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Wheat grain number: Identification of favourable physiological traits in an elite doubled-haploid population

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ABSTRACT

A detailed and accurate phenotyping of mapping populations is an important “bottleneck” for the understanding of the phenotype–genotype relationships. Grain number per unit area (GN), the main wheat yield component, can be analyzed through physiological components as spike dry weight at flowering, determined by crop growth rate and biomass partitioning to spike during stem elongation phase, and fruiting efficiency. The phenotypic variability of these physiological traits responsible for variation in GN and the relationships among them was analyzed in an elite wheat doubled-haploid (DH) population grown in two different environments. Positive transgressive segregation (i.e. DH lines that exceed parental phenotypic values) was observed for all GN determining traits, suggesting that increases in GN could be achieved through their improvement. However, focusing on top DH lines, which represent a feasible genetic improvement, fruiting efficiency was the most relevant physiological trait for consistently improving GN, and thereby grain yield, in both environments.

1. Introduction

Wheat (*Triticum aestivum* L.) is a key component of food security (it provides ca. 20% of the calories to the world’s population) and the crop most widely grown worldwide, being adapted to a broad range of environments (Reynolds et al., 2012). As wheat global demand is projected to increase during coming decades, it is broadly agreed that improvements in yield potential must be accelerated to achieve a sustainable production increment. Current rates of wheat genetic gains in many countries (largely inferior to 1% per year) are lower than those required to meet the projected cereal demand (Reynolds et al., 2012; Hall and Richards, 2013). It has been proposed that indirect selection based on physiological traits would help achieving the required rates of genetic gains. Consequently, many efforts have been made to understand the association between grain yield improvements and changes in physiological traits. Currently, there are several proposals that support the feasibility of using this physiological assistance to improve yield potential (Slafer, 2003).

Recent advances in molecular biology have developed the potential to identify and map genes or quantitative trait *loci* related to any trait, and phenotyping has become the “bottleneck” delaying progress in breeding for complex traits (Furbank and Tester, 2011; Fiorani and Schurr, 2013). In order to use physiological criteria in a breeding program, it is first required to identify traits that determine grain yield and then to detect genetic factors controlling them in order to make their manipulation easier and/or to predict their selection response (Slafer, 2003). The usefulness of physiological information obtained by accurate phenotyping is unquestionable, not only for a better understanding of the relationships between

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Abbreviations: GN, grain number per m^2; SDW, spike dry weight at flowering; FE, fruiting efficiency; SEP, stem elongation phase; CGR, crop growth rate; BPS, biomass partitioning to spike; RUE, radiation use efficiency; DH, doubled-haploid; BA, Buenos Aires; CO, Ciudad Obregón; PAR, photosynthetically active radiation; Ri, incident solar radiation; Rt, transmitted solar radiation; RIE$_{midday}$, radiation interception efficiency at midday; RIE$_{day}$, daily radiation interception efficiency; BLUE, best linear unbiased estimation; B, Bacanora; W, Weebil.

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grain yield and its determining traits, but also to improve, in combination with molecular tools, the current knowledge about the genotype–phenotype relationship (Slafer, 2003; Edmeades et al., 2004). On the other hand, phenotyping, an "elite" population, has an evident practical application, as breeding programs routinely make progress with elite lines and are interested in improved combinations among them (Rattey et al., 2009).

Grain number per unit area (GN) is the main yield component in wheat as in the majority of grain crops (Fischer, 2008). Improvement of GN is critical to achieve genetic gains in wheat yield, particularly if large increases are required (Slafer et al., 2014), as it was the main component associated with yield progress through breeding and it is still the main component limiting yield in many regions of the world (e.g. Peltonen-Sainio et al., 2007). A common approach to understand GN (and yield) determination is to dissect it into their numerical components, i.e. spike number per unit area and grain number per spike (Slafer et al., 2014 and references quoted therein). Even though this approach is useful to analyze grain yield strategies (e.g. differences between cultivars) or a management practice effect (e.g. different sowing rates), from a physiological perspective, it is inefficient for predicting the impact of manipulating a single trait on GN determination. This limitation arises because a trade-off between spike number and grain number per spike almost inevitably appears, implying that improvements in one of these components is negatively counterbalanced by reductions in the other one, failing to deliver more grains (Fischer, 1983; Slafer, 2003), particularly for modest to moderate yield improvements (Slafer et al., 2014). Therefore, GN determination would be better analyzed in terms of crop dry matter economy during the critical period (Fischer, 2008).

The critical period for GN determination in wheat occurs when the spikes are actively growing during the stem elongation phase, from a few weeks before to immediately after anthesis (Fischer, 1985). During this critical period, GN determination is strongly source-limited and the degree of such limitation is reflected in the proportion of both floret primordia able to reach the stage of fertile florets, avoiding floret death (Kirby, 1988), and tillers surviving to become fertile spikes (Thorne and Wood, 1987). Thus, different evidence shows a strong positive association between GN and spike dry weight at flowering (Fischer, 2011). However, GN may vary among genotypes beyond differences in spike dry weight due to differences in fruiting efficiency, i.e. the number of grains set per unit of spike weight (Abbate et al., 1998; González et al., 2011). Therefore, GN can be analyzed in terms of spike dry weight at flowering determinants [i.e. stem elongation phase (SEP), crop growth rate (CGR) and biomass partitioning to spike (BPS) both during SEP] and fruiting efficiency (FE; Eq. (1)) (Fischer, 1983, 2008).

$$\mathrm{GN} = \mathrm{SEP} * \mathrm{CGR} * \mathrm{BPS} * \mathrm{FE} \qquad (1)$$

This assimilate-based approach considers that if: (i) more solar radiation is intercepted, and/or (ii) this radiation is more efficiently converted into biomass, and/or (iii) this biomass is more favorably partitioned to the juvenile spikes, and/or (iv) spike biomass is more efficiently used to set grains, an increment in GN could be achieved. This approach represents a useful guide to carry out a detailed and accurate phenotyping of elite mapping populations.

As stated above, spike dry weight at flowering is a good indicator of wheat GN (Fischer, 2011) and most of the efforts to improve GN are focused in its linked traits. The idea of manipulating the stem elongation phase through photoperiod sensitivity in order to increase spike dry weight has been suggested (Slafer et al., 2001). The positive impact of longer stem elongation phase on spike dry weight at flowering and GN has been experimentally tested (Miralles et al., 2000; González et al., 2003; Serrago et al., 2008), however this trait could have an important genotype by environment interaction which affects its early selection (García et al., 2011). The improvement of crop growth rate through higher pre-flowering radiation use efficiency (RUE) has contributed to yield progress of UK cultivars released between 1970s to 1990s (Shearman et al., 2005), and today several works aim to improve RUE for increasing GN and yield (Reynolds et al., 2012). The biomass partitioning to spike, a key trait during the Green Revolution, must also be improved without affecting the root system functionality or increasing the lodging risk (Berry et al., 2007). On the other hand, although the importance of the fruiting efficiency is recognized, its relationship with the spike dry weight has been scarcely studied. Works that evaluated the genetic progress or the performance of modern cultivars have reported a positive association between fruiting efficiency and GN, in both bread (Abbate et al., 1998; Acreche et al., 2008; González et al., 2011) and durum wheat (Ferrante et al., 2012). These results, together with evidence of cultivar's variability (Shearman et al., 2005; Serrago et al., 2008; González et al., 2011) and likely responsiveness to selection (Abbate et al., 2013), position fruiting efficiency as a relevant trait to improve GN, although keeping in mind that a trade-off between fruiting efficiency and spike dry weight may occur (Dreccer et al., 2009; Ferrante et al., 2012; Lázaro and Abbate, 2012). Therefore, when testing the opportunities to raise GN through improved fruiting efficiency, it is necessary to evaluate whether the improved in this trait does bring about a trade-off in spike dry weight.

The two main objectives of this work were: (i) to analyze the phenotypic variability in physiological traits responsible for genotypic variation in GN (Eq. (1)) and (ii) to identify possible trade-offs among those traits, in an elite wheat doubled-haploid (DH) population grown in two contrasting environments. The relevance of the present work lies both in (i) the phenotyping of GN determination based on the physiological approach proposed by Fischer (1983), rarely reported for large populations, and (ii) the use of a population derived from high-yielding CIMMYT cultivars contrasting in grain yield components. Crop-physiological studies based in this sort of population are far less common than those based on populations derived from wide crosses. The latter normally offer wide ranges of variation exacerbating the breadth of expression of physiological traits, but using populations derived from two high-yielding cultivars provides more meaningful conclusions for breeding programs, as when breeders aim to increase grain yield potential normally cross elite-by-elite materials and search for transgressive segregations. Furthermore, this population is being genotyped at the John Innes Centre (UK) and therefore it might be possible to count in the near future with genetic markers associated to the traits identified in the present work, which may become tools for empirical application of these conclusions in the selection process.

2. Material and methods

2.1. Plant material and environments

The wheat population used in this work consisted of 105 DH lines derived from a cross between two well-adapted and high-yielding cultivars of spring wheat, Bacanora and Weebil, with similar phenology but consistently differing in yield components: Bacanora normally has more grains than Weebil, while the latter has heavier grains than Bacanora (García et al., 2013). The cross was carried out in CIMMYT (Mexico) and the DH lines, derived from F_1 using the maize cross method (Laurie and Bennett, 1988), were developed by the John Innes Centre (UK). Both parents are modern cultivars within the elite CIMMYT germplasm. The population was phenotyped under field conditions in two environments: (i) the experimental field of Facultad de Agronomía - Universidad de Buenos Aires (34°35′S, 58°29′W, 26 masl) in Buenos Aires (Argentina) during the 2009 growing season (BA), and (ii) the