Fruiting efficiency in wheat (*Triticum aestivum* L): Trait response to different growing conditions and its relation to spike dry weight at anthesis and grain weight at harvest

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A R T I C L E   I N F O

A B S T R A C T

The use of physiological traits for indirect selection may help to increase wheat yield potential. Fruiting efficiency (FE, grain number per unit of spike dry weight at anthesis −SDWa-) may be an alternative to increase grain number per unit area (GN), but the possible cross-over genotype (G) × environment (E) interaction and trade-off with SDWa and grain weight (GW) may limit its usefulness. The present paper aimed to determine (i) the degree of G × E interaction of FE at plot, main stem and tiller levels, (ii) the relationship between GN and FE, and (iii) the possible trade-off between FE and (a) SDWa, and (b) GW. Three FE contrasting genotypes (B11 and B19 – high FE, and B2002 – low FE) were grown under different Nitrogen (N) availability at sowing [(i) low – Ni: ca. 50 kg N ha^{-1}; (ii) middle −130 kg N ha^{-1} and (iii) high −200 kg N ha^{-1}). Two other treatments were applied within the 200N: (iv) late sowing, i.e. delaying sowing 30 days in relation to optimum date (200N + LS) and (v) shading the canopy during stem elongation (200N + SH). The FE showed G × E interaction (year × genotype and genotype × treatment) but it only explained 13.4% of its variation. The environment (year) had similar impact than the genotype, explaining both ca. 38% of FE variation (19% each). The FE of tiller spikes was higher than that of main stem spikes, but the difference among cultivars was maintained. Thus, canopies of the same genotype with different proportion of main stem and tiller spikes may present different FE value at plot level. Nevertheless, a high correlation (r = 0.82, p < 0.0001) and a close 1:1 relationship was observed between FE at plot level and FE in main stems, for all treatments and cultivars, suggesting that sampling the main stem spikes represents the FE at plot level in dense canopies. A G × E cross-over interaction was observed when the sowing was delayed one month (200N + LS) from the optimum date because B19 reached anthesis later than B2002, exploring higher heat stress index (°Ch > 27 °C) around anthesis, which reduced FE. The correlation of GN with FE was high and significant (r = 0.74, p < 0.00001) for all treatments and for a wide range of SDWa values (from 90 to 188 g m^{-2}). The B19, selected as a high FE genotype, showed higher GN than B2002 (selected as a low FE genotype) under all treatments, while B11 (also of high FE) showed similar or higher GN than B2002, depending on treatment. Thus, despite the G × E interaction, the genotypes with higher FE had more GN under a wide range of environments. Nevertheless, the SDWa and GW were negatively correlated with FE (for SDWa r = −0.73 p < 0.005, without considering 200N + SH; and for GW r = −0.48 p < 0.01 for all treatments or r = −0.75 p < 0.08 for genotypes only). Then, special attention should be given to SDWa and GW when selecting for higher FE in a breeding program.

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1. Introduction

Wheat yield potential has been greatly increased during the second half of last century through improvement in harvest index (Austin et al., 1980, 1989; Siddique et al., 1989b; Slafer and Andrade, 1991; Sayre et al., 1997; Calderini et al., 1999), and after mid 80's due to higher biomass at harvest (Reynolds et al., 1999; Donmez

et al., 2001; Shearman et al., 2005). The relative rate of yield increase, nevertheless, has decreased from 3.5% to less than 1.0% comparing from 1960 to 2010, being this rate less than that required to fulfil the projected increased demand of wheat production by 2050 (Reynolds et al., 2012; Hall and Richards, 2013; Fischer et al., 2014). The use of physiological traits for indirect selection, i.e. analytical or physiological breeding, may help to increase yield potential at the pace it is required (Slafer, 2003; Araus et al., 2008).

Wheat yield is the result of the number of grains set by unit area (GN) and the average grain weight achieved by these grains (GW). As wheat is mainly limited by sinks during grain filling (Borrás et al., 2004; Pedró et al., 2011; Serrago et al., 2013; González et al., 2014), increasing GN usually results in yield increments (Slafer et al., 1990; Canevara et al., 1994; Calderini et al., 1995; Sayre et al., 1997; Shearman et al., 2005; Fischer, 2007; Acreche et al., 2008). According to the model proposed by Fischer (1984, 2011), GN is the result of the spike dry weight at anthesis (SDWa) and the reproductive efficiency of those spikes, i.e. fruiting efficiency (FE): the number of grains set by unit of spike dry weight at anthesis. Past breeding success was associated with increased SDWa due to higher partitioning of biomass to the spikes during the pre-anthesis period as consequence of reduced stem growth and height (Siddique et al., 1989a; Slafer et al., 1990; Richards, 1992; Slafer and Andrade, 1993; Miralles and Slafer, 1995a; Calderini et al., 1999). As the modern high-yielding cultivars are within the optimum height to maximize yield (Richards, 1992; Miralles and Slafer, 1995a, 1997; Flintham et al., 1997), new ways to further improve SDWa are been studied (see Slafer et al., 2001; Miralles and Slafer, 2007; Parry et al., 2011; González et al., 2011; Reynolds et al., 2012). Alternatively, GN could be improved via increasing FE (Abbate et al., 1998; González et al., 2011; García et al., 2014; Slafer et al., 2015; Mirabella et al., 2016), as genetic variation in that trait has been reported in modern cultivars (Abbate et al., 1998; Shearman et al., 2005; González et al., 2011; García et al., 2014; Mirabella et al., 2016), which was positively associated to GN (Abbate et al., 1998; González et al., 2011; Lázaro and Abbate, 2012; García et al., 2014). Nevertheless, the degree of cross-over genotype (G) × environment (E) interaction of FE and the magnitude of the trade-off between (i) FE and SDWa, and (ii) GW and FE, should be better understood to define its actual usefulness to improve GN and yield potential (particularly when breeding for wide adaptation).

It has been traditionally considered that the main factor affecting FE is the genotype, except for water stress around flowering (Fischer, 1984), but it is also evident that there can be some environmental effects (Fischer, 2011). Reduction in FE has been reported when wheat grows under low incident radiation prior to anthesis (more than 50% reduction) (Fischer and Stockman, 1980) or low nitrogen (Abbate et al., 1995). If the impact of the environment on FE is not similar among genotypes, then cross-over interaction could be observed. González et al. (2011) showed that the ranking of FE across years in contrasting cultivars can be maintained despite the significant G × E interaction. Mirabella et al. (2016) studying different cultivars, locations and years showed similar results: significant FE interaction between genotypes and environments (locations and years) but a high impact of genotype as source of variation. The number of spikes per unit area, established from fertile tillers, is one of the important yield components to define GN. Wheat cultivars may differ in the number of tillers produced (e.g. Shearman et al., 2005; González et al., 2011) and the productivity of those tillers may change depending on the spike-type, frequently referred to as large and small (e.g. Gaju et al., 2009), and on tiller position within the plant (primary, secondary or tertiary tillers) (Xu et al., 2015). Differences in tiller productivity had been associated with grain number per spike due to fertile spikelets per spike (Xu et al., 2015). It is unknown whether (i) the average FE of tiller spikes is similar to the one of main stem spikes, and (ii) how the number of tillers produced may affect the FE when it is measured at plot level. Unraveling the underlying crop physiological bases of FE in response to a wide range of environments in contrasting cultivars (at plot, main stem and tiller level) will help to understand the possible genotype × environment interaction.

The conceptual model proposed by Fischer (1984) suggests that FE and SDWa are partially independent, thus, improving one trait would not greatly reduce the other resulting in an increased GN. Previous results indirectly support the idea of independence as a strong relationship between GN and SDWa has been reported when SDWa was changed by dwarfism genes (Fischer and Stockman, 1980; Brooking and Kirby, 1981; Miralles et al., 1998), nitrogen availability (Demotes-Mainard et al., 1999; Fischer et al., 1993; Demotes-Mainard and Jeuffroy, 2001), and incident radiation during stem elongation (Fischer, 1985; Savin and Slafer, 1991). On the other side, the different works that particularly studied the possible trade-off between FE and SDWa are inconclusive as the relationship between both traits has been reported as negative by some authors (Dreccer et al., 2009; Ferrante et al., 2012; Lázaro and Abbate, 2012) but not significant by others (González et al., 2011; García et al., 2014).

Additionally, GN increases via FE would result in low yield potential advantage if GW is highly reduced due to a trade-off between FE and GW (Slafer et al., 2015). Some authors (Fischer and HilleRisLambers, 1978; Gaju et al., 2009; Ferrante et al., 2012) reported a negative relationship between FE and GW, while others (González et al., 2014) working with higher number of cultivars showed no general relationship between FE and the potential GW. Then, the few works reporting about the relationship between FE and GW are not conclusive, highlighting the importance of studying the possible trade-off between them.

The objective of the present paper was to study the GN, GW, SDWa and FE in contrasting FE cultivars grown under different environments (nitrogen, sowing dates, shading during stem elongation and years) to understand and quantify (i) the degree of G × E interaction of FE (at plot, main stem and tiller levels), (ii) the relationship between GN and FE, and (iii) the possible trade-off between FE and (a) SDWa, and (b) GW.

2. Materials and methods

2.1. General conditions

Field experiments were carried out during 2010 and 2011, at Pergamino Research Station of INTA (Instituto Nacional de Tecnología Agropecuaria) in the north of Buenos Aires Province (33°51′sl, 60°56′wl), Argentina. The soil is classified as Typic Argiudol (USDA Taxonomy). The available water in the soil at sowing was 136 and 91 mm (1 m depth, for 2010 and 2011, respectively). The natural rainfall of the season was complemented by irrigation to avoid water stress (Table 1). The photosynthetic active radiation (PAR) accumulated during growth cycle was 1196 and 1055 Mj m^{-2} for 2010 and 2011, respectively. Lower minimum and higher maximum temperatures were explored during 2011 compared to 2010 (Table 1). At sowing, 105 (2010) and 115 (2011) kg ha^{-1} of a starter fertilizer (0N, 20P, 0K, 13Ca) were incorporated into the soil for all treatments. Seed sowing population was 250 plants m^{-2}, during both years for optimum sowing date and 320 plants m^{-2} for late sowing date. Plots were 7 rows 5 m long and 0.20 m apart. Pests, diseases and weeds were controlled by appropriate chemical applications during crop cycle.

Table 1
Growth conditions. Rain, irrigation, accumulated photosynthetic active radiation (PAR), average maximum (Max) and minimum (Min) temperature during 2010 and 2011 seasons.

2010	Rain (mm)	Irrigation (mm)	PAR (Mj m^{-2} month^{-1})	Max Temp (°C)	Min Temp (°C)
June	8.5	–	114	16.5	4.0
July	24.0	–	139	14.6	2.0
August	0.3	40.0	174	16.4	1.5
September	86.8	–	209	20.0	7.5
October	84.4	42.0	274	22.4	7.8
November	26.9	30.0	287	27.9	11.4

2011	Rain (mm)	Irrigation (mm)	PAR (Mj m^{-2} month^{-1})	Max Temp (°C)	Min Temp (°C)
June	24.0	–	102	14.8	3.6
July	15.0	–	136	15.3	0.3
August	2.0	–	114	15.9	2.2
September	35.9	155.0	208	22.3	5.9
October	76.0	145.0	244	21.8	8.2
November	52.5	34.0	252	29.4	13.2

2.2. Treatments and experimental designed

Two cultivars of high fruiting efficiency (FE), Baguette Premium 11 (B11) and Baguette 19 (B19), and one of low FE, BioINTA 2002 (B2002), all selected from González et al. (2011), were used. These cultivars showed a similar cycle to anthesis when sown at optimum date and height is within the optimum range (70–100 cm) for yield potential (González et al., 2011). To explore the magnitude of genotype × environment interaction, the cultivars were grown under different conditions. The first was nitrogen (N) availability: (i) low N (Ni: 58.5 and 41.6 kg N ha^{-1} at sowing from 0 to 0.4 m for 2010 and 2011, respectively); (ii) middle N (130 kg N ha^{-1}) and (iii) high N (200 kg N ha^{-1}). The UREA fertilizer was used to elevate soil N from Ni to 130 or 200 kg N ha^{-1}. The other two treatments were applied within the 200N: (iv) late sowing, i.e. delaying sowing 30 days in relation to optimum date (200N + LS) and (v) shading the canopy during stem elongation (200N + SH, from Z31 to Z65, Zadoks et al., 1974), where a net intercepting 55% of incoming radiation was put 20 cm above the canopy surface. Sowing was within the optimum date for all treatments (10th and 11th June for 2010 and 2011, respectively), except for the 200N + LS where sowing date was delayed one month (12th and 8th July for 2010 and 2011, respectively). The experiment was arranged in a factorial combination of cultivars (3) × treatments (5), in a randomized complete block designed with three replications.

2.3. Measurements and analyses

When each plot reached anthesis (50% of the plot at Z65, Zadoks et al., 1974), a sample of 1 m long from the central row was harvested, and the main stem (MS) and tiller (TL) spikes were separated from the rest of the aerial biomass and put into an air forced oven at 70 °C to constant weight to estimate the spike dry weight at anthesis per unit area (SDWa). When each plot reached maturity (14% grain moisture content), another sample of 1 m long was harvested, to estimate yield and its components. The number of main stem (NS-MS) and tiller spikes (NS-TL) were counted, separated from the rest of the aerial biomass and dried in the oven. For both samples, at anthesis and harvest, it was considered that the tallest stem within the plant holds the main spike and the rest were assumed as tiller spikes. At harvest, the spikes were threshed manually to estimate yield and components: grain number m^{-2} (GN) and thousand grain weight (GW), which were estimated using an automatic seed counter (Pfeuffer GmnH, Kitzingen, Germany). The grains m^{-2} produced by main stems (GN-MS) and tillers (GN-TL) were also calculated. The grain number produced per main stem (NGS-MS) and tiller spike (NGS-TL) were estimated as the ratio between grain number and number of spikes. Fruiting efficiency was calculated at

plot level (FE) and for main stem (FE-MS) and tiller (FE-TL) spikes as the relationship between GN and SDWa (Fischer, 1984).

To determine the environment, i.e. growth treatments (T: Ni, 130N, 200N, 200N + LS, 200N + SH) and years (Y: 2010 and 2011), the genotype (B19, B11 and B2002), and the G × E interaction (G × T and G × Y), ANOVA was performed considering the years as random effects and the genotypes and treatments as fixed effects. The LSD Fischer protected (α = 0.05) was used to compare means. The linear regression and Pearson correlation analyses were used to estimate the association between variables. For all the analyses the Infostat software (Di Rienzo et al., 2012) was used.

3. Results

3.1. Yield, grain number and grain weight

Grain yield ranged from 227 to 696 g m^{-2} and, as expected, it was highly associated to GN (Fig. 1a) and no significant relationship was observed with GW. Differences in GW, for the same value of GN, explained all-out 1.5 ton difference in yield (Fig. 1a). GW ranged from 26 to 38 mg, depending on genotype and growth treatment (p < 0.05). The genotype B2002 showed the heaviest GW (35.6 mg) followed by B11 and B19 (33.1 and 28.7, respectively, LSD = 1.36). The treatments Ni and 130N showed heavier grains (33.9 and 33.5 mg, respectively) than the 200N, independently of sowing date or shading (31.9 and 31.4 for 200N + LS and 200N/200N + S, respectively, LSD = 1.76).

The genotypes with higher FE produced more GN under a wide range of environments. When the GN produced by each genotype was plotted against the environmental index (calculated as the average GN of all genotypes in each environment), the genotype with higher FE, B19, produced more GN than the genotype with the lowest FE, i.e. B2002, while B11 showed intermediate GN values for all the range of the index (ranging from 8700 to 21000 grains m^{-2}) (Fig. 1b).

Although the growth treatments explained most of the variation in GN (ca. 55%), it depended on year (6%) and genotype × treatment interaction (6%, Table 2). GN was lower during 2010 compared to 2011 (15370 vs 17628 grains m^{-2}, respectively). Increases in N availability from Ni to 200N promoted a higher GN in B19 and B2002, without significant response in B11 (Fig. 2a). When sowing was delayed at the highest N rate (200N + LS), B19 and B2002 reduced GN compared to the early sowing by ca. 25 and 16%, respectively; but B11 did not change (Fig. 2a and b). As it was expected, the three cultivars produced less GN when crop was shaded (200N +SH), reducing it 49 (B19), 48 (B11) and 57% (B2002) compared to the 200N treatment (Fig. 2a and b). Then, considering the genotypes within the same growth treatment, B19 always showed higher GN
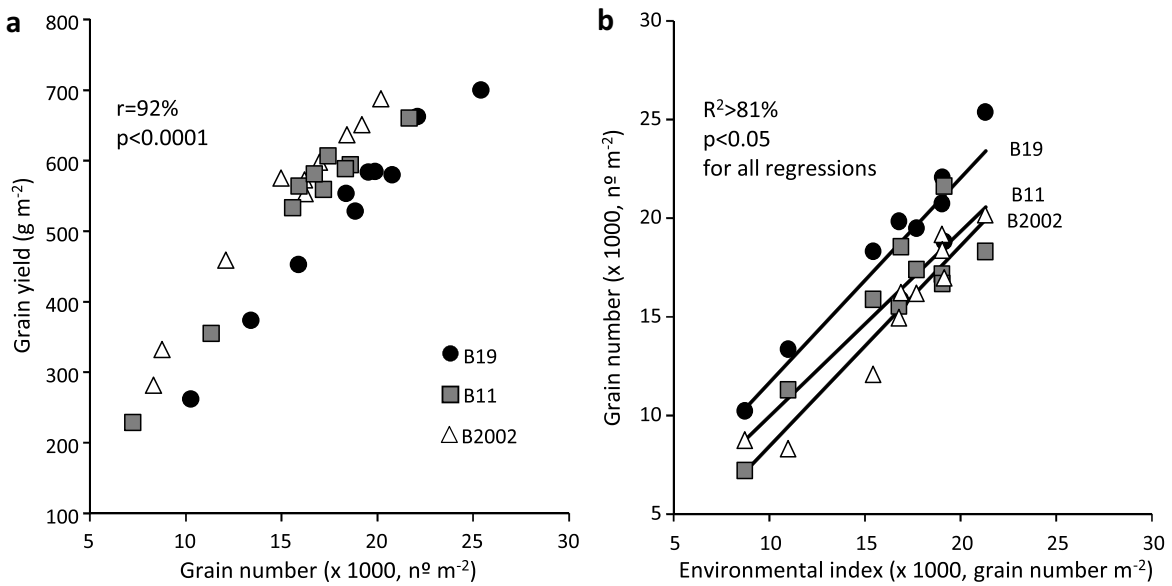
Fig. 1. Relationship between (a) grain yield and grain number, and (b) grain number and environmental index for the three genotypes (2 years × 5 treatments presented).

Table 2
ANOVA results for GN, SDWa and FE. Percent of total sum of squares (%SS) explained by each source of variation (year, genotype and treatment) and probability for grain number per unit area (GN), spike dry weight at anthesis per unit area (SDWa) and fruiting efficiency in (a) Plot, (b) Main stem −MS- and (C) Tiller −TL- levels. The number of spikes per unit area (NS) for tillers and the grain number per spike (NGS) at MS and TL level are shown in b and c.

a) Plot

	GN		SDWa		FE	
S.V.	% SS	p	% SS	p	% SS	p
Year (Y)	6.0	**	3.9	*	19.0	*
Genotype (G)	9.2	****	7.2	***	19.9	****
Treatment (T)	56.6	****	55.1	****	2.5	
Y × G	0.2		2.4		3.7	*
G × T	6.1	*	2.6		9.7	*
Y × G × T	2.1		6.0	*	9.1	t

b) Main stem

	GN-MS		SDWa-MS		FE-MS		NGS-MS	
S.V.	% SS	p	% SS	p	% SS	p	% SS	p
Y	0.1		3.4	*	5.6		0.2	
G	3.9	t	25.5	****	20.9	***	3.3	*
T	47.0	****	31.2	****	14.3	***	45.5	****
Y × G	0.1		1.0		2.0		3.2	t
G × T	2.7		4.4		6.0		6.2	
Y × G × T	4.4		5.2		7.6		10.0	*

c) Tiller

	GN-TL		SDWa-TL		FE-TL		NS-TL		NGS-TL	
S.V.	% SS	p	% SS	p	% SS	p	% SS	p	% SS	p
Y	12.0	*	2.1		21.5	t	25.5	****	0.2	
G	13.5	****	1.6		4.0	t	0.8		24.1	****
T	43.0	****	54.9	****	5.7		28.2	****	37.8	****
Y × G	1.1		2.4	t	2.2		0.8		1.1	
G × T	5.3	t	2.6		7.0		11.4	**	3.9	*
Y × G × T	2.7		8.5	*	5.3		4.3		3.9	

t: trend <0.08.
S.V. source of variation.
* <0.05.
** <0.01.
*** <0.001.
**** <0.0001.

than B2002 (except for the 200N + LS), while B11 showed similar or higher GN than B2002 depending on treatment (Fig. 2a and b).

The contribution of main stems (GN-MS) to GN ranged from 37 to 50%. The GN-MS was similar between years, but tended to differ among genotypes and was affected by growth treatments (Table 2),
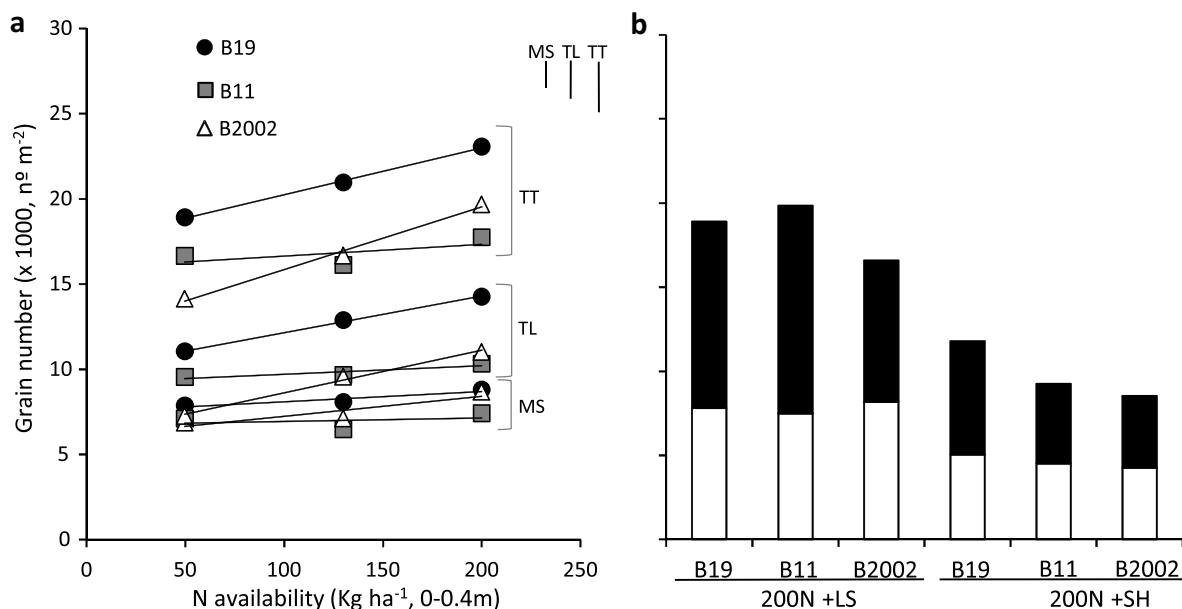
Fig. 2. Grain number produced per unit area (TT) and the contribution from tillers (TL, close bars) and main stems (MS, open bars) for (a) nitrogen availability (Ni: 49.8, 130N and 200N), and (b) late sowing (200N + LS) and shading (200N + SH) treatments. The average over years (a and b) and trend lines (a) are presented. The lines in the middle top indicate the values of LSD (Fischer protected, $\alpha = 0.05$) for genotype × treatment interaction in a and b.

particularly by the 200N + SH (Fig. 2a and b). B19 tended to show higher GN-MS than B2002 in most of the treatments (Fig. 2a and b). The contribution of grains produced by tillers (GN-TL) ranged from 50 to 63%, depending on years, genotypes and treatments (Table 2). GN-TL was lower during 2010 compared to 2011 (8363 vs. 10713 grains m^{-2}). Considering the genotypes, B19 produced the highest GN-TL (11197 grains m^{-2}) followed by B11 and B2002 (9134 and 8102 grains m^{-2}, respectively, LSD = 1003). The trend to interactive effect G × T (Table 2) was a consequence of the response of B11 to N availability and delayed sowing date. As N availability was higher GN-TL increased in B19 and B2002 but B11 showed a small response (Fig. 2a). When sowing was delayed GN-TL reduced by 23% in B19 and B2002 while B11 showed again a small response (Fig. 2b). When crop was shaded (200N +SH) GN-TL decreased by 54% for B19 and B11, and 61% for B2002 (Fig. 2b).

The GN depends on the number of spikes m^{-2} (NS) and the number of grains $spike^{-1}$ (NGS), contributed by main stems (MS) and tillers (TL). The number of grains $spike^{-1}$ of main stem (NGS-MS) was greatly affected by treatments (Table 2) but its value depended on the year × genotype × treatment interaction. The growth treatments explained 45% variation in NGS-MS with values of 37.5, 35.5 and 36.0 grains $spike^{-1}$ for Ni, 130N and 200N, respectively; while late sowing (200N + LS) slightly increased (7%) and SH strongly decreased (27.7%) the NGS-MS respect to the 200N treatment (LSD = 3.1). The average values of NGS-MS for genotypes were 36.4, 33.3 and 34.7 grains $spike^{-1}$ (LSD = 2.4) for B19, B11 and B2002, respectively. The interaction year × genotype × treatment was consequence of the cross response of B11 and B2002 during 2010 under 200N + LS (31.6 vs 44.9 grains $spike^{-1}$, respectively, LSD = 14.4) and during 2011 under 200N + SH (32.6 vs 19.5 grains $spike^{-1}$, respectively, LSD = 14.4).

The number of spikes m^{-2} produced by tillers (NS-TL) was highly associated with GN (r = 0.81 p < 0.001) and greatly affected by treatments but its actual value depended on year and genotype × treatment interaction (Table 2). In line to the GN-TL, the NS-TL was lower in 2010 than in 2011 (345 vs. 434 spikes m^{-2}). The treatments explained 28% of variation in NS-TL (Table 2). As N availability increased, the NS-TL was higher for B19 and B2002 while B11 only showed a trend to increase (Fig. 3a). When sowing was delayed
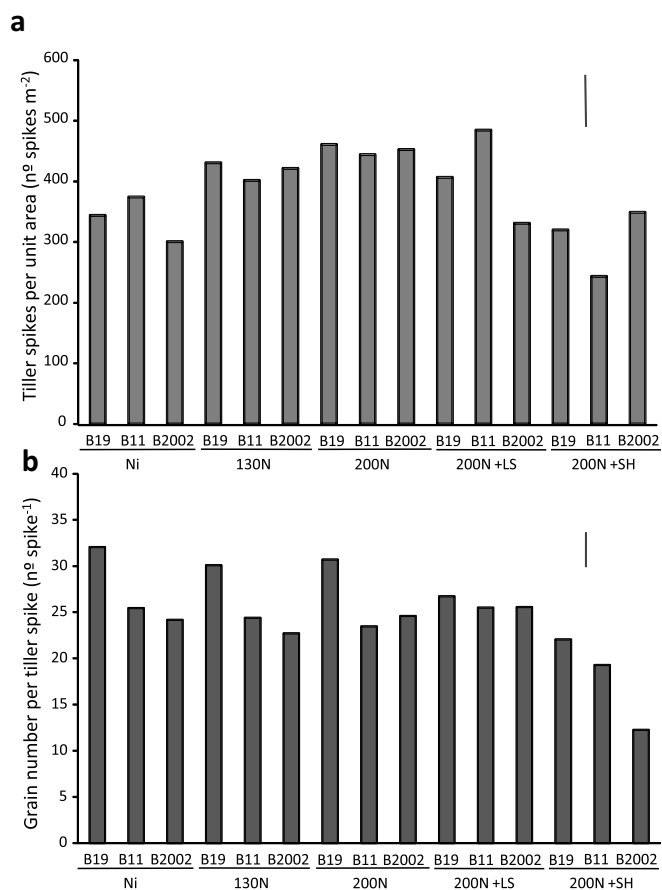

Fig. 3. (a) Number of tiller spikes m^{-2} (NS-TL) and (b) grain number per tiller spike (NGS-TL). The three genotypes (B19, B11 and B2002) in the five treatments (Ni, 130N, 200N, 200N + LS and 200N + SH) averaged over years are presented. The lines in the top right indicate the value of LSD for genotype × treatment interaction.
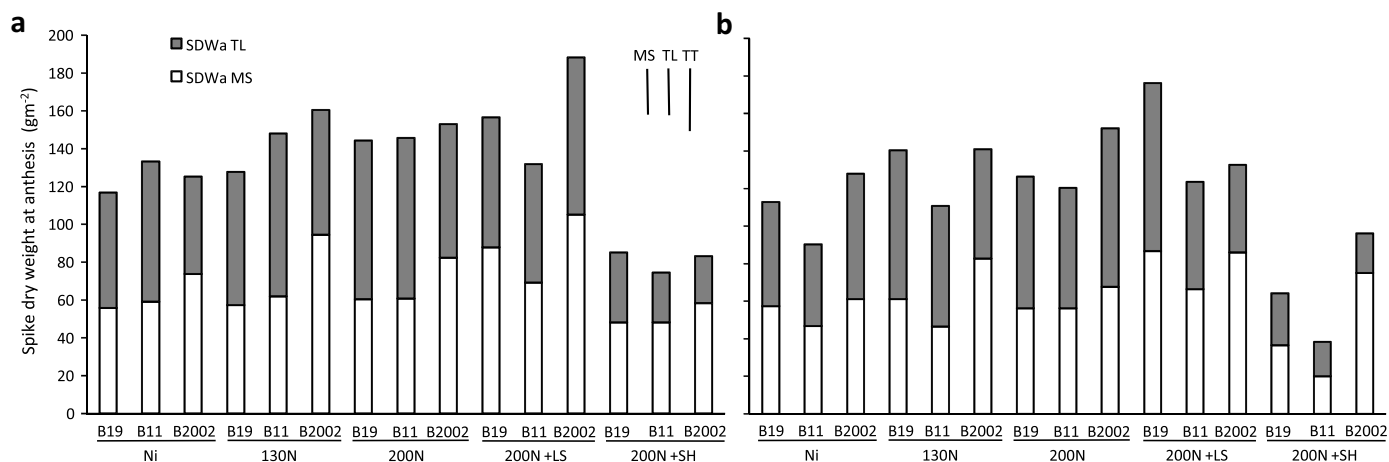
Fig. 4. Spike dry weight at anthesis per unit area (SDWa, total: TT) and the contribution from main stems (SDWa-MS) and tillers (SDWa-TL) for the interaction genotype (B19, B111 and B2002) × treatment (Ni, 130N, 200N, 200N + LS, 200N + SH) for (a) 2010 and (b) 2011. The lines in the top right of (a) indicate the value of LSD for year × treatment × genotype interaction.
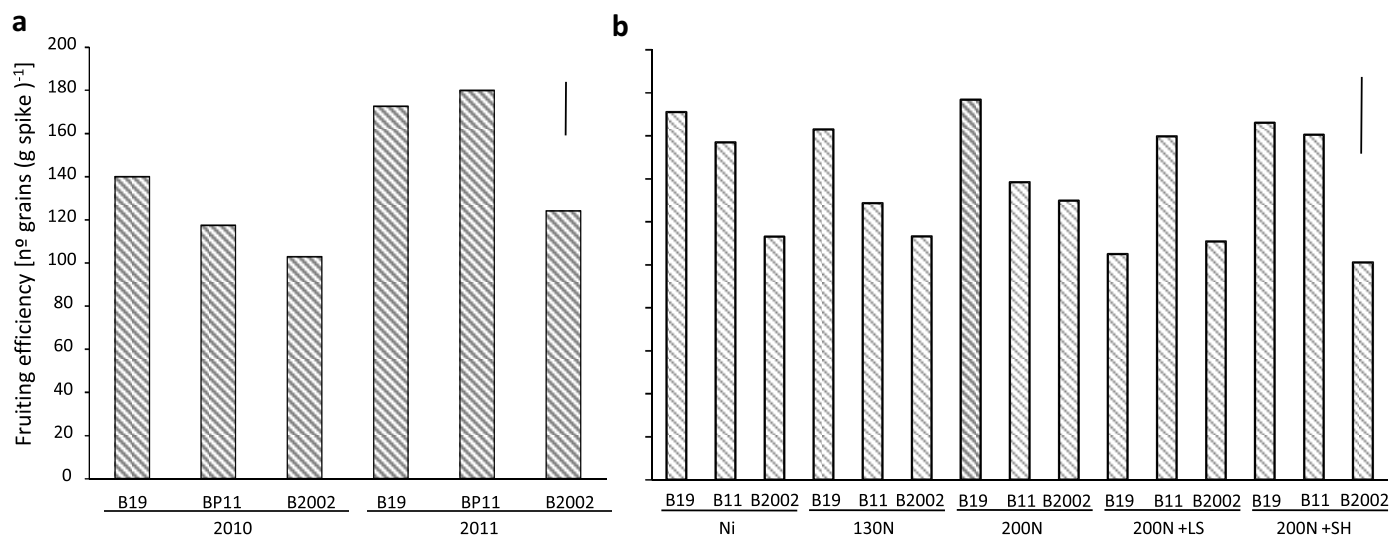

Fig. 5. Fruiting efficiency at plot level [n° grains (g spike at anthesis)$^{-1}$] for (a) the interaction year × genotype (2010 and 2011 × B19, B11 and B2002), and (b) genotype × treatment (Ni, 130N, 200N, 200N + LS, 200N + SH), average of two years. The lines in the top right of (a) indicate the value of LSD for year × genotype, and the one in (b) of genotype × treatment.

and crop was shaded the NS-TL decreased for all the genotypes, except for B11 under 200N + LS that maintained the value of spikes similar to the 200N treatment (Fig. 3a). The number of grains per tiller spike (NGS-TL) was highly dependent on the genotype (24% of variation) and treatments (38% of variation), evidencing also a significant genotype × treatment interaction (Table 2). The genotype B19 always showed higher NGS-TL than B11 and B2002, except for the 200N + LS treatment (Fig. 3b), while B11 showed similar or higher NGS-TL than B2002, depending on the treatment (Fig. 3b). As N availability was higher, NGS-TL tended to reduce (Fig. 3b) due to the increment in NS-TL (Fig. 3a). The genotype × treatment interaction was consequence of a decrease of NGS-TL in B19 (13% compared to 200N) and an increase in B11 and B2002 (9 and 4% compared to 200N, respectively) under 200N + LS (Fig. 3b).

3.2. Spike dry weight at anthesis

The spike dry weight at anthesis (SDWa) ranged from 38 to 188 g m^{-2} mainly due to treatment effects (ca. 55%, see Table 2), although a significant year × genotype × treatment interaction was observed. Considering the high N availability and shading

(200N + SH) treatment, B2002 showed similar or higher SDWa than B19 and B11 during both years (Fig. 4). The interaction was observed in the late sowing treatment (200N + LS), where B2002 showed higher SDWa during 2010 but smaller during 2011 than B19. The contribution of main stem spikes (SDWa-MS) to SDWa ranged from 42 to 78%, depending on year, genotype and treatment (Table 2). The values of SDWa-MS were lower during 2010 compared to 2011 (60.4 vs. 68.2 g m^{-2}, respectively). The genotypes B19, B11 and B2002 averaged SDWa-MS values of 60.8, 53.5 and 78.6 g m^{-2} (LSD = 7), respectively. The treatment that produced the lowest SDWa- MS was 200N + SH (47.7 g m^{-2}), followed by Ni, 200N, 130N and 200N + LS (58.9, 63.9, 67.3, and 83.5 g m^{-2}, respectively, LSD = 9) (Fig. 4). The relative contribution of tillers spike dry weight (SDWa-TL) to SDWa ranged from 22 to 58% depending on year × genotype × treatment interaction, while the growth treatments had a significant high impact (55%, Table 2). Considering the high N availability and shading (200N + SH) treatment B2002 showed similar SDWa-TL than B19 and B11 during both years, but tended to be smaller in 5 out of 8 cases (Fig. 4). Once again, the main interaction was observed in the 200N + LS treatment where B2002 tended to show higher SDWa-TL than B11 and B19 during 2010 but
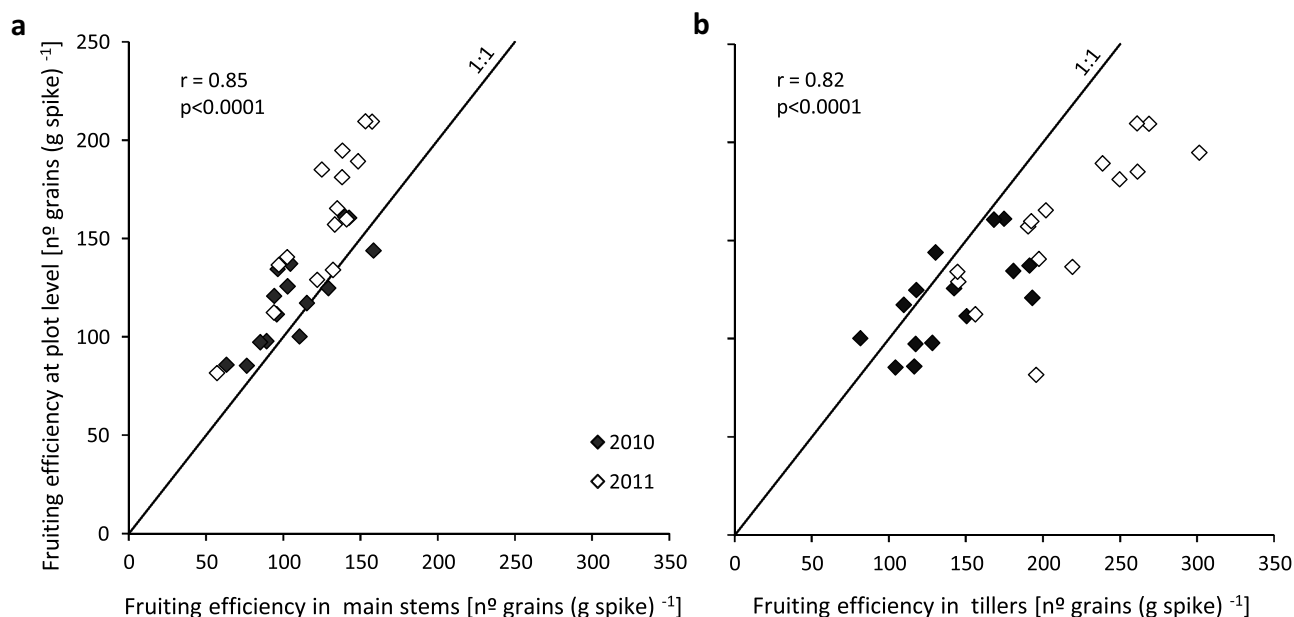
Fig. 6. Correlation between fruiting efficiency [n° grains (g spike at anthesis)$^{-1}$] at plot level and (a) fruiting efficiency in mains stems (FE-MS) and (b) fruiting efficiency in tillers (FE-TL). All data included.

it was statistically lower to B19, though similar to B11, during 2011 (Fig. 4).

3.3. Fruiting efficiency

The variation of FE at plot level was mainly explained by the year (19%) and the genotype (20% see Table 2), although significant year × genotype and genotype × treatment interactions were observed (Table 2). During both years, B2002 showed lower FE than B19, but it was similar to and lower than B11 during 2010 and 2011, respectively (Fig. 5a). Considering the genotype × treatment interaction, B2002 always showed the lowest and B19 the highest FE values, except for the 200N + LS where it was similar due to a reduction in the FE value in B19 (Fig. 5b). Comparing with B11, B2002 showed lower (Ni, 200N + SH, 200N + LS) or similar (130N, 200N) FE values (Fig. 5b). The FE of main stem spikes (FE-MS) depended on genotype (20%) and growth treatments (Table 2). The genotypes B19 and B11 showed higher values (130 and 125 grains g^{-1}, respectively) than B2002 (93 grains g^{-1}, LSD = 14.4). The treatment with higher N and optimum sowing date (200N) showed the highest FE value (134.5 grains g^{-1}) followed by Ni, 130N, 200N + SH and 200N + LS (127.2, 114.6, 107.2 and 96.3 grains g^{-1}, respectively, LSD = 18.6). The FE in tiller spikes (FE-TL) tend to respond to year and genotype (Table 2), with values of 140 and 215 grains g^{-1} during 2010 and 2011, respectively (LSD = 33.6), and 197.3, 178.6 and 157.7 grains g^{-1} for B19, B11 and B2002, respectively (LSD = 43.6). The correlation between FE at plot level and the FE-MS or the FE-TL was high (>0.80), but the FE-MS values were closer to the FE at plot level than the FE-TL (Fig. 6, see 1:1 line). The maximum values explored by FE-TL were higher than the ones explored by FE-MS (Fig. 6).

3.4. Relation between grain number and fruiting efficiency

When GN was plotted against FE, there was not a unique relationship due to the differences observed in SDWa (Fig. 7), particularly due to the great impact of shading treatment, 200N +SH (see iso-line of 60 g m^{-2} in Fig. 7). The GN was highly associated with SDWa within each cultivar (r = 0.53, 0.64 and 0.74, p < 0.05, for B19, B11 and B2002, respectively). Considering all data
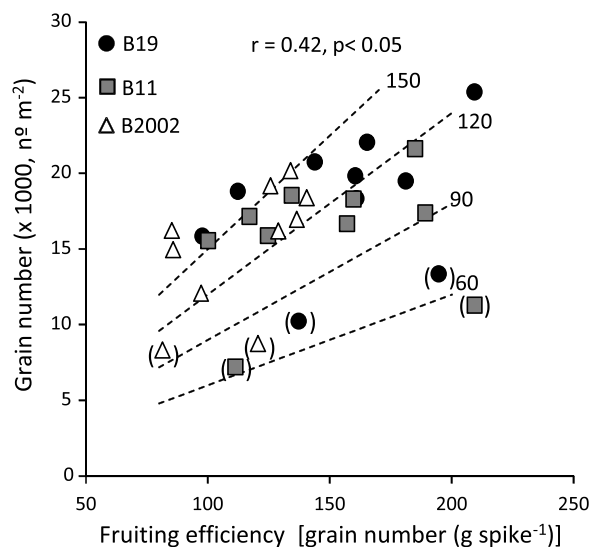

Fig. 7. Relation between grain number and fruiting efficiency for the three cultivars. The dotted lines indicate iso-lines for spike dry weight at anthesis (60–90–120 and 150 g m^{-2}). The correlation coefficient for all data was 0.42 (p < 0.05), for all treatments except 200N + SH (points within brackets) was 0.74 (p < 0.00001), and for 200N + SH treatment was 0.86 (p < 0.005).

the correlation between GN and FE was 0.40 (p < 0.05), however, when correlation was done for all treatments except the 200N + SH treatment, the value increased up to 0.74 (p < 0.00001), despite the important differences in SDWa that ranged between 90 and 188 g m^{-2} (Fig. 7). For the shading treatment, the correlation was also high, ca. 0.86 (p < 0.005), considering the three cultivars. As FE increased there was a trend to cross the iso-lines of SDWa from higher to lower values (Fig. 7). It is noteworthy that GN higher than 20000 grains m^{-2} was obtained with FE higher than 150 grains g^{-1} and SDWa similar or higher to 120 g m^{-2} (Fig. 7).
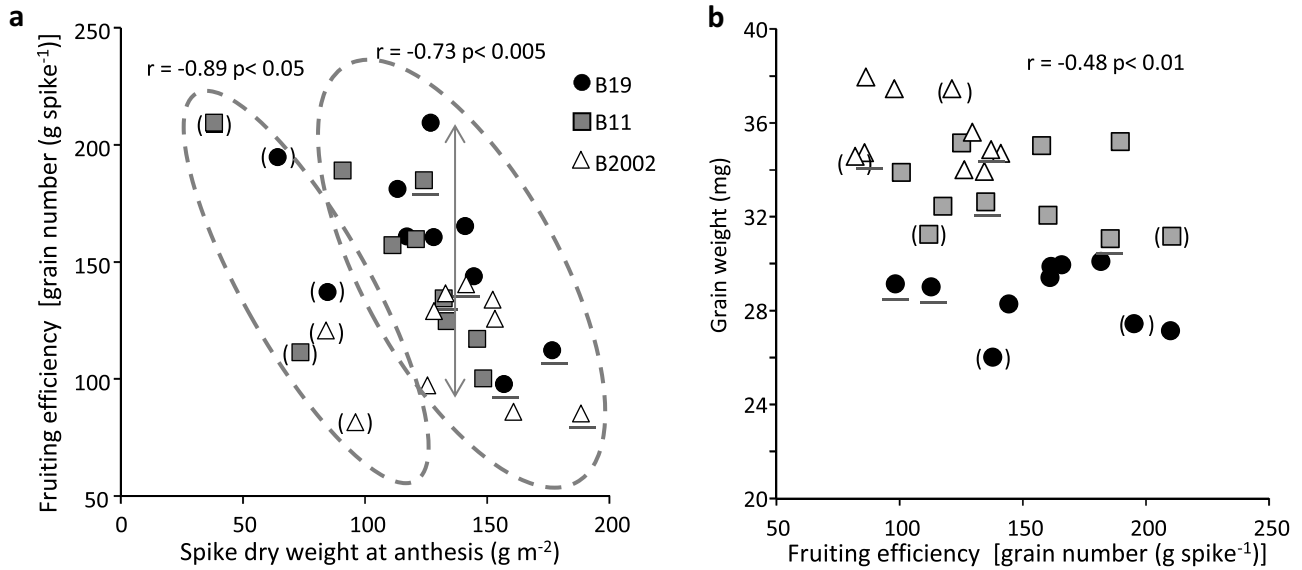
Fig. 8. Relationship between (a) fruiting efficiency and spike dry weight at anthesis and (b) grain weight and fruiting efficiency. The brackets indicate the 200N + SH and the line the 200N + LS. The correlation coefficients are shown inside.

3.5. Spike dry weight at anthesis and grain weight: association with fruiting efficiency

The FE showed a general negative correlation with SDWa (Fig. 8a). Considering all the genotypes, treatments and years, with the exception of the 200N + SH, the correlation was −0.73 (p < 0.005). The shading treatment also showed a high negative correlation, but exploring lower values of SDWa, pointing out the greater impact of shading on SDWa than on FE. Despite the high negative correlation, a wide range of variation in FE was observed for each value of SDWa, for example, for 125 g m^{-2} of SDWa a range of FE from 100 to 200 grains g^{-1} was observed depending on genotype (mainly) and year.

The GW decreased as FE increased (r = −0.48, p < 0.01) (Fig. 8b). A clear genotype impact on GW was observed for a wide range of FE variation due to years and treatments. When correlation was tested considering only data for the three genotypes at the best growth condition (200N) during both years, the negative correlation tend to increase to −0.75 (p < 0.08), highlighting the genotype effect.

4. Discussion

The use of physiological traits for indirect selection may help to increase yield potential at the pace it is required (Slafer, 2003; Araus et al., 2008) to fulfil the increasing production demand (Reynolds et al., 2012; Hall and Richards, 2013; Fischer et al., 2014). The FE has been suggested as secondary trait to increase GN (Abbate et al., 1998; González et al., 2011; García et al., 2014; Slafer et al., 2015; Mirabella et al., 2016), but its possible cross-over genotype (G) × environment (E) interaction and trade-off with SDWa and GW may limit its usefulness. In the present paper three FE contrasting cultivars were sown under different environments and yield numerical components (GN and GW) and crop physiological traits (SDWa and FE) were studied at plot level and as the outcome of main stem and tillers response.

Yield variations were mostly explained by changes in GN which was at the same time negatively associated with GW (Fig. 9), as it was expected from the literature (Slafer et al., 1990; Canevara et al., 1994; Calderini et al., 1995; Sayre et al., 1997; Shearman et al., 2005; Fischer, 2007; Acreche et al., 2008). The GN and SDWa responded to treatments according to bibliography (Fischer, 1985;
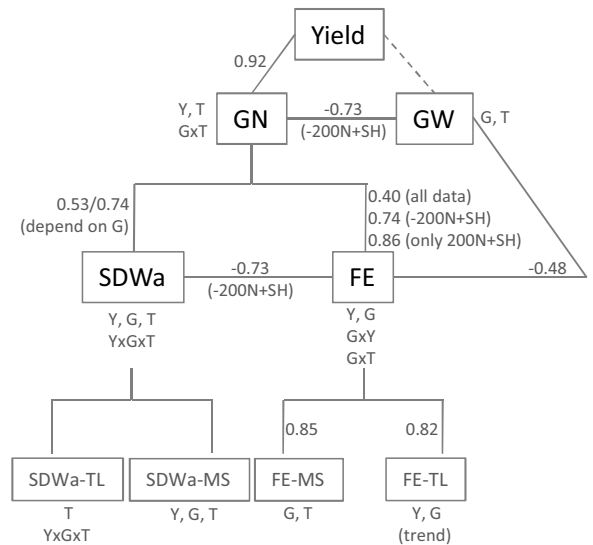

Fig. 9. Resume of genotype and environment impact on main variables and their relationships. The values connecting variables represent the Pearson correlations.

Fischer et al. 1993; Savin and Slafer, 1991; Demotes-Mainard et al., 1999; Demotes-Mainard and Jeuffroy, 2001). Regarding the cultivars, B19 (high FE) produced more GN than B2002 (low FE) under all treatments, while B11 (high FE) showed similar or higher GN than B2002, depending on treatment. The difference in GN produced by genotypes was more associated to the GN produced in tillers (GN-TL) than in MS (GN-MS). As the number of tiller spikes m^{-2} (NS-TL) was not different among genotypes, the number of grains spike^{-1} (NGS-TL) was the trait that better explained the differences in GN-TL. In fact, NGS-TL was consistently higher in B19 followed by B11 and B2002, except for the late sowing date (where B19 showed similar values than B11 and B2002). At the main stem level a trend of B19 to produce more grains per spike (NGS-MS) was also evident. The SDWa of B19 was similar or lower than the one of B2002 (except for the late sowing during 2011), which was consequence of reduced SDWa-MS but similar or higher SDWa-TL. The correlation of GN with FE, excluding shading treatment, was high (Fig. 9) for a wide range of variation in SDWa (90–188 g m^{-2}),

agreeing with previous results (Abbate et al., 1998; González et al., 2011; Lázaro and Abbate, 2012; García et al., 2014) but disagreeing with others published in the literature (Shearman et al., 2005).

The FE at plot level was affected by genotype and year and also by genotype × year and genotype × treatment (late sowing) interaction (Fig. 9). FE was not modified by shading treatments in line to that reported by Lázaro and Abbate (2012). However, others evidences showed reductions in FE due to N shortage and/or shading (Fischer and Stockman, 1980; Abbate et al., 1995). The genotype had similar impact than the year, explaining each one 19% of FE variation, while the G × Y interaction only explained 3.7%. González et al. (2011) also observed a higher impact of genotype (52–67%) than G × Y interaction (19–11%). Similarly, Mirabella et al. (2016) measuring FE for different genotypes, locations and years, reported a coefficient of variation lower than 20% for G × E against a range from 30 to 90% for genotypes. The FE has always been studied at plot level (eg. Fischer, 1984; Abbate et al., 1998; González et al., 2011; García et al., 2014; Slafer et al., 2015; Mirabella et al., 2016). Nevertheless, as the FE at plot level comes from the combination of FE in main stems (FE-MS) and tillers (FE-TL), changes in the relative proportion of each stratum into the canopy could modify the values of FE at plot level. Regarding the environments, the changes in FE at plot level between years may be a consequence of the FE-TL response. The phototermal quotient (Q, MJ per °Cd) during the critical period (−20 + 10 days from anthesis) was higher during 2011 vs. 2010 (ca. 0.82 vs 0.77 Mj per °Cd), allowing the establishment of more tiller spikes m^{-2}. As the FE-TL was higher than FE-MS, the FE at plot level may have increased associated with better environmental conditions for tiller survival (the FE-MS tended to increase also during 2011, but it was not statistically different). It is noteworthy that, in contrast to FE at plot level and FE-TL, the FE-MS responded to shading treatment (Fig. 9). It maybe that under a growth restriction, the only mechanism of response of main stem spikes is to adjust growth and efficiency at the spike level, whereas the mechanism at tillers level is to reduce the number of spikes. If this is the case, canopies with different structure (that is different relative proportion of mains stem and tiller spikes) may respond different to shading at plot level, explaining some of the contrasting reports in bibliography.

A cross-over interaction between B2002 and B19 was observed when the sowing was delayed one month (200N + LS) from the optimum date, because B19 greatly reduced its FE compared with the other genotypes. The anthesis of B19 was later than the other two genotypes when sowing was delayed, exploring higher maximum temperatures during the critical period (taken from 20 days previous to, and 10 after, anthesis). To test if the heat stress explored by each genotype was associated with the FE when sowing date was delayed, a stress index was calculated quantifying the hours that the crops were exposed to temperatures above 27 °C (°Ch > 27 °C), temperature used by Semenov (2009) as threshold for heat stress around anthesis. In Fig. 10 a clear decrease in FE can be observed when the stress index increased, for the three genotypes, B19 being the one that experienced the highest heat stress condition. The decrease in FE at plot level was consequence of a decrease mainly in FE- MS (though FE-TL tended to be reduced). As far as we are aware, no previous paper reported about a possible cross-over G × E interaction of FE. The results of the present study suggest that selection for FE into a breeding program should be carried out within environments with low probability of any stress around anthesis or within cultivars of similar anthesis date.

It has been stated that FE at spike level is a good estimator of FE at plot level, suggesting that this trait could be selected in early generations of breeding programs (Abbate et al., 2013). In the present study a high correlation and a close 1:1 relationship was observed between FE at plot level and FE in main stems (Fig. 9), for all treatments and cultivars, suggesting that main stem spikes should be
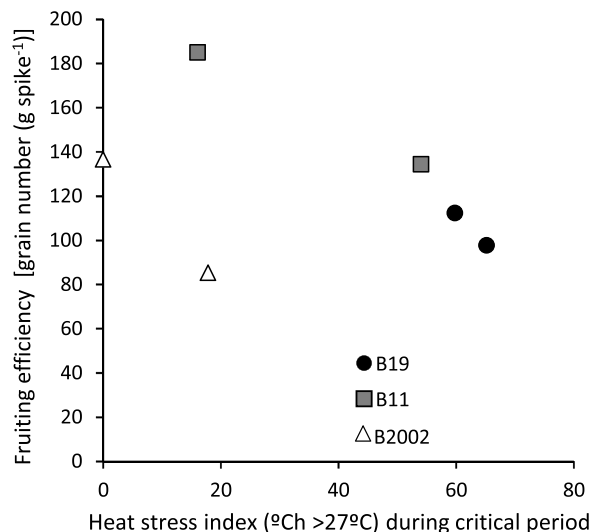

Fig. 10. Relationship between fruiting efficiency and heat stress index (Σ°Ch > 27 °C) during critical period (−20 + 10 days from anthesis) for 200N + LS treatment during both years.

sampled to represent the FE values at the plot level. Nevertheless, it remains to be studied in more detail the correlation of FE at plot and at plant level (which is used in early generations of breeding programs), as the results of the present paper showed that tiller spikes are more efficient to produce grains than main stem spikes and that the FE at plot (or plant) level may be the outcome of the proportion of them.

The negative correlation between FE and SDWa observed in the present study, agrees with some previous reports (Dreccer et al., 2009; Ferrante et al., 2012; Lázaro and Abbate, 2012), but disagrees with others (González et al., 2011; García et al., 2014). It was noteworthy the parallel negative correlation of shading treatment, highlighting the greater impact of shading on SDWa than on FE. It should be noted that there may be some artifact in the correlation as naturally when the SDWa increases, the FE may decrease as it is calculated as the ratio between GN and SDWa (this would reflect a lower functionality of FE as a trait to improve grain number as increases in the value of FE may be more associated to a reduction in SDWa than to increment in GN, reflecting somewhat the case of B11). But, if this negative correlation is constitutive, that is, increasing FE by breeding will result in less SDWa, the GN maybe little increased when selecting for higher FE. The study of partitioning of dry matter within the spikes (rachis, glumes and grains) could help to understand the nature of this relationship, which is still uncertain (Slafer et al., 2015). Nevertheless, there are some examples in literature showing that this possible trade-off can be overcome by breeding as high yielding materials were associated with higher GN due to both, higher FE and SDWa (García et al., 2014).

The negative correlation between GW and FE may limit yield increments when GN is increased via higher FE. In the present paper there was a negative correlation between these two traits, (Fig. 9) and clearly the genotype with higher FE showed lighter grains and *vice versa*, agreeing with some previous results (Fischer and HilleRisLambers, 1978; Ferrante et al., 2012), but disagreeing with others (González et al., 2014). When FE was altered by treatments within each genotype, the GW did not change, agreeing with the observation that GW has extremely low plasticity (Sadras and Slafer, 2012). The negative correlation between both traits maybe apparent if increasing FE does not affect potential GW and the increments in GN are consequence of more grains from distal positions which naturally have lower GW potential (Miralles and Slafer, 1995b; Ferrante et al., 2015). But, if increases in FE reduce potential

GW, then the negative correlation may be a truly trade-off (Slafer et al., 2015). The weight of grains in particular positions of the spike and/or the weight of floret carpels should be studied to determine the nature of the relationship between FE and GW.

5. Conclusions

The FE at plot level showed moderate G × E interaction (ca. 13%), while the impact of genotype (20%) and environment (19%) were higher. Cross-over G × E interaction was observed when sowing was delayed because the higher heat stress experienced by some genotypes reduced FE. Therefore, it can be concluded that the genotype ranking for FE will not change in environments without abiotic stress around anthesis (not only water, but also temperature).

The FE of tiller spikes was higher than that of main stem spikes and responded differently to environment. The proportion of tiller into a canopy may change the FE response at plot level. However, measuring the FE at main stem spike level seems to be a good estimation of FE at plot level in dense canopies.

The GN was correlated with FE for a wide range of SDWa ($90-188\,\mathrm{g\,m^{-2}}$) and the cultivars with higher FE showed higher GN in a wide range of environmental index (ranging from 8700 to $21000\,\mathrm{grains\,m^{-2}}$). Thus, improving FE may result in higher GN in wide-ranging environments. Nevertheless, special care should be taken when selecting for higher FE in a breeding program as a strong negative correlation between FE and both SDWa and GW was observed.

Acknowledgements

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