Wheat spike fertility: inheritance and relationship with spike yield components in early generations

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Abstract

In wheat, grain number is considered as the product of spike dry weight (SDW) and the number of grains per unit of SDW, that is an indicator of spike fertility (SF). The aim of this study was to determine the heritability of SF and the effect of early selection for high SF on its relationship with other spike yield components. Two field experiments were conducted in the south-eastern Pampas (Argentina) with 400 F_2 and $F_{2:3}$ families obtained from two crosses between varieties with contrasting SF (PIG/SSN and B10/KCJ). Heritability estimates in PIG/SSN and B10/KCJ were, respectively, 0.60 and 0.51 by variance component analysis, 0.43 and 0.43 by $F_2 : F_3$ parent–offspring regression and 0.30 and 0.28 by realized heritability analysis. The existence of transgressive segregation (i.e. the occurrence of families with SF values that were more extreme than those of the parents) was observed. The top 25% F_3 families with the highest SF had 12% more grains per spike, despite a 13% and 5% decrease in SDW per spike and weight per grain, respectively, than the remaining families. These results give support to the application of early selection for high SF.

Key words: genetic × environmental interaction — grain number — spike dry weight — yield improvement — early selection

Bread wheat (*Triticum aestivum* L.) is one of the most important crops in the world, and grain yield improvement is one of the main targets of most wheat breeding programmes. Wheat yield can be considered as the product of the number of grains (GN) per unit area and weight per grain (WG). Of these, GN/m^2 is the component which best explains yield variations (Fischer 1985, Abbate et al. 1995, Calderini et al. 1999). Therefore, selection for high GN/m^2 seems an obvious approach that breeders could apply for improving grain yield. One of the problems with using variables that are quantified per unit area is obtaining reliable data in early generations of breeding programmes, which are usually grown in small plots because only little seed is available.

Actually, GN/m^2 can be considered as the product of spike dry weight (SDW)/m^2 and the number of grains per unit of SDW, that is an indicator of spike fertility (SF; Fischer 1984, Abbate et al. 1998). Improvement in wheat grain yield over the last 50 years, particularly the one associated with shorter stature, has mainly been based on increasing GN/m^2 via an increase in SDW through a higher crop dry weight partitioning to spikes (Brooking and Kirby 1981, Fischer and Stockman 1986, Siddique et al. 1989, Youssefian et al. 1992, Slafer and Andrade 1993). On the other hand, several authors (Abbate et al. 1998, Shearman et al. 2005, Acreche et al. 2008, González et al. 2011) have observed that GN/m^2 variation among cultivars often encompasses variation in SF. In addition, research by Abbate et al. (2013) has shown that SF is fairly independent of the sample size; thus, SF could be determined from early generations of a breeding programme.

Nevertheless, some aspects need to be dealt with before considering the use of SF as a breeding target. Firstly, the effectiveness of selection for a given trait depends, among other things, on the relative importance of genetic and non-genetic factors in the expression of phenotypic differences between genotypes in a population, that is its heritability (Falconer and Mackay 1996). Virtually, no such information is available in the case of SF.

Secondly, several authors (Abbate et al. 1995, 1997, Reynolds et al. 2001, Dreccer et al. 2009, Lázaro and Abbate 2012, among others) have reported the existence of a negative relationship between SF and SDW, whereas Abbate et al. (1998) and González et al. (2011) observed no such relationship, in commercial cultivars. No information on this relationship has been generated, however, in segregating lines not subject to selection. Also, whether an eventual negative relationship between SF and SDW would hinder the increase in GN/m^2 through selection for high SF remains to be determined.

Thirdly, a negative relationship between SF and WG has been reported in commercial cultivars (Fischer 2007). As this negative relationship could potentially counteract the positive effect of increasing SF on GN/m^2, it needs to be investigated in segregating materials as well.

The aim of this study was to determine the mode of the inheritance of SF and the effect of selection for high SF on other spike yield components, in order to generate information on the feasibility of using SF as a selection criterion in bread wheat breeding programmes aimed at increasing grain yield.

Materials and Methods

Characterization of the experimental sites, experiments and plant material: Field experiments were carried out during the 2009/2010 and 2010/11 crop seasons at the Estación Experimental Agropecuaria

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Abbreviations: GN, grain number; WG, weight per grain; SDW, spike dry weight; SF, spike fertility; YLD, grain yield; PIG/SSN, PROINTA Pigüé/Soissons cross.; B10/KCJ, Baguette 10/Klein Chajá cross.

Balcarce, Instituto Nacional de Tecnología Agropecuaria (INTA) (Balcarce, Argentina; 37°45′S, 58°18′W, 130 m ASL) and during the 2010/11 crop season at the Chacra Experimental Miramar, Ministerio de Asuntos Agrarios de la Provincia de Buenos Aires (Miramar, Argentina; 38°10′S, 58°0′W, 45 m ASL). Soils at both sites were loamy, illitic, thermic, typical Argiudolls (Soil Survey Staff, 1994) with 5.5–6.3% organic matter in the first 25 cm of depth. Both experiments were conducted under conventional tillage, with chemical pest and disease control and no nutrient limitations. Irrigation was applied only in Balcarce.

During the 2009/2010 crop season, ~1500 F_2 plants derived from each of two crosses between varieties contrasting for SF were grown at Balcarce in 11-m-long plots of seven rows distanced at 0.2 m. Seeding was performed mechanically at a mean density of 20 seed/m of row. The two crosses were (i) 'PROINTA Pigüé' and 'Soissons' of low and high SF, respectively (PIG/SSN), and (ii) 'Baguette 10' and 'Klein Chajá' of high and low SF, respectively (B10/KCJ). Two hundred random F_2 plants per population were individually harvested as described below, and each individual plant constituted an experimental unit for SF determination.

The derived $F_{2:3}$ families were evaluated in 2010/2011 crop season at Balcarce and Miramar, under a randomized complete block design with two replications. The experimental unit consisted of a 1-m-long single row, 20 cm apart from adjacent rows in which cv. 'Baguette 10' was sown, to make competition between experimental units more uniform. Treatments consisted of (i) 400 $F_{2:3}$ families (200 of each PIG/SSN and B10/KCJ crosses) and (ii) the four parental cultivars. Seeding was carried out manually at a seeding rate of 300 seeds/m^2.

Measurements: At physiological maturity, all shoots from each experimental unit (individual F_2 plant or F_3 row) were cut above ground level. Subsequently, spikes were cut at the lowest spikelet level, counted, weighed and threshed. Grain was then weighed and a sample of them was weighed and counted in an electronic counter. Yield per spike (YLD/spike) was calculated as the quotient between grain weight and the number of spikes from each experimental unit. Weight per grain (WG) was obtained as the quotient between grain weight and the number of grains from each experimental unit. Grain number per spike (GN/spike) was calculated as the quotient between grain number and the number of spikes from each experimental unit. Spike dry weight per spike (SDW/spike) was calculated as the difference between total SDW (before threshing) and grain weight, both as per plant or row scale, divided by the number of spikes. Then, SF was calculated as the quotient between GN/spike and SDW/spike (Abbate et al. 2013).

Spike fertility in parental cultivars: Differences in SF between contrasting parental cultivars were corroborated by ANOVA, using a fixed effects linear model which included cultivars, environments, replicates within environments and cultivar by environment interaction as factors.

Frequency distribution of spike fertility in the populations: Histograms for frequency distribution of SF of $F_{2:3}$ families were built for each of the populations in each site of evaluation. They were expressed as density, that is the quotient between relative frequency and class width.

Spike fertility and other spike yield components in segregant families: A linear mixed model was fitted for each trait which included populations as a fixed effects factor and environments, replicates within environments, families and genotype by environment interaction as random effects factors within each population. Best linear unbiased predictors (BLUP) for each family and trait at each environment were obtained and used to estimate genetic correlations between traits.

Variance components and heritability of spike fertility: Variance components of SF were estimated for $F_{2:3}$ families (without including the parental cultivars present in the experiment) by restricted maximum likelihood (REML) method, proposed by Milliken and Johnson (1992). Broad-sense heritability of SF was estimated with the variance components, considering the average of each $F_{2:3}$ family as the selection unit, using the method proposed by Falconer and Mackay (1996):

$$\hat{H}^2 = \frac{\hat{\sigma}_{\text{g}}^2}{\hat{\sigma}_{\text{e}}^2/rt + \hat{\sigma}_{\text{ge}}^2/t + \hat{\sigma}_{\text{g}}^2},$$

where: $\hat{H}^2$, estimated broad – sense heritability; $\hat{\sigma}_{\text{g}}^2$, estimated genetic variance; $\hat{\sigma}_{\text{e}}^2$, estimated experimental error variance; $\hat{\sigma}_{\text{ge}}^2$, estimated genotype × environment interaction variance; r = number of replications; t = number of test environments.

Parent–offspring regression: Heritability was also estimated with the slope (b) of the linear regression between the SF of parents (F_2 generation, x) and that of their offspring ($F_{2:3}$ generation, y), following the method proposed by Lush (1940). To reduce the effect of the environment, the regression was performed with standardized SF data of offspring vs. standardized SF of the corresponding parent (Frey and Horner 1957). The standardization was performed as:

$$Z_{if_p} = \frac{\bar{X}_{if_p} - \bar{X}_{ip}}{S_{ip}},$$

where: i, each environment; $\bar{X}_{if_p}$, SF mean value of the fth family in the pth population in the ith environment; $\bar{X}_{ip}$, SF mean value of the pth population in the ith environment; S_{ip}, SF standard deviation of the pth population in the ith environment; Z_{if_p}, standardized SF value of the fth family of the pth population in the ith environment.

Realized heritability: According to Falconer and Mackay (1996), the heritability of a trait can be estimated by the quotient between the response to selection (difference between the average performance of the offspring of the selected parents and that of all progeny) and the selection differential (difference between the mean of the selected individuals of a population and the general mean of the population from which they were selected). The heritability obtained by this procedure is called 'realized heritability'. In this work, we performed selection of the 50 F_2 plants with the highest SF in each of the two populations under study (i.e. the top 25%). The formula used was as follows:

$$H_{\text{R}}^2 = \frac{\bar{X}_{\text{s.F}_3} - \bar{X}_{\text{F}_3}}{\bar{X}_{\text{s.F}_2} - \bar{X}_{\text{F}_2}},$$

where: H_{R}^2, realized heritability; $\bar{X}_{\text{s.F}_3}$, mean SF of F_3 families derived from selected F_2 plants; $\bar{X}_{\text{F}_3}$, mean SF of all F_3 families; $\bar{X}_{\text{s.F}_2}$, mean SF of selected F_2 plants, $\bar{X}_{\text{F}_2}$, mean SF of all F_2 plants; $\bar{X}_{\text{s.F}_3} - \bar{X}_{\text{F}_3}$, response to selection; $\bar{X}_{\text{s.F}_2} - \bar{X}_{\text{F}_2}$, selection differential.

Effect of selection for high spike fertility on spike yield components: To analyse the effect of selection for high SF on other spike yield components in the F_3 generation, we calculated the increase/decrease in WG, GN/spike and SDW/spike of the 50 $F_{2:3}$ families with the highest SF values (termed 'selected group') as compared to the remaining, unselected group. Student's t-test was used for establishing the statistical significance of these comparisons.

All statistical analyses were performed using the R program (RCore-Team 2012), and mixed models were fitted with function LMER from package LME4 (Bates et al. 2013). The critical level of significance used was 0.05 in all statistical tests.

Results
Meteorological and environmental conditions

Crops grown in Balcarce and Miramar during the 2009/10 and 2010/11 crop season had radiation, temperature and water availability similar to the respective historical average values, which allowed a normal growth and development (Table S1). None of

the sites suffered freezing during reproductive stages, which could have adversely affected the crop.

Average flowering time was similar in both populations and evaluation sites, and virtually all families flowered within ~1 week in mid-November (Table S2).

Spike fertility in parental cultivars

Parent SF values (Table 1) were consistent with those obtained in previous experiments (P.E. Abbate, unpublished results). 'Soissons' and 'Baguette' 10 had greater SF than 'PROINTA Pigüé' and 'Klein Chajá' ($P < 0.05$), whereas no interaction effect between parental cultivars and environments was detected ($P > 0.05$).

Frequency distribution of spike fertility in the population

Bell-shaped, nearly symmetrical distributions of SF were observed in both populations and sites (Fig. 1). In all cases, the existence of substantial transgressive segregation (i.e. the occurrence of families with SF values that were more extreme than those of the parents) was observed.

Estimation of variance components and heritability of spike fertility

Broad-sense heritability of SF calculated from variance components was 0.60 and 0.51 for PIG/SSN and B10/KCJ population, respectively (Table 2). Although there was a strong environmental effect on SF, evidenced when comparing results at Balcarce and Miramar (see below), significant genotype × environment variance interaction was detected only in population B10/KCJ (Table 2) and its value represented only 14% of the total variation.

Table 1: SF value for parental cultivars at each location (Balcarce and Miramar) and overall mean of each cultivar

Cultivar	SF (grains/g)		
	Balcarce	Miramar	Mean[1]
Soissons	72	101	87 a
PROINTA Pigüé	54	72	63 b
Baguette 10	73	99	86 a
Klein Chajá	54	70	62 b

[1] Means with the same letter are not significantly different (LSD = 17.5 grains/g).

Parent–offspring regression

Heritability estimate by parent–offspring regression analysis was 0.43 in both populations (Fig. 2). This is, on average, 0.13 lower than heritability estimates obtained by variance components (average 0.56, Table 2).

Realized heritability

Realized heritability was 0.30 and 0.28 for populations PIG/SSN and B10/KCJ, respectively (Table 3). These values were, on average, 0.27 lower than those calculated using variance components and 0.14 lower than those obtained by parent–offspring regression.

Spike yield components

Average YLD/spike was higher in Miramar (1.5 and 1.4 g/spike in PIG/SSN and B10/KCJ, respectively) than in Balcarce (1.3 and 1.1 g/spike in PIG/SSN and B10/KCJ, respectively). These differences were mainly due to increased GN/spike,
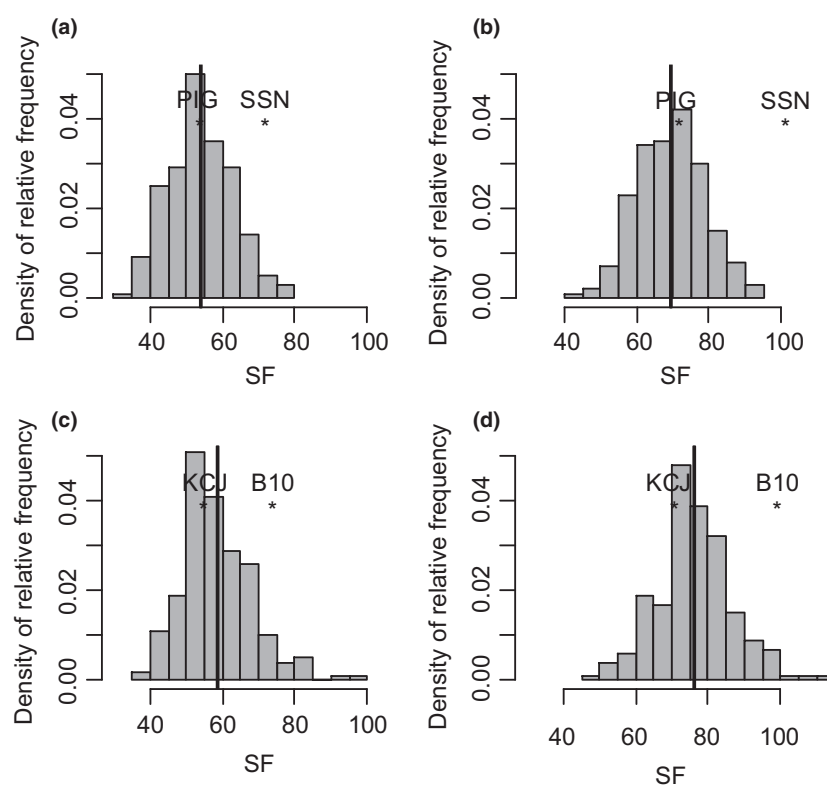

Fig. 1: Frequency distribution of spike fertility (grains/g) in the F_3 generation of population PIG/SSN in (a) Balcarce and (b) Miramar, and population B10/KCJ in (c) Balcarce and (d) Miramar. Vertical black lines indicate the mean of each distribution, and asterisks indicate the mean of each parent in each location. Mean standard error of the parents: 6.54 SF grains/g

Table 2: Estimated variance components and heritability of spike fertility (SF) for populations PIG/SSN and B10/KCJ. Genetic variance (V_g), genotype × environment interaction variance (V_{ge}), error variance (V_e) and broad-sense heritability (H^2). Data of two locations (Balcarce and Miramar)

Estimated variance components	PIG/SSN	B10/KCJ
V_g	35.5	34.1
V_{ge}	0.5 ns	18.1
V_e	92.7	92.7
H^2	0.60	0.51

ns, non-significant (by χ^2 restricted maximum likelihood ratio test $P > 0.05$).

which was 13% and 21% higher in Miramar than in Balcarce, whereas WG was only 4% and 10% higher in Miramar than in Balcarce for populations PIG/SSN and B10/KCJ, respectively. Average SF was higher in Miramar for both populations, exceeding that obtained in Balcarce by 29% and 30% for population PIG/SSN and B10/KCJ, respectively. On the other hand, SDW/spike was higher in Balcarce than in Miramar by 17% and 20% for populations PIG/SSN and B10/KCJ, respectively. Table 4 describes the mean of all spike yield components mentioned above for populations PIG/SSN and B10/KCJ in Balcarce and Miramar.

Spike fertility was positively correlated with GN/spike in both sites and segregating populations (0.50 and 0.47 for population PIG/SSN in Balcarce and Miramar, respectively, and 0.51 and 0.50 for population B10/KCJ in Balcarce and Miramar, respectively; Fig. 3). Two negative relationships were found between SF and other spike yield components: (i) SF vs. SDW/spike and (ii) SF vs. WG (Fig. 3). The first one had the highest correlation coefficients (−0.73 for population PIG/SSN in both environments, and −0.39 and −0.42 for population B10/KCJ in Balcarce and Miramar, respectively). A weaker negative relationship was detected between SF and WG in both populations (−0.20 and −0.32 for population PIG/SSN in Balcarce and Miramar, respectively, and −0.31 and −0.39 for population B10/KCJ in Balcarce and Miramar,

respectively). All these correlation coefficients were significant ($P < 0.05$).

Effect of selection for high spike fertility on spike yield components

Table 4 shows the effect of selection for high SF (i.e. selection of the top 25% of the $F_{2:3}$ families) in the selected group as compared with the remaining, unselected one. In both sites and segregating populations, the mean GN/spike of the selected group was higher than that of the remaining one ($P < 0.05$). On the other hand, the selected group's mean SDW/spike and WG were lower than the remaining group's mean ($P < 0.05$) in both sites and populations.

Selection of the top 25% $F_{2:3}$ families with the highest SF resulted in a 12% increase in GN/spike, despite a 13% and 5% decrease in SDW/spike and WG, respectively, on average across environments and populations, as related to the unselected families (Table 4).

Discussion

The idea of SF as a key determinant of yield in wheat was first postulated by Fischer (1984) and later demonstrated in commercial cultivars by Abbate et al. (1998). However, virtually no studies were available so far on the genetic control of this trait and its heritability. The present study shows that SF is apparently controlled by several genes, as reflected by the occurrence of substantial transgressive segregation in both populations and evaluation sites. Results obtained in both segregating populations with three different estimation methods also suggest that SF is a moderately heritable trait.

Parent–offspring regression and realized heritability estimations were lower than those obtained by variance components, probably due to the fact that data from the F_2 generation derived from a different environment than the ones used for evaluating the F_3 generation. On the other hand, the estimation of variance components reported here was performed with data of the F_3 generation evaluated in replicated trials in two different
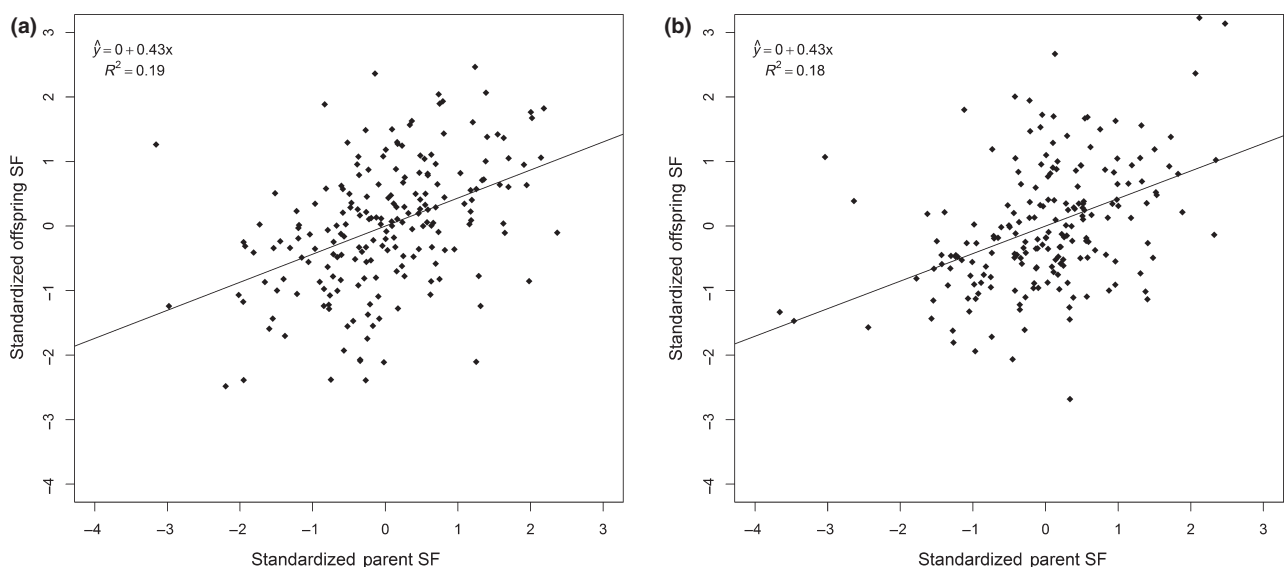

Fig. 2: Linear regression of spike fertility (SF) of the offspring (F_3 generation) on the SF of the parents (F_2 generation), in standardized values averaged across locations (Balcarce and Miramar), for (a) PIG/SSN population and (b) B10/KCJ population

Table 3: Mean spike fertility (SF) of a group of families selected in the F_2 generation (top 25% of the population) and that of their offspring (F_3 generation), general mean of the F_2 and F_3 generations (i.e. without selection) and realized heritability of populations PIG/SSN and B10/KCJ (mean of two locations: Balcarce and Miramar)

Population	Variable	F_2	F_3
PIG/SSN	Mean SF of the selected group (top 25%; grains/g)	94.5	66.7
	General SF mean (grains/g)	75.4	61.6
	Realized heritability		0.30
B10/KCJ	Mean SF of the selected group (top 25%; grains/g)	99.2	74.1
	General SF mean (grains/g)	78.3	67.4
	Realized heritability		0.28

Table 4: Mean ($Mean_{op}$) for original populations PIG/SSN and B10/KCJ, mean of selected group ($Mean_{sg}$) for high SF (top 25% of the $F_{2:3}$ families) and mean of the remaining group ($Mean_{rg}$) in spike fertility (SF, grains/g), grain number per spike (GN/spike), spike dry weight per spike (SDW/spike, g/spike) and weight per grain (WG, mg/grain) in Balcarce and Miramar. The percentage of change in spike yield components after selection for high SF per population and location, and across populations and locations

		SF (grains/g)		GN/spike (grains/spike)		SDW/spike (g/spike)		WG (mg/grain)	
	Population	Balcarce	Miramar	Balcarce	Miramar	Balcarce	Miramar	Balcarce	Miramar
$Mean_{op}$	PIG/SSN	54.0	69.5	36.3	40.9	0.7	0.6	35.0	36.3
	B10/KCJ	58.4	76.2	31.8	38.6	0.6	0.5	34.0	37.4
$Mean_{sg}$[1]	PIG/SSN	65.7	81.3	39.3	42.4	0.6	0.5	34.3 ns	34.3
	B10/KCJ	71.0	89.5	35.8	41.9	0.5	0.5	33.0	35.6
$Mean_{rg}$	PIG/SSN	50.1	65.6	35.3	40.3	0.7	0.6	35.2	36.9
	B10/KCJ	54.2	71.7	30.4	37.5	0.6	0.5	34.3	38.0
% change after selection for high SF	PIG/SSN	31.3	24.0	11.3	5.3	−15.7	−15.9	−2.6	−7.1
	B10/KCJ	31.0	24.7	17.8	11.9	−10.1	−10.8	−3.9	−6.2
% change after selection for high SF across populations and locations		28		12		−13		−5	

[1]All effects ($Mean_{sg}$ vs. $Mean_{rg}$ at each population and location) were significant ($P < 0.05$) except where denoted by 'ns' (non-significant).

environments. This allowed a more accurate estimation of the genetic component of phenotypic variation, of the genetic × environment interaction, and thus of heritability. Interestingly, realized heritability values were greater than zero for both populations, which indicates that selection carried out as early as in the F_2 generation would generate, in the F_3 generation, a mean SF greater than that of the original population.

The two environments used in the present work were different enough as to produce significant environmental variances and very different means in all variables under study (Tables 2 and 4); this was probably due to intrinsic differences in field conditions of each experiment. In turn, a significant genotype × environment interaction effect was detected for SF in only B10/KCJ population, but it represented a small proportion of the total variation. Similarly, Abbate et al. (1998, 2007) observed no genotype × environment interaction for SF in cultivars evaluated across environments. A more precise estimation of such variance components is likely to be obtained using more environments, which could be possible in more advanced generations, when enough seed is available.

Parental SF means were as expected, based on data from previous experiments carried out in 7.7 m^2 plots for several years at Balcarce (P.E. Abbate, unpublished results); these data had been used to choose the parents for developing the populations under study. This indicates that the size of the experimental units used in this work was adequate as to evidence differences in SF between genotypes.

This study also analysed the effect of selection for high SF on GN/spike, SDW/spike and WG in segregating populations. The use of segregating populations allowed detecting a greater magnitude of trait variability than the one observed in studies performed with commercial cultivars, for both each trait *per se* and its association with the remaining traits. In both sites and segregating populations, the selected group's average GN/spike was higher than that of the remaining, unselected population. This suggests that SF could be a surrogate for GN, although further studies are needed to ascertain whether this association, observed at the individual spike level, holds true with GN/m^2 in segregating lines. Actually, P.E. Abbate (personal communication), when analysing field experiments carried out in Balcarce from 1996 to 2011 with at least 15 cultivars each, never found a negative relationship between GN/m^2 and SF. Nevertheless, the findings shown here should be corroborated in advanced breeding lines, in which the use of larger experimental plots allows evaluating GN/m^2 and yield/m^2.

The selected group's average SDW/spike was lower than that of the unselected group in both sites and segregating populations, and also a negative correlation between this trait and SF was detected (Fig. 3). Similarly to what was discussed above, this should be verified as per unit area in more advanced generations. Dreccer et al. (2009) and Lázaro and Abbate (2012) also reported the existence of a strong negative correlation between SF and SDW in commercial cultivars. However, no such correlation was found by Abbate et al. (1998) or González et al. (2011). These apparently conflicting results could suggest differences in the genetic constitution for the traits under study or the genetic background from which these cultivars were derived after selection. Nevertheless, the data obtained in this work as per spike and in Lázaro and Abbate (2012) as per unit area show that the decrease in SDW/spike and SDW/m^2 driven by selection
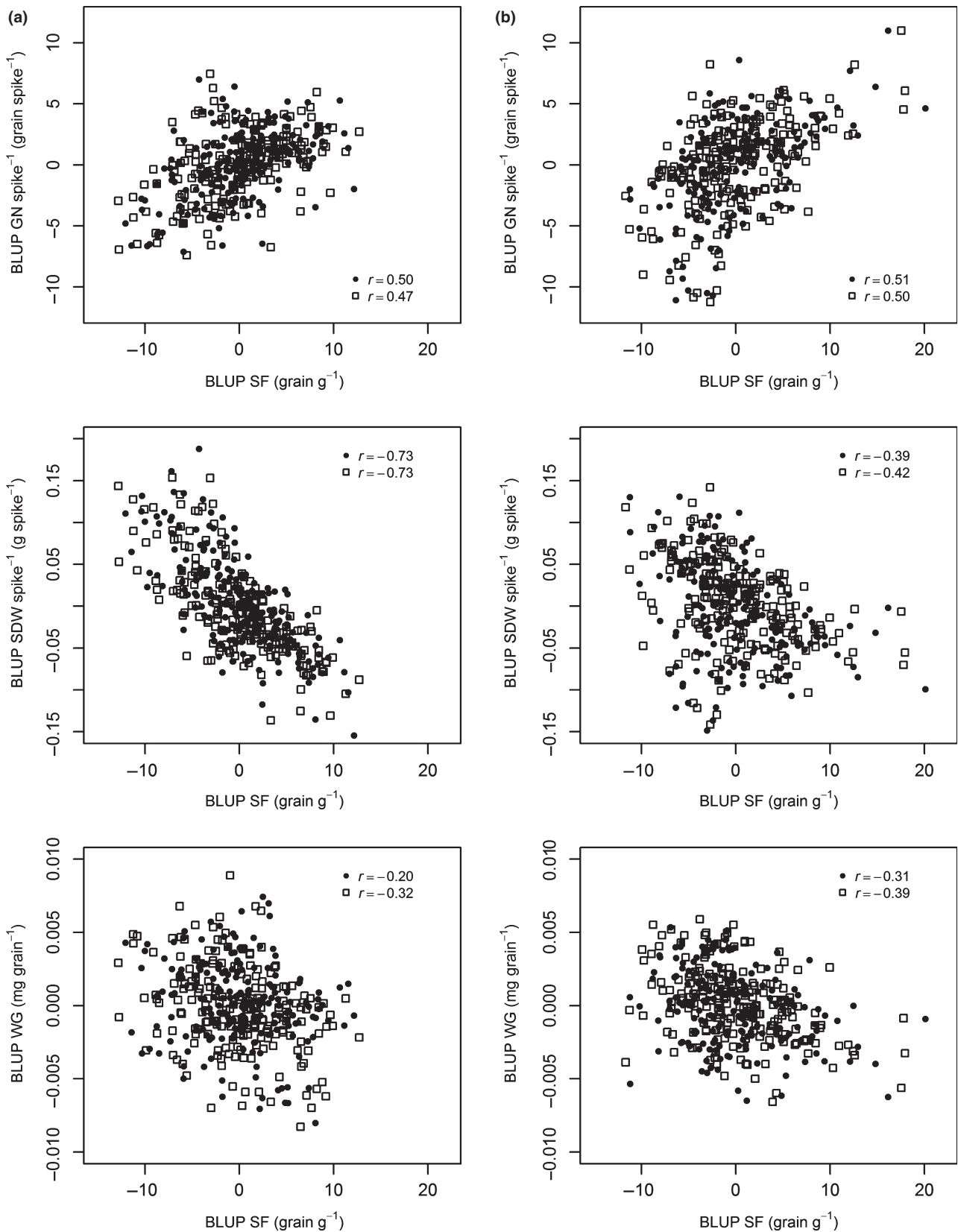
Fig. 3: Correlation of best linear unbiased predictors for grain number per spike (GN/spike, grains/spike) vs. spike fertility (SF, grains/g), spike dry weight per spike (SDW/spike, g/spike) vs. SF and weight per grain (WG, mg/grain) vs. SF for populations (a) PIG/SSN and (b) B10/KCJ, at Balcarce (full symbols) and Miramar (empty symbols). All correlation coefficients were significant (P < 0.05)

for high SF is not important enough to prevent the increase in GN/spike and GN/m^2, respectively.

Although GN/m^2 is the component which best explains yield variations (Fischer 1985, Abbate et al. 1995, Calderini et al. 1999), the negative relationship between WG and SF that was found here, although weak, could eventually counteract the positive effect of SF on GN (Fischer 2007). Nevertheless, the data obtained in this work as per spike and in Abbate et al. (1998) and Lázaro and Abbate (2012) as per unit area show that the decrease in WG driven by selection for high SF is not important enough to prevent the increase in YLD/spike and YLD/m^2, respectively. Similarly to what was stated previously, further studies are warranted to determine this association in advanced breeding lines.

In conclusion, it has been shown that SF appears to be a moderately heritable trait with low genetic × environmental interaction and that selection for high SF, which can be performed from early generations, appears to result in increased GN/spike despite a negative but incomplete association with SDW/spike and WG. This gives support to the application of early selection for high SF in breeding programmes, although future research should analyse the relationship between SF, WG, and GN and YLD per unit area in advanced breeding lines.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Mean temperature, photosynthetically active radiation and precipitation plus irrigation from sowing to physiological maturity for the 2009/10 and 2010/11 crop seasons at Balcarce, and for the 2010/11 crop season at Miramar, and historical average values.

Table S2. Date on which 5, 50 and 95% of the $F_{2:3}$ families of each PIG/SSN and B10/KCJ populations reached flowering stage at Balcarce and Miramar in the 2010/2011 crop season.