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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

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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 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 $\geq 800\ g\ m^{-2}$ 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 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)

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

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

Table 1
Mean daily temperature (Tmean, °C), radiation (MJ m^{-2}) and photothermal quotient (Q; MJ m^{-2} d^{-1} $°C^{-1}$) for three crop seasons (2013, 2014 and 2015) and the historical means (from 1983 to 2015) in Balcarce, Argentina. Each crop season was divided into an initial period (IP; from sowing to 20 days before anthesis), critical period (CP; from 20 days before to 7 days after anthesis) and grain filling period (GFP; from 7 days after anthesis to physiological maturity).

	Tmean (°C)			Radiation (MJ m^{-2})			Q (MJ m^{-2} d^{-1} $°C^{-1}$)
	IP	CP	GFP	IP	CP	GFP	CP
2013	10.0	15.4	19.4	10.0	17.4	22.2	0.80
2014	12.1	17.5	19.8	11.0	19.7	23.0	0.76
2015	10.9	16.1	18.6	10.8	18.4	21.5	0.79
Historical mean	10.0	15.1	18.2	10.0	17.4	22.2	0.90

statistical analyses were performed using the R software, and the critical level of significance used was 0.05.

3. Results

3.1. Weather conditions and phenology

Mean daily temperature, radiation and photothermal quotient values for each crop season are shown in Table 1. On average, all seasons were warmer than the historical mean. Particularly, in 2014 the crop grew under unusually high temperature, with the lowest Q value. The last season showed the lowest temperature during the grain filling period.

Regarding crop phenology, flowering date for the RIL population, parents and commercial cultivars in all crop seasons was concentrated within ~10 days in early November (Fig. S1); thus, environmental conditions during the critical period were fairly similar for all genotypes at each experiment. On average, the combined initial plus critical period lasted 137, 105 and 119 days in the 2013, 2014 and 2015 crop seasons, respectively. The grain filling period was 5–10 days longer in 2015 (43–49 days) than in the remaining seasons.

In order to rule out effects of phenology on DSL and SICA, the association between (i) DSL and grain filling duration, (ii) SICA and flowering date, and (iii) DSL and flowering date, was tested at each crop season. As a result, no significant association was found for any of these pairs ($p > 0.05$).

3.2. Yield and associated traits

Grain yield, yield components and other traits of interest determined in the RIL population, their parents and commercial cultivars are shown in Table 2 for the three crop seasons. On average, grain number was greatest in 2013, intermediate in 2015 and lowest in 2014. The latter was probably a consequence of a low Q during the critical period, as well as of a warmer and shorter initial plus critical period which led to a low number of tillers and suboptimal leaf area (data not shown).

Mean grain weight was greater in 2015 than in 2013 or 2014 (Table 2), probably due to the fact that in 2015 the grain filling period was longer than in the remaining crop seasons (Fig. S1), as a consequence of milder temperatures (Table 1). Yield and SICA were more related to variations in grain number than they were to variations in grain weight or potential grain weight, regardless of the genotype or environment (Table 2). Nevertheless, RILs' median grain yield was greater in 2015 (764 g m^{-2}) than in 2013 (719 g m^{-2}) despite greater median grain number in 2013 (21.4 10^3 grains m^{-2}) than in 2015 (17.8 10^3 grains m^{-2}) and because of greater median grain weight in the latter crop season (43 mg vs. 33 mg in 2013). On the other hand, both parents and commercial cultivars yielded more in 2013 than in 2015 (Table 2).

Sink capacity varied significantly between crop seasons, with higher mean values in 2013, and lower values in 2014 (Table 2; Fig. 1). The combination of three years of experiments and over 150 genotypes resulted in a wide range of SICA and grain yield values (Fig. 1), due to high variability at both variables in the population and among cultivars and different environmental conditions between crop seasons. Fig. 1 shows a high association between grain yield and SICA, with a breaking point on 795.8 g m^{-2} (~8 tons ha^{-1}) of grain yield in which the slope of this relationship departed from the expected 1:1 ratio and beyond which all genotypes (be it RILs or cultivars) showed some degree of source limitation.

There were significant negative correlations between SICA and DSL for all crop seasons ($r = -0.53$ for 2013, $r = -0.46$ for 2014 and $r = -0.38$ for 2015; $p < 0.0001$) (Fig. 2). The slopes of these relations were significantly different among years, whereas cultivars and RILs within each year were evaluated together as no difference was found between these two groups in their relation between SICA and DSL. This indicates that, when SICA increases, the degree of source limitation increases as well; hence, sink is no longer the sole limiting factor for achieving yield potential. In addition, this relation depended on the weather conditions during the critical period (when SICA is defined) and during grain filling. For instance, in 2014, DSL values were close to 1 (median of RIL population and mean of parents and commercial cultivars) due to weather conditions that led to lower grain number, and thus to lower SICA, than in the remaining seasons (Tables 1 and 2; Fig. 3). In the 2013 and 2015 crop seasons, in which SICA reached the highest values, average DSL values were lower than in 2014, with more extreme values in 2013.

Median DSL of RILs and commercial cultivars were not significantly different at each crop season (Fig. 3). Both RILs and commercial cultivars presented median DSL significantly lower than 1 in 2013 and

Table 2
Minimum, median and maximum grain yield (GY), grain number (GN), grain weight (GW), potential grain weight (PGW), sink capacity (SICA) and degree of sink limitation (DSL) for the RIL population; means of parental cultivars Baguette 10 and Klein Chajá and minimum, mean and maximum values of other commercial cultivars for the same variables. Standard deviation (SD) of each variable at each experiment is shown at the bottom. Data from 2013, 2014 and 2015 crop seasons at Balcarce, Argentina.

		GY (g m^{-2})			GN (grains m^{-2})			GW (mg)			PGW (mg)			SICA (g m^{-2})			DSL		
		2013	2014	2015	2013	2014	2015	2013	2014	2015	2013	2014	2015	2013	2014	2015	2013	2014	2015
RILs	Mín	274	194	439	8634	5284	9738	23	25	30	28	28	37	311	182	459	0.61	0.73	0.74
	Median	719	365	764	21413	9961	17824	33	38	43	39	39	46	818	380	830	0.87	0.96	0.93
	Max	1081	555	893	36407	17835	25308	42	50	53	46	50	56	1436	605	1005	1.00	1.10	1.01
Baguette 10 Klein Chajá	Mean	1025	373	790	29523	9208	19015	35	40	42	39	40	47	1142	365	890	0.91	1.00	0.90
	Mean	760	459	672	23097	10618	15297	34	41	44	43	41	45	1006	434	684	0.79	1.01	0.99
Other commercial cultivars	Mín	654	353	581	17004	9208	12296	31	28	37	39	34	37	773	343	595	0.79	0.83	0.88
	Mean	844	468	719	24211	12323	16322	35	38	43	42	40	46	1005	482	753	0.85	0.97	0.93
	Max	1025	581	806	29523	16145	21187	38	43	54	45	46	58	1252	614	890	0.91	1.08	0.99
	SD	187	93	124	6357	2744	3474	4.2	4.6	3.9	3.4	4.8	3.7	259	113	140	0.10	0.13	0.06

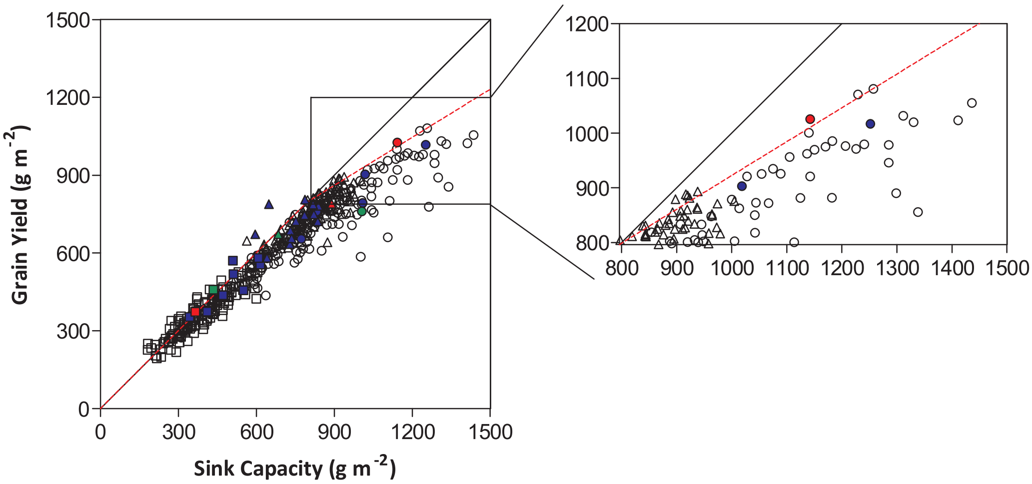

Fig. 1. Average grain yield as a function of average sink capacity (SICA) in 146 RILs, for 2013 (circles), 2014 (squares) and 2015 (triangles) crop seasons at Balcarce, Argentina. Commercial cultivars are shown in blue and parents of the RIL population in red (Baguette 10) and green (Klein Chajá). The black dotted line is the 1:1 relationship, in which grain yield is equal to SICA. The red dashed line is a boundary function (Q95) of grain yield as a function of SICA.

2015 ($p < 0.05$) (Table 2). Moreover, the variation within RILs was substantially higher than it was within cultivars (Table 2; Fig. 3). In fact, standard deviation of DSL in the 2013, 2014 and 2015 crop seasons was respectively 40, 43 and 67% higher for RILs than it was for cultivars (SD of RILs and cultivars = 0.07 and 0.05 in 2013; 0.10 and 0.07 in 2014; 0.05 and 0.03 in 2015). Particularly in the 2013 crop season, when the lowest DSL values were observed, the minimum DSL value among cultivars was 0.79, whereas some RILs showed much lower DSL values (minimum = 0.61), indicating that they were more source-limited.

Differences in DSL between genotypes that exhibited mean grain yield values greater than 8 tons ha^{-1} were detected by mean comparisons of 31 such genotypes (27 RILs and four commercial cultivars, including 'Baguette 10'). Taking 'Baguette 10' as a reference (due to its high mean grain yield, SICA and DSL −close to 1), none of the remaining three cultivars had a different DSL; however, nine out of 27 RILs had a significantly lower DSL than that of 'Baguette 10' ($P < 0.001$).

4. Discussion

The idea of wheat being predominantly sink-limited during grain filling (regardless of the growing environment) is widespread and well documented (reviewed in Borrás et al., 2004). Nevertheless, in this study, several lines and cultivars showed source limitation when grown under non-limiting conditions. This source limitation was mainly observed at yield levels above ~800 g m^{-2} (*i.e.* ~8 tons ha^{-1}), in line with what had been reported by Abbate et al. (2005) for foreign and local cultivars evaluated in Balcarce.

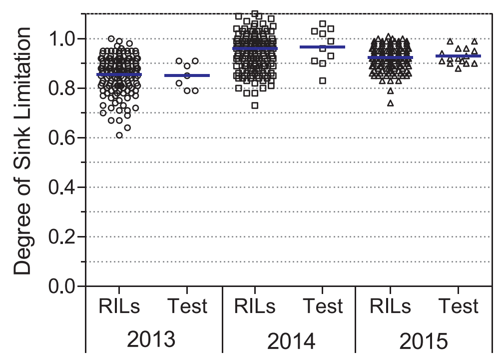

Fig. 3. Scatter plot of the degree of sink limitation in the RIL population (RILs) and their parents and other commercial cultivars (Test) for the 2013, 2014 and 2015 crop seasons. Median values are shown with horizontal blue lines.

The experiments carried out in this study included both commercial cultivars and advanced lines not subject to selection, as opposed to previous studies, which were mainly based on commercial cultivars. Moreover, the contrasting weather conditions observed between years allowed an accurate assessment of yield and yield-related traits and their relation with the environment. The fact that the flowering date of the RIL population and cultivars was mostly concentrated within ~1 week in all crop seasons is relevant because, otherwise, confounding effects of differences in phenology would have interfered in the resulting yield and the remaining, associated variables.

As expected, yield was more related to grain number than it was to grain weight and potential grain weight. The average DSL of

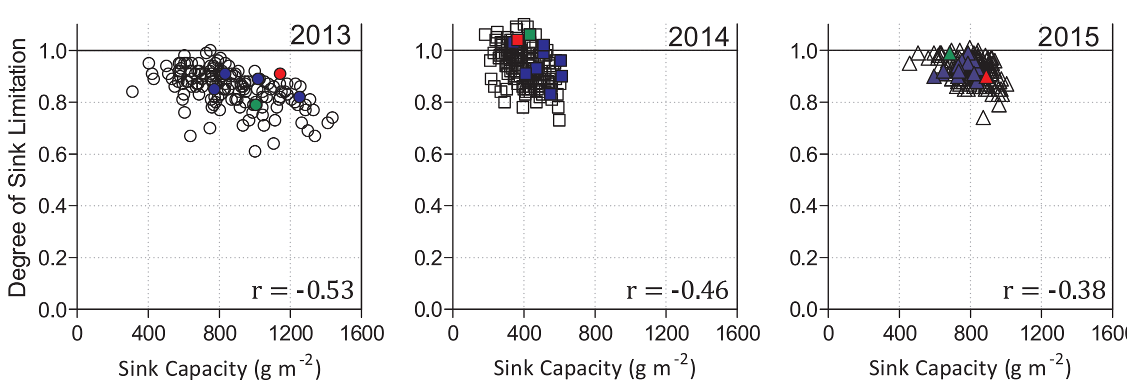

Fig. 2. Degree of sink limitation (DSL) as a function of sink capacity (SICA, g m^{-2}) for 2013 (circles), 2014 (squares) and 2015 (triangles) crop seasons at Balcarce, Argentina. RILs are shown with open symbols, commercial cultivars are shown in blue and parents in red (Baguette 10) and green (Klein Chajá). Significant negative correlations between DSL and SICA were determined at each crop season for all genotypes (p-value < 0.05).

commercial cultivars with wide diffusion in Balcarce was similar to that of RILs (*i.e.* unselected advanced lines), and it occurred in all three crop seasons, under contrasting weather conditions. Moreover, in 2013 and 2015, average DSL for cultivars was lower than 1. That means that even genetic materials selected for or adapted to this high yielding environment showed some degree of source limitation during grain filling. Nevertheless, when analyzed at the individual genotype level, source limitation was greater in some of the high yielding RILs than in the cultivars. Trujillo-Negrellos et al. (2014) found that some modern CIMMYT cultivars of high yield potential showed a lower degree of sink limitation than did their predecessors. Our analysis shows that, in Balcarce, genetic materials with high yield potential are likely to be source-limited especially above a yield potential of 8 tons ha^{-1}. Many authors consider that the most obvious way to increase yield potential is by increasing grain number (Abbate et al., 1995; Fischer, 2011; Reynolds et al., 2012). However, given that a significant negative correlation between DSL and SICA was observed at each crop season, the pursuit of a breeding strategy for increasing grain number which disregarded the possibility of source limitation could lead to selecting materials with source (-sink co-) limitation, especially in high yield-potential target environments. As a result, this limitation would become more frequently observed.

Our study indicates that, within the bread wheat gene pool, certain genetic combinations can arise which lead to source limitations under high-yielding environments, even though subsequent natural or artificial selection has normally operated against this (Sadras, 2007). However, grain selection (against shriveling or other signs of filling problems) would only reduce the occurrence of severe source limitations, but it would fail to completely prevent it. As a matter of fact, in the present study we seldom observed shriveled grains whereas source limitations occurred in many of the RILs and cultivars that were evaluated. Therefore, while grain number is improved/increased, it is necessary to continue improving the source, through increases in the radiation use efficiency, capacity of soluble carbohydrate storage and remobilization, green leaf area duration, etc. (e.g. Reynolds et al., 2012), and thus maximize progress in breeding of yield potential under non-limiting conditions. In order to achieve this, simple methods for detecting source limitations in the context of a breeding program are needed. Its availability would allow establishing the sink/source balance of the genetic pool at each target environment and, in extension, optimizing breeding strategies.

This study presents a novel approach to address sink/source relations in wheat during grain filling. The high variability found in the RIL population allowed us to observe phenotypes that would normally be discarded by the breeder, in contrast with previous works, that only evaluated a narrow range of cultivars selected for the same target environment. The latter approach hinders the possibility of distinguishing between attributes that are inherent to the species (i.e. fixed during domestication) and those that are outcomes of artificial selection (i.e. breeding). Our work is a first attempt to separate these effects. However, to fully clarify whether the prevalence of sink over source limitation in wheat is inherent of the species, a wider range of genotypes, including cultivars bred for different environments and/or in different eras, as well as wild relatives, should be explored.

5. Conclusion

Our comprehensive analysis of sink/source relations in over 150 genotypes comprising both commercial cultivars and unselected lines (RIL population), carried out in high yielding environments under contrasting weather conditions, shows that all genotypes analyzed presented some degree of source limitation at high SICA values. Therefore, it would be inaccurate to assume that sink limitation during grain filling in wheat is an ubiquitous attribute. Moreover, further improvement of grain number could lead to source limitations; therefore, the sink/source balance should not be disregarded in the breeding process.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.eja.2017.11.007.

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