

Grain Weight Response to Different Postflowering Source:Sink Ratios in Modern High-Yielding Argentinean Wheats Differing in Spike Fruiting Efficiency

Fernanda G. González,* María L. Aldabe, Ignacio I. Terrile, and Deborah P. Rondanini

ABSTRACT

Improving wheat (*Triticum aestivum* L.) yield potential via higher grain number per unit area (GN) may reduce average grain weight and consequently the yield increment would be low. Thirty-nine high-yielding modern cultivars differing in spike fruiting efficiency (FE) (number of grains per gram of no-grain spike) were grown under potential conditions during two temperature-contrasting years to study the level of source limitation during grain filling and rank the main physiological determinants of potential grain weight (PGW) and actual grain weight. The response of grain weight to a 100% higher source ranged from 0 to 25%, depending on cultivar and year. No general relationship was observed between PGW and FE. The stabilized grain water content, which was partially correlated with the endosperm cell number per grain ($r^2 = 48\%$, $p < 0.05$), was the main variable associated to grain weight variation ($r^2 = 77\%$, $p < 0.00001$) in both temperate and warm years. Genetic improvement focused on increasing the sink strength through higher GN is still an alternative to increase yield potential in modern cultivars as no source limitation during grain filling was observed. The improvement of FE could be used to increase GN and yield as no general negative relationship was observed between PGW and FE.

F. G. González and D.P. Rondanini, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), EEA Pergamino-INTA, Ruta 32, Km 4.5, Pergamino 2700, Buenos Aires, Argentina; M. L. Aldabe, Facultad de Agronomía, UBA. Av. San Martín 4453, C1417DSE, Ciudad Autónoma de Buenos Aires, Argentina; I.I. Terrile, EEA Pergamino-INTA, Ruta 32, Km 4.5, Pergamino 2700, Buenos Aires, Argentina; D.P. Rondanini, Depto. Producción Vegetal, Facultad de Agronomía, UBA. Av. San Martín 4453, C1417DSE, Ciudad Autónoma de Buenos Aires, Argentina. Received 11 Mar. 2013. *Corresponding author (fgonzalez@pergamino.inta.gov.ar).

Abbreviations: °Cd, grade centigrade days; A304, Aca 304; AGW, average grain weight; AMDW, adjusted maximum grain dry weight; B1002, BioINTA 1002; B1005, BioINTA 1005; B2002, BioINTA 2002; B3000, BioINTA 3000; BG9, Baguette 9; BGT, Buck Guatimozin; BNR, Buck Norteño; CGW, grain weight in control spikes; DGF, duration of grain filling; DON, DM Onix; EC, early cultivars; ECN, endosperm cell number per grain; FE, fruiting efficiency; G1, grain number 1 within the spikelet; G2, grain number 2 within the spikelet; GC, growth condition; GN, grain number per unit area; ICH, INIA Churrinche; ITR, INIA Torcaza; KCS, Klein Castor; KTR, Klein Tauro; KZR, Klein Zorro; LC, late cultivars; PGW, potential grain weight; PM, physiological maturity; RDW, relative dry weight; RGF, rate of grain filling; RGWRT, relative grain weight response to trimming; RUE, radiation used efficiency; SGRG, spike growth rate per grain; SGWC, stabilized grain water content; TGW, grain weight in trimmed spikes.

WHEAT PRODUCTION has to increase approximately 50% from actual volumes to fulfill the global increase of food demand (Chand, 2009; Hall and Richards, 2012). As land cropped with wheat will hardly increase, most of this increment should be achieved through higher on-farm yields, which are closely linked to cultivars yield potential (Fischer and Edmeades, 2010; Hall and

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Richards, 2012). Wheat yield potential is highly correlated with grain number per unit area (GN), which depends on the resource availability during preanthesis (Fischer, 1984; Sinclair and Jamieson, 2008). Yield improvement of wheat cultivars was based on the increment of GN, not only under potential growing conditions but also under sub-optimal ones (Fischer, 1984, 2007; Calderini and Slafer, 1998; Slafer and Araus, 2007; Fischer and Edmeades, 2010). Therefore, when yield of cultivars released under different breeding eras is plotted against GN, a linear positive relationship is usually found (Calderini et al., 1999). Nevertheless, this relationship could become curvilinear as GN is further increased by genetic gains (Miralles and Slafer, 2007), evidencing a negative association between average grain weight (AGW) and GN that may have two possible causes. The first one considers that the reduction in AGW is a consequence of increased proportion of grains of lower potential grain weight (PGW) placed in distal position within the spikelets and/or the spike and/or in secondary spike tillers (Miralles and Slafer, 2005; Acreche and Slafer, 2006). The second one considers that reductions in AGW are due to competition among grains by limited source during grain filling. Although the first noncompetitive hypothesis is the most validated up to date (Slafer and Savin, 1994; Borrás et al., 2004; Ahmadi et al., 2009; Zhang et al., 2010), recent studies revealed that source-sink co-limitation could occur in modern wheat cultivars (Acreche and Slafer, 2009; Sandaña et al., 2009). Determining the degree of source and/or sink limitation in wheat cultivars recently released to the market will help to draw strategies to improve yield potential in the future.

The increment of GN through breeding in Argentina was achieved not only by increasing partitioning of dry matter to spikes at anthesis but also by improving the fruiting efficiency (FE) of the spikes (the grain number produced by unit of no-grain spike dry weight at anthesis or maturity) (Abbate et al., 1998). It has been recently suggested that GN could be further improved by increasing the FE as the modern high-yielding cultivars released to the market during the last decade still show great variation of FE associated to GN (González et al., 2011). Nevertheless, some studies using a reduced number of cultivars reported a negative trade-off between FE and AGW in old (Fischer and HilleRisLambers, 1978) and modern high-yielding cultivars (Ferrante et al., 2012). It has been suggested that this negative relationship would be the consequence of reduced PGW in cultivars with higher FE (Fischer, 2011; Ferrante et al., 2012). Therefore, increasing GN via higher FE of cultivars may result in a small yield improvement if AGW is decreased due to a concomitant reduction in PGW (Ferrante et al., 2012). As far as we are aware there are no studies reporting the relationship between PGW and FE and even fewer reporting that relationship in a large set of modern high-yielding cultivars.

The PGW is determined around anthesis, that is, ovary growth of fertile florets during preanthesis and endosperm cell number per grain (ECN) during postanthesis (Calderini et al., 1999, 2001). The realization of this PGW and the final grain weight achieved would depend on grain growth (and the supply of assimilates) during postanthesis (Fischer, 2011). Grain growth during postanthesis is usually studied as the product between the rate of grain filling (RGF) and the duration of grain filling (DGF). The RGF, associated to the number of cells present in the endosperm (Brocklehurst, 1977; Gleadow et al., 1982), frequently explains the differences in grain weight among cultivars (Sofield et al., 1977; Bruckner and Froberg, 1987; Egli, 2004; Ehdaie et al., 2008). The grain growth is accompanied by changes in grain water content, and the stabilized grain water content (SGWC) during the water plateau is positively associated with final grain weight (Schnyder and Baum, 1992; Lizana et al., 2010). To breed for maintaining the AGW when GN is increased, it will be useful to determine the available variability in PGW among recent released cultivars and also the physiological processes associated with realization of that PGW during postanthesis (i.e., degree of source limitation, RGF, DGF, and SGWC).

In this paper the physiology of grain weight determination was studied in a set of 39 modern high-yielding cultivars differing in FE, which were grown during two seasons under potential growing conditions (without hail, frost, or lodging and without water, nutrient, or biotic stress) (Fischer and Edmeades, 2010). The specific objectives were to determine (i) the degree of source limitation during grain filling, (ii) the variability of PGW, (iii) the relationship between PGW, FE, and source limitation during grain filling, and (iv) the variability of RGF, DGF, SGWC, and ECN and their relationships with final grain weight.

MATERIALS AND METHODS

Growing Conditions and Plant Materials

The experiments were performed during 2007 and 2008 at Pergamino Research Station (33°51' S, 60°56' W), National Institute for Agriculture, Technology, and Husbandry, Pergamino, Ciudad de Buenos Aires, Argentina. The soil type is Arguidol and the N content (0–20 cm) reached approximately 200 kg N ha⁻¹ through fertilization. The natural rainfall was complemented by irrigation, and pests, diseases, and weeds were chemically controlled. The temperature was very contrasting between years, particularly during July, August, and November (Fig. 1a).

The 39 cultivars studied were released to the market from 2000 to 2008 and are the highest yielding cultivars recommended for the north Argentine Pampas (most of them tested under high input technology in the National Wheat Cultivar Yield Testing Trials) (Table 1). The cultivars represent a continuous twofold variation in FE ranging from 60 to 130 grains g⁻¹ (González et al., 2011). They were grouped according to the crop length cycle to anthesis in late cultivars (LC) and early

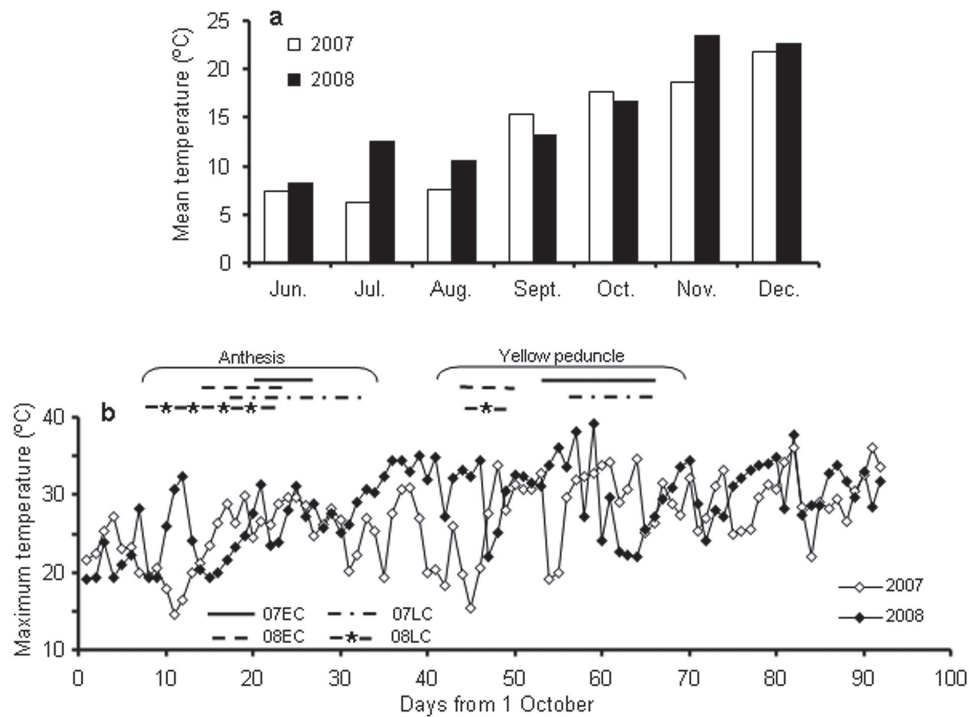


Figure 1. (a) Mean and (b) maximum temperature during crop length cycle in 2007 and 2008. The range of dates when anthesis and maturity (estimated as yellow peduncle) were achieved in each cultivar group and year are insert in Fig. 1b. 07EC, year 2007 early cultivars; 07LC, year 2007 late cultivars; 08EC, year 2008 early cultivars; 08LC, year 2008 late cultivars.

Table 1. Name of wheat cultivars studied with abbreviation (Abbrev.) used and year of release (YR) to the market. Modified from González et al. (2011).

Late cultivars			Early cultivars		
Name	Abbrev.	YR	Name	Abbrev.	YR
Aca 303	A303	2002	Aca 601	A601	2003
Aca 304	A304	2004	Aca 801	A801	2004
Aca 315	A315	2006	Aca 901	A901	2006
Baguette P11	BG11	2004	Baguette P13	BG13	2001
Baguette 19	BG19	2006	Baguette 9	BG9	2007
BioINTA 2002	B2002	2006	BioINTA 1001	B1001	2004
BioINTA 3000	B3000	2004	BioINTA 1002	B1002	2005
BioINTA 3004	B3004	2006	BioINTA 1003	B1003	2005
Buck Baqueano	BBQ	2007	BioINTA 1005	B1005	2008
Buck Guatimozin	BGT	2001	Buck Bigua	BBG	2002
Buck Malevo	BML	2006	Buck Brasil	BBR	2000
Buck Norteño	BNR	2006	Buck Pingo	BPN	2002
Buck Ranquel	BRN	2006	DM Cronox	DCR	2005
DM Themix-L	DTH	2007	DM Onix	DON	2004
INIA Tijetera	ITJ	2001	INIA Churrinche	ICH	2005
INIA Torcaza	ITR	2005	INIA Condor	ICN	2005
Klein Capricornio	KCP	2004	Klein Castor	KCS	2005
Klein Gavilan	KGV	2004	Klein Tauro	KTR	2005
Klein Guerrero	KGR	2007	Klein Zorro	KZR	2007
Sursem Nogal	SNG	2006			

cultivars (EC). Each group was sown at optimum date (first days of June for LC and first days of July for EC) and optimum planting populations (250 plants m⁻² for LC and 300 plants m⁻² for EC) in seven rows 0.2 m apart and 5-m-long plots. Further details about growing conditions and plant material can be found in González et al. (2011).

Measurements and Analyses

When anthesis began in 50% of the plants in each plot (Z6.1) (Zadoks et al., 1974), 60 spikes of similar length and anthesis date (mostly from main stem and primary tiller) were tagged with two different colors: 30 white-tagged spikes were the control spikes and the other 30 blue-tagged spikes were trimmed

Table 2. List of cultivars used to study the dynamics of grain growth.

2007		2008	
LC†	EC‡	LC	EC
Aca 304	Aca 601	BioINTA 2002	BioINTA 1005
Buck Guatimozin§	Aca 901	BioINTA 3000	BioINTA 1002
Baguette P11	Buck Brasil	Baguette 19	Baguette 9
BioINTA 3000	DM Onix	Buck Guatimozin	DM Onix
INIA Tijetera	Klein Tauro	Buck Norteño	INIA Churrinche
INIA Torcaza	Klein Zorro	INIA Torcaza	Klein Castor
Klein Capricornio	INIA Condor	Klein Gavilan	Klein Tauro
Sursem Nogal		Klein Guerrero	

†LC, late cultivars.

‡EC, early cultivars.

§In bold, cultivars studied during both years.

10 d after anthesis. In the trimmed treatment all of the spikelets from one side of the spike were removed. At harvest, these spikes were cut by hand and dried in an air forced oven for 72 h. They were drilled in a single-spike machine and the number of grains (two subsamples of 2 g each) was measured with an automatic counter to obtain the grain weight in trimmed spikes (TGW) (used as an estimate of PGW) and grain weight in control spikes (CGW). Once the CGW and TGW were estimated, the relative grain weight response to trimming (RGWRT) was calculated (Eq. [1]):

$$RGWRT = [1 - (CGW/TGW)] \times 100, \quad [1]$$

Dynamics of grain weight was studied on 12 main stem spikes tagged at anthesis. Fifteen different cultivars were studied each year, with only three LC and two EC measured in both years (Table 2). Twice a week one spike per plot was cut and 15 basal grains (grain number 1 [G1] plus grain number 2 [G2]) of central spikelets were sampled to obtain fresh and dry weight after 72 h in an air forced oven. The RGF and DGF were calculated from the bilinear regression model (Eq. [2]) fitted to the relation between dry weight and time from anthesis, expressed as calendar time (days) or thermal time (grade centigrade days [°Cd]) (base temperature 4.5°C):

$$Y = A + B(X) (X < C) + B \times C (X \geq C), \quad [2]$$

in which Y is dry weight, B is RGF, and C is the time of maximum grain dry weight (i.e., DGF). The maximum dry weight achieved by the grain (or adjusted maximum grain dry weight [AMDW]) was calculated from adjusted Eq. [2] when $X = C$. This bilinear regression model (Eq. [2]) was also fitted to the relation between the relative dry weight (RDW) and percent water content of the grain {percent water content = [(fresh weight - dry weight)/fresh weight] × 100} to estimate grain moisture at physiological maturity (PM). The RDW of the grains, which was used to eliminate differences in the AMDW among cultivars, was calculated by Eq. [3]:

$$RDW_i = (DW_i/AMDW) \times 100, \quad [3]$$

in which RDW_i is relative dry weight at time i and DW_i is dry weight at time i , for i ranging from 10 d postanthesis to the end of grain filling.

Grain water content (mg water per grain) was calculated as the difference between fresh and dry weight while the SGWC was estimated as the average water content observed during the water plateau, according to Lizana et al. (2010) and Hasan et al. (2011). The ECN was counted for samples from 2008 in four LC (Buck Norteño [BNR], BioINTA 2002 [B2002], BioINTA 3000 [B3000], and Buck Guatimozin [BGT]) and four EC (Baguette 9 [BG9], Klein Castor [KCS], Klein Tauro [KTR], and INIA Churrinche [ICH]), which were contrasting in PGW during 2007 (within each cultivar group two cultivars showed heavier grains than the other two). The number of nuclei was counted according to Rijven and Warlaw (1966) modified by Singh and Jenner (1982) and Gleadow et al. (1982) in all the grains of the spike (i.e., G1, G2, and grain number 3 [G3] within all the spikelets of the spike) 20 d after anthesis (estimated to be the end of lag phase of endosperm cell division). The AGW and the FE were calculated at harvest from all the spikes (main stem and tillers) and grains obtained from 0.5 m of a central row (further details in González et al. [2011]).

Experimental Design and Statistics

Each group of cultivars (LC and EC) consisted of a single experiment, which was sown during both years as a randomized complete block design with three replications. As the trimming treatment was performed inside each cultivar plot, it was assumed to be a subplot. The model used for ANOVA analyses was a split plot in blocks combined over years, considering the cultivars as main plot and the trimming treatment as subplot. For the analyses of ECN, the model used was a randomized complete block design as cultivars were randomly assigned to plots within blocks and ECN was measured only during 2008 on control spikes. The Tukey test ($p < 0.05$) was used for comparison using the Infostat/P software (Di Rienzo et al., 2010). The regression analyses were performed with Table Curve 2D (Jandel Scientific, 1992) and the 95% confidence interval was used for comparison of parameters obtained.

Table 3. Grain weight in control spikes (CGW) and trimmed or potential grain weight (T/PGW) in all cultivars and both years.

LC [†]	CGW (mg)		T/PGW (mg)		EC [‡]	CGW (mg)		T/PGW (mg)	
	2007	2008	2007	2008		2007	2008	2007	2008
Aca 303	32.1	28.8	33.3	28.7	Aca 601	33.4	24.8	38.4	27.2
Aca 304	33.7	30.5	34.3	30.1	Aca 801	32.3	27.6	36.4	28.7
Aca 315	31.9	29.1	33.2	27.8	Aca 901	34.5	27.2	39.9	28.9
Baguette P11	33.8	27.9	36.2	26.1	Baguette P13	35.0	23.8	38.7	26.8
Baguette 19	30.6	23.8	33.7	23.0	Baguette 9 [§]	40.8	25.1	45.7	29.1
BioINTA 2002 ^{2§}	35.5	32.0	38.9	35.6	BioINTA 1001	32.2	25.1	36.6	27.5
BioINTA 3000 ¹	37.9	28.9	43.1	34.8	BioINTA 1002 ⁹	35.4	22.9	43.7	23.7
BioINTA 3004	34.5	25.9	35.8	26.7	BioINTA 1003	34.9	24.6	39.7	27.9
Buck Baqueano	35.0	23.6	36.9	26.1	BioINTA 1005 ⁴	35.4	26.7	46.8	33.4
Buck Guatimozin	30.4	21.3	33.9	23.1	Buck Bigua	33.2	26.6	39.4	26.8
Buck Malevo	33.7	24.1	34.6	24.2	Buck Brasil	31.6	27.8	38.7	27.1
Buck Norteño	30.3	24.7	31.5	27.3	Buck Pingo	31.6	26.0	38.8	28.1
Buck Ranquel	30.2	28.2	31.5	29.8	DM Cronox	31.4	27.5	38.6	28.8
DM Themix-L	32.8	26.0	34.9	24.2	DM Onix	31.9	26.1	36.8	26.9
INIA Tijetera	32.5	23.5	33.9	26.1	INIA Churrinche ⁶	31.4	22.6	34.5	25.2
INIA Torcaza ³	29.5	21.4	31.8	23.2	INIA Condor	34.1	27.6	40.9	31.6
Klein Capricornio	34.0	23.4	35.3	27.3	Klein Castor ⁷	32.4	22.0	35.2	23.5
Klein Gavilan	36.2	26.7	38.7	28.1	Klein Tauro ⁵	38.9	27.6	43.6	31.5
Klein Guerrero	35.3	25.1	38.3	29.3	Klein Zorro	36.1	28.4	40.9	30.1
Sursem Nogal	32.6	27.5	36.8	29.2					
T _{YXC} [¶]	2.79				T _{YXCXT}	4.72			
T _{CXT}	2.85								

[†]LC, late cultivars.

[‡]EC, early cultivars.

[§]The uppercase letters (from 1 to 9) indicate the cultivars highlighted in Fig. 2a as the most responsive ones to trimming and in Fig. 4 as contrasting for potential grain weight.

[¶]The Tukey values for comparison is presented (Tukey value for year × cultivar [T_{YXC}], Tukey value for cultivar × trimming [T_{CXT}], and Tukey value for year × cultivar × trimming [T_{YXCXT}]; *p* = 0.05).

RESULTS

Phenology, Grain Number per Unit Area, and Average Grain Weight

Anthesis date for both cultivar groups and years took place from mid October to the end of October (Fig. 1b). The maturation dates ranged from the end of November to first days of December during 2007 (for both cultivar groups) and from mid November to the end of November during 2008 (for both cultivar groups) (Fig. 1b). The earlier maturation dates during 2008 compared to 2007 were associated with the higher mean temperature during November (Fig. 1a) and also with maximum temperatures higher than 30°C during the first 15 d of November (Fig. 1b). During October (when preanthesis period took place in all cultivars) no heat stress was observed (no temperature higher than 30°C was observed, except for four nonconsecutive days) (Fig. 1b). Within each year, the cultivars showed a negative relationship between AGW (grain weight obtained from 0.5 m harvest in central rows considering main stem and tiller spikes) and GN (except for EC during 2008) ($r^2 = 35\%$ $p < 0.00005$, $n = 39$ for LC plus EC during 2007 and $r^2 = 16\%$ $p < 0.05$, $n = 20$ for LC during 2008) (González et al., 2011). The contrasting temperature between years, especially during grain filling, had a great impact on AGW and yield. The range

of GN produced was similar between years (from 16 to 23 × 10³ for LC and from 15 to 22 × 10³ for EC) but the AGW ranged from 27 to 40 mg for 2007 and from 16 to 30 mg for 2008 (González et al., 2011). Therefore, the average yield reduction during the hotter year (2008) was 1.6 t, ranging from 0.04 to 3.24 t, depending on cultivar. Further details about the environment (rain plus irrigation and photosynthetic active radiation) and responses of phenology, GN, and AGW to environment can be found in González et al. (2011).

Grain Weight Response to Different Postflowering Source:Sink Ratios

Grain weight ranged from 21 to 46 mg among cultivars, years, and trimming treatments (Table 3). Significant year × cultivar and cultivar × trimming interaction were observed for LC while year × cultivar × trimming interaction was observed for EC (Table 4). Despite these interactions, cultivars showing heavier grains during the two contrasting years in control and trimmed spikes were identified (e.g., B2002 and B3000 in LC and BG9, BioINTA 1005 (B1005), and KTR in EC) (Table 3). The grain weight increment due to trimming (i.e., the response to higher source:sink ratio) was lower for LC compared to EC during 2007 (when temperature was moderate) while it was similar for

Table 4. Mean squares of the ANOVA for grain weight considering cultivars, years, and trimming treatments as source of variation.

Source of variation	LC [†]	EC [‡]
Year (Y)	2913***	5685***
Cultivar (C)	1267***	915***
Y × C	377***	390***
Trimming (T)	244***	865***
Y × T	4 NS [§]	152***
C × T	98***	118***
Y × C × T	33 NS	68*
Error	109	158

*Significant at the 0.05 probability level.

***Significant at the 0.001 probability level.

[†]LC, late cultivars.

[‡]EC, early cultivars.

[§]NS, not significant.

both cultivars groups during 2008 (when temperature was higher) (Fig. 2a). For LC the response to trimming ranged from 1.6 to 12% during 2007 (i.e., 0.6 to 5.2 mg) (see Aca 304 [A304] and B3000 in Table 3) and from 0 to 17% during 2008 (i.e., 0 to 5.9 mg) (see Aca 303 [A303], A304, Aca 315 [A315], DM Themix-L [DTH], Buck Malevo [BML], and B3000 in Table 3) (Fig. 2a). For EC the response to trimming ranged from 8 to 25% during 2007 (i.e., 2.8 to 11.4 mg) (see KCS and B1005 in Table 3) and from 0 to 20% during 2008 (i.e., 0 to 6.7 mg) (see Buck Brasil [BBR] and B1005 in Table 3) (Fig. 2a). No relationship was observed between grain weight response to trimming (expressed in mg or as RGWRT) and GN or yield ($p > 0.10$). Also no relationship was observed between RGWRT and FE for any combination of cultivar group (LC and EC) and year or considering all data together (Fig. 2b).

Potential Grain Weight Variation and Its Relation to Relative Grain Weight Response to Trimming and Fruiting Efficiency

A clear year effect was observed as the PGW of cultivars was lower during 2008 vs. 2007 (Table 3; Fig. 3a), according to the higher temperatures registered during November 2008 (Fig. 1). The PGW in LC ranged from 32 to 43 mg and from 23 to 36 mg during 2007 and 2008, respectively, while in EC it ranged from 35 to 47 mg and from 24 to 33 mg during 2007 and 2008, respectively (Table 3; Fig. 3a). Interactions between cultivars and years were observed (Table 1); for example, BioINTA 1002 (B1002) presented high PGW during 2007, approximately 44 mg, but it decreased to 24 mg during 2008, being one of the lowest PGW cultivars during that year (see data point identified as 9 in Fig. 3a). Regardless of these interactions, some cultivars with high and low PGW did not change the ranking between years: B3000 and B2002 vs. INIA Torcaza (ITR) in LC and B1005, KTR, and BG9 vs. ICH and KCS in EC (Fig. 3a).

The cultivars with higher PGW showed the highest response to trimming during both years (except for B1002 in 2008) (see B3000, B2002, B1005, KTR, and BG9 in Fig. 2a). The RGWRT increased with PGW for LC during 2007 ($r^2 = 11%$, $p < 0.05$) and for EC during both years ($r^2 = 17%$ during 2007 and $r^2 = 22%$ during 2008, $p < 0.05$). Within the LC during 2008, B3000 and B2002 were positioned in the range of medium-high response to trimming (17 and 10% of increment, respectively) (Table 3; Fig. 2a).

When PGW was plotted against FE (Fig. 3b) no relationship was observed for any combination of cultivar group and year. Nevertheless, some particular cultivars identified in LC as contrasting in PGW (Fig. 3a) seemed to show a negative relation with FE within each year; that is, the cultivars with heavier grains were associated with lower FE and vice versa (Fig. 3b). But it is worth noting that for a given value of FE there was a great variation in PGW. Contrary to LC, the EC identified as contrasting for PGW showed no relationship with FE (Fig. 3b).

Grain Weight Relation to Rate of Grain Filling, Duration of Grain Filling, Stabilized Grain Water Content, and Endosperm Cell Number per Grain

No difference in grain moisture content at PM was observed among years and cultivars (Table 5). Considering all available data the grain growth ceased (PM) in average when grain moisture content reached $40.9 \pm 0.39\%$ ($r^2 = 95%$, $p < 0.00001$) (data not shown). The RGF ranged from 8.04×10^{-2} (ITR) to 10.37×10^{-2} (B3000) mg per °Cd and from 7.01×10^{-2} (BGT) to 9.80×10^{-2} (B2002) mg per °Cd for the LC studied during 2007 and 2008, respectively (Table 5). Extreme RGF for EC ranged from 8.46×10^{-2} (Aca 601 [A601]) to 10.83×10^{-2} (Klein Zorro [KZR]) mg per °Cd during 2007 and from 7.08×10^{-2} (B1002) to 12.81×10^{-2} (DM Onix [DON]) mg per °Cd during 2008 (Table 5). The differences in the RGF were statistically significant between B3000 and ITR (LC in 2007) (Table 5) and between DON and B1002, ICH, KCS, and KTR (EC in 2008) (Table 5). The high temperature during November 2008 tended to (B3000 and ITR) or significantly reduced (BGT and KTR) the RGF (except for DON) (Table 5). The DGF ranged from 34 to 38 d considering LC and EC during 2007, but it was greatly reduced in the cultivars studied during 2008 (the hottest year) ranging from 21 to 27 d (except for B2002, which lasted 33 d). When DGF was expressed as thermal time (base temperature 4.5°C), some statistically significant differences among cultivars were observed. For example, during 2007, B3000 showed a longer DGR than A304, Baguette P11 (B611), and BGT (within the LC) and Aca 901 (A901), INIA Condor (ICD), and KZR (within the EC) (Table 5). During 2008, B2002 showed longer DGF than B3000, BGT, BNR, and Klein Capricornio (KCP) (within the LC) and DON, ICH, and KCS (within the EC) (Table 5). The impact

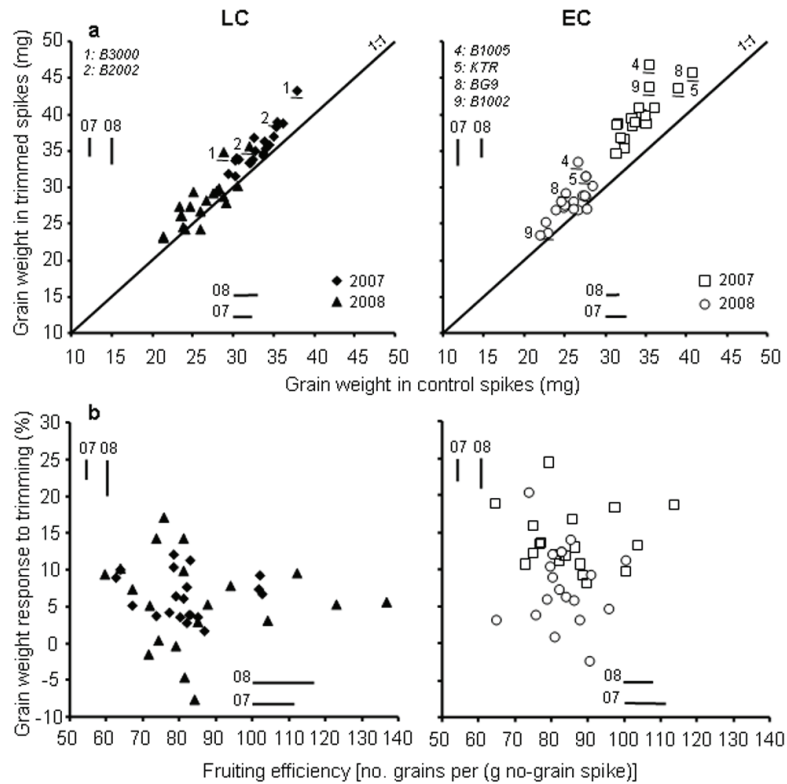


Figure 2. (a) Relationship between grain weight in trimmed vs. control spikes for late cultivars (LC) and early cultivars (EC) during both years. The cultivars with the highest response to trimming during both years are identified with numbers near data points. (b) Relationship between relative grain weight response to trimming and spike fruiting efficiency for LC and EC during both years. The lines parallel to the axis indicate the pooled SE. 07, year 2007; 08, year 2008; B1002, BioINTA 1002; B2002, BioINTA 2002; B1005, BioINTA 1005; B3000, BioINTA 3000; BG9, Baguette 9; KTR, Klein Tauro.

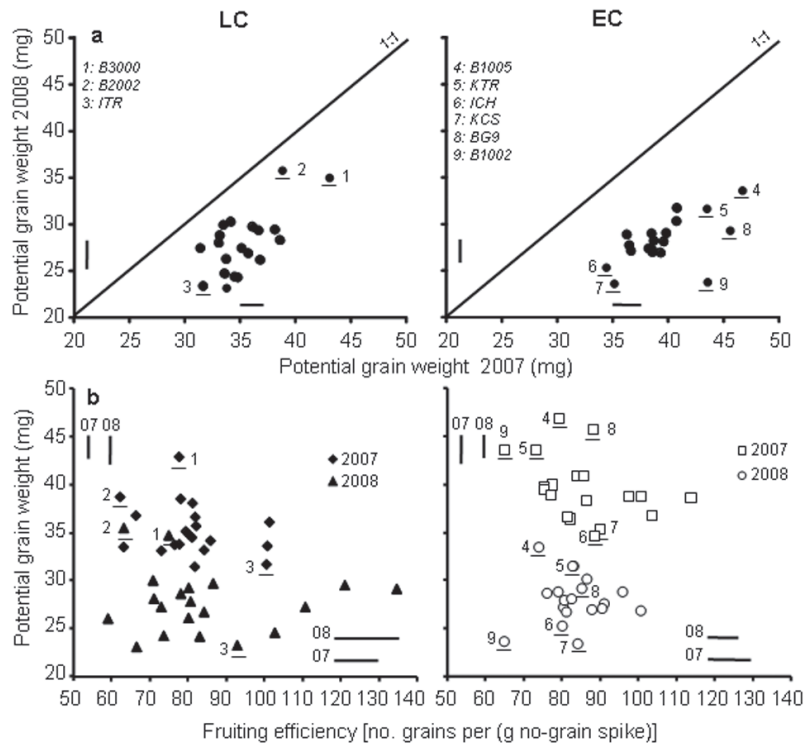


Figure 3. Relationship between (a) potential grain weight (PGW) during 2008 and 2007 and (b) PGW and spike fruiting efficiency for late cultivars (LC) and early cultivars (EC) during 2007 and 2008. The cultivars with contrasting PGW during both years are identified with numbers near data points. The lines parallel to the axis indicate the pooled SE. 07, year 2007; 08, year 2008; B1002, BioINTA 1002; B1005, BioINTA 1005; B2002, BioINTA 2002; B3000, BioINTA 3000; BG9, Baguette 9; ICH, INIA Churrinche; ITR, INIA Torcaza; KCS, Klein Castor; KTR, Klein Tauro.

Table 5. Rate of grain filling (RGF), duration of grain filling (DGF), and moisture at physiological maturity (PM). Means and 95% confidence interval are presented.†

Cultivar group	2007			2008		
	RGF	DGF	PM	RGF	DGF	PM
	mg per °Cd [§] (× 10 ⁻²)	°Cd	%MC [¶]	10 ⁻² mg per °Cd	°Cd	%MC
LC[‡]						
Aca 304	9.67 (8.46–10.87)	495 (463–526)	42 (39–45)			
BioINTA 2002				9.80 (8.82–10.79)	483 (457–508)	43 (40–45)
BioINTA 3000	10.37 (9.48–11.25)	555 (527–582)	37 (31–42)	9.55 (7.87–11.24)	411 (377–445)	44 (41–48)
Baguette P11	10.07 (8.92–11.21)	494 (466–522)	38 (36–41)			
Baguette 19				8.59 (6.11–11.06)	397 (345–449)	44 (39–48)
Buck Guatimozin	9.65 (8.35–10.95)	487 (455–520)	42 (39–46)	7.01 (5.73–8.28)	385 (356–413)	44 (39–49)
Buck Norteño				9.17 (6.89–11.44)	385 (339–430)	42 (35–50)
INIA Tijetera	9.77 (8.39–11.16)	506 (469–543)	41 (37–45)			
INIA Torcaza	8.04 (6.84–9.24)	514 (474–555)	41 (38–43)	7.26 (4.57–9.96)	385 (322–448)	45 (38–51)
Klein Capricornio	9.72 (8.76–10.68)	506 (479–532)	42 (40–45)			
Klein Gavilan				7.74 (6.11–9.37)	427 (383–471)	45 (40–49)
Klein Guerrero				8.16 (5.17–11.15)	426 (351–501)	43 (35–50)
Sursem Nogal	9.39 (8.46–10.32)	510 (484–536)	40 (36–44)			
EC[#]						
Aca 601	8.46 (6.73–10.19)	528 (472–584)	39 (37–41)			
Aca 901	10.28 (9.35–11.24)	502 (479–525)	39 (35–43)			
BioINTA 1005				9.48 (5.37–13.59)	432 (338–527)	45 (35–54)
BioINTA 1002				7.08 (4.44–9.72)	422 (354–490)	44 (35–52)
Baguette 9				8.67 (4.81–12.54)	402 (320–484)	44 (36–52)
Buck Brasil	8.88 (7.05–10.72)	506 (452–559)	40 (37–43)			
DM Onix	9.34 (7.74–10.95)	481 (440–523)	40 (36–44)	12.83 (9.81–15.85)	351 (314–388)	42 (37–47)
INIA Churrinche				7.85 (6.72–8.97)	425 (397–454)	41 (33–49)
INIA Condor	10.00 (9.06–10.95)	502 (478–527)	42 (35–45)			
Klein Castor				7.64 (6.01–9.28)	404 (361–447)	43 (32–48)
Klein Tauro	10.70 (9.44–11.96)	537 (504–570)	38 (31–44)	7.99 (6.87–9.10)	462 (427–497)	38 (35–42)
Klein Zorro	10.83 (9.08–12.58)	485 (448–522)	40 (35–45)			

†*r*² ranging from 90 to 99%, *p* < 0.001 for all regressions.

[‡]LC, late cultivars.

[§]°Cd, grade centigrade days.

[¶]%MC, percent moisture content.

[#]EC, early cultivars.

of year on DGF was highly significant, reducing DGF in a range from 75 to 144 °Cd (see B3000, BGT, ITR, DON, and KTR in Table 5).

Considering all available data, the variation in AMDW (the maximum grain weight obtained from regression curves) was associated with both DGF (*r*² = 76%, *p* < 0.00001) and RGF (*r*² = 69%, *p* < 0.00001) (Fig. 4a and 4b). With the exception of EC during 2008, the DGF also explained some of the variation in AMDW when data of each combination of cultivar group × year were regressed (*r*² = 62, 29, and 79% for EC in 2007, LC in 2007, and LC in 2008, respectively; *p* < 0.05 for all regressions). Similarly, the RGF explained approximately 40% (*p* < 0.05) of the variation observed in AMDW when regressions of data for each cultivar group × year were performed (except for EC during 2008). No relationship was observed between RGF and DGF within each year (Fig. 4c).

The SGWC ranged from 20 to 35 mg per grain, considering all available data (Fig. 5). The SGWC explained

a great proportion (i.e., 77%) of the variation observed in AMDW (Fig. 5a). When cultivars were studied within each year, the SGWC explained from 55 to 87% of AMDW (except for EC during 2007, *r*² = 55, 84, and 87% for EC in 2008, LC in 2007, and LC in 2008, respectively; *p* < 0.05 for all regressions). The SGWC was positively associated with the RGF and the DGF, explaining approximately 50% of the variation observed in both variables (Fig. 5b and 5c). Nevertheless, when cultivars were studied within each year, significant regression between the RGF and the SGWC were observed only for LC (*r*² = 47 and 21% during 2007 and 2008, respectively; *p* < 0.05). Also, the DGF was significantly related to SGWC only for LC in 2008 (*r*² = 81%, *p* < 0.005).

The ECN showed fourfold variation among cultivars and grain positions within the spikelet (Table 6). For both cultivars groups, there was a statically significant (*p* < 0.05) impact of cultivar on the ECN in the three grain positions (Table 6). For LC the ECN was higher in the three grains

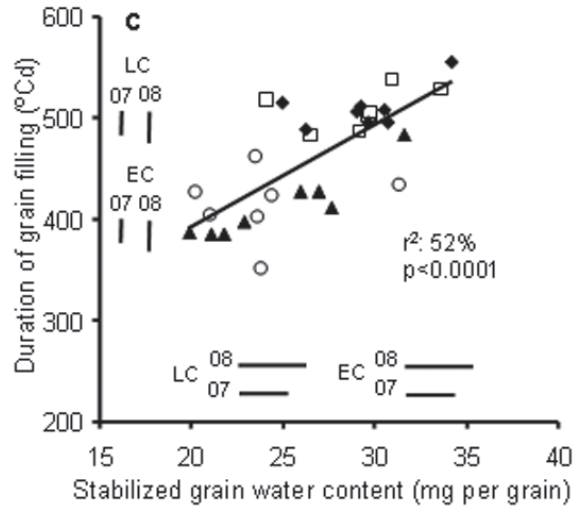
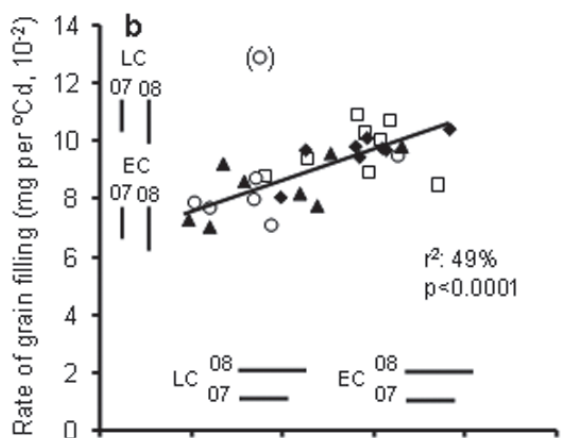
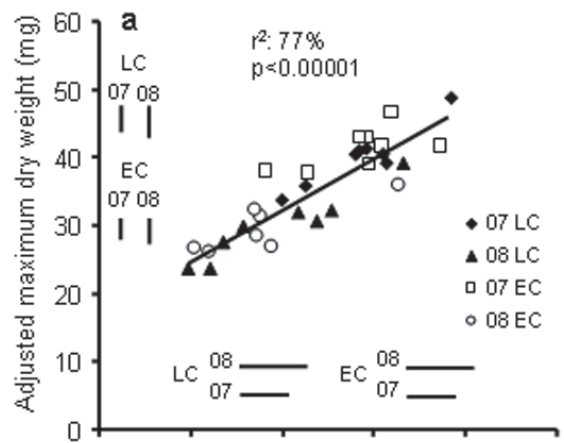
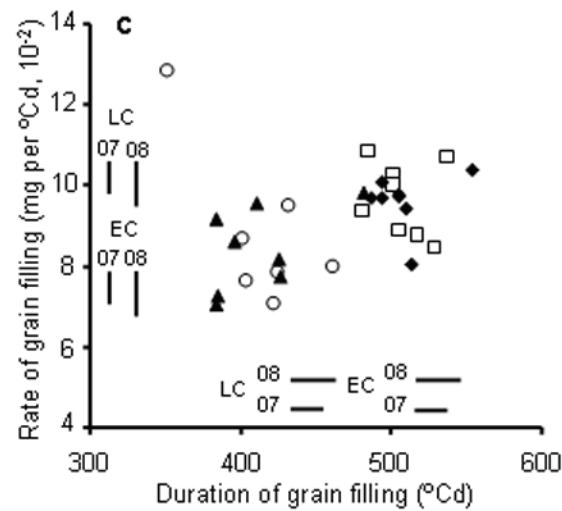
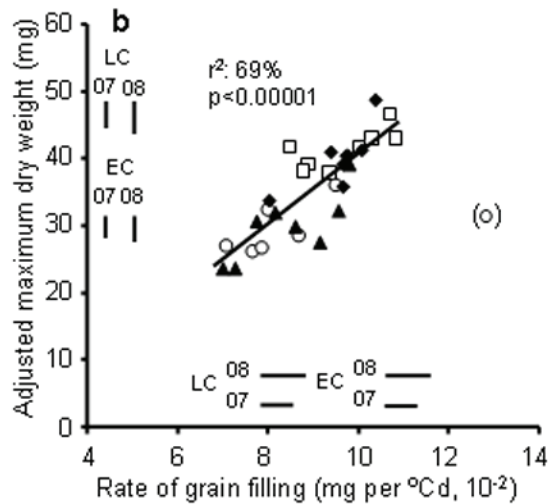
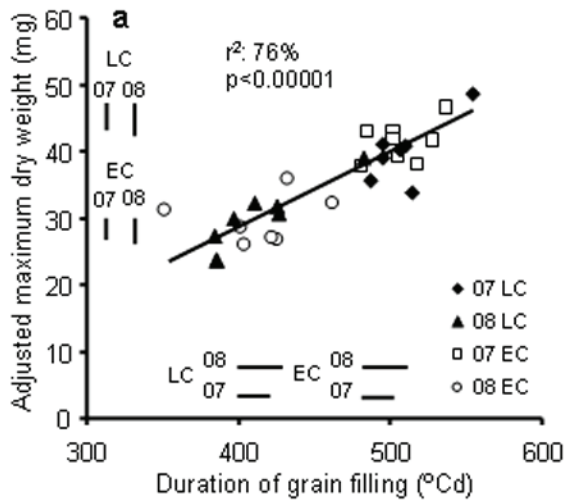


Figure 4. Relationship between adjusted maximum grain dry weight and (a) duration of grain filling (DGF) [$y = -15 (\pm 5) + 0.11 (\pm 0.01) \times X$] and (b) rate of grain filling (RGF) [$y = -13 (\pm 6) + 536 (\pm 64) \times X$]. In (c) the relation between the RGF and the DGF is shown. All cultivars and years included (except for the data between brackets in Fig. 5b, which was excluded from the regression). The lines parallel to the axis indicate the pooled SE. °Cd, grade centigrade days; LC, late cultivars; EC, early cultivars; 07, year 2007; 08, year 2008.

Figure 5. Relationship between (a) adjusted maximum grain dry weight [$y = -4.9 (\pm 3.9) + 1.49 (\pm 0.14) \times X$], (b) rate of grain filling [$y = 0.037 (\pm 0.009) + 0.0019 (\pm 0.0003) \times X$], and (c) duration of grain filling [$y = 189 (\pm 45) + 10.1 (\pm 1.7) \times X$] and stabilized grain water content. All cultivars and years included (except for the data between brackets in Fig. 6b, which was excluded from the regression). The lines parallel to the axis indicate the pooled SE. °Cd, grade centigrade days; LC, late cultivars; EC, early cultivars; 07, year 2007; 08, year 2008.

Table 6. Number of endosperm cells in grains of different positions (grain number 1 within the spikelet [G1], grain number 2 within the spikelet [G2], and grain number 3 within the spikelet [G3] from proximal to distal position) of the spikelets (average of all the spikelets of the spike).

LC [†]	Endosperm cell number (cells per grain)			EC [‡]	Endosperm cell number (cells per grain)		
	G1	G2	G3		G1	G2	G3
BioINTA 2002	87,362	85,903	59,375	Baguette 9	47,440	58,899	56,347
BioINTA 3000	70,382	82,660	53,760	INIA Churrinche	35,227	33,968	29,097
Buck Guatimozin	52,576	58,125	20,542	Klein Castor	61,209	61,973	47,444
Buck Norteño	34,552	38,583	28,203	Klein Tauro	65,415	65,913	54,443
Tukey	47,260	47,184	25,203	Tukey	18,503	15,080	8,287
$p = 0.05$				$p = 0.05$			

[†]LC, late cultivars.

[‡]EC, early cultivars.

positions for the cultivars showing heavier grains (CGW and PGW) compared with the other two cultivars showing lighter grains (see B2002 and B3000 vs. BGT and ICH in Table 6 and data of 2008 in Table 3). For EC the ECN follow the same response observed in the LC (see BG9 and KTR vs. ICH in Table 6 and data of 2008 in Table 3), except for KCS (Table 6 and Table 3). When the AMDW (measured in G1 and G2) was plotted against the average ECN of G1 and G2, a linear positive relationship was observed ($r^2 = 30\%$, $p < 0.05$), which seemed to be explained by the positive relationship between the SGWC (measured in G1 and G2) and the average ECN (of G1 and G2) ($r^2 = 48\%$, $p < 0.05$). Contrary to expectations, no positive relationship was observed between the RGF and the ECN.

DISCUSSION

Despite the negative relationship between AGW and GN observed in the modern high-yielding Argentinean wheats (González et al., 2011), the response of grain weight to an increment of 100% in the source per grain during grain filling ranged from 0 to 25% depending on cultivar and year. The maximum response to trimming observed in the present paper was lower than the one reported by Acreche and Slafer (2009), suggesting a source–sink co-limitation during grain filling in the most responsive cases and a complete sink limitation in the least responsive ones. Also, there was no relationship between grain weight response to trimming and GN or yield. These results support the idea that grain growth in wheat is generally not source limited during grain filling (Slafer and Savin, 1994; Borrás et al., 2004; Ahmadi et al., 2009; Zhang et al., 2010) even in high-yielding modern cultivars. Therefore, increasing the sink strength (GN or PGW) may still be an alternative to improve yield potential.

The increment of GN due to genetic improvement of yield potential has led to cultivars with reduced source–sink relation during grain filling (Slafer and Andrade, 1991; Acreche and Slafer, 2009) but with increased post-flowering radiation used efficiency (RUE) (Reynolds et al., 2005; Acreche and Slafer, 2009). The evolutionary aspects related to best fitted reproductive output discussed

by Sadras (2007) and Sadras and Denison (2009) implies that parental fitness benefits from changes in PGW (i.e., offspring size) beyond certain size (i.e., the optimum offspring size) are offset by benefits from adjusting GN (i.e., offspring number). Considering this idea, it could be hypothesized that RUE may be less affected when the sink strength is increased via heavier grains instead of more GN (despite that the total sink strength may be the same), and then increasing the PGW would result in crops that are more source limited during grain filling. The results of the present paper are in line with this idea as the cultivars showing higher probability of source–sink co-limitation, consistently during both years, were those with heavier grains as in Acreche and Slafer (2009) and Calderini et al. (2006), and the response was independent of GN (Calderini et al., 2006). Therefore, to improve yield potential with minimum increment in source limitation, producing more GN with medium PGW seems more efficient than producing less GN with higher PGW.

The negative relationship between PGW and FE previously reported (Fischer and HilleRisLambers, 1978; Ferrante et al., 2012) was observed only when particular cultivars were analyzed but not as a general relationship including all cultivars and both years. Differences in the availability of resources per grain around the grain set period may determine differences in PGW, as shown for maize (*Zea mays* L.) and sorghum [*Sorghum bicolor* (L.) Moench] (Gambín et al., 2006, 2008) and for comparison across species with contrasting PGW (Gambín and Borrás, 2010), that may be masking the possible negative relationship between PGW and FE. To test this idea, the resource per grain during the grain set period was estimated as the spike growth rate per grain (SGRG) (mg d^{-1} per grain) for all cultivars and both years (using data from González et al. [2011]). When PGW was plotted against the SGRG no relationship was observed during 2008, which could be consequence of the warm temperatures during that year. Nevertheless, for 2007 (which was a temperate year) there was a positive relationship between PGW and SGRG only for EC, explaining 15% of variation in PGW ($p < 0.005$), and no relationship for LC (Fig. 6a and 6b). Similar results

were observed for an independent data set from Ferrante et al. (2012) (for potential growth condition [GC] 2, GC4, and GC6) (Fig. 6c) ($r^2 = 8\%$, $p = 0.11$). Within the EC during 2007, for cultivars with similar SGRG there was no negative relationship between PGW and FE (see insets in Fig. 6a). Therefore, the differences in the availability of resources per grain around the grain set period were not masking a possible negative relationship between PGW and FE. The lack of relationship between the response to trimming, which was associated with PGW, and the FE supports the idea that there is not a general trade-off between PGW and FE (at least in the range of PGW considered in this work, 23 to 43 mg). Further experiments aimed to understand why some cultivars show a negative relationship (and whether this would actually be a trade-off between FE and grain size) (Ferrante et al., 2012) while others do not would be very valuable to determine the general usefulness of FE to improve yield potential (González et al., 2011).

Significant variability in PGW among cultivars was observed in both LC and EC, agreeing with previous studies reporting genetic variation in grain weight (Ehdaie et al., 2008; Dreccer et al., 2009; Rattey et al., 2009; Fischer, 2011; Tiwari et al., 2012). The physiological mechanism determining grain weight have been studied in isolation during the last two decades, but efforts to integrate and give hierarchy to them under potential conditions are being developed (Hasan et al., 2011). The present paper adds to give hierarchy to them under contrasting seasons (heat stressed and unstressed) during grain filling in a set of high-yielding modern cultivars. The SGWC was the main variable explaining the differences in AMDW not only under moderate temperature but also under heat stress, and it was positively associated with the RGF and the DGF when all the data set was used. The ECN (measured only during 2008, when the heat stress was present) explained half of the variation observed in the SGWC. The lower PGW during 2008 was also associated to a reduced DGF with less impact of RGF (both expressed in thermal time basis), agreeing with previous reports in wheat (Bagga and Rawson, 1977; Stone and Nicolas, 1995), barley (*Hordeum vulgare* L.) (Wallwork et al., 1998; Savin and Nicolas, 1996), corn (Monjardino et al., 2005), and sunflower (*Helianthus annuus* L.) (Rondanini et al., 2006). Not only the RGF, as it was expected (Brocklehurst, 1977; Sofield et al., 1977; Wiegand and Cuellar, 1981; Bruckner and Froberg, 1987; Egli, 2004; Ehdaie et al., 2008), explained a great proportion of the differences in AMDW among cultivars but also the DGF did, as recently reported by Tiwari et al. (2012). The RGF and DGF were not associated, suggesting that they could be manipulated without compensatory mechanisms, as suggested for several grain crops (Egli, 1981; Egli et al., 1984; Mov and Kronstrad, 1994; Borrás et al., 2009).

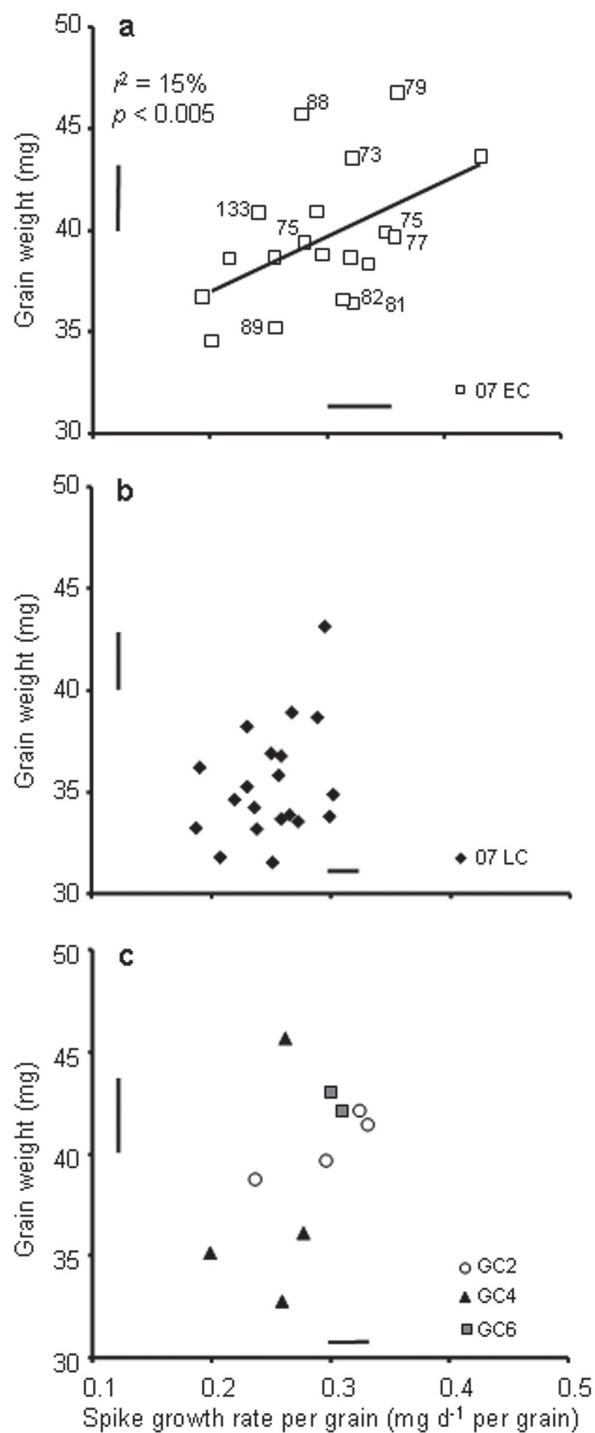


Figure 6. Relationship between grain weight and spike growth rate per grain (SGRG) for (a) early cultivars during 2007 ($y = 31.6 + 27.4 \times X$), (b) late cultivars during 2007, and (c) data reanalyzed from Ferrante et al. (2012) for potential growing conditions (GCs) (GC2, GC4, and GC6). For (a) and (b) the potential grain weight is shown; for (c) the achieved grain weight is shown. The numbers in panel (a) indicate the fruiting efficiency for cultivars with similar SGRG. Lines parallel to the axis indicate the pooled SE. 07 EC, year 2007 early cultivars; 07 LC, year 2007 late cultivars.

CONCLUSIONS

The results showed in the present paper support the idea that wheat yield potential could be further improved via

increasing the sink strength as most of the modern high-yielding cultivars showed sink limitation during grain filling and few cultivars showed source–sink co-limitation (25% at most). No clear negative relationship was observed between PGW and FE, suggesting that increasing GN via higher FE may not necessary reduce PGW.

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