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Heterosis and combining ability of seed physiological quality traits of single cross *vs.* three-way sorghum hybrids

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ABSTRACT. The aim of this research was to compare genetic parameters for traits related with seed germination and seedling vigour of single cross (SCH) *vs*. three-way (TWH) sorghum hybrids. The study was conducted in a sand bed under a greenhouse; 67 genotypes (four pairs of A- and B- lines, four R- lines, 13 SCH and 42 TWH) were allocated in a randomized complete blocks experimental design with three replications. Statistical analysis included ANOVA's and Student "t" tests, while Tukey test ($p \leq 0.05$) was applied for mean comparisons. The R-lines showed better physiological seed quality attributes than the A- and B- lines. The seed quality and heterosis values of SCH *vs.* that of TWH did not show significant differences ($p > 0.05$) for any variable; however, heterobeltiosis of SCH was higher than that of TWY for normal seedlings, dry weight of plumule and seedling emergence rate. The A2- line and R14 restorer line showed the highest GCA values in both types of hybrids. No differences ($p \leq 0.05$) were found between maternal and paternal effects of the A- and B- lines involved in the male sterile cross (female parent) of the TWH, except for plumule length in Line 5.

Keywords: *Sorghum bicolor* L. Moench, maternal effects, seedling emergence, sorghum lines, top-cross tests.

Heterose e capacidade de combinação de traços fisiológica qualidade de single cross *Vs.* a três híbridos de sorgo

RESUMO. O objetivo desta pesquisa foi comparar parâmetros genéticos para características relacionadas com germinação das sementes e vigor de plântulas de cruzamentos simples (SCH) *vs.* três vias (TWH) híbridos de sorgo. O estudo foi realizado em substrato a base de areia em estufa; 67 genótipos (4 pares de linhas A- e B-, 4 linhas R-, 13 SCH e 42 TWH) foram alocados em blocos completos com delineamento experimental inteiramente casualizado, com três repetições. A análise estatística incluiu testes de ANOVA e "t" Student; o teste de Tukey ($p \leq 0,05$) foi aplicado para comparação de média. As linhas – R apresentaram melhores atributos fisiológico de sementes de qualidade do que as linhas A- e B. Os valores de qualidade e de heterose de sementes de SCH *vs.* que TWH não apresentaram diferenças significativas ($p > 0,05$) para qualquer variável. No entanto, heterobeltiose de SCH foi maior do que a de TWH de plântulas normais, peso seco de plúmula e velocidade de emergência de plântulas. A Linha A2 e linha restauradora R14 apresentou os maiores valores da CGC nos dois tipos de híbridos. Não foram encontradas diferenças ($p \leq 0,05$) entre os efeitos maternos e paternos das linhas A- e B- envolvidas em cruzamentos entre plantas esteriles do sexo masculino (progenitor feminino) do TWH, exceto para o comprimento plúmula na Linha 5.

Palavras-chave: *Sorghum bicolor* L. Moench, efeitos maternos, emergência de plântulas, linhas de sorgo, testes top-cruzadas.

Introduction

In commercial seed production of single cross hybrids of grain sorghum [*Sorghum bicolor* (L.) Moench] two lines are involved: a male-sterile line (A- line, female), and a male fertile line (R- line, restorer) (León-Velasco, Mendoza-Onofre, Castillo-González, Cervantes-Santana, & Martínez-Garza, 2009a). In the three-way sorghum hybrids three lines are used since the female parent is a male-sterile cross of an A- line and a B- non isogenic line, and the male parent is an R- line. In both hybrid types, the progenie may express a higher plant vigour than the parents, an effect named heterosis, which is a relevant genetic trait frequently measured and used in plant breeding.

Mean heterosis (called as heterosis hereafter) is calculated based on the performance of the F1 hybrid with regard to the average performance of both parental lines (Kumar, Reedy, Ramaiah, &

Sharma, 2011); the high parent heterosis (called as heterobeltiosis hereafter) refers to the F1 hybrid behaviour with respect to the best parental line (Hayes & Rooney, 2014). Heterosis brings gains in grain yield, earlier flowering, greater number of leaves, taller plants, more tillers and panicles per plant, heavier seeds, more seeds per panicle (Acquaah, 2012), a faster seedling emergence rate, more vigourous seedlings and a higher plumule dry weight (Yu & Tuinstra, 2001; Cisneros-López, Mendoza-Onofre, Mora-Aguilera, Córdova-Téllez, & Livera-Muñoz, 2007; León-Velasco et al., 2009a). Compared to the three-way experimental sorghum hybrids, the single cross hybrids show a higher heterosis for grain yield (Rooney, 2004).

The three-way sorghum hybrids are not commercially grown in México (Montes-García, Williams-Alanís, Moreno-Gallegos, Cisneros-López, & Pecina-Quintero, 2012) nor anywhere else. However, in corn (*Zea mays* L.) these hybrids are highly profitable for seed producing companies due to the high heterosis obtained for seed yield in the female single cross (female parent of this type of hybrid), as contrasted to the lower seed yield harvested from a female pure-line (female parent of the single cross hybrid) (Beck, 2002).

Several A-, B- and R- sorghum lines adapted to the Mexican Highlands have been developed and single cross hybrids have been evaluated under field conditions for different purposes (Osuna-Ortega et al., 2000; Cisneros-López et al., 2007; 2010; Cisneros-López, Mendoza-Onofre, & González-Hernández, 2012; León-Velasco et al., 2009a). In this region (mean annual rainfall, 655 mm; average daily temperature, 16.3°C; 2,250 m of altitude) seedling growth of experimental conventional (single cross) sorghum hybrids is slow at the beginning of the growing season. In seedling emergence tests conducted in sand beds, seed size has not been the main responsable factor of this slow sorghum seedling growth (Cisneros-López et al., 2007; Valadez-Gutiérrez et al., 2007). On the other hand, the physiological seed quality traits of three-way sorghum hybrids are unknown. Therefore, it is necessary to compare these traits in three-way hybrids *vs.* single cross hybrids, assuming that in the three-way hybrids the single cross female parent seeds will have better physiological attributes than those produced by the pure female line.

A genetic trait closely related to heterosis is the combining ability of the parents. The general combining ability (GCA) is the capacity of an individual or a population of individuals to combine with others, and it is estimated by the average performance in their hybrid combinations, whereas the specific combining ability (SCA) is the particular performance of two parental lines in a hybrid combination. These two responses are useful to select parental lines of sorghum hybrids (Kenga, Alabi, & Gupta, 2004; Solanki, Patel, Patel, & Desai, 2007; León-Velasco, Mendoza-Onofre, Castillo-González, Cervantes-Santana, & Martínez-Garza, 2009b).

The diallel crosses are widely used for measuring the GCA and SCA effects of agronomic traits in plant breeding programs. The top-cross test that involves crosses of corn lines with a tester, is another option to estimate GCA (Bradshaw, 2016). In three-way corn hybrids the more common tester is a single cross hybrid or a pure-line (Beck, 2002), whereas in single cross hybrids the elite lines are used as testers (Hallauer, Carena, & Miranda Filho, 2010). According to Castañón, Jeffers, Hidalgo, & Tosquy (1998), the top-cross test has successfully substituted the diallel crosses because it reduces pollination costs.

The aim of this research was to compare the magnitude of the heterosis, heterobeltiosis, and the general and specific combinig ability on seed physiological quality traits of single cross hybrids *vs.* three-way hybrids of sorghum, as well as maternal *vs.* paternal effects of single AxB crosses for those traits.

Material and methods

Seed of isogenic and non isogenic single crosses AxB was increased in the spring-summer growing season of year 2012, according to a diallel squeme (Figure 1). Four pairs of A- and B- lines were included, so sixteen AxB male-sterile crosses were obtained. Four of these crosses correspond to isogenic AxB crosses; it means these are seed increments of the A- line (the female parental line of single cross hybrids). The other twelve are non isogenic crosses that correspond to the female parental single cross of the three-way hybrids. In addition, in this diallel we can also differentiate maternal *vs.* paternal effects of the isogenic A- and B- lines. For example, the average of A1xB2, A1xB3 and A1xB5 crosses will correspond to the performance of the A1- line as a female parent (maternal effects), and the average of A2xB1, A3xB1 and A5xB1 crosses will correspond to the performance of the B1- line (known as the maintainer line, isogenic of the A1- line) as a male parent (paternal effects).

Seed from the single cross hybrids and the three-way hibrids was increased in the 2013 growing season, by hand made pollinations between the sixteen AxB crosses and four R- lines (R14, R17, R19, and R25).

Male sterile lines	Maintainer lines			
	B1	B2	B3	B5
A1	A1xB1	**A1xB2**	**A1xB3**	**A1xB5**
A2	*A2xB1*	A2xB2	A2xB3	A2xB5
A3	*A3xB1*	A3xB2	A3xB3	A3xB5
A5	*A5xB1*	A5xB2	A5xB3	A5xB5

Figure 1. Diallel scheme of isogenic and non isogenic AxB crosses. Isogenic crosses (boxes in white); non isogenic crosses (boxes in grey). Non isogenic crosses to analize maternal effects of the A1 line (bold letters) and paternal effects of the B1 line (italics letters).

Seedling emergence test

This experiment was established in June 2014, including 67 genotypes (four pairs of A- and B- lines; four R- lines; 13 out of the expected 16 single cross hybrids, and 42 out of the 48 possible three-way hybrids), according to seed availability. Seed was sown in sand beds within a greenhouse. The experimental units were rows of 50 cm length, 5 cm apart. In each row 25 seeds were placed every 2 cm at 5 cm depth. Treatments were allocated in a randomized blocks design with three replications.

Variables measured in each plot were:

Seedling emergence rate (SER): Seedlings were counted daily (as soon as the plumule became visible) until no more seedlings emerged in three consecutive days. Then SER was estimated with the equation of Maguire (1962): $SER = \Sigma^{n}_{i} (Xi/Ni)$, where Xi = number of emerged seedlings on day i, and Ni = number of days after sowing including day i.

Normal seedlings (NS), abnormal seedlings (AS) and dead seeds (DS) were also counted at the end of the essay, as specified by International Seed Testing Association (ISTA, 1999) rules, and its respective percentages were calculated. Aditionally, plumule length (PL) and plumule dry weight (PDW) from 10 normal seedlings were measured; PL was the length (cm) from the base of the stem to the apex of the youngest leaf; and PDW (mg per seedling) was recorded after seedlings were dried in an oven at 75°C for 72h.

Heterosis [(Performance of the F1/Average performance of the parental lines: two in single cross hybrids and three in three-way hybrids) x 100] and heterobeltiosis [(Performance of the F1/Performance of the best parent) x 100] (Hayes & Rooney, 2014) were calculated for each hybrid. Data of the fertile lines (B and R) was used in these calculations to assure a full seed set of the panicles.

Estimates of GCA and SCA in both types of hybrids were obtained considering top-cross tests. In these tests, the term "lines" were assigned to each A-line in the analysis of single cross hybrids, and to the non isogenic AxB crosses in the three-way hybrids. The term "tester" was assigned to the R- lines. Therefore, the GCA of lines and testers were estimated through their respective averages; the SCA corresponded to the interaction of line x tester.

Maternal effects *vs.* paternal effects were compared for each AxB non isogenic crosses participating in the three-way hybrids. Maternal effects correspond to hybrids in which the version A of the line acted as female parent (direct cross), while paternal effects were those hybrids in which the maintainer B-line participated as the male parent (reciprocal cross) (Figure 1) of the male sterile single crosses. Therefore, the statistical contrast between maternal *vs.* paternal effects of Line 1, would correspond to the average performance of A1xB2, A1xB3, A1xB5 crosses (direct crosses, maternal effects) *vs.* the average performance of A2xB1, A3xB1 and A5xB1 crosses (reciprocal crosses, paternal effects), crossed to each R-line.

Statistical analyses

The statistical package SAS (2002) was used. Prior to the statistical analyses, an angular transformation [arcosin $(Yi)^{1/2}$] to the percentage data (Yi) was applied but results are shown in percentages. Mean comparison tests were applied (Tukey, $p \leq 0.05$) among genotype groups (A-, B-, R- lines, single cross hybrids and three-way hybrids). Since each hybrid group was represented by different number of observations (because there was not enought seed in some hybrids), PROC GLM of SAS (2002) was used to carry out the ANOVA's analysis. Statistical contrasts between the averages of the heterosis estimates of the 13 single cross hybrids *vs.* that of the 42 three-way hybrids were made by the Student "t" base on an unpaired design. To compare the differences of maternal effects *vs.* paternal effects the Student "t" test was also performed.

Results and discussion

Comparisons of groups of genotypes

There were significant differences ($p \leq 0.05$) among genotypes for all the genotypes groups (grouped according to their role in a sorghum breeding program), for all seed physiological quality traits, except for abnormal seedlings (Table 1).

Among parental lines, the male R-lines group showed much better seed physiological quality attributes than the A- and B- line groups; *i.e.*, higher percentage of normal seedlings, faster seedling emergence, as well as longer and heavier seedling plumules (Table 2). Most interestingly, the seed from the R- lines group was as good as the seed from the single cross and three-way hybrids regarding sed physiological quality traits.

Instead, the A- and B- inbred lines groups showed similar seed quality due to their isogenic nature. Under field conditions these lines are "3-dwarf" types (Brown, Rooney, Franks, & Kresovich, 2008) although our R- lines are usually more vigouous and reach higher stem size than isolines at harvest (León-Velasco et al., 2009a). There were no differences in seed physiological quality traits between the single cross hybrids and the three-way hybrids. These results clearly show that morphological differences in plant vigour can be detected as early as the seedling growth stage.

Cisneros-López et al. (2007) compared also seed germination and seedling emergence rate of single cross hybrids and their parental lines under field (same location as the present study), and laboratory conditions. They did not find either any significant difference between the hybrids and the R- lines, for percentages of normal seedlings, abnormal seedlings and dead seeds, plumule length and seedlings emergence rate. Yu &Tuinstra (2001) found similar results for variables related with seedling emergence rate in sorghum. That is, the *per se* seed performance of our group of R- lines is as good as that of seed obtained from hybrids. The absence of significant differences between the means of both groups of hybrids also suggest that the seed physiological quality traits do not rely on the female parents involved (pure-line for single cross hybrids or AxB non isogenic crosses for three-way hybrids), since all our male parents (R- lines) were the same in both types of hybrids.

Heterosis

Table 3 shows three features on the heterosis and heterobeltiosis results: (i) There were not significant differences ($p > 0.05$) for heterosis between single cross and three-way hybrids, in any of the four seed quality traits; (ii) Heterosis had greater values than those of heterobeltiosis for all traits in both types of hybrids; (iii) Single cross hybrids had higher heterobeltiosis than three-way hybrids for normal seedlings, plumule dry weight and seedling emergence rate.

Heterotic effects are expected to be maximized in single crosses depending upon the genetic diversity of the parental lines and the homocigous level of these lines. Contrary to cross pollinated species such as maize, sorghum is a self pollinated specie in which homocigosity can be reached without an important decrease in vigour. The high heterosis values obtained here for the single cross hybrids (from 126 and 166 % depending upon to the trait involved) indicate that in this group of parental lines exist genetic divergence between the A- lines and the R- lines.

Table 1. Square means and significance of the source of variation of the groups of genotypes for seed physiological quality traits.

Source of variation	DF	Normal seedlings	Abnormal seedlings	Dead seeds	Plumule length	Plumule dry weight	Seddlings emergence rate
Groups	4	1337.76**	47.17ns	1267.43**	30.12**	334.11**	8.43**
Replications	2	97.62ns	821.93ns	87.90ns	38.53**	146.59**	0.41ns
Error	194	85.88	70.70	79.19	1.40	12.59	0.51
VC (%)		17	62	28	13	26	28

DF: Degrees of freedom; VC: variation coefficient; **: Significance of the F test ($p \leq 0.01$): ns: not significant.

Table 2. Means of seed physiological quality traits for each group of sorghum genotypes.

Genotype group	Normal Seedlings (%)	Abnormal Seedlings (%)	Dead Seeds (%)	Plumule Length (cm)	Plumule dry weight (mg)	Seed e mergence rate (Nd^{-1})
A- lines (n=4)	45 b	9 a	44 b	7.78 b	8.5 b	1.76 b
B- lines (n=4)	40 b	6 a	52 b	6.24 c	6.1 b	1.42 b
R- lines (n=4)	73 a	5 a	19 a	8.75 ab	13.7 a	2.93 a
Single cross hybrids (n=13)	74 a	6 a	20 a	9.55 a	16.5 a	3.03 a
Three-way hybrids (n=42)	64 a	5 a	28 a	9.08 a	14.0 a	2.50 a

A: Male sterile lines; B: Maintainer lines; R: Restorer lines; (n): Number of genotypes involved in the average; Values with the same letter in each column are not significant different (Tukey, $p \leq 0.05$).

Table 3. Values of heterosis and heterobeltiosis for seed physiological quality traits for single cross and three-way sorghum hybrids.

Type of hybrids	Normal seedlings	Plumule length	Plumule dry weight	Seedling emergence rate
		Heterosis		
Single cross hybrids (n=13)	126 a	126 a	166 a	137 a
Three-way hybrids (n=42)	125 a	132 a	164 a	130 a
		Heterobeltiosis		
Single cross hybrids (n=13)	100 a	111 a	126 a	104 a
Three-way hybrids (n=42)	88 b	105 a	105 b	86 b

n: Number of genotypes involved in the average; values with the same letter in each column, are not significant different (Student "*t*" test, $p \leq 0.05$).

After evaluating parental lines with similar pedigrees under field conditions, Cisneros-López et al. (2007) found lower heterosis values (normal seedlings, 90%; plumule length, 98% and seedling emergence rate, 107%) for single cross hybrids than in our study. These differences in heterosis might be due to differences in environmental conditions, more adverse in the field for seed germination and seedlings emergence rate with respect to the sand bed test done under greenhouse conditions in our study. Heterosis in biomass production at early stages of development has also been observed under chilling temperatures in sorghum (Windpassinger et al., 2016) as well as in classical molecular biology studies on *Arabidopsis* (Meyer, Törjék, Becher, & Altmann, 2004).

According to Márquez (1988), heterosis will decrease as the number of parental lines involved in a hybrid increases (two in a single cross hybrid, three in a three-way hybrid or four in a double cross hybrid), probably because it is less likely that all pairs of genes will combine for favourable characters. Our results indicate that in this group of parental lines this phenomenon do not occur, as three-way crosses and single crosses has similar heterosis values (Table 2). This response may be related to a similar proportion of allelic additively expressed genes associated with heterosis in the early stage of development of both types of hybrids.

The heterobeltiosis values were of lower magnitude that those of heterosis in both types of hybrids. Cisneros-López et al. (2007) also found that heterobeltiosis values of the group of single cross hybrids were lower that the heterosis values (normal seedlings, 89 *vs*. 90%; plumule length, 94 *vs*. 98%; seed emergence rate, 92 *vs*. 107%). However, heterobeltiosis data represents greater agronomical importance than heterosis as the first indicates the superiority of the hybrid compared to the best parental line

General and specific combining ability

Lines and testers in single cross hybrids

No significant difference ($p > 0.05$) were found in the GCA of lines and testers for most of the seed quality measured traits, but line A2- tended to be better than the other females A- lines. There were not significant differences among testers either, except for seedling emergence rate of R 14 and R19 male lines (Table 4). Regarding the specific combining ability (SCA), the best combination for normal seedlings and seedlings emergence rate was the A2xR14 single cross hybrid.

Lines and testers in three-way hybrids

Similar to the single cross hybrids results, in the three-way hibrids the A and B versions of Line 2, and R14 among testers, were the only ones with high values of GCA for normal seedlings, plumule dry weight and sedling emergence rate (Table 5). Regarding SCA estimates, the superiority of R14 tester is evident, because when it is crossed to any female single cross, seeds of the three-way hybrids produce more normal seedlings, which can emerge at a faster rate (Table 5).

Table 4. Estimated values of general and specific combining ability (GCA and SCA) for seed physiological quality traits of female and male lines in single cross hybrids.

Female lines	Testers (male lines)				GCA
	R14	R17	R19	R25	
	Normal seedlings (%)				
A1	67 ab	--	--	79 ab	73 AB
A2	85 a	77 ab	83 a	81 ab	82 A
A3	82 a	65 ab	64 ab	--	70 AB
A5	72 ab	47 ab	74 ab	69 ab	66 B
GCA	77 W	63 W	74 W	76 W	
	Plumule length (cm)				
A1	8.53 a	--	--	9.40 a	8.97 A
A2	9.80 a	10.50 a	9.93 a	9.67 a	9.98 A
A3	10.07 a	9.40 a	9.70 a	--	9.72 A
A5	8.70 a	9.10 a	9.50 a	9.80 a	9.27 A
GCA	9.27 W	9.67 W	9.71 W	9.62 W	
	Plumule dry weight (mg)				
A1	12.4 a	--	--	16.4 a	14.4 A
A2	18.1 a	18.2 a	20.6 a	17.7 a	18.7 A
A3	18.0 a	15.1 a	19.1 a	--	17.4 A
A5	12.8 a	14.6 a	15.4 a	16.3 a	14.8 A
GCA	15.3 W	16.0 W	18.4 W	16.8 W	
	Seedlings emergence rate (N d^{-1})				
A1	2.62 ce	--	--	3.38 ad	3.00 B
A2	4.14 a	3.04 bd	3.72 ab	3.69 ac	3.65 A
A3	3.37 ad	2.71 be	2.40 de	--	2.83 B
A5	2.70 be	1.93 e	2.68 be	3.06 ad	2.59 B
GCA	3.21 W	2.56 X	2.93 WX	3.38 W	

GCA values with the same capital letter, or SCA values with the same lower case letter in each trait, are not significant different (Tukey, $p \leq 0.05$); --: hybrid not included in test.

Table 5. Estimated values of general and specific combining ability (GCA and SCA) for seed physiological quality traits of female and male lines in three-way hybrids.

	Testers (male lines)				
Female lines	R14	R17	R19	R25	GCA
	Normal seedlings (%)				
A1/B1	80 a	48 e	61 ce	61 ce	63 A
A2/B2	72 ac	55 de	68 ad	73 ac	67 A
A3/B3	78 ab	58 ce	54 de	65 bd	64 A
A5/B5	69 ad	53 de	63 ce	60 ce	61 A
GCA	75 W	53 Y	62 X	65 X	
	Plumule length (cm)				
A1/B1	9.47 a	9.66 a	8.64 a	8.41 a	9.05 A
A2/B2	8.98 a	9.59 a	9.20 a	8.87 a	9.16 A
A3/B3	9.65 a	9.71 a	8.72 a	8.77 a	9.21 A
A5/B5	9.28 a	9.04 a	8.82 a	8.56 a	8.93 A
GCA	9.35 WX	9.50 W	8.84 XY	8.65 Y	
	Plumule dry weight (mg)				
A1/B1	15.1 a	14.8 a	13.7 a	12.3 a	14.0 A
A2/B2	14.1 a	14.9 a	16.1 a	13.1 a	14.6 A
A3/B3	16.0 a	15.3 a	13.2 a	13.5 a	14.5 A
A5/B5	14.9 a	12.4 a	14.0 a	11.8 a	13.3 A
GCA	15.0 W	14.3 WX	14.3 WX	12.7 X	
	Seedlings emergence rate (Nd^{-1})				
A1/B1	3.36 a	1.67 g	2.27 dg	2.37 dg	2.42 AB
A2/B2	3.12 ac	2.10 eg	2.57 ce	2.90 ad	2.67 A
A3/B3	3.31 ab	2.25 dg	1.97 eg	2.64 be	2.54 AB
A5/B5	2.82 ad	1.85 fg	2.21 dg	2.49 cf	2.34 B
GCA	3.15 W	1.96 Z	2.25 Y	2.60 X	

GCA values with the same capital letter, or SCA values with the same lower case letter in each trait, are not significant different (Tukey, $p \leq 0.05$).

Maternal *vs*. paternal effects in the non isogenic female cross of three-way hybrids

There were not significant differences between maternal effects (the A- versions) *vs*. paternal effects (the B- versions) of each pair of A/B lines, except for the plumule length of Line 5. Three-way hybrids in which the A- version was involved showed longer plumule (9.22 cm) than those hybrids in which the female crosses included the B- version (8.61 cm). These results indicate that there are not nuclear and mitochondrial gene interactions in the seedling growh response of our A/B elite lines.

Conclusion

There were significant differences among genotypes for physiological quality traits of sorghum seeds. The R- lines group showed better seed quality traits than A- and B- lines groups. Single cross hybrids and three-way hybrids showed similar seed quality and heterosis values. The A2-line and the R14 restorer line stand out as the best candidates to be used as parental lines for seed physiological quality traits. There were not significant differences between maternal *vs*. paternal effects in physiological quality traits of sorghum seeds. Morphological differences in plant vigour can be detected in the seedling growth stage.

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