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Grain Weight of Durum Wheat Cultivars Released in Italy and Spain during the 20th Century as Affected by Source-Sink Manipulations

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The present work analysed whether grain weight is affected by changes in source:sink ratio in twenty-four durum wheat cultivars from Italy and Spain released through the 20th century grown under Mediterranean conditions. For this purpose, a field experiment was conducted during the 2002 growing-season in southeastern Spain. Sink strength was modified by removing half of the spikelets, of one side of the spike, one week after anthesis. Spikelet trimming had different effects on both average grain weight and individual grain weight at different positions within the spike. While old cultivars did not respond positively to spikelet trimming, and appear to be mainly sink-limited, intermediate and modern cultivars from Spain increased their grain weight in response to sink reductions, suggesting co-limitation by the sink and source. On the contrary, grain weight of intermediate and modern Italian cultivars remained relatively unchanged suggesting a sink-limitation to grain yield. The differential response to source-sink manipulations observed between Italian and Spanish cultivars could be attributed to their different genetic background, which determines their level of adaptation to harsh Mediterranean environments.

Keywords: grain weight, source-sink manipulations, durum wheat, southeastern Spain, Mediterranean conditions

Introduction

It is well known that increases in the number of grains per unit area has been the yield component most related to yield variations due to breeding efforts in bread wheat (McCaig and Clarke 1995); durum wheat (García del Moral et al. 2003) and barley (García del Moral et al. 1991), whereas changes in mean grain weight have been generally non-significant (McCaig and Clarke 1995; Royo et al. 2007), or negative (Brancourt-Hulmel et al. 2003). Regarding this point, evidences for a negative relationship between average grain weight and the number of grains per unit area are largely reported in the literature (Slafer and

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Savin 1994; Miralles and Slafer 1995; Kruk et al. 1997; Borrás et al. 2004; Acreche and Slafer 2006). Such negative association is often interpreted as a competition among growing grains for a limited supply of assimilates during grain filling. However, other alternative non-competitve hypothesis was suggested based on the assumption that reduction in grain weight is associated with an increased proportion of grains of lower potential weight generally placed in distal positions within the spikelets and/or tiller-spikes (Miralles and Slafer 1995). The competitive hypothesis implies that grain yield is mainly source-limited, while the non-competitive hypothesis support the idea that grain yield is mostly sink-limited.

The simplest approach to determine whether, and to what extent, grain yield is sink- or source-limited during grain filling has been to modify the source-sink ratio by different treatments (e.g. defoliation, shading, trimming or degraining). Several works have been carried out in order to investigate the effects of source-sink manipulations during grain filling on average grain weight, but have led to conflicting conclusions. Thus, while some studies revealed that grain weight is mostly sink-limited when wheat is grown under optimal growing conditions (Slafer and Savin 1994; Miralles and Slafer 1995), other authors reported that grain weight was somewhat limited by the ability of the source to provide assimilates during grain filling (Ma et al. 1990). However, under rainfed conditions, Blade and Baker (1991) showed that grain weight increased in response to a sink reduction treatment that can be interpreted as a source-limitation to grain growth.

Only few evidences showed the effect of breeding comparing old and modern bread wheat cultivars released in different periods (Koshkin and Tararina 1989; Kruk et al. 1997). Nevertheless, other works on source-sink manipulations carried out in northern Spain showed a major degree of source-limitation in barley (Voltas et al. 1997), while in bread wheat Cartelle et al. (2006) concluded that grain yield was mainly sink-limited during the grain-filling period.

The aims of the present study were (i) to examine the effect of spikelet trimming (i.e. doubling the source-sink ratio) on grain weight in durum wheat cultivars released in different periods during the 20th century in Italy and Spain, and (ii) to ascertain whether breeding in both countries have changed yield from sink- to source-limited during grain filling under the Mediterranean conditions of southern Spain.

Materials and Methods

General

A field experiment was carried out during the 2002 growing season in Granada (37º08’N, 3º49’W), in a representative area of the cereal growing region of south-eastern Spain characterised by a typical Mediterranean climate. Twelve durum wheat cultivars from Italy and twelve ones from Spain were selected to represent the germplasm grown in both countries during the 20th century. Based on the year of release (Table 1), the cultivars were separated in three periods, namely old (before 1945), intermediate (released between 1950 and 1985) and modern (from 1988 to 2000).

Table 1. Cultivars used in the study released in different periods in Italy and Spain

Italian	Year of release	Presence of *Rht-B1* gene	Spanish	Year of release	Presence of *Rht-B1* gene
Old					
Balilla Falso	<1930	–	Blanco Verdeal	<1930	–
Carlojucci	1945	–	Clarofino	<1930	–
Razza 208	1930	–	Pinet	<1930	–
Senatore Capelli	1930	–	Rubio de Belalcázar	<1930	–
Intermediate					
Adamello	1985	–	Bidi 17	1950	–
Capeiti 8	1955	–	Camacho	1975	+
Creso	1974	+	Esquilache	1976	+
Trinakria	1970	–	Mexa	1980	+
Modern					
Cirillo	1992	+	Ariesol	1992	+
Flavio	1992	+	Astigi	1999	+
Simeto	1988	+	Boabdil	2000	+
Zenit	1992	+	Senadur	1995	+

Note: Within each country, cultivars were grouped in old, intermediate and modern according to the year of release. Presence and absence on dwarfing gene Rht-B1 is indicated.
Source: Álvaro et al. 2008.

Seasonal precipitations were 328 mm and experiment was conduced under no irrigation conditions. Mean temperature during grain filling was 19.2 ºC, with average maximum temperature of 27.1 ºC. Soil was loamy Calcixerolic Xerochrept with a silty-clay texture. Cultivars were sown on November 27, 2001 at a rate of 350 seeds per m^2 and grown in plots of 12 m^2 (eight rows 10 m long and 0.15 m apart). Basic fertilization consisted of a mixture of NPK (15:15:15) applied in the seedbed and top-dressed with ammonium nitro sulphate (26% N). Taking into consideration the soil characteristics, total fertilization in kg ha^{-1} was: 52 + 26 N, 52 P, and 52 K. Pests, diseases and weeds were chemically controlled following the recommendations at the region of study.

Treatments

Cultivars and source-sink manipulation treatments were arranged in a split-plot design, with cultivars assigned to main plots and source-sink ratios to sub-plots, using three replicates per treatment.

Source-sink ratios were modified by manipulating the number of spikelets per spike. For this purpose, at anthesis 20 main-stem spikes (having similar number of spikelets per spike) were randomly selected from the central rows of each plot and tagged. One week after anthesis, all spikelets from one side of 10 spikes, chosen randomly from the 20 spikes labelled before, were removed by hand (trimming treatment); while the other 10 spikes remained unaltered as controls.

Sampling, measurements and analyses

Plants contained in 1-m-long rows were pulled out in a central row of each plot at ripening and the number of grains in the sample was recorded. A sub-sample of 10 randomly selected plants was used to determine the number of main and tiller-spikes as well as average grain weight in main and tiller-spikes, separately. The average grain weight (from the main and tiller-spike mixture) was then calculated for each sub-sample. Plots were mechanically harvested at ripening and grain yield was adjusted to a 12% moisture level.

To investigate whether the relationship between average grain weight and the number of grains per unit area might be related to the competitive or non-competitive hypothesis above mentioned, the behaviour of basal grains in "near apical" and "near basal" spikelets as well as grains from different positions in central spikelets was determined. For that purpose, at maturity the control and trimmed spikes were harvested in each plot and grains in whole spike and those from the selected positions within the spike were counted, oven-dried and weighed separately. Thus, grains were taken from different positions within the central spikelets and were named (from closest to distal position respect to the rachis) as: G1C (closest), G2C (second), G3C (third) and G4C (fourth). Similarly basal grains placed (i.e. G1) in both the "near apical" and "near basal" spikelets were sampled and subsequently referred to as G1A and G1B. Statistical analyses were performed with the SAS–STAT package (SAS Institute 2000).

Results

As expected, modern cultivars, both from Italy and Spain, exhibited higher grain yields than old cultivars (Table 2). This was mainly due to breeding effects on the number of grains per m^2. In fact, increases in grain number were ca. 25% and 40% from old to modern cultivars from Italy and Spain, respectively (Table 2).

Table 2. Mean values of grain yield, number of grains per m^2, and grain weight averaged across main and tiller spikes and in control and trimmed spikes of the main stems of 24 durum wheat cultivars released in different periods (old, intermediate and modern) in Italy and Spain

Period of release	Grain yield (kg ha^{-1})	Grains m^{-2}	Average grain weight (mg)		
			Main and tiller spikes	Main spikes	
				Control	Trimmed
Italian					
Old	2809 b	6125 c	47.8 a	47.3 a	44.0 a*
Intermediate	3032 ab	6955 b	45.0 a	43.0 b	42.1 a
Modern	3249 a	7644 a	44.0 a	43.9 ab	43.4 a
Spanish					
Old	2735 b	6178 c	45.6 a	46.7 a	43.4 b
Intermediate	3433 a	7721 b	45.6 a	45.8 ab	48.9 a*
Modern	3527 a	8631 a	42.5 a	42.3 b	46.7 a*

Notes: Means within columns and countries followed by the same letter are not significantly different according to Duncan's test at $P = 0.05$.
* = spikelet trimming significantly altered grain weight when compared to the control.

Relationship between average grain weight and number of grain per m²

Old cultivars with lower grain number per m^2 form Italy and Spain showed higher grain weights, when averaged across main and tiller spikes (Table 2), as well as when considered grain weight from main spikes, respect to intermediate and modern cultivars which registered the lower values. However, in statistical terms, the differences were significant only when grain weight from main spikes was compared (Table 2). Average grain weight showed a negative linear regression when was regressed against the number of grain per m^2 both in Italian (r = –0.78**) and Spanish cultivars (r = –0.37 ns) (Fig. 1a). When average grain weight was regressed against the year of release, the fit was weak and only a slight decrease in grain weight with the year of release (i.e. slope of –0.05 mg $grain^{-1}$ y^{-1}) was observed in both Italian and Spanish cultivars (Fig. 1b).

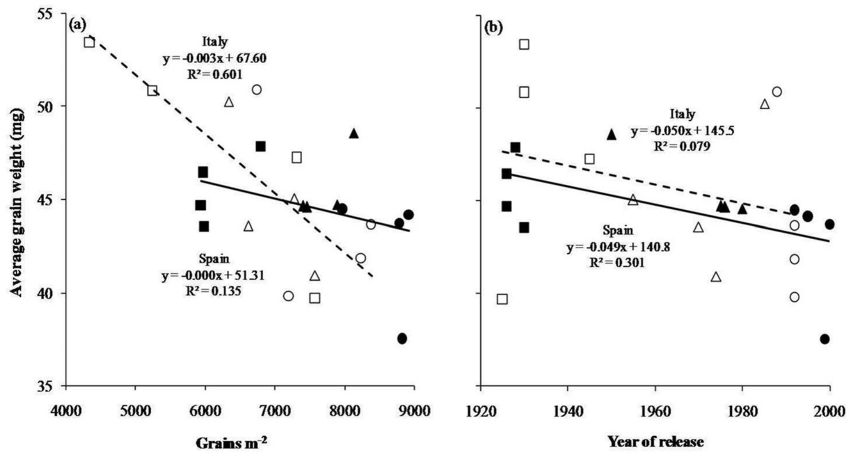

Figure 1. Relationships between average grain weight and (a) number of grains per m^2 and (b) year of release for Italian (open symbols) and Spanish (closed symbols) durum wheat cultivars grouped in old (squares), intermediate (triangles), and modern (circles). Linear regressions were fitted for the Italian (dotted lines) and Spanish (solid lines) cultivars

Individual weight of grains from different positions within the spike

Both in Italian and Spanish cultivars, basal grains in central spikelets (G1C) were heavier than those placed in apical (G1A) and basal (G1B) spikelet positions (Table 3). Averaged by country, individual weights of G1A, G1B and G1C were 45.8, 45.1 and 47.8 mg $grain^{-1}$ for Italian set and 47.6, 47.5 and 49.6 mg $grain^{-1}$ for Spanish set, respectively. In central spikelets, the ranking of individual grain weights was G2C>G1C>G3C>G4C, with 47.8, 52.0, 43.3 and 34.7 mg $grain^{-1}$ for Italian set and 49.6, 52.1, 42.3 and 35.5 mg $grain^{-1}$ in Spanish set, respectively. For all categories of grains, old cultivars showed higher grain weights compared with modern cultivars (Table 3). The relative reduction in individual grain weight was, in general terms, similar to that described for average grain weight in Table 2.

Average grain weight responses to spikelet trimming

Cultivars from Italy and Spain showed different responses to spikelet trimming (Table 2). In fact, while significant increments in grain weight were observed for intermediate (7%) and modern (10%) Spanish cultivars, on the contrary, the treatment slightly and not significantly reduced grain weight in intermediate (2%) and modern (1%) Italian cultivars. When considered old cultivars, and in both countries, spikelet trimming reduced grain weight ca. 7% (Table 2).

According to Figure 2, where grain weight in trimmed spikes was plotted against grain weight in control spikes, cultivars from Italy appear to be mostly sink-limited as suggested by the slope of 0.83 mg mg^{-1}, which is close to 1:1 line. In fact, no significant effects were observed in grain weight when spikes were trimmed respect to the control spikes. A different scenario was observed in Spanish cultivars, as grain weights from trimmed spikes were higher than those of control spikes in intermediate and modern cultivars suggesting a source-limitation. Conversely, grain weight of old cultivars placed below the 1:1 line evidenced a reduced grain weight due to trimming (Fig. 2).

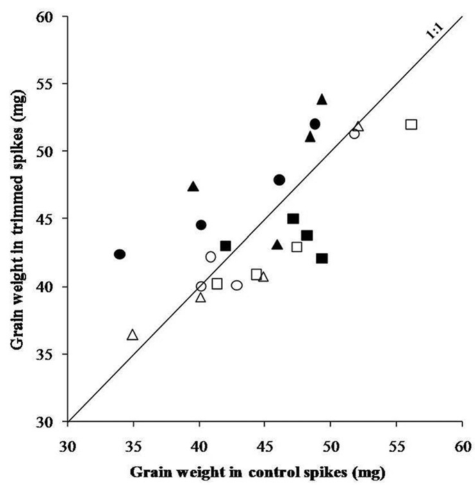

Figure 2. Average grain weight in control spikes plotted against average grain weight in trimmed spikes of 12 Italian (open symbols) and 12 Spanish (closed symbols) durum wheat cultivars grouped in old (squares), intermediate (triangles), and modern (circles)

Figure 3a shows the relative change in grain weight (the increase in average grain weight due to spikelet trimming as a percentage of the average grain weight in control spikes) as a function of the year of release. It appears that the response to trimming is increased from old to modern cultivars in both countries but particularly in Spain. This trend of responsiveness is also observed when the relative change in grain weight is plotted against the number of grains per m^2 (Fig. 3b). The change in grain weight due to trimming is proportional to increases in grain per unit area. Old cultivars with low number of grains had the lowest response while intermediate and modern cultivars, particularly from Spain with a large number of grains, exhibited an increased grain weight and appear to be more source-limited. In contrast, Intermediate and Modern Italian cultivars, although having higher number of grains, did not respond to trimming suggesting to be sink-limited.

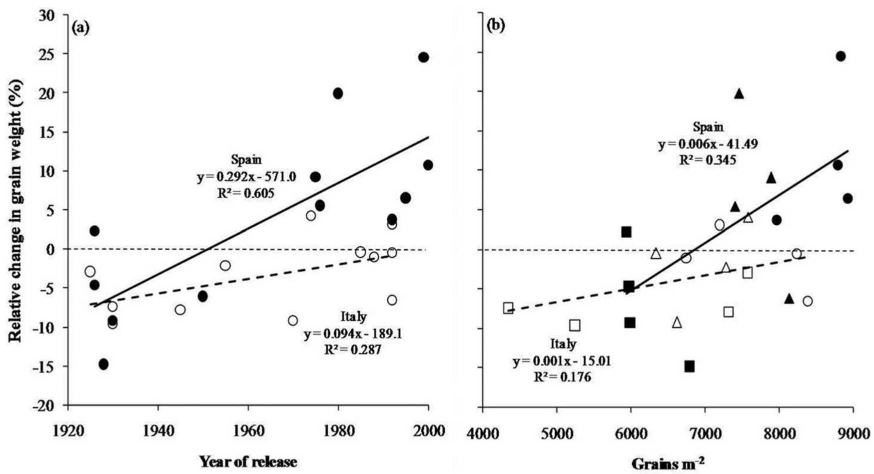

Figure 3. Relative change in grain weight plotted against (a) the year of release and (b) the number of grains per m^2 (b) for Italian (open symbols) and Spanish (closed symbols) durum wheat cultivars grouped in old (squares), intermediate (triangles), and modern (circles). Linear regressions were fitted for the Italian (dotted lines) and Spanish (solid lines) cultivars

The possible explanation of the different responses to trimming among Spanish and Italian cultivars could be found in Figure 4. In fact, when the relative change in grain weight is plotted against the relative change in assimilate availability per grain (i.e. the percentage change of the source-sink ratio), it can be observed that intermediate and modern Spanish cultivars have the lowest capacity to accumulate photosynthetic assimilates and appear to have some limitation by the source. Intermediate and modern cultivars from Italy exhibited an acceptable capacity of accumulation and then did not respond positively to spikelet trimming. Old cultivars from both countries exhibited the largest capacity of accumulation and seem, probably, to have a sink limitation due to their lower number of grain per m^2 (see Fig. 3b)

Supporting the trend described above in average grain weight, sink halving reduced grain weight of proximal grains (G1A, G1B, G1C and G2C) by an average of ca. 6 and 11% in old Italian and Spanish cultivars, respectively (Table 3). Similarly, reductions in distal positions (G3C and G4C) were about 4% and 9% in old Italian and Spanish cultivars. In intermediate and modern cultivars, different responses to trimming were observed between Italian and Spanish sets (Table 3). While grain weight in intermediate Italian cultivars showed a slight reduction in proximal (1%) and distal (4%) grains, it was increased in intermediate Spanish cultivars by 4% and 7% in proximal grains and distal

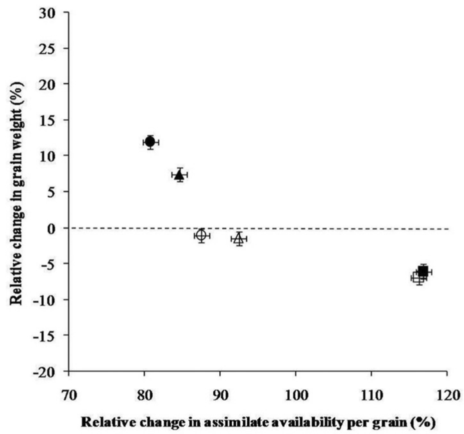

Figure 4. Relationship between the relative change in grain weight and the relative change in potential assimilate availability per grain for Italian (open symbols) and Spanish (closed symbols) durum wheat cultivars grouped in old (squares), intermediate (triangles), and modern (circles). Points represent the average values over cultivars and repetitions belonging to each period of release (old, intermediate and modern). Horizontal and vertical bars attached to each symbol indicate the standard error of means corresponding to each axis

Table 3. Individual weight (mg) of the grain corresponding to the most proximal position to the rachis (G1) in "near apical" (G1A), and "near basal" (G1B) spikelets as well as the grain weight for different positions within central spikelets (from G1C most proximal to the rachis to G4C the most distal) in control (C) and trimmed (T) spikes of 24 durum wheat cultivars released in different periods (old, intermediate and modern) in Italy and Spain

Grain position	Period of release	Italy		Spain	
		C	T	C	T
G1A	Old	48.4 a	45.3 a	50.3 a	45.7 b*
	Intermediate	44.1 b	44.0 a	48.5 a	50.0 a
	Modern	44.9 ab	45.0 a	44.2 b	49.3 a*
G1B	Old	45.9 a	44.5 a	48.8 a	42.3 b*
	Intermediate	43.9 a	44.3 a	48.1 a	50.6 a
	Modern	45.5 a	46.8 a	45.5 a	48.9 a*
G1C	Old	49.4 a	46.5 a	50.3 a	45.9 b*
	Intermediate	46.7 a	46.2 a	50.9 a	52.7 a
	Modern	47.1 a	49.1 a	47.6 a	52.3 a*
G2C	Old	53.7 a	49.8 a*	54.1 a	47.1 b*
	Intermediate	51.0 a	49.3 a	53.6 a	56.0 a
	Modern	51.2 a	51.5 a	48.7 b	52.8 a*
G3C	Old	45.6 a	43.7 a	42.9 ab	41.5 b
	Intermediate	40.8 b	41.6 a	45.5 a	49.7 a*
	Modern	43.6 ab	41.9 a	40.5 b	46.6 a*
G4C	Old	36.6 a	35.6 a	40.0 a	34.5 a*
	Intermediate	29.6 b	26.9 b	34.5 ab	36.6 a
	Modern	37.8 a	31.1 ab*	32.1 b	38.4 a*

Note: Means within columns and grain positions followed by the same letter are not significantly different according to Duncan's test at P = 0.05.
* = spikelet trimming significantly altered grain weight when compared to the control.

grains, respectively, when spikes were trimmed. Modern cultivars responded also differently to trimming. Thus, Italian cultivars showed a non-significant increase of ca. 2% in grain weight at proximal positions and conversely an important decrease of 11% in grain weight at distal positions. Modern Spanish cultivars exhibited consistent grain weight increases of 9% and 17% at proximal and distal positions, respectively, in response to trimming.

Discussion

The significant rise in grain yield in Italian and Spanish durum wheats from old to modern cultivars was consequence of increases in the number of grain per m^2 as was also reported in durum (Royo et al. 2007) and bread wheat (Austin et al. 1989). This increased grain number could be attributed to a higher number of fertile florets per spikelet in modern cultivars compared to the old ones (Royo et al. 2007) as a consequence of higher assimilate partitioning to the spike during the pre-flowering critical period (Miralles et al. 2002).

A negative relationship, particularly in Italian cultivars, was found between average grain weight and the number of grains per m^2 in coincidence to that reported by other works carried out in the Mediterranean basin on wheat (Acreche and Slafer 2006; Cartelle et al. 2006) and barley (Voltas et al. 1997) and in other regions of the world (Slafer and Savin 1994; Kruk et al. 1997). However, in proportional terms the increases in grain number were higher than the decreases observed in grain weight, determining finally increases in yield and suggesting that crops under Mediterranean conditions are co-limited by sink and source without a complete compensation between both attributes.

Different patterns of responsiveness to source-sink manipulations were observed in our study between Italian and Spanish cultivars and could be probably due to its different sensitivity to scarce source conditions during grain filling. Thus, while intermediate and modern Spanish cultivars showed a significant increase in grain weight in response to doubling source-sink ratio without significant change in the proportion of each grain category (proximal or distal grains), on the contrary, grain weight of intermediate and modern Italian cultivars was slightly reduced. This irrelevant change in grain weight could be interpreted as a sink-limitation to grain yield in the Italian cultivars. The same picture was observed when examining the relative change in grain weight in response to changes in assimilate availability. Thus, the results of the present study suggest that old cultivars, with lower sink capacity than the modern ones, appear to be more sink-limited. Intermediate and modern Spanish cultivars with lower capacity of accumulation increased their grain weight in response to trimming but their values were distant from the 1:1 ratio and appear to be co-limited by both source and sinks during grain filling, as suggested by Slafer and Savin (1994). In contrast, intermediate and modern Italian cultivars, with more capacity to accumulate photosynthetic assimilates compared to Spanish ones, did not change their grain weight in response to trimming with values not significantly different from zero and are then sink-limited.

Under Mediterranean conditions, similar results were obtained in northern Spain by Álvaro et al. (2008) in durum wheat and by Voltas et al. (1997) in barley indicating a co-limitation of grain growth by the sink and the source. However, in the same region and working with bread wheat Acreche and Slafer (2006) showed that wheat is largely sink-limited. In addition, the results in the present study under harsh Mediterranean conditions are in some extent in disagreement with those described in the literature for other regions that final grain weight in wheat is largely unresponsive to changes in sink size (see Borrás et al. 2004 and references quoted therein, Miralles and Slafer 2007). Moreover, while Koshkin and Tararina (1989) reported that grain growth was more limited by the strength of the source in the newest than in the oldest cultivars, several studies mostly carried under favourable conditions indicate that grain yield is sink-limited during grain filling (e.g. Slafer and Savin 1994; Miralles and Slafer 1995). This lack of consistency in the response of grain weight to spikelet trimming was also found in our study probably due to the different genetic background of Italian and Spanish cultivars. In addition, the competitive hypothesis was confirmed, in the present work, by the positive response of intermediate and modern Spanish cultivars to sink halving under stressed conditions during grain growth. In fact, it has been reported that even in areas where grain filling take place under dry conditions, where it is expected that sink-limitation to grain yield rarely occurs, plant breeding has increased grain weight through changes in the number of grains m^2 (Siddique et al. 1989).

The different patterns observed in the response of intermediate and modern cultivars from Italy and Spain to source-sink manipulations could be attributed to the different breeding strategies followed in these countries. The importance of durum wheat in Italian agriculture and pasta consumption has led breeding to be initiated from the beginning of the 20th century (with selection for shorter genotypes carrying dwarfing genes from the Japanese variety Akagomughi *(Rht9),* Saitama 27 *(Rht1 s)* and probably minor genes (Borghi 2001). In Italian cultivars, increments in the number of grains per m^2 were explained by both significant increases in the number of fertile florets and the percentage of grain setting, which have probably improved the adaptation of Italian cultivars to Mediterranean environments, where abiotic stresses during grain filling are the main cause of floret abortion (Miralles et al. 2002). On the other hand, durum wheat breeding was not a traditional activity in Spain because barley and bread wheat were the most cultivated cereals (Royo et al. 2007). Breeding progress in Spain relied on CIMMYT germplasm introduced during the second half of the 20th century (Royo 2005) and were therefore not constructed incorporating the genetic background of old cultivars (Martos et al. 2005).

Thus, it appears that the continuous breeding efforts since 1900 in Italy resulted in well-adapted cultivars to harsh Mediterranean environments with increased grain setting that determined a clear sink-limitation to grain yield. In contrast, intermediate Spanish cultivars with CIMMYT background (which relies on genotypes developed under environmental conditions somewhat different from the typically found in Spain) and modern ones (locally improved) might not be sufficiently adapted to the rainfed areas of southern Spain. Consequently, reduction in average grain weight of recently introduced cultivars in Spain was mainly due to the effect that abiotic stresses during grain filling may have on the availability of assimilates (with accentuated competition among grains and accelerated senescence) indicating a major degree of source-limitation to grain yield.

Conclusions

Grain yield of durum wheat grown in Mediterranean environments is co-limited by the availability of assimilates during grain filling and the sink strength without a complete compensation between both attributes. The different patterns of responsiveness to source-sink treatments among Italian and Spanish cultivars, observed in the present study, were probably due to its different sensitivity to water shortage during grain filling and to different breeding activities conducted in both countries. While old cultivars from both countries appear to have a sink-limitation to grain yield, intermediate and modern Spanish cultivars seem to be co-limited by the sink and the source during grain filling. Conversely, intermediate and modern Italian cultivars proved to be sink-limited.

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