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CROPS AND SOILS RESEARCH PAPER
Genetic variation for wheat spike fertility in cultivars and early breeding materials

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SUMMARY

Grain yield in bread wheat is often tightly associated with grain number/m^2. In turn, spike fertility (SF), i.e., the quotient between grain number and spike chaff dry weight, accounts for a great proportion of the variation in grain number among cultivars. In order to examine the potential use of SF as a breeding target, (1) variation for the trait was assessed in six datasets combining commercial cultivars under different environmental conditions, (2) trait heritability was estimated in a set of F_1 hybrids derived from controlled crosses between cultivars with contrasting SF and (3) SF distribution pattern was analysed in two F_2 segregating populations. Analysis of commercial cultivars revealed considerable variation for SF, under both optimal and sub-optimal conditions. In addition, genotypic variation was consistently larger than genotype × environment interaction variation in all datasets. Narrow sense heritability, estimated by the mid-parent-offspring regression of 20 F_1 hybrids and their respective parents, was 0·63. Data from two F_2 populations exhibited bell-shaped and symmetric frequency distributions of SF, with a SF mean intermediate between the parental values. Substantial transgressive segregation was detected in both F_2 populations. In conclusion, SF appears to be a heritable trait with predominantly additive effects. This warrants further investigation on the feasibility of using SF as an early selection criterion in wheat breeding programs aimed at increasing grain yield.

INTRODUCTION

Increasing grain yield is one of the primary objectives of most bread wheat (*Triticum aestivum* L.) breeding programmes worldwide. During the last 50 years, most yield progress in wheat has been associated with increased harvest index. In particular, breeding efforts in raising grain yield have mainly modified one of the yield components, namely grain number/m^2 (GN; Austin 1982; Slafer & Andrade 1989; Slafer *et al.* 1990). Grain number continues to be the component which best explains yield variations (Shearman *et al.* 2005), but it is a difficult trait to select for in early generations of a breeding programme, in which not enough seed is available for

accurately determining traits per unit area. Therefore, understanding the physiology of GN determination is a good way to identify traits to further improve yield potential. Fischer (1984) proposed that, under optimal growing conditions (i.e., without water or nutrient limitations and in the absence of pests and diseases), GN in wheat can be considered as the product of (i) the duration of the rapid spike growth period (SGP), (ii) the crop growth rate during the SGP, (iii) the dry weight partitioning to spikes during the SGP and (iv) the number of grains per unit of spike chaff dry weight, i.e., a measure of spike fertility (SF).

Data from Stapper & Fischer (1990) revealed differences in SF among Australian wheat cultivars; however, the authors considered that SF differences were not relevant in GN determination. Later, Abbate *et al.* (1998) observed that increased GN in

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high yielding Argentine cultivars was actually associated with higher SF values. Since then, several authors have reported the existence of substantial variation in SF among modern cultivars (Shearman *et al.* 2005; Fischer 2007; Acreche *et al.* 2008; González *et al.* 2011, Lázaro & Abbate 2012; Abbate *et al.* 2013). In addition, a few studies (Abbate *et al.* 1997, 1998, 2007, 2013) have provided some proof of stability of the trait under different environments, although this needs to be further investigated.

Based on this evidence, several authors have suggested that this ecophysiological trait could be used as a selection criterion in breeding programs aiming at increasing grain yield (Fischer 2007, 2011; Foulkes *et al.* 2011; González *et al.* 2011; Lázaro & Abbate 2012; Abbate *et al.* 2013). Also, Abbate *et al.* (2013) have proposed a fast and simple method to screen for SF at maturity in a small sample of individual spikes. Hence, SF could be used as a selection criterion in early generations of a breeding programme. However, no information has yet been generated on the genetic basis of phenotypic variation for the trait and its mode of inheritance. The current paper reports (1) evidence of variation and stability of SF in six datasets combining commercial cultivars under different environments, (2) the estimation of trait heritability in F_1 hybrids derived from controlled crosses between commercial cultivars with contrasting SF and (3) an analysis of SF distribution pattern in two F_2 segregating populations.

MATERIALS AND METHODS

Assessment of spike fertility in commercial cultivars

Characteristics of experiments and datasets

A wide set of partially published data (Abbate *et al.* 1998, 2005, 2007, 2013; Cantarero *et al.* 1998; Abbate & Demotes-Mainard 2001; Lázaro & Abbate 2012) from 17 field experiments (Table 1) was used for analysing SF variation and stability in wheat commercial cultivars. Six datasets were built by combining two to five experiments per dataset, which were carried out under similar management practices but in different locations or years, and included at least three cultivars in common, all with chemical control of weeds, pests and fungal diseases. An overview of each dataset is presented in Table 1 and the distinctive characteristics of each dataset are described herein.

In Dataset 1, two Argentine and two British cultivars were compared, while two Argentine and two

Mexican cultivars were evaluated in Dataset 2. Both datasets comprised experiments carried out without water or nutrient limitations (i.e., under potential conditions) at Balcarce, Argentina. Dataset 3 included one Mexican and three Argentine cultivars evaluated under potential conditions in Azul, Argentina, in 3 years with contrasting temperature and radiation. Dataset 4 compared three Argentine cultivars in three contrasting locations: Balcarce, Córdoba (Argentina) and Grignon (France), under potential conditions. Dataset 5 comprised experiments with four Argentine cultivars at five Argentine locations spanning 10° of latitude in the Argentine wheat belt, under rainfed conditions. In all cases, a randomized complete block design with three or four replications was used, and the experimental unit for each plot consisted of seven to nine rows wide (inter-row distance 17–20 cm) and at least 5 m long. Dataset 6 comprised two experiments with 15 cultivars of diverse origin which were used in controlled crosses, as detailed below.

Determination of spike fertility

Spike fertility was calculated as the quotient between grain number and spike chaff dry weight, either at 'anthesis' (growth stage GS62; Zadoks *et al.* 1974), as proposed by Abbate *et al.* (1997), or at 'maturity' (GS90) as proposed by Abbate *et al.* (2013). The first approach involved the determination of spike dry weight/m^2 7 days after anthesis, and grain number/m^2 at maturity, both by sampling 60–80 cm from the five central plot rows. Spike fertility determination at maturity was performed by taking two samples of at least 15 spikes each, in which spike chaff dry weight and grain number were determined. All samples were dried at 56 °C until constant weight before being processed.

Statistical analysis

A combined ANOVA was performed for each dataset (Annicchiarico *et al.* 2002) with fixed effects of cultivar (genotype), environment (location and/or year) and their interaction. Coefficients of variation of the ANOVA factors were calculated as follows:

$$CV_G = \frac{\sqrt{MS_G}}{\bar{x}}$$

$$CV_E = \frac{\sqrt{MS_E}}{\bar{x}}$$

$$CV_{G \times E} = \frac{\sqrt{MS_{G \times E}}}{\bar{x}}$$

Table 1. *Commercial cultivars evaluated and distinctive characteristics of each field experiment in six datasets of combined experiments used for examining SF variation*

Dataset number	Cultivars analysed in each dataset*	Characteristics of experiments in each dataset						
		Expt code	Site*	Location	Year of sowing	Growing conditions	Moment of SF determination†	Reference
1	Granero INTA (AR), PROINTA Puntal (AR), Hereward (UK), Rialto (UK)	BC98	Balcarce (AR)	37°45′S, 58°18′W, 130 m a.s.l.	1998	Irrigated	Anthesis	Abbate et al. (2005)
		BC99	Balcarce (AR)	37°45′S, 58°18′W, 130 m a.s.l.	1999	Irrigated	Anthesis	Abbate et al. (2005)
2	Granero INTA (AR), Baviacora (MX), Bacanora (MX)	BY95	Balcarce (AR)	37°45′S, 58°18′W, 130 m a.s.l.	1995	Irrigated	Anthesis	Abbate et al. (1998, 2005)
		BC96	Balcarce (AR)	37°45′S, 58°18′W, 130 m a.s.l.	1996	Irrigated	Anthesis	Abbate et al. (2005, 2013)
		BC98	Balcarce (AR)	37°45′S, 58°18′W, 130 m a.s.l.	1998	Irrigated	Anthesis	Abbate et al. (2005)
3	Buck Ámbar (AR)‡, Buck Ombú (AR), Granero INTA (AR), Bacanora (MX)	AP00	Azul (AR)	36°45′S, 59°50′W, 132 m a.s.l.	2000	Irrigated	Anthesis	Lázaro & Abbate (2012)
		AP99	Azul (AR)	36°45′S, 59°50′W, 132 m a.s.l.	1999	Irrigated	Anthesis	Lázaro & Abbate (2012)
		APC01	Azul (AR)	36°45′S, 59°50′W, 132 m a.s.l.	2001	Irrigated	Anthesis	Lázaro & Abbate (2012)
4	Granero INTA (AR), PROINTA Oasis (AR), PROINTA Puntal (AR)	BC95	Balcarce (AR)	37°45′S, 58°18′W, 130 m a.s.l.	1994	Irrigated	Anthesis	Abbate et al. (1997, 1998)
		BC96	Balcarce (AR)	37°45′S, 58°18′W, 130 m a.s.l.	1996	Irrigated	Anthesis	Abbate et al. (1998, 2005, 2013)
		BC97	Balcarce (AR)	37°45′S, 58°18′W, 130 m a.s.l.	1997	Irrigated	Anthesis	Abbate et al. (1998, 2013)
		CC97	Córdoba (AR)	31°33′S, 64°00′W, 360 m a.s.l.	1997	Irrigated	Anthesis	Cantarero et al. (1998)
		GN99	Grignon (FR)	48°59′N, 1°54′E, 700 m a.s.l.	1999	Irrigated	Anthesis	Abbate & Demotes-Mainard (2001)

Table 1. (*Cont.*)

Dataset number	Cultivars analysed in each dataset*	Characteristics of experiments in each dataset						Reference
		Expt code	Site*	Location	Year of sowing	Growing conditions	Moment of SF determination†	
5	BIOINTA 1001 (AR), BIOINTA 1002 (AR), Klein Chajá (AR), Klein Tauro (AR), BIOINTA 1001 (AR), BIOINTA 1002 (AR), Klein Chajá (AR), Klein Tauro (AR)	BO06	Bordenave (AR)	37°51′S, 63°01′W, 212 m a.s.l.	2006	Rainfed	Maturity	Abbate *et al.* (2007)
		BA06	Balcarce (AR)	37°45′S, 58°18′W, 130 m a.s.l.	2006	Rainfed	Maturity	Abbate *et al.* (2007)
		MI06	Miramar (AR)	38°10′S, 58°00′W, 64 m a.s.l.	2006	Rainfed	Maturity	Abbate *et al.* (2007)
		PE06	Pergamino (AR)	33°56′S, 60°33′W, 65 m a.s.l.	2006	Rainfed	Maturity	Abbate *et al.* (2007)
		RE06	Reconquista (AR)	29°18′S, 60°00′W, 42 m a.s.l.	2006	Rainfed	Maturity	Abbate *et al.* (2007)
6	Arche (FR), Bacanora (MX), Baviacora (MX), Baguette 10 (FR), BIOINTA 1001 (AR), Bourgogne (FR), Buck Charrúa (AR), INIA Churrinche (UR), INIA Torcaza (UR), Klein Chajá (AR), Klein Sagitario (AR), PROINTA Cinco Cerros (AR), PROINTA Pigüé (AR), PROINTA Puntal (AR), Soissons (FR)	Expt 1	Balcarce (AR)	37°45′S, 58°18′W, 130 m a.s.l.	2008	Rainfed	Maturity	
		Expt 2	Balcarce (AR)	37°45′S, 58°18′W, 130 m a.s.l.	2009	Rainfed	Maturity	

* Country of origin (in parenthesis): AR, Argentina; UK, United Kingdom; MX, Mexico; FR, France; UR, Uruguay.

† Anthesis: Spike dry weight measured 7 days after anthesis and grain number at maturity; Maturity: spike dry weight and grain number measured at maturity.

‡ Durum wheat.

where CV_G: genotype coefficient of variation, CV_E: environment coefficient of variation, $CV_{G \times E}$: genotype × environment interaction coefficient of variation, $\bar{x}$: general mean of variable, MS_G: genotype mean square, MS_E: environmental mean square, $MS_{G \times E}$: genotype × environment interaction mean square.

Assessment of spike fertility in parental cultivars and F_1 and F_2 generations

Crossing work

Fifteen bread wheat cultivars of diverse genetic background, contrasting for SF, were used in controlled crosses during the 2007/08 cropping season at the experimental field of the Unidad Integrada Balcarce, Argentina. Cultivars used were from Argentina (Baguette 10, BIOINTA 1001, Buck Charrúa, Klein Chajá, Klein Sagitario, PROINTA Cinco Cerros, PROINTA Pigüé and PROINTA Puntal), France (Arche, Bourgogne and Soissons), Mexico (Bacanora and Baviacora) and Uruguay (INIA Churrinche and INIA Torcaza). Flowers from several spikes per female parent were emasculated and bagged to avoid contamination with foreign pollen. Pollen was collected from each male parent immediately before pollination, which was done 2–3 days after emasculation. At maturity, seeds from each cross were harvested and stored individually. Most of the crosses, except a few, were made between cultivars of contrasting SF. Crosses performed depended on the coincident availability of spikes for both flower emasculation and pollen collection. This resulted in 20 crosses that yielded enough seed quantity for further experiments.

Crop husbandry

Two field experiments (termed Expt 1 and Expt 2) were conducted at Balcarce. Experiment 1 was carried out during the 2008/09 cropping season under a randomized complete block design with three replications. Treatments consisted of the parents and F_1 hybrids, grown at *c.* 65 seeds/m in a single 1 m-long row, 0·2 m from adjacent rows, as the experimental unit. Experiment 2 was carried out in the 2009/10 cropping season. Seeds of the 15 parental cultivars and of two F_2 populations (Baguette 10/Klein Chajá and Prointa Pigüé/Soissons) were sown in randomized 11 m-long plots consisting of seven rows spaced 0·2 m from adjacent ones, at *c.* 20 seeds per linear metre. Experiments

were conducted under no nutrient or water limitations, and weeds, pests and fungal diseases were controlled chemically.

Determination of spike fertility

In Expt 1, all spikes per experimental unit were collected at maturity for SF determination. In Expt 2, all spikes from five random plants per parental cultivar and from 200 random F_2 plants per cross (Baguette 10/Klein Chajá and ProINTA Pigüé/Soissons) were harvested at maturity. Spike fertility was calculated following Abbate *et al.* (2013)'s protocol as described above, except for the fact that samples were air-dried in order to preserve seed viability.

Statistical analysis

An estimation of the narrow sense heritability (h^2) of SF was obtained by the mid-parent-offspring regression of data from the parental cultivars and their respective F_1 hybrids. According to Lush (1940), the regression coefficient (*b*) can be considered an estimator of h^2. However, the use of parent and offspring data collected in the same environment and year could lead to inflated h^2 values due to significant genotype × environment interaction and error covariances (Casler 1982). One way to overcome this is to use parent data from 1 year and offspring data from a different year (Casler 1982). Also, Frey & Horner (1957) recommend performing the regression analysis with standardized data to reduce the effect of the environment. Therefore, a regression analysis was carried out with the standardized SF of the parents determined in Expt 2, on standardized data of their respective F_1 determined in Expt 1. Standardization was done with the quotient between the residuals of the mean of each experiment and their standard deviation.

Histograms for frequency distribution of SF were built for each of the two F_2 populations evaluated in Expt 2. They were expressed as density of relative frequency, i.e., the quotient between relative frequency and class width. Normality of these distributions was tested with a Shapiro–Wilk test. In order to obtain the percentage of transgressive individuals in each population (i.e., the occurrence of F_2 plants with SF values that were more extreme than those of the parents) 95% confidence intervals were made for parental cultivars. Confidence intervals were made for each parental

Table 2. *Maximum, minimum and mean SF values per dataset of combined experiments; significance level of environment (E), genotype (G) and G × E effects of ANOVA*

Dataset*	Number of cultivars	Number of environments	SF (grains/g)			$P (F > Fp)$†		
			Max.	Min.	Mean	G	E	G × E
1	4	2	102	79	90	<0·01	NS	NS
2	3	3	113	76	92	<0·001	NS	<0·05
3	4	3	113	58	86	<0·001	NS	<0·01
4	3	5	103	74	87	<0·001	<0·05	<0·05
5	4	5	71	58	65	<0·001	<0·001	NS
6	15	2	95	56	76	<0·001	<0·001	<0·001

NS, not significant.

* See Table 1.

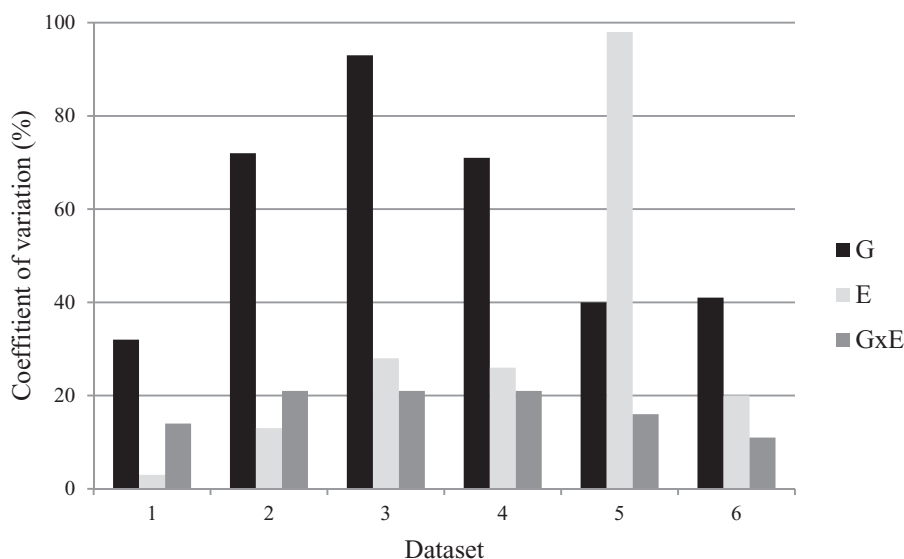† Probability of *F*-test (Fp) from ANOVA.

Fig. 1. Coefficient of variation of SF in ANOVA factors – genotype (G), environment (E) and genotype × environment interaction (G × E) – of six datasets of combined experiments with commercial cultivars.

cultivar as follows:

$$CI(95\%) = \bar{x} \pm t_{(n-1); \left(1 - \frac{0.05}{2}\right)} \times \frac{S}{\sqrt{n}}$$

where $\bar{x}$: mean of the cultivar; *t*: value of independent random variable of *t* distribution, with $n - 1$ degrees of freedom and $P < 0.05$; *n*: sample size; *S*: sample standard deviation.

RESULTS

Table 2 shows the maximum, minimum and mean SF values per dataset of commercial cultivars, as well as the significance level of ANOVA factors.

Considerable variation for SF among cultivars was observed in all datasets, under both optimal and sub-optimal growth conditions. Significant effects of genotypes were detected in all datasets, whereas genotype × environment interaction effects were significant in half of them; in addition, the $CV_{G × E}$ was always lower than the CV_G (3·3 times lower, on average; Fig. 1).

Narrow sense heritability of SF, as estimated by the mid-parent-offspring regression method with data from the 20 F_1 hybrids and their parents, was 0·63 ($R^2 = 0.38$, D.F. = 19, $P < 0.05$; Fig. 2; Table 3).

The density of frequency distribution of SF in the two F_2 populations is shown in Fig. 3. Both populations exhibited bell-shaped, symmetrical
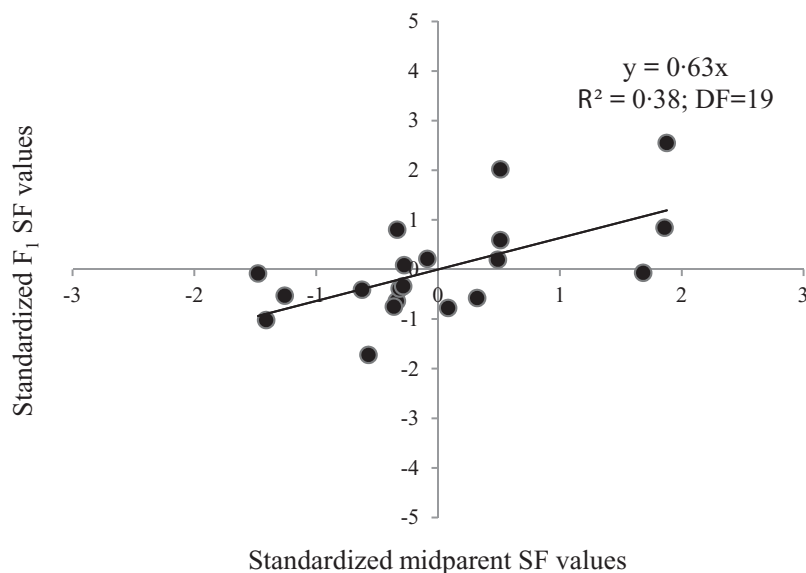
Fig. 2. Regression of SF of the offspring (20 F_1 hybrids; data from Expt 1, Table 3) on the mid-parent SF value (data from Expt 2), in standardized units.

distributions with mean values intermediate between those of their parents. Transgressive segregation was detected in both populations. The F_2 population derived from the cross between Baguette 10 and Klein Chajá showed 7% of individuals with SF lower than that of Klein Chajá and 7% of individuals with SF higher than that of Baguette 10, while the F_2 population derived from the cross between PROINTA Pigüe and Soissons showed 33% of individuals with SF lower than that of PROINTA Pigüe and 10% of individuals with SF higher than that of Soissons (Fig. 3).

DISCUSSION

The successful use of a given trait as a breeding target depends upon four pre-requisites: it should (1) be positively associated with crop performance, (2) be easily determined in early generations, (3) exhibit genetic variation and (4) have medium to high heritability (Andrade *et al.* 2009). The association of SF with GN and, ultimately, yield in wheat was first anticipated by Fischer (1984) through his 'assimilate approach', and then empirically confirmed by many authors (e. g. Abbate *et al.* 1997, 1998; Shearman *et al.* 2005; Fischer 2007; Acreche *et al.* 2008; González *et al.* 2011; Lázaro & Abbate 2012; Abbate *et al.* 2013). Regarding the ease of determination of the trait, Abbate *et al.* (2013) proposed a simple, fast method of assessing SF, amenable to high throughput application in the context of a breeding programme. On

the other hand, although many authors (cited above) have reported the existence of variability for SF among wheat cultivars, little information has been made available so far on the trait's stability under different environmental conditions and the genetic basis of phenotypic variation.

Analysis of several datasets of combined experiments with cultivars of diverse origin in different environments confirmed the existence of wide variation for SF among wheat cultivars, under both optimal and sub-optimal growth conditions. Different SF mean values observed among datasets were probably due to differences in environmental conditions, in the genetic constitution of the cultivars under study and/or in both. Despite the number of cultivars analysed here was not high (3–4 per dataset except for Dataset 6, with 15 cultivars), differences in SF were found in all datasets. Additionally, SF determination in cultivars more recently released in Argentina has revealed highly coincident results (P. E. Abbate and A. C. Pontaroli, personal communication).

Even though each dataset sampled a combination of a few cultivars and environments, a high number of experiments were analysed overall. In addition, genotypic variation was larger than genotype × environment interaction variation in all datasets, as reflected by comparing CV_G and $CV_{G \times E}$ at each dataset. This was observed consistently, regardless of the growing conditions, the method of SF determination used or the array of cultivars and environments under analysis.

Table 3. *Spike fertility values in parental cultivars and* F$_1$ *hybrids, used for the estimation of narrow sense heritability by mid-parent-offspring regression*

| Cross (female/male parent) | Year | SF (grains/g) | | | |
		Female parent	Male parent	P (F>Fp) for female/ male comparison*	F_1
Arche/Buck Charrúa	2008	71·8	62·0	<0·05	65·1
	2009	77·1	57·3	<0·05	
Arche/Klein Sagitario	2008	71·8	55·7	<0·05	70·7
	2009	77·1	55·8	<0·05	
BIOINTA 1001/Klein Chajá	2008	80·0	63·1	<0·05	50·1
	2009	73·3	72·0	<0·05	
Bourgogne/Klein Chajá	2008	105·6	63·1	<0·05	97·1
	2009	83·4	72·0	<0·05	
Bourgogne/PROINTA Cinco Cerros	2008	105·6	53·5	<0·05	63·8
	2009	83·4	57·4	<0·05	
Buck Charrúa/PROINTA Puntal	2008	62·0	90·9	<0·05	66·9
	2009	57·3	88·1	<0·05	
INIA Churrinche/PROINTA Pigüé	2008	81·4	65·9	<0·05	66·6
	2009	80·9	60·4	<0·05	
INIA Torcaza/Soissons	2008	97·6	94·4	<0·05	82·3
	2009	83·5	90·1	<0·05	
INIA Torcaza/Bourgogne	2008	97·6	105·6	<0·05	103·8
	2009	83·5	83·4	NS	
Klein Chajá/Bourgogne	2008	63·1	105·6	<0·05	79·1
	2009	72·0	83·4	<0·05	
Klein Sagitario/Baguette 10	2008	55·7	98·4	<0·05	67·5
	2009	55·8	89·4	<0·05	
PROINTA Cinco Cerros/Baguette 10	2008	53·5	98·4	<0·05	72·8
	2009	57·4	89·4	<0·05	
PROINTA Cinco Cerros/BIOINTA 1001	2008	53·5	80·0	<0·05	58·9
	2009	57·4	73·3	<0·05	
PROINTA Cinco Cerros/Bourgogne	2008	53·5	105·6	<0·05	81·8
	2009	57·4	83·4	<0·05	
PROINTA Pigüé/Soissons	2008	65·9	94·4	<0·05	62·0
	2009	60·4	90·1	<0·05	
PROINTA Puntal/INIA Torcaza	2008	90·9	97·6	<0·05	70·9
	2009	88·1	83·5	<0·05	
PROINTA Puntal/Klein Chajá	2008	90·9	63·1	<0·05	64·5
	2009	88·1	72·0	<0·05	
PROINTA Puntal/PROINTA Pigüé	2008	90·9	65·9	<0·05	74·4
	2009	88·1	60·4	<0·05	
Soissons/Klein Chajá	2008	94·4	63·1	<0·05	74·2
	2009	90·1	72·0	<0·05	
Soissons/Klein Sagitario	2008	94·4	55·7	<0·05	62·3
	2009	90·1	55·8	<0·05	

* Least significant difference for female/male parent comparison: 1·239. In all cases, significant differences were detected at $P < 0.05$, except where noted (NS).

The estimation of narrow sense heritability by mid-parent-offspring regression of F_1 hybrids and their respective parents suggests that additive effects play a relevant role in SF determination. The fact that symmetrical frequency distributions of SF were observed in two different F_2 populations segregating for the trait gives additional support to this hypothesis. Substantial transgressive segregation was also
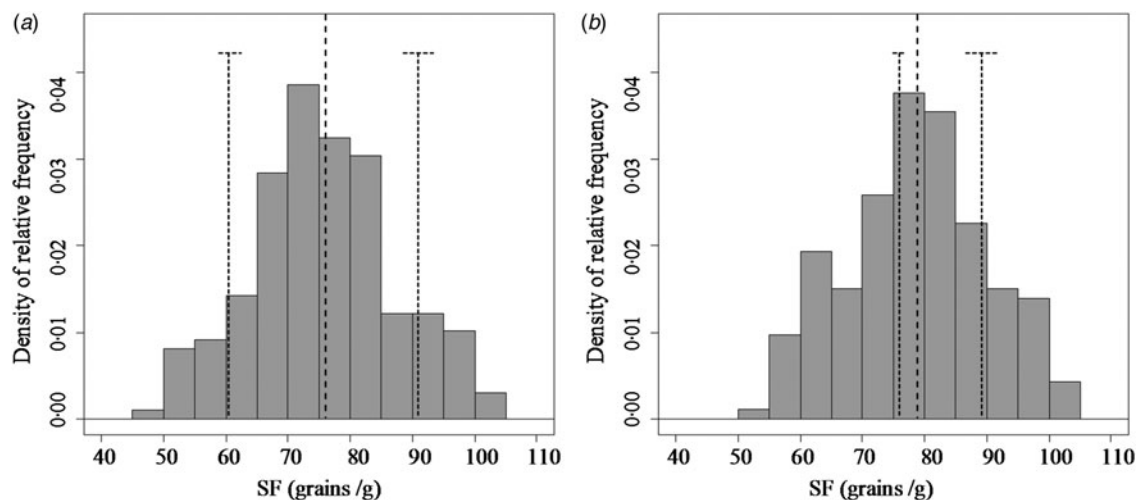
Fig. 3. Density of frequency distribution of SF in two F_2 populations: (A) PROINTA Pigüé/Soissons, $n = 197$; (B) Baguette 10/ Klein Chajá, $n = 186$. Population means are shown in thick, dashed vertical lines. Spike fertility of the parental cultivars are shown in thin, dashed vertical lines, with their respective standard deviation represented by a horizontal line at the top (A: left = PROINTA Pigüé; right = Soissons; B: left = Klein Chajá, right = Baguette 10).

detected in both F_2 populations, which may indicate that several genes are involved in the control of SF. The fact that at least 7% of individuals showed higher SF values than the parental cultivar of high SF in both populations under study is encouraging in terms of the feasibility of achieving genetic progress for the trait. Notwithstanding, and despite environmental and genetic × environmental interaction effects might be low in comparison with genetic effects, as was detected in cultivars, F_2 data might be slightly biased due to the fact that each plant is a unique genotype that cannot be replicated. Thus, the occurrence of a significant percentage of transgressive segregants with greater SF than the superior parent should be confirmed in more advanced generations, in which more seed is available for carrying out field trials with increased replications and/or more than one environment.

Although heritability may be meaningful only when related to the specific genetic population structure from which it was estimated and to the environmental conditions in which the plants were grown (Fehr 1987), the estimation of heritability in a set of F_1 hybrids gives support to the idea that SF is a heritable trait with predominance of additive (and possibly additive by additive) effects. This is of great importance in the context of a breeding programme aimed at increasing yield. In addition, selection in early generations seems feasible because of the high narrow sense heritability observed in the current study. Further work is needed to determine whether early selection increases SF in subsequent generations and, ultimately, leads to increased grain number (and yield) in advanced generations of a breeding programme.

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