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Analysis of sink/source relations in bread wheat recombinant inbred lines and commercial cultivars under a high yield potential environment

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ABSTRACT

Grain yield in wheat is generally considered to be sink-limited during grain filling. But is this limitation inherent to the crop species or a consequence of the breeding process? A way to ascertain this is by using genetic materials not subject to selection. Grain yield could be analyzed as the product between: (i) grain number per unit area, (ii) the potential grain weight (i.e. weight per grain obtained without source limitation); and (iii) the degree of sink limitation (DSL). The product of the first two components defines the crop sink capacity (SICA), and the DSL could be assessed as the quotient between weight per grain and its potential weight. Such an analysis was carried out in a RIL population derived from the cross between Baguette 10 and Klein Chajá (Argentinean cultivars with contrasting grain number). Three field experiments were conducted at Balcarce, Argentina during the 2013, 2014 and 2015 crop seasons, under non-limiting conditions; 146 recombinant inbred lines (RILs), the parental cultivars and other commercial cultivars were evaluated. At maturity, grain yield and grain weight were determined. The potential grain weight was obtained by thinning rows at the beginning of grain filling. Grain number m^{-2} was calculated as grain yield/grain weight. Grain yield was highly associated with SICA; the slope of the relationship between grain yield and SICA was lower than the expected 1:1 ratio above ~8 tons ha^{-1}, indicating that the source for grain filling becomes a limiting factor when SICA increases, particularly in the RILs. This suggests that much of the sink limitation observed in modern wheat cultivars may be the result of genetic improvement.

1. Introduction

Bread wheat (*Triticum aestivum* L.) is one of the most important food crops in the world. An estimated 30 million poor farmers in the developing world rely on wheat system innovations to increase their cereal production, improve their incomes, and adapt to climate change. Demand for wheat by 2050 is predicted to increase by 70 percent from today's levels, but the challenges to wheat production are stark and growing (CIMMYT, 2017).

Grain yield in wheat can be considered as the product between grain number per unit area and grain weight. Breeding efforts to improve wheat yield have been mainly focused on increasing grain number, which is closely related to this trait (Fischer, 2011; Sadras and Slafer, 2012). As a consequence, differences in yield between wheat cultivars have been classically analyzed in terms of changes in grain number. The period during which grain number is set, *i.e.* 30–20 days before the grain filling period, is considered as the critical period for yield determination (Fischer, 1984; Abbate et al., 1997; Fischer, 2008; Lázaro and Abbate, 2012). However, such an approach overlooks differences in grain number, which may be substantial between cultivars (Abbate et al., 2005).

Alternatively, grain yield could be considered in terms of balance between sink capacity and the source of photo-assimilates for grain filling (Gifford et al., 1973; Evans et al., 1975; Fischer and HilleRisLambers, 1978). Under this approach, grain yield would be limited by the smaller of these two components (sink capacity or source). However, it is not easy to use this analysis, mainly because it is difficult to quantify the source. Thus, Abbate et al. (2005) proposed to analyze wheat grain yield as the product between: (i) grain number, (ii) potential grain weight (*i.e.* the weight per grain obtained without

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source limitation) and (iii) the degree of sink limitation (DSL). Then, sink capacity (SICA) can be estimated as the product between grain number and potential grain weight. The DSL could be assessed as the quotient between grain number and potential grain weight (Abbate et al., 2005; Lázaro et al., 2010). Then, the DSL can take theoretical values between 0 and 1; DSL = 1 indicates that the crop is fully sink-limited, DSL = 0 indicates full source limitation, and intermediate values indicate different degrees of sink limitation (also called sink/source co-limitation). As a result, 1-DSL represents the degree of source limitation.

Fischer and HilleRisLambers (1978) investigated the degree of source limitation of wheat cultivars across contrasting environments under no water, nutrient or disease/pest limitations, by changing the source/sink ratio either by trimming out spikelets or by crop thinning. They found source limitations for all the "modern", semidwarft cultivars analyzed, and they concluded that the potential grain weight attained was a cultivar-specific trait. Several other studies, carried out in different parts of the world, have addressed the response of wheat grain weight to changes in source/sink ratios by mechanical or chemical defoliation, grain removal, stand reduction or shading. As a result, a low degree of source limitation in the absence of water stress and other adversities (biotic and abiotic) during grain filling has consistently been reported (Slafer and Savin, 1994; Miralles and Slafer, 1995; Abbate et al., 1997; Cruz-Aguado et al., 1999; Calderini et al., 2006; Lázaro et al., 2010; Zhang et al., 2010; Mohammadi, 2012; Saeidi et al., 2012; Abdoli et al., 2013; Serrago et al., 2013; Trujillo-Negrellos et al., 2014; Cantarero et al., 2016). Accordingly, Borrás et al. (2004) reappraised an extensive dataset comprising 18 studies published between 1975 and 1995 and examined the response of grain weight to the availability of assimilates during grain filling, finding that wheat grain yield was barely source-limited.

Most of these investigations on the degree of source/sink limitation were performed with the use of elite germplasm, *i.e.* advanced lines or commercial cultivars, under similar environmental conditions as the target environment for which they were selected. In fact, genetic materials with shriveled grains are normally discarded during the breeding process, starting as early as in the F_2 generation (Fischer and HilleRisLambers, 1978; Rajaram et al., 2002). Hence, only those lines that do not show a significant source limitation at the target environment are prone to be released as commercial cultivars. In this regard, Abbate et al. (2005) showed that foreign cultivars selected for environments with higher yield potential conditions presented source limitations at grain yield levels $\geq 800\ \mathrm{g\ m^{-2}}$ when grown at Balcarce, Argentina.

If, as a result of the breeding process, wheat grain yield continues to rise through an increase in SICA without a concomitant increase in the source, problems of source limitation might arise. For instance, Trujillo-Negrellos et al. (2014), when studying modern CIMMYT spring wheat cultivars with high yield potential, suggested that the DSL have decreased with breeding, due to a greater increase in grain number (and presumably in SICA) than in the source of assimilates for grain filling across years of cultivar release.

The aim of this study was to analyze sink/source relations in over 150 genotypes comprising both recombinant inbred lines and commercial cultivars, in order to provide insight into whether sink limitation during grain filling in wheat is a ubiquitous attribute or a consequence of breeding and/or the yield potential of the target environment.

2. Materials and Methods

2.1. Plant material

A mapping population of 146 recombinant inbred lines (RILs) derived from the cross between 'Baguette 10' and 'Klein Chajá', Argentinean spring bread wheat cultivars respectively released in 2000 and 2002 and contrasting for grain number, was used in all field experiments. Both parental cultivars were also included, along with other commercial cultivars (5–14, depending on the experiment; Table S1).

2.2. Field experiments

During the 2013, 2014 and 2015 crop seasons, field experiments were carried out at the experimental station of the Instituto Nacional de Tecnología Agropecuaria (INTA) Balcarce (37°45′ S; 55°18′ W; 130 m a.s.l.), Buenos Aires Province, Argentina. In each experiment (one per crop season), 146 RILs, their parents and 5–14 commercial cultivars were grown under a randomized complete block design with two replications. The experimental unit consisted of a 5 m-long, seven-row plot with 0.2 m inter-row distance. All experiments were conducted under no nutritional or water limitations, with chemical control of weeds, pests and fungal diseases. Sowing dates were June 27th 2013, July 24th 2014 and July 15th 2015. Anthesis and physiological maturity dates of each plot were registered in field when 50% of its spikes reached those phenological stages. Physiological maturity was determined as loss of green from the peduncle. Seven days after anthesis of each particular plot, one meter of row was thinned except for the second and the fifth rows, in order to increase their source to reach potential grain weight (Fischer and Laing, 1976; Fischer and HilleRisLambers, 1978; Abbate et al., 2005; Fischer, 2011). Weather conditions were recorded daily with a standard meteorological station located in the experimental station. Temperature and radiation means were calculated for the initial period [from sowing to 20 days before anthesis (anthesis–20d)], the critical period [(from anthesis–20d to seven days after anthesis (anthesis + 7d)] and the grain filling period (from anthesis + 7d to physiological maturity) of each experiment (Fischer, 1985; Lázaro and Abbate, 2012). In addition, the photothermal quotient (Q; Fischer, 1985) was calculated for the critical period.

2.3. Grain measurements and calculations

At maturity, grain yield was measured by mechanical harvest of the five central rows of the unthinned part of each plot. In order to determine potential grain weight and grain weight, subsamples of ca. 40 g of grains were collected respectively from the thinned and unthinned parts of the plot before harvest. Grains were counted and weighed after drying samples for 48 h at 65 °C. Grain number $\mathrm{m^{-2}}$ was calculated as the quotient between grain yield and grain weight. The grain weight of the thinned part of the plot was considered to be the potential grain weight. Sink capacity was calculated as the product of grain number and potential grain weight, whereas DSL was calculated as the quotient between grain weight and potential grain weight.

In order to determine the SICA value at which the slope of the relationship between grain yield and SICA departs from the expected 1:1 ratio, a segmented boundary function was fitted (Eq. (1), Koenker, 2005)

$$Grain\ \ Yield = \min_{SICA \in [0,1500]} \{SICA;\ a + b \times SICA\} \tag{1}$$

where a and b are parameters estimated with the *quantreg* package (Koenker, 2007) of the R software (R-Core Team, 2016).

2.4. Statistical analysis

In order to establish differences between treatment means, an ANOVA was performed for SICA and DSL using a fixed effects model which included nested effects of replicates, flowering date and grain filling duration within environments, environments, genotypes (both cultivars and RILs) and the genotype x environment interaction. Differences between treatment means were determined with the least significant difference (LSD) test when ANOVA was significant. All

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