stresses) may be the good news. The bad news is that it does not seem to be easy to raise the yield potential further, because modern cultivars already possess a relatively high yield potential (as a positive consequence of successful breeding in the past). In fact, there is some evidence that in recent years genetic gains in yield potential have been far lower than what is required to keep pace with the increase in demand (e.g., Denison et al. 2003). We believe that further improvements need the integration of new tools and strategies to complement traditional breeding approaches. Two candidate disciplines that might contribute to complementing traditional breeding are molecular biology and crop physiology.

MOLECULAR BIOLOGY NEEDS SOUND CROP PHYSIOLOGY

Molecular biology can help in identifying and introgressing genetic factors responsible for traits in which breeders may be interested. When these traits are relatively simple the usefulness of these techniques is beyond questioning. However, when it comes to yield potential (or any other complex trait) the identification of a genetic basis (quantitative trait loci, QTLs) has proven of little empirical value. One example may be found by the fact that while literature is full of papers reporting QTLs for yield in wheat and barley, there are no examples of breeding programmes introgressing those QTLs and ending up with a consistent yield gain (Slafer 2003)². As indicated by Goodman (2004), molecular biotechnologies will add little to actual breeding for improved yield until these technologies acquire capabilities to manipulate predictably complex traits.

If we were able to identify relatively simple traits putatively associated with yield potential, there would be a way to take advantage of the enormously powerful tools developed by molecular biology for improving yield potential. The whole effort would require joining the know-how of molecular biologists with expertise of conventional breeders and rigorous developments made by crop physiologists (Slafer 2003; Sinclair et al. 2004; Slafer et al. 2005; Wollenweber et al. 2005). In other words, these emerging technologies may have no value for improving yield potential without an improved ecophysiological assessment of relatively simple traits associated with yield under a wide range of conditions (Araus et al. 2003; Slafer 2003).

ARE THERE PHYSIOLOGICAL TRAITS CONTRIBUTING TO YIELD IN A WIDE RANGE OF CONDITIONS?

Most literature in crop physiology related to breeding does focus on either yield potential or yield under stressful conditions. This influences our perception on whether there might be a possibility to identify traits that being relatively simple

would be mechanistically associated with crop yield, naturally under field conditions and for a wide range of conditions. By trying to identify such traits, it may seem that we are stretching too much the potential impact of physiological traits for future breeding. However, some traits may allow the crop to capture more effectively its most limiting resources, or may improve the overall efficiency of use of resources.

In this section, we will first illustrate that identifying traits combining both simplicity and virtually global impact is possible by describing the trait 'semi-dwarfism'. Then we will speculate on two other alternative traits that may also be selected to provide a yield advantage under a wide range of conditions: one is related to the use of more resources (increasing ^{13}C discrimination: $\Delta^{13}\text{C}$), and the other by exploiting more resources for accumulation of reserves by extending the duration of carbon allocation to stems and spikes.

Semi-dwarfism

Most genetic gains in wheat yield potential were mainly achieved by means of improvements in harvest index with marginal or no modification of biomass (see: Spiertz and De Vos 1983; Slafer and Andrade 1991; Feil 1992; Calderini et al. 1999), though recently some papers reported slight increases in biomass in spring wheat (Reynolds et al. 1999) and winter wheat (Shearman et al. 2005). Although trends in harvest index with the year of release of cultivars were slightly positive before the introgression of semi-dwarf genes, the incorporation of genes derived from Norin 10 (*Rht1* and *Rht2*) into wheat-breeding programmes has been decisive to increase harvest indices to a great extent (Gale and Youssefian 1985; Calderini et al. 1999). These genes reduce culm elongation, which is associated with an effect on the sensitivity to endogenous gibberellic acid.

The large and consistent (across genetic backgrounds) increase in yield potential has been physiologically explained by a relatively simple model. Briefly, semi-dwarf genes impose a genetic restriction to culm growth at the time when most assimilates are being competitively used for culm and spike growth, few weeks before anthesis. Compared with the tall genotype, more assimilates are available for spike growth resulting in higher weight in spike dry matter per unit land area at anthesis. Because of a consistent relationship between number of grains per unit land area and the spike dry mass at anthesis the impact of semi-dwarf genes is an increase of the number of grains per m^2 (e.g., Brooking and Kirby 1981; Gale and Youssefian 1985; Fischer and Stockman 1986; Youssefian et al. 1992; Miralles and Slafer 1995; Flintham et al. 1997; Miralles et al. 1998).

The increased yield potential due to the introgression of semi-dwarf genes was very consistent not only because it occurred in virtually all genetic backgrounds studied, but also because the yield advantage was still evident under a wide range of environments including stress conditions. With the exception of very severe stresses (say, yields $< 2.0 \text{ Mg ha}^{-1}$), semi-dwarfism consistently combined improved yield potential with improved performance across a wide range of conditions (e.g., Laing and Fischer 1977; Richards 1992; Miralles and Slafer 1995). The natural consequence of improving yield potential and concomitantly actual yields in a wide

range of agro-ecological conditions explains the huge success this characteristic had in most breeding programmes of the world. Nowadays, semi-dwarf wheats are cultivated virtually throughout the world.

Unfortunately, we cannot further reduce plant height, as the relationship between height and yield is parabolic and modern cultivars already possess a height that optimizes yield (Fischer and Quail 1990; Richards 1992; Miralles and Slafer 1995; Flintham et al. 1997). Semi-dwarfism constitutes a clear example that it is possible to find a relatively simple trait (controlled by major genes, expressed in most genetic backgrounds and environments) gaining yield improvements under a wide range of conditions. To further raise yield potential and constitutively increase actual yields, we must find alternative traits to improve spike growth before anthesis. These alternative traits should still be much simpler than the complex genes controlling ultimately yield itself under a wide range of conditions.

Increasing $\Delta^{13}C$

For C_3 species such as wheat, carbon isotope discrimination ($\Delta^{13}C$), when measured in plant tissues, constitutes an integrated record of the ratio of intercellular to atmospheric partial pressure of CO_2 (C_i/C_a) and therefore of the transpiration efficiency of the plant (A/T , the ratio of net assimilation to water transpired), over the period during which the dry matter is assimilated. Thus, $\Delta^{13}C$ measured in dry matter is widely accepted as an indicator of crop water use efficiency (WUE) of dry-matter production. Because $\Delta^{13}C$ is genetically correlated with grain yield and shows a higher broad-sense heritability than yield itself, it has been proposed as trait for breeding (Araus et al. 2002). As C_i/C_a is positively related with $\Delta^{13}C$ and negatively with A/T , then $\Delta^{13}C$ is negatively related with WUE (Farquhar and Richards 1984). Genetic gains in yield may then be expected by selecting for lower $\Delta^{13}C$ (and, thus, higher WUE) if the released cultivar is to be grown under severe water restrictions, such as when the crop grows primarily on water stored in the soil (e.g., Rebetzke et al. 2002).

However, in many environments in which water restrictions may limit yield, $\Delta^{13}C$ has been found positively correlated with grain yield (Condon et al. 1987; 1993; 2004; Richards 1996; Araus et al. 1998; 2002; 2003; Slafer and Araus 1998; Slafer et al. 1999; Voltas et al. 1999). This is likely because of the fact that a genotype possessing higher $\Delta^{13}C$ must have maintained a higher CO_2 conductance due to a better water status, the higher $\Delta^{13}C$ then likely reflecting avoidance to stress by either faster development or better access to soil water (Araus et al. 2002; Condon et al. 2004).

Several explanations may account for such positive correlation between $\Delta^{13}C$ and yields. Differences among genotypes in phenology may affect yield and also $\Delta^{13}C$, especially in drought-prone environments. For example, under Mediterranean conditions genotypes with fewer days from sowing to flowering show higher $\Delta^{13}C$ values (Richards 1996; Araus et al. 1998) probably because they attain grain filling with more water in the soil whereas the evapo-transpirative demand is lower. Nevertheless, in bread wheat (Sayre et al. 1997), durum wheat (Araus et al. 1998)

and barley (Voltas et al. 1999) large genotypic variability in $\Delta^{13}\text{C}$, independent of phenology, has been reported.

Therefore, additional causes for such positive relationship may be envisaged. Positive relationships between $\Delta^{13}\text{C}$ and grain yield are mostly found under moderately to well watered conditions, whereas for severely stressed environments (characterized by yields below 2.0 Mg ha^{-1}) relationships are absent or negative (Voltas et al. 1999; Araus et al. 2003). In fact, a higher $\Delta^{13}\text{C}$ may be just the result of more water captured and used by the crop. Thus, a strong positive relationship between total water input during grain filling and grain $\Delta^{13}\text{C}$ has been reported (Araus et al. 1997c; 1999; 2003), which supports the fact that $\Delta^{13}\text{C}$ is also a good indicator of total crop water availability (Stewart et al. 1995; Araus et al. 2002; see also Blum 2005). Other causes for a positive relationship are less common and may arise usually under well-watered conditions due to miscellaneous causes, such as leaf structure (Araus et al. 1997a; 1997b), a higher transpirative cooling or a higher stomatal conductance associated with a larger photosynthetic sink (Richards 2000).

Summarizing higher $\Delta^{13}\text{C}$ has been proposed as a breeding criterion for increasing yield in wheat and other temperate cereals under a wide range of conditions, where yield formation is, at least in part, determined by in-season rainfall. The reason for the positive relationship between $\Delta^{13}\text{C}$ and yield is that a genotype exhibiting higher $\Delta^{13}\text{C}$ is probably able to maintain a better water status (Araus et al. 2002; Condon et al. 2004). Where additional water is not available to the crop (i.e., all the stored soil moisture is exhausted during the crop cycle), increased WUE appears to be an alternative strategy for improving crop performance (Araus et al. 2002; Blum 2005).

Lengthening stem elongation

An alternative approach recently hypothesized (and therefore not widely tested in many different environments and genetic materials) is to extend the duration of the stem elongation phase, from jointing to anthesis, at the expense of shortening of vegetative and early reproductive phases, with no major changes in time to flowering (e.g., Slafer et al. 1996; 2001).

In principle, the rationale for the hypothetical overall benefit of this characteristic is in line with the overwhelming evidence of the impact of introgressing semi-dwarfing genes: yield potential, and actual yields in a wide range of conditions, would be increased if we could further increase the spike dry weight, per unit land area, at anthesis. Lengthening the duration of the phase when spike growth takes place would result in higher spike dry matter at anthesis and subsequently more grains per m^2 . In fact, artificially extending the duration of stem elongation by exposing the crop to different photoperiods did raise the number of grains (Miralles et al. 2000; González et al. 2003; 2005a).

It is clear that substantial genetic variation in duration of the stem elongation phase exists (Slafer and Rawson 1994; Kernich et al. 1997; Slafer 2003), though we need to identify specific genetic factors responsible for this variability. Main developmental traits that might be related to the variability in stem elongation

duration are sensitivity to photoperiod (rate of development during stem elongation seems to be governed by photoperiod response, Slafer and Rawson 1997; Miralles and Richards 2000; González et al. 2002) or differences in earliness *per se* (genotypes may differ in their duration of stem elongation when photoperiod is long and plants were fully vernalized, Slafer 1996).

For the particular case of photoperiod sensitivity during stem elongation, it was suggested that this sensitivity would be independent from that of previous phases (Slafer and Rawson 1994; González et al. 2002), which is required if the total time to anthesis is to be maintained. However, we must learn much more on the genetic bases determining sensitivity to photoperiod during stem elongation before this information may be useful for practical breeding.

Most attempts to identify a clear and consistent genetic basis for this particular response have failed (González et al. 2005b). This is likely because we only know (and have worked with) few of the hypothesized genes for photoperiod sensitivity (Snape et al. 2001). There are now other approaches in ongoing projects attempting to determine what genes are down- or up-regulated when responses to photoperiod occur or to identify genes/QTLs for differences in length of different phases within mapping populations.

NOTES

¹ It must be noticed, however, that selecting for better performance under stressful conditions may likely be useful only when the type and intensity of the stress are rather homogeneous. In regions where stressful conditions vary temporally and/or specially in type, intensity and opportunity, the approach may not be useful: cultivars selected in particular stressful conditions may not behave well in other stressful environments, with a different combination (or periodicity) of interacting stresses (Cooper et al. 1997).

² Although some results, yet unpublished, presented in the 3rd Cereal Genetics and Genomics Workshop may provide empirical advantages of a QTL for yield under post-flowering drought conditions in pearl millet, the relatively little breeding of pearl millet as compared to that in wheat and barley should be taken into account before accepting simple extrapolations (Catherine Howarth, IGER-Aberystwyth, pers. comm. 2006).

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