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Genetic control of soybean seed quality using partial diallel

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ABSTRACT: The selection of soybean genotypes with seeds of high physiological quality is key to increasing the likelihood of establishment and success in the field and thus reaping higher yields. The aim of this study was to evaluate the genetic control of the physiological quality of soybean seeds from a partial diallel cross. Six previously selected soybean cultivars, group 1 (CD 201, CA 115, MS 8400) and group 2 (CD 202, Syn 1263, Syn 1279), were intercrossed by a partial diallel cross, totalizing 24 treatments. Seeds from these cultivars and crosses were evaluated for seed physiological quality based on germination tests, first germination count, accelerated aging, seedlings emergence, and emergence speed index. The lignin content in the soybean seed coat was evaluated. The effects on general and specific combining ability and reciprocal effects were analyzed. There were significant additive and non-additive effects of the genes on the seed quality traits and pronounced effects on the reciprocal traits, which suggest the presence of a maternal effect. Lignin content was not correlated with the physiological test results in the studied genotypes.

Index terms: combining ability, diallel analysis, *Glycine max* L., maternal effect.

RESUMO: A seleção e utilização de genótipos de soja com sementes de alta qualidade fisiológica é importante para possibilitar maior probabilidade de estabelecimento e sucesso da cultura em campo, e, consequentemente, alcançar altas produtividades. Objetivou-se neste trabalho avaliar o controle genético da qualidade fisiológica de sementes de soja a partir de um dialelo parcial. Seis cultivares de soja, previamente selecionadas, grupo 1 (CD 201, CA 115, MS 8400) e grupo 2 (CD 202, Syn 1263, Syn 1279), foram intercruzadas utilizando-se um esquema de dialelo parcial, gerando 24 tratamentos. Sementes dessas cultivares e destes cruzamentos foram avaliadas quanto à qualidade fisiológica das sementes a partir de testes de germinação, primeira contagem de germinação, envelhecimento acelerado, emergência e índice de velocidade de emergência de plântulas. Foram avaliados os teores de lignina nos tegumentos das sementes de soja. Foram analisados os efeitos da capacidade geral (CGC) e específica de combinação (CEC) e os efeitos recíprocos. Há efeito significativo dos genes aditivos e não aditivos para os caracteres de qualidade de sementes, e efeito pronunciado de recíprocos, o que sugere a presença do efeito materno. Não há correlação entre o teor de lignina e testes fisiológicos para os genótipos estudados.

Termos de indexação: capacidade de combinação, análise dialélica, *Glycine max*, efeito materno.

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INTRODUCTION

The physiological quality of seeds can be influenced by the genotype, edaphoclimatic conditions during the production phase, and management conditions adopted at harvest, processing, and storage (Gris et al., 2010). The good performance of soybean crops depends on seed quality (Pereira et al., 2015; Dantas et al., 2017), as the use of high-quality seeds, as evaluated by germination and vigour tests, can provide yield gains (Tavares et al., 2013; Bagateli et al., 2019).

In soybean seeds, seed coat lignin is one of the components that can influence the quality of the variety (Bellaloui et al., 2017), vary depending on the genetic characteristics of the cultivar, but can also be influenced by the environment (Lewis and Yamamoto, 1990).

For the development of superior cultivars, the genetic variance obtained by crossing different strains may allow breeders to explore the maximum quality potential (Gondim et al., 2006). However, one of the greatest difficulties is the large number of crosses and segregating populations that need to be handled (Ferreira-Júnior et al., 2015).

The development and selection of soybean genotypes with high performance in multiple traits simultaneously is complex and difficult (Volpato et al., 2020), and few studies on the genetic control of seed quality are found in the literature. Menezes et al. (2009) tested the existence of genetic variability in soybean seed quality and observed a significant reciprocal effect of the lignin content of soybean seeds. Vasconcelos et al. (2012) analysed some genetic parameters of soybean seeds in germination and seedling emergence tests using soybean seeds, such as quadratic genotypic components and genotypic coefficient of determination. However, the importance of the additive, dominant, and maternal effects have not yet been fully elucidated and need to be further investigated.

Additional studies on the genetic control of the physiological quality of seeds may facilitate the choice of parents for future hybridizations and may help obtain cultivars with high physiological quality. The aim of this study was to evaluate the genetic control of the quality of soybean seeds from a partial diallel cross.

MATERIALS AND METHODS

The experiments were conducted at the Centre for Development and Technology Transfer (CDTT), latitude 21° 09’ 49.97” S and longitude 44° 55’ 00.58” O, located in the municipality of Ijaci, and at the Central Seed Laboratory, located in Lavras, belonging to *Universidade Federal de Lavras* (UFLA), both located in Minas Gerais, Brazil.

Six soybean cultivars were used, divided into two groups, and classified according to the results obtained by Menezes et al. (2009), Gris et al. (2010), Baldoni et al. (2013), Baldoni et al. (2019), and Moreno et al. (2019). For the choice of contrasting cultivars, the results obtained by these authors were considered, since variations in the results are expected in different seasons, since the physiological quality is a quantitative characteristic with genotype and environment interaction. Group 1 (G1) consisted of three cultivars with seeds of high physiological quality (CD 201, CA 115, MS 8400), and group two (G2) consisted of three cultivars of low physiological quality (CD 202, Syn 1263, Syn 1279). Seeds of each cultivar were manually sown at six different times to ensure coincidence of flowering between the parents. The plants of the two groups were manually intercrossed using a partial diallel cross design to obtain the F_1 generation.

The experiment was conducted in an area with semi-protected cultivation. It had a plastic cover on the upper part of the structure and open sides. The seeds were treatment with Carboxina and Tiram (Vitavax®) at a dose 250 mL.100 kg^{-1} of seeds and inoculated with *Bradyrizobium japonicum* at a dose 1 mL.5kg^{-1} of seeds. Each plot consisted of four 5-m rows, with 18 plants meter and the spacing used between lines was 0.5 m, two central lines were used as useful areas. Fertilization at sowing was performed according to the soil analysis and the interpretation according to the recommendations of Ribeiro et al. (1999). The irrigation was drip irrigation daily until R7 stage (Fehr and Caviness, 1977). The F_1 and reciprocals were manually harvested at the R8 stage (Fehr and Caviness, 1977) and dried in the shade until the seeds reached a water content of approximately 12%. After being threshed manually, the seeds were separated using

5.55 mm and 6.35 mm sieves for size standardization for later evaluations. The seeds were treated at the time of testing with the fungicide Carboxina e Tiram (Vitavax®) at a dose of 250 mL.100 kg^{-1} of seeds. The traits related to seed quality and seed coat were measured in the F_2 generation, which was obtained by self-fertilization of the F_1 generation.

Seed quality was assessed by means of germination and vigour tests. For all tests, four replications of 50 seeds were given each of the 24 treatments, with six cultivars and 18 populations obtained from each cross and its reciprocal, as can be observed in the first column of Table 1.

For the germination test, the seeds were sown on three leaves of germination paper moistened with distilled water in an amount equivalent to 2.5 times the dry paper weight. The rolls were kept in a germinator at 25 °C. The evaluations were performed at 5 days (first count) and 8 days (final count) after test setup, and the results are expressed as the percentage of normal seedlings (Brasil, 2009).

Table 1. Mean values obtained through the first germination count (G1 - %), germination (G - %), early aging test (EA -%), seedling emergence (E - %), emergence speed index of seedlings (ESI) and lignin (L - mg.g^{-1}) from seeds of soybean genotypes and their crosses.

Genotypes	G1[1]	G[1]	EA	E[1]	ESI	L
CD 201 (G1)	92 b	97 b	41 f	96 b	10.92 b	0.587 b
CA 115 (G1)	98 a	100 a	99 a	100 a	12.84 a	0.410 c
MS 8400 (G1)	49 e	61 d	46 e	63 d	6.79 d	0.370 d
CD 202 (G2)	98 a	100 a	99 a	100 a	12.10 a	0.405 c
Syn 1263 (G2)	98 a	99 a	88 b	100 a	11.63 a	0.215 h
Syn 1279 (G2)	92 b	97 b	78 c	99 a	12.08 a	0.310 f
Syn 1263(F) x CA 115(M)	92 b	97 b	29 g	100 a	12.34 a	0.202 h
CA 115(F) x Syn 1263(M)	94 b	99 a	79 c	100 a	13.04 a	0.400 c
Syn 1263(F) x MS 8400(M)	91 b	98 a	51 e	100 a	12.08 a	0.217 h
MS 8400(F) x Syn 1263(M)	70 d	85 c	40 f	79 c	8.70 c	0.355 d
Syn 1263(F) x CD 201(M)	85 c	97 b	52 e	100 a	12.25 a	0.225 h
CD 201(F) x Syn 1263(M)	65 d	77 c	23 g	76 c	7.67 d	0.615 a
CD 202(F) x MS 8400(M)	97 a	100 a	98 a	100 a	11.91 a	0.420 c
MS 8400(F) x CD 202(M)	85 c	94 b	58 d	93 b	10.39 b	0.363 d
CD 202(F) x CD 201(M)	99 a	100 a	97 a	100 a	12.11 a	0.600 b
CD 201(F) x CD 202(M)	67 d	85 c	33 f	84 c	8.81 c	0.378 d
CD 202(F) x CA 115(M)	96 b	100 a	88 b	99 a	11.97 a	0.448 c
CA 115(F) x CD 202(M)	98 a	99 a	97 a	100 a	12.51 a	0.408 c
Syn 1279(F) x CA 115(M)	87 c	95 b	59 d	96 a	11.55 b	0.260 g
CA 115(F) x Syn 1279(M)	93 b	98 b	65 d	100 a	12.52 a	0.428 c
Syn 1279(F) x MS 8400(M)	96 a	97 b	81 c	100 a	12.57 a	0.303 f
MS 8400(F) x Syn 1279(M)	84 c	89 c	53 e	88 c	10.88 b	0.373 d
Syn 1279(F) x CD 201(M)	93 b	99 a	91 a	100 a	12.37 a	0.325 e
CD 201(F) x Syn 1279(M)	83 c	93 b	36 f	100 a	11.16 b	0.638 a
CV (%)	6.85	3.9	10.65	4.73	6.61	4.8

Means followed by the same letters, in the columns, do not differ by the Scott-Knott test, at 5% probability. [1]Scott-Knott test result with data transformed into arc sine$\sqrt{(x/100)}$. CV: coefficient of variation.

The accelerated aging test was conducted in plastic gerbox germination boxes. The seeds were placed in a single layer on a suspended screen in the plastic boxes containing 40 mL of distilled water. These boxes stayed at 42 °C in a biochemical oxygen demand incubator for 82 hours (Moreno et al., 2019), and this period was determined. Due to edaphoclimatic conditions were favorable to obtain seeds with high physiological quality, it was necessary to extend the accelerated aging test period of the seed so that the genotypes could be discriminated. Then the seeds were subjected to the germination test as described above.

The seedling emergence test was performed under controlled conditions in a plant growth chamber at 25 °C under a 12-hour photoperiod. Sowing was performed in plastic trays containing soil:sand at a 2:1 ratio as substrate. After the first seedling emerged, daily evaluations were performed, calculating the number of seedlings that emerged until stabilization. The percentage of emerged seedlings at 14 days was calculated (Krzyzanowski et al., 2020).

The emergence speed index (ESI) was performed in conjunction with the seedling emergency test and determined by evaluating seedling emergence every 48 hours until the 21st day. Seedlings with cotyledons above the soil surface were considered. At the end of the test, the ESI was calculated using the formula proposed by Maguire (1962).

The lignin content in the seed coat was evaluated in all 24 groups using four replications of 50 seeds. The seed coats were removed and macerated in a crucible using liquid nitrogen, and lignin extraction was performed as described by Capeleti et al. (2005) and the result expressed in mg of lignin per dry tissue grams.

All data were subjected to the normality test of Shapiro and Wilk (1965) to check whether data transformation was needed. The first germination count, final germination count, and emergence data that did not show normality were $arc\ sine\sqrt{\frac{x}{100}}$ transformed for analysis.

The means of all traits were grouped by the Scott-Knott test at 5% probability using Genes software (Cruz, 2013). Pearson correlations between these traits were estimated pairwise, and analysis of variance was performed using the PROC GLM procedure of the Statistical Analysis System (SAS) statistical package (SAS, 2002). The estimates of general and specific combining ability and reciprocal effect were obtained for the physiological quality traits using the PROC IML procedure of SAS The genetic parameters were estimated according to Model I proposed by Griffing (1956), adapted to partial diallel crosses (Cruz and Regazzi, 1994). The model used was $Y_{ij} = m + g_i + g_j + s_{ij} + r_{ij} + e_{ij}$, where Y_{ij} is the mean value of the hybrid combination (i ≠ j) or the parent (i = j); m is the overall mean; g_i is the effect of the general combining ability of the ith parent of G1; g_j is the effect of the general combining ability of the jth parent of 2; s_{ij} is the effect of the specific combining ability between the parents of order i and j of G1 and G2, respectively; r_{ij} is the reciprocal effect that measures the differences provided by parent i or j when used as the male or female in the cross i×j; and e_{ij} is the mean experimental error associated with the observation of order ij.

In addition to Griffing's Model I adapted to the partial diallel cross, to estimate the reciprocal effect, the estimator described by Menezes et al. (2009) was used $rij = \frac{(Yij - Yji)}{2}$, where refers to the reciprocal effect of the i×j cross, which measures the differences provided by parent i or j when used as the male or female in cross i×j; refers to the mean of the F_2 progeny obtained by cross i×j when used as a female; and is the mean of the F_2 progeny obtained by cross i×j when j or i is used as the male. The coefficient of determination (R^2) obtained by the ratio of the sum of squares of the combining abilities was also estimated.

RESULTS AND DISCUSSION

Significant effects were found for all parameters used to evaluate the physiological quality of the seeds, with differences in the performance of the cultivars between and within the strain groups and between the progenies obtained from the crosses. G1 had worse mean seed quality than G2, and other variables differed as well (Table 1).

Moreno et al. (2019) also studied the physiological quality of these cultivars, but their materials came from seeds obtained from different harvests than the one used in the present study, so the different edaphoclimatic conditions of the production environment underlie the discrepancy in the results observed in the two harvests among most cultivars. As the physiological quality of soybean seeds has a quantitative character and is controlled by several genes, Vasconcelos et al. (2012) observed that individual selection of soybean genotypes, based on the physiological quality of seeds by location, can maximize genetic gains when compared to selection considering the environments together. This explains the variation in relation to the classification of soybean genotypes for this trait in different cultures and locations. These authors also observed a significant interaction between genotypes x environments for germination and emergence traits, and a genotypic determination coefficient of 57.16% for soybean seedling emergence.

Soybean seeds are very sensitive to environmental effects (Silva et al., 2017), which can result in different interactions between cultivars and cultivation environments (Marques et al., 2011; Meotti et al., 2012). An effect of the genotype × environment interaction on seed germination traits was observed in other studies on soybean seeds (Menezes et al., 2009; Vasconcelos et al., 2012; Silva et al., 2017). According to Volpato et al. (2020), the environmental effect and the presence of genes involved in genetic control influence the phenotypic expression and continuous distribution of segregating populations.

Regarding the seeds of the cultivars, all mean values of first germination count, final germination count, and emergence percentage parameters were above 92%, except for seeds of cultivar MS 8400 (Table 1). Regarding the ESI and accelerated aging, in addition to cultivar MS 8400 – which showed low germination – seeds of cultivar CD 201, despite their high germination rate, also showed low vigour. In all tests, the highest germination and vigour values were observed in seeds of cultivars CA 115 and CD 202 (Table 1). CA 115 was classified as high quality but CD 202 as low quality in the study by Moreno et al. (2019).

There were significant differences in lignin content in the seed coat of the cultivars and crosses, with the formation of eight statistically distinct groups. Intermediate lignin contents were observed in seeds of cultivars with better physiological quality (CA 115 and CD 202). The MS 8400 cultivar, which had the poorest seed quality, had lower lignin content than high-quality cultivars (Table 1). Lignin may influence the physiological quality of seeds (Baldoni et al., 2019, Castro et al., 2019) when evaluating germination, water permeability, and resistance to seed deterioration (Bellaloui et al., 2017). Lignin may contribute to obtaining seeds with greater resistance to mechanical damage (Alvarez et al., 1997), greater tolerance to pathogens (Peltier et al., 2009), and greater vigour as evaluated by the accelerated aging test (Menezes et al., 2009). In the present study, high germination rate, vigour, and lignin content were found in seeds from the CD 202(F) × CD 201(M) cross. However, the seeds of the CD 201(F) × Syn 1263(M) and CD 201(F) × Syn 1279(M) crosses, with higher lignin content, had low seed quality (Table 1). These results corroborate those obtained by Carvalho et al. (2014), who found that seeds of soybean cultivars with high lignin content (0.5951 g%) in the seed coat do not necessarily have better physiological quality.

For the progenies generated from the crosses of the six strains, there were variations in performance for all traits evaluated. In seeds of the progenies obtained from the cross between the two cultivars with higher physiological quality and their reciprocals (CD 202 and CA 115), high physiological quality was observed according to the germination, seedling emergence, and ESI tests, as well as intermediate levels of lignin, as was observed in their parents (Table 1).

High germination rate, vigour, and lignin content were observed in seeds from the CD 202(F) × CD 201(M) cross. Another interesting result is related to the reciprocal of this cross, which exhibited inferior performance, with lower germination and seed vigour values, revealing the existence of variation in the performance of the progeny depending on the parent used as mother and father in the cross. The maternal effect was also evidenced in the cross and its reciprocal between the cultivars CD 202 and MS 8400, which showed high and low vigour, respectively. High germination and vigour values were observed when cultivar CD 202 was used as the female parent, and low values were observed when cultivar MS 8400 was used as the female parent (Table 1).

The study of genetic variability in soybean populations provides important information for breeding programmes, and the physiological quality of seeds is a key trait to ensure an adequate stand and vigorous and productive plants in the field. Some studies have shown the existence of variability in several parameters. Kurasch et al. (2017) studied partial diallel crosses and observed significant genotypic variations, high heritability ($h^2 > 0.7$) and transgressive segregation for grain yield, 1000-grain weight, plant height, protein content, and soybean oil content. Vasconcelos et al. (2012) studied some germination genetic parameters at different sites and found the presence of genotype × environment interactions and moderate to low coefficients of determination, suggesting that at sites with higher selection coefficients, the potential for gain is greater.

Leite et al. (2016) found that the number of nodes and the number of pods had high positive genotypic and phenotypic correlations with grain yield, and these were the traits that most contributed to grain production. The estimation of heritability, genetic gain, and genetic correlations allows breeders to choose the best breeding strategy (Hamawaki et al., 2012), but selecting superior progenies requires much work because most traits of agronomic importance have low heritability (Bárbaro et al., 2009).

In the field, some soybean cultivars, although highly productive, have low-quality seeds, thus hindering their permanence on the market (Baldoni et al., 2013). Thus, studies aiming at a better understanding of genetic control through combining ability may allow gains in the form of the selection and generation of cultivars with better performance in the field and higher-quality seeds. Santos et al. (2012) reported that breeding programmes have prioritized obtaining cultivars with high productivity and seed physiological quality.

Our diallel analysis showed that GCA was significant for all parameters evaluated in both groups. This indicates that genotype contributed differently to the means of the crosses and that the additive effects were significant for the traits evaluated. SCA was also significant for most of the parameters evaluated, suggesting the participation of non-additive effects (Table 2).

Table 2. Diallel analysis of the data obtained for the tests of first germination count (G1), germination (G), accelerated aging (EA), seedling emergence (E), emergence speed index (ESI) and lignin (L), including the parents, the seeds of the F2 plants and their reciprocals.

Source of variation	GL	G1[1]	G[1]	EA	E[1]	ESI	L
Treatments	23	0.145**	0.122**	2869.927**	0.158**	11.064**	0.053**
Parents (P)	5	0.282**	0.257**	2693.367**	0.262**	19.090**	0.061**
Group 1 (G1)	2	0.523**	0.487**	4206.333**	0.465**	38.213**	0.054**
Group 2 (G2)	2	0.039*	0.023**	420.333**	0.005NS	0.287NS	0.036**
G1 vs G2	1	0.284**	0.264**	4213.500**	0.367NS	18.454**	0.128**
Crossings (C)	17	0.111**	0.136**	2928.163**	0.089**	9.245**	0.054**
GCA1	2	0.149**	0.112**	1230.056**	0.130**	16.763**	0.109**
GCA2	2	0.121**	0.060**	6437.389**	0.039**	4.257**	0.060**
SCA	4	0.025NS	0.032**	436.639**	0.078**	3.593**	0.003*
Reciprocal	9	0.139**	0.116**	3633.037**	0.185**	11.194**	0.063**
P vs C	1	0.029NS	0.0001 NS	2762.722**	0.011 NS	1.864 NS	0.0002 NS
Error	72	0.011	0.008	48.833	0.008	0.558	0.001
CV (%)		8.4	6.35	10.64	6.13	6.60	6.54
Means		87.333	94.305	62.528	95.194	11.384	0.386
R^2 GCA		0.287	0.227	0.308	0.147	0.267	0.368
R^2 GCA (G1)		0.158	0.148	0.049	0.112	0.213	0.238
R^2 GCA (G2)		0.128	0.079	0.259	0.034	0.054	0.131
R^2 SCA		0.053	0.084	0.0351	0.135	0.091	0.014
R^2 Reciprocal		0.660	0.689	0.657	0.718	0.641	0.618

[1]Analysis with data transformed into arc sine√(x/100); *,** significant at 5% and 1%, respectively, and NS not significant. CV: coefficient of variation.

The relative contribution of the sums of squares of the additive and dominant effects can be judged from their coefficients of determination (R^2). In all traits, the R^2 of GCA (which ranged from 0.034 to 0.368) was higher than that of SCA (which ranged from 0.014 to 0.135), indicating that the participation of additive effects was more significant than that of non-additive effects. For most of the parameters evaluated, the additive effects were greater in G1, except for the accelerated aging parameter. Further, the reciprocal effect was even more evident than the other effects in all evaluated traits, contributing 61 to 72% of the variation found (Table 2), as observed in several crosses shown in Table 1.

There are few studies of the genetic control of soybean seed quality. Menezes et al. (2009) studied the additive and non-additive genetic effects on the thickness of seed coat layers and lignin content present in these layers and found, as we did, the contribution of additive and non-additive effects.

GCA was highest in the cultivar CA 115, followed by CD 202, for the first germination count, germination, and accelerated aging parameters (Table 3). These observations suggest that on average, these strains contributed more to seed quality and probably have a higher proportion of favourable alleles. This can be confirmed by the physiological quality results observed for these cultivars (Table 1). For the MS 8400, CD 201, and Syn 1263 strains, low GCA values were observed for most of the traits studied, indicating that on average, these cultivars lowered seed quality. Estimates of GCA effects indicate the importance of additive gene effects in the manifestation of a trait and have been useful for the choice of parents in breeding programmes (Cruz et al., 2012).

When comparing these results with those observed by Moreno et al. (2019), there was consistency in the CA 115 and Syn 1263 genotypes, which contributed positively and negatively, respectively, to the physiological quality of seeds.

Estimates of SCA suggested the existence of genes with non-additive action in the genetic control of the traits, and the non-significance for most crosses suggested that the genotypes were not contrasting for the traits (Cruz et al., 2012). The highest SCA estimates were observed for the CD 201 × Syn 1279 cross for most parameters and for the CA 115 × Syn 1263 cross (Table 4), which indicates a better complementation of favourable alleles. Considering only accelerated aging and lignin content, the highest SCA was observed in seeds of the CA 115 × CD 202 cross. This cross was not contrasting for most of the evaluated traits but can be considered promising since a high GCA was observed, and the seeds of the parents and their crosses had high quality (Table 1). According to Cruz et al. (2012), the best progeny is the one that has the highest SCA estimate and that has at least one parent with high GCA.

GCA and SCA estimates are useful for choosing parents. However, another important and complementary piece of information in breeding programmes is the study of reciprocal crosses, which allows verification of the maternal

Table 3. Estimates of the effects of the general combining abilities (GCA) and the respective standard deviations (SD) for the vigor of seeds evaluated by the tests of first germination count (G1), germination (G), accelerated aging (EA), seedling emergence (E), emergence speed index (ESI), and lignin contents (L).

	General combination ability (GCA)					
Crossings	G1[1]	G[1]	EA	E[1]	ESI	L
CD 201 (G1)	-0.075**	-0.054**	-7.60**	-0.034*	-0.65**	0.0769*
CA 115 (G1)	0.083**	0.077**	6.65**	0.085**	0.94**	-0.0289*
MS 8400 (G1)	-0.008NS	-0.022NS	0.74NS	-0.050**	-0.29*	-0.0481*
CD 202 (G2)	0.065**	0.056**	15.64**	0.009NS	-0.10NS	0.0494*
Syn 1263(G2)	-0.076**	-0.041**	-17.03**	-0.044**	-0.36**	-0.0506*
Syn 1279(G2)	0.010NS	-0.015NS	1.39NS	0.036*	0.46**	0.0011NS
SD	0.018	0.0147419	1.16	0.015	0.12	0.0042

[1]Analysis with data transformed into arc sine$\sqrt{(x/100)}$; *,** significant at 5% and 1%, respectively, and NS not significant.

effect on the traits. The reciprocal effect may be due to genes found in cytoplasmic organelles (mitochondria and chloroplasts), genes related to endosperm nuclei, or a maternal nuclear gene product (Ramalho et al., 2008; Baldissera et al., 2012). In this study, the reciprocal effect had high significance (R^2 of 0.62 to 0.72) in relation to GCA and SCA for all physiological quality parameters, which indicates a large influence of the maternal genotype on seed quality (Table 2), and this effect was evident in most crosses (Table 5).

Cultivar MS 8400, when used as a female parent, contributed to progeny with lower seed quality than the reciprocal cross had, indicating that this cultivar lowered the seed quality of the progenies (Table 1). The results also suggest a maternal effect (Table 5).

The importance of the reciprocal effect to traits underlying the physiological quality of soybean seeds was reported by Menezes et al. (2009), who observed that the reciprocal effect was superior to the additive and dominant effects

Table 4. Estimates of the effects of specific combining abilities (SCA) and the respective standard deviations (SD) for the vigor of seeds evaluated by the tests of first germination count (G1), germination (G), accelerated aging (EA), seedling emergence (E), emergence speed index (ESI), and lignin contents (L).

	Specific combining abilities (SCA)					
Crossings	G1[1]	G[1]	EA	E[1]	ESI	L
CD 201 x CD 202	-0.00^{NS}	-0.022^{NS}	-6.14**	-0.061**	-0.17^{NS}	-0.0240**
CD 201 x Syn 1263	-0.036^{NS}	-0.054*	-0.47^{NS}	-0.056**	-0.40*	0.0072^{NS}
CD 201 x Syn 1279	0.043^{NS}	0.076**	6.61**	0.117**	0.58**	0.0168**
CA 115 x CD 202	0.017^{NS}	0.022^{NS}	7.36**	-0.005^{NS}	0.02^{NS}	0.0206**
CA 115 x Syn 1263	0.054**	0.042*	1.28^{NS}	0.078**	0.74**	-0.0057^{NS}
CA 115 x Syn 1279	-0.071**	-0.064**	-8.64**	-0.073**	-0.75**	-0.0149*
MS 8400 x CD 202	-0.009^{NS}	0.000^{NS}	-1.22^{NS}	0.067**	0.16^{NS}	0.0035^{NS}
MS 8400 x Syn 1263	-0.018^{NS}	0.012^{NS}	-0.81^{NS}	-0.022^{NS}	-0.33^{NS}	-0.0015^{NS}
MS 8400 x Syn 1279	0.027^{NS}	-0.012^{NS}	2.03^{NS}	-0.044*	0.18^{NS}	-0.0019^{NS}
SD	0.025	0.021	1.65	0.021	0.18	0.0059

[1]Analysis with data transformed into arc sine√(x/100); *,** significant at 5% and 1%, respectively, and NS not significant.

Table 5. Mean effect of reciprocals and the t test for first germination count (G1), germination (G), accelerated aging (EA), seedling emergence (E), emergence speed index (ESI), and lignin contents (L) of the partial diallel.

Crossings	G1[1]	G[1]	EA	ESI	E[1]	L
CD 201 x CD 02	-16**	-7.75**	-32**	-1.655**	-8.25**	-0.111**
CD 201 x Syn 1263	-10**	-10**	-14.5**	-2.285**	-12**	0.195**
CD 201 x Syn 1279	-5*	-2.75*	-27.5**	-0.61*	0^{NS}	0.1565**
CA 115 x CD 202	1^{NS}	-0.5^{NS}	4.25^{NS}	0.27^{NS}	0.75^{NS}	-0.02*
CA 115 x Syn 1263	1^{NS}	1.25^{NS}	25**	0.35^{NS}	0^{NS}	0.0985**
CA 115 x Syn 1279	3.25^{NS}	1.5^{NS}	3^{NS}	0.485^{NS}	2*	0.084**
MS 8400 x CD 202	-6.25**	-3*	-19.75**	-0.765**	-3.5**	-0.0285**
MS 8400 x Syn 1263	-10.75**	-6.5**	-5.5^{NS}	-1.695**	-10.5**	0.0685**
MS 8400 x Syn 1279	-5.75**	-4**	-14.25**	-0.84**	-6.25**	0.035**

[1]Analysis with data transformed into arc sine√(x/100); *,** significant at 5% and 1%, respectively, and NS not significant.

Table 6. Estimated Pearson correlation between the results of the accelerated aging test (EA), first germination count (G1), seedling emergence (E), emergence speed index (ESI), germination (G) and lignin contents (L).

	G1	E	G	ESI	L
EA	0.63**	0.50*	0.55*	0.58**	-0.06^{NS}
G1		0.78**	0.92**	0.78**	-0.08^{NS}
E			0.85**	0.89**	-0.13^{NS}
G				0.81**	-0.12^{NS}
ESI					-0.23^{NS}

*,** significant at 5% and 1%, respectively, and NS not significant.

for lignin content in soybean seeds. In a study of popcorn by Cabral et al. (2013), this effect was also pronounced, and there was a reciprocal effect on both germination parameters and vigour. Cruz et al. (2011) studied Asian soybean rust infection and found that the use of cultivars as female vs. male parents in crosses causes variation in the progression of Asian rust among F_3 progenies. Roveri José et al. (2004) studied vigour in maize strains with high and low desiccation tolerance and identified the significance of the reciprocal effect on seed quality. According to Ramalho et al. (2012), the reciprocal effect indicates the strength of the maternal effect.

Another aspect that may contribute to breeding programmes is the correlations, as they allow us to verify whether some characters are associated with others, and for characters with high correlations with each other, selecting for one of them allows us to infer the response of others. In this study, all evaluated parameters were positive and correlated with each other, except for lignin content (Table 6).

The correlation estimates were considered moderate to high, with results similar to those observed by Diniz et al. (2013) for the first germination count, germination, emergence, and accelerated aging. Results similar to those observed in Table 6 were reported by Barbieri et al. (2013), who found correlations between different traits related to soybean seed quality, especially emergence in the field with germination, electrical conductivity, and accelerated aging.

Botelho et al. (2019) studied the application of desiccants and their relationships with the physiological quality of soybean seeds with different lignin contents and observed a negative relationship between lignin content and quality. However, Menezes et al. (2009) observed a positive correlation between lignin content and the percentage of normal seedlings in the accelerated aging test, which they took as an indication that lignin content is related to seed quality. Thus, even though this study did not observe a positive correlation between germination traits or vigour and lignin content, factors such as seed production in weather-free conditions and manual harvesting may have influenced and studies on this relationship are important to improve our understanding of and make advances in the selection of genotypes with better physiological seed quality.

CONCLUSIONS

There are additive and non-additive genetic effects on the physiological quality of soybean seeds. There is a reciprocal effect on the physiological quality of soybean seeds. Lignin content is not correlated with physiological test results in the studied genotypes.

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