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Combining ability of common bean in a complete diallel cross under water deficit

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ABSTRACT: The aim of this study was to identify drought-tolerant parents and combinations of common bean based on general and specific combining abilities. A complete diallel was conducted, including the reciprocals, among 12 parents, obtaining 132 populations. These populations and respective parents were evaluated in pots in a greenhouse in a randomized block experimental design with three replications and placed under intermittent water deficit applied in the pre-flowering. Physiological, morphological, and agronomic traits were evaluated, and general combining ability (GCA), specific combining ability (SCA), and reciprocal effect (RE) were estimated. Significant effects were found among the genotypes for most of the traits confirming genetic variability among populations. The additive effects were more expressive than the non-additive effects, with reciprocal effect for some traits. The Carioca Precoce and SER 16 parents exhibited significant GCA, contributing alleles favorable to additive effects for increasing grain yield and harvest index. Significance of SCA and RE was not observed for grain yield. However, the SEA 5 (pollen receptor) × SER 16, Carioca Precoce (pollen receptor) × BRS FP403, and the reciprocal Carioca Precoce (pollen donor) × BRS FP403 hybrid combinations achieved positive estimates for harvest index, which is an indirect selection trait for grain yield. This study allowed selection of progenies coming from the parents Carioca Precoce and SER 16, as manifested favorable traits related to grain yield.

Key words: *Phaseolus vulgaris*, abiotic stress, drought, grain yield.

INTRODUCTION

The common bean (*Phaseolus vulgaris* L.) holds significant global economic and nutritional importance as a staple food, with Brazil being one of the major producers. According to Companhia Nacional de Abastecimento (2023), the 2022/2023 crop year saw the total production of 2,481 thousand tons, covering 1,488.8 thousand ha and yielding an average of 1,649 kg·ha^{-1}.

Despite efforts to mitigate climate change, drought remains a primary constraint on grain yield. According to Intergovernmental Panel on Climate Change (IPCC) studies (2012), since the 1950s, certain regions have witnessed prolonged droughts, impacting rainfall and temperature. With medium confidence, the IPCC predicts intensified droughts in the 21st century due to decreased precipitation and/or increased evapotranspiration, particularly in southern Europe, the Mediterranean, central Europe, central North America, Central America, Mexico, northeast Brazil, and southern Africa. The IPCC (2018) anticipates a potential 2°C global temperature rise in the next three decades, leading to potentially irreversible damage. The reduction of at least 0.5°C could mitigate sea level rise and preserve ecosystems.

Drought severely impacts plant growth and grain yield. Understanding the physiological and molecular changes in plants is crucial for selecting drought-tolerant genotypes (Farooq et al. 2016, Wu et al. 2016). Common beans are highly sensitive to water scarcity, necessitating the identification of tolerant genotypes through genetic variability exploration for hybridization and selection (Beebe et al. 2014). According to Beebe et al. (2008), about 60% of the global production of common beans faces the threat of drought. Studies by Androcioli et al. (2020) in a greenhouse and by Assefa et al. (2015, 2017) in field conditions found significant reductions, up to 56%, in common bean grain yield due to water deficit. The extent of yield reduction varies based on region, crop season, year, and cultivar.

Daronch et al. (2014) stated that breeding program success depends on efficiently selecting parents for promising hybrid and segregating populations. Various techniques, including the widely used diallel cross (Bolson et al. 2016, Fasahat et al. 2016, Rodrigues et al. 2018), aim to enhance the likelihood of obtaining superior segregating populations. This method provides estimates of useful genetic parameters that allow selection of promising parents for obtaining hybrids, assisting understanding of the genetic effects responsible for expression of a determined trait (Cruz, 2006). Studies conducted by Gonçalves et al. (2015) and Arruda et al. (2019) working with common bean and Rodrigues et al. (2018) with cowpea, using associated diallel analysis, emphasized the importance of this analysis in selection of parents for extraction of drought-tolerant lines.

The aim of this study was to conduct a complete diallel cross with 12 parents, to identify and select parents and hybrid combinations tolerant to drought through combining ability, obtaining information regarding the gene activity that controls expression of the traits evaluated.

MATERIALS AND METHODS

Twelve genotypes of common bean with genetic variability regarding plant cycle, plant architecture, tolerance to biotic and abiotic factors, seed coat color, and yield potential (Table 1) were crossed in a complete diallel design (12 × 12) in a greenhouse, resulting in 132 hybrid combinations, including the reciprocal crosses. After obtaining the F_1 generation by natural self-fertilization of the plants, the F_2 generation was obtained, with only one plant per pot in an automated irrigation system to avoid contamination.

Table 1. Description of the 12 parents used in the diallel regarding genealogy, origin, seed coat color, and agronomic traits.

Genotype	Genealogy	Origin	Seed coat color	Traits
SER 16	(RAB 651 × TIO CANELA 75) × (RAB 608 × SEA 15)/-MC-2P-MQ-MC-27C-MC-MC	CIAT	Red	Drought tolerance
SEA 5	BAT 477/San Cristobal 83/ Guanajuato 31/Rio Tibagi	CIAT	Mulatinho	Drought tolerance
Carioca Precoce	Cultivar improved from the landrace Pitoco	CATI	Carioca	Early cycle, short plant, and resistance to golden mosaic virus
BRSMG Majestoso	Pérola/Ouro Negro	Embrapa	Carioca	Resistance to common mosaic virus and anthracnose, high yield, and grain quality
BRS FP403	POT 51/ICA Pijao/XAN 170/ BAC 16/XAN 91	Embrapa	Black	Moderate resistance to Fusarium wilt, early cycle, upright plant architecture, and high yield
G 19841	Unknown	CIAT	Cranberry	High grain weight and hardiness
Wild Mex	Crioulo	Wild variety	Gray with beige streaks	Hardiness and resistance to weevils
Gen TS 3-2	SEA 5/IAC Carioca Tybatã	IAC	Cream	Drought tolerance
Gen TS 3-3	SEA 5/IAC Carioca Tybatã	IAC	Carioca	Drought tolerance
Gen TS 4-8	SEA 5/IAC Alvorada	IAC	Carioca	Drought tolerance
IAC Sintonia	RC2 IAC Alvorada/Pérola	IAC	Carioca	Resistance to Fusarium wilt
IAC Imperador	Carioca Eté/Carioca Precoce/Carioca Eté	IAC	Carioca	Resistance to anthracnose and early cycle

CIAT: International Center for Tropical Agriculture; CATI: Coordenadoria de Assistência Técnica Integral; Embrapa: Empresa Brasileira de Pesquisa Agropecuária; IAC: Instituto Agronômico de Campinas.

Experimental plots consisted of three pots with two plants, coming from the F_2 seeds of the 132 progenies, together with the 12 parents that gave rise to them. One plant from each pot was used for the morphophysiological evaluations, considering the following traits: leaf area, root collar diameter, and total shoot dry matter. The remaining plant was kept under intermittent water deficit until physiological maturity.

The plants were grown in a greenhouse, in 10 dm^{-3} pots filled with a mixture of soil and mineral substrate at the ratio of 3:1. Chemical analysis of the soil used as a substrate for conducting the experiment reveled: 25 $g·dm^{-3}$ of organic matter, 48 $mg·dm^{-3}$ of P, 0,9 $mmol·dm^{-3}$ of K, 72 $mmol·dm^{-3}$ of Ca, 25 $mmol·dm^{-3}$ of Mg, potential acidity (H + Al) of 37 $mmol·dm^{-3}$, exchangeable base sum of 97 $mmol·dm^{-3}$, cation exchange capacity of 134 $mmol·dm^{-3}$, base saturation percentage (V%) of 72 and 5,4 of pH. Fertilization was carried out according to Raij et al. (1997), consisting of application at sowing of 625 $kg·ha^{-1}$ of the formulation 4-14-8, corresponding to 25 $kg·ha^{-1}$ N (125 mg of N per pot); 87.5 $kg·ha^{-1}$ P_2O_5 (437.5 mg of P_2O_5 per pot), and 50 $kg·ha^{-1}$ K_2O (250 mg of K_2O per pot). In the V3-V4 stage of plant development, N fertilization was top dressed, using 225 $kg·ha^{-1}$ urea (1.125 g of N per pot).

A randomized block experimental design was used, with three replications. Irrigation of the pots was monitored throughout the cycle to maintain the soil matric potential at approximately -30 Centibar/kPa up to the time water deficit began to be applied in the pre-flowering stage (R5 stage). Soil moisture sensors were used, distributed at random in the pots. The plants received two automated waterings per day, with application of 140 mL in each pot, using lateral lines and one microtube (spaghetti line) per pot (Gonçalves et al. 2019). The number of days to flowering (DF) was verified and, when more than 50% of the plants were in the R5/R6 stages, between anthesis and opening of the first flowers, irrigation was suspended, beginning application of the water deficit periods. Intermittent water deficit was applied, and the first cycle was six days because of accelerated senescence and curling of leaves. At that time, the matric potential of the soil was -125.75 Centibar/kPa.

After that period, irrigation was reestablished for three days, and then four days of water deficit was applied, with soil matric potential at -147.88 Centibar/kPa. This period lasted less than the first one, because the soil was not saturated in rehydration after the first deficit was applied. Thus, the plants had more accentuated stress symptoms, including leaf abscission and accentuated closing of stomates.

At this time of maximum stress, the following evaluations were made:

- Relative chlorophyll index (RCI) by chlorophyll meter (Konica Minolta model SPAD-502 Plus) on leaves of the lower part of the plant;
- Leaf temperature (LT), using an infrared thermometer (Telatemp model AG-42D) with the reading taken at 50 cm from the leaf surface at a 45° angle;
- Stomatal conductance (SC) by a porometer (Delta T Devices model AP4) in a state of dynamic equilibrium;
- Leaf area (LA) by an area integrator meter (LI-COR model LI-3100C);
- Partitioned dry matter: leaf dry matter (LDM); stem dry matter (SDM); and total shoot dry matter (TSDM), in which the plants used for LA evaluation were dried in a forced air circulation laboratory oven at 60ºC until reaching constant weight;
- Root collar diameter (RCD) using a digital caliper rule;
- Number of nodes per plant (NN);
- Plant height (PH).

At physiological maturity, the following determinations were made: number of viable pods per plant (NVP), number of unviable pods per plant (NUP), number of viable seeds per plant (NS), number of empty locules (NEL), grain yield (GY), days to maturity (DM), and harvest index modified (HI), proposed by Costa et al. (1985), estimated by Eq. 1:

$$HI = \left(\frac{GY}{TSDM}\right) * 100 \tag{1}$$

Analysis of variance and diallel analysis were performed using method 1 of Griffing (1956), considering the parents, crosses, and reciprocals. Diallel analyses were carried out using the AGD-R software (Rodríguez et al. 2015), considering the effects of genotypes as fixed and using the F test and the Student's *t* test at < 0.05 and < 0.01 of probability. Pearson's correlation was carried out with ggcorrplot R-package.

RESULTS

Diallel analysis (Table 2) revealed significant genotype (G) differences in most variables, except LT and RCI. General combining ability (GCA) mean squares were significant for most traits, except LT, RCI, and SC, implying certain parents influence hybrid performance. Specific combining ability (SCA) was significant for PH, LDM, TSDM, SC, DF, and HI. Reciprocal effects (RE) were significant for PH, LDM, TSDM, LA, SC, DF, and HI. Experimental accuracy (CV%) ranged from 5.71 to 37.83%, with the highest values for NVP (37.83%), NS (36.43%), and NUP (22.29%), indicating environmental impact on these variables.

Table 2. Mean squares of diallel analysis for the variables leaf temperature (LT); relative chlorophyll index (RCI); stomatal conductance (SC); root collar diameter (RCD); number of nodes per plant (NN); plant height (PH); leaf dry matter (LDM), stem dry matter (SDM), and total shoot dry matter (TSDM); leaf area (LA); number of viable pods per plant (NVP); number of unviable pods per plant (NUP); number of viable seeds per plant (NS); number of empty locules (NEL); days to flowering (DF): days to maturity (DM); grain yield (GY); and harvest index (HI) of the 144 common bean genotypes.

Source of variation	Mean Squares									
	df	LT	RCI[1]	SC[1]	RCD	NN	PH[1]	LDM[1]	SDM[1]	TSDM[1]	LA[1]
Genotype	143	2.95	59.09	1,006.28**	1.22**	9.77**	6,076.69**	1.06**	0.79**	3.13**	1,156,261.39 **
GCA	11	10.08	106.84	868.48	10.54**	60.98**	5,6647.6**	2.62**	2.53**	7.33**	4,466,184.56 **
SCA	66	2.19	69.56	972.65 **	0.40	5.93	1,997.55**	0.92*	0.60	2.72*	822,361.20
Reciprocal	66	2.54	41.53	1,062.22**	0.49	5.21	1,759.36**	0.94*	0.69	2.85*	943,200.21 **
Mat[1]	11	2.63	54.95	1,006.60	0.25	7.24	2,308.03**	0.62	0.60	2.28	620,294.60
No Mat[2]	55	2.53	38.85	1,073.34**	0.54	4.81	1,649.63**	1.00	0.71	2.97	1,007,781.34
Residual	286	3.43	62.40	592.12	0.37	4.44	864.05	0.62	0.55	1.98	620,529.81
CV%		6.64	17.18	21.44	14.07	19.84	19.36	19.04	12.57	10.47	12.45
Source of variation	df	NVP	NUP[1]	NS[1]	NEL[1]	DF	DM	GY[1]	HI[1]		
Genotype	143	19.01**	5.96	201.53**	24.20*	26.01**	65.40**	4.56**	0.39**		
GCA	11	134.49 **	20.68 **	1,473.70**	52.20**	220.11**	301.10**	17.26**	1.34**		
SCA	66	8.26	4.44	95.43	21.62	9.57**	48.76	3.67	0.31**		
Reciprocal	66	10.39	5.04	96.01	21.82	10.00**	44.97	3.33	0.31*		
Mat	11	12.18	7.03	75.69	28.44	8.00*	43.86	2.10	0.44*		
No Mat	55	10.03	4.64	100.07	20.50	10.40**	45.19	3.57	0.28*		
Residual	286	8.01	4.78	86.22	18.88	4.00	44.74	2.97	0.20		
CV%		37.83	22.29	36.43	18.50	5.71	9.91	12.04	7.05		

*Significant at 5% probability by the F-test; **significant at 1% probability by the F-test. Transformed data $\sqrt{x+1}$; df: degrees of freedom; GCA: general combining ability; SCA: dpecific combining ability; [1]maternal effects; [2]no Maternal effects; CV%: coefficient of variation.

Selection of the genotypes evaluated by estimates of GCA (Table 3), SCA (Table 4), and RE (Table 5) were carried out considering the significant values obtained by the Student's t test. As expected in an autogamous crop, the predominance of additive effects was found in expression of the traits due to the significance of the GCA, ensuring the transfer of these traits to the following generations, favoring the process of selection of drought-tolerant common bean genotypes (Table 2).

The Parent Carioca Precoce demonstrated significant and positive estimates for NS (2.60 units), GY (0.81 g·plant^{-1}), and HI (0.25), highlighting its potential yield under drought stress.

For drought tolerance, genotypes SEA 5 and SER 16 from International Center for Tropical Agriculture (CIAT) (Gonçalves et al. 2015, Klaedtke et al. 2012, Polania et al. 2016) can serve as parents to decrease DF (-2.54 and 2.01 days), PH (-24.84 and -13.46 cm), and positively affect NN (by -1.01 units) and RCD (by 0.27 mm). SER 16, a parent with favorable GCA estimates for drought adaptation, enhanced NVP (1.75 units), NS (6.25 units), HI (21%), reduced plant cycle (DM: -2.54 days), and increased GY (0.76 g·plant^{-1}).

Table 3. Estimates of effects of general combining ability (ĝi) for the following variables: days to flowering (DF); root collar diameter (RCD); number of nodes per plant (NN); plant height (PH); leaf dry matter (LDM), stem dry matter (SDM), and total shoot dry matter (TSDM); leaf area (LA); number of viable pods per plant (NVP); number of unviable pods per plant (NUP); number of viable seeds per plant (NS); number of empty locules (NEL); days to maturity (DM); grain yield (GY); and harvest index (HI) of the 12 common bean parents.

Parent	$\hat{g}_i$							
	DF	RCD	NN	PH	LDM	SDM	TSDM	LA
	(days)	(cm)	(un.)	(cm)	--------(g)-------			cm^2
IAC Imperador	0.44	0.10	-0.37	-7.64*	-0.03	-0.05	-0.08	-22.41
SEA 5	-2.54**	0.27**	-1.01**	-24.84**	-0.07	-0.22**	-0.30	-119.47
Carioca Precoce	-0.27	0.03	0.01	0.54	0.09	0.03	0.13	89.95
BRS Majestoso	0.88**	0.24**	0.04	0.35	0.09	0.05	0.14	-39.04
SER 16	-2.01**	-0.05	-0.50	-13.46**	0.17	0.01	0.18	181.66
G 19841	0.88**	-0.48**	0.22	21.15**	-0.22*	-0.09	-0.31	-394.75**
Wild Mex	3.65**	-1.01**	2.72**	80.33**	-0.29**	0.26**	-0.03	369.06**
GEN TS 3-2	0.63*	0.19*	0.00	-12.05**	-0.07	-0.15	-0.22	-104.69
GEN TS 3-3	-2.44**	0.11	-0.33	-19.12**	-0.20*	-0.25*	-0.46*	-431.18**
GEN TS 4-8	0.73**	0.16*	-0.32	-6.14	0.00	-0.06	-0.07	-31.19
IAC Sintonia	0.65*	0.31**	0.02	-0.48	0.26*	0.39	0.65**	183.91
BRS FP403	0.87**	0.11	-0.47	-18.62**	0.29**	0.08	0.37*	318.15**
Parent	$\hat{g}_i$							
	NVP	NUP	NS	NEL	DM	GY	HI	-
	---------------------(un.)---------------------				(days)	(g·plant^{-1})		
IAC Imperador	-0.29	0.83**	-0.63	-0.18	-1.18	0.21	-0.01	-
SEA 5	-0.05	-0.37	0.60	0.88	0.31	0.11	0.04	-
Carioca Precoce	0.32	-0.21	2.60*	0.45	0.06	0.81**	0.25**	-
BRS Majestoso	-0.68	-0.26	-2.89*	-0.05	0.42	-0.24	-0.01	-
SER 16	1.75**	0.43	6.25**	1.77**	-2.54**	0.76**	0.21**	-
G 19841	-1.17**	0.58*	-6.37**	-0.69	1.61	-0.06	-0.06	-
Wild Mex	3.49**	-0.62*	10.01**	-0.14	4.65**	-0.83**	-0.27**	-
GEN TS 3-2	-0.18	-0.06	0.47	-0.17	-2.10*	0.19	0.04	-
GEN TS 3-3	-1.10**	0.87**	-2.31*	-0.51	-2.83*	-0.50*	-0.06	-
GEN TS 4-8	-1.25**	-0.26	-4.14**	-0.72	0.22	-0.44*	-0.06	-
IAC Sintonia	-0.30	-0.37	-1.92	-1.37*	0.70	0.20	-0.02	-
BRS FP403	-0.52	-0.55*	-1.71	0.75	0.66	-0.21	-0.04	-

*Significant at 5% probability by the Student's t test; **significant at 1% probability by the Student's t test.

In contrast, Wild Mex, a robust anthracnose-resistant variety, yielded abundant pods and seeds per plant, evident in its positive and significant GCA effects (Table 3), with 3.49 pods and 10.01 seeds per plant. Its small seeds accompanied a climbing, indeterminate growth habit (type IV). However, its GY (-0.83 g·plant^{-1}), HI (-27%), and LDM (-0.29 g) values were unfavorable, elevating PH by 80.33 cm and mean plant cycle (DM) by 4.65 days. The parents Gen TS 3-3 and Gen TS 4-8 exhibited negative, significant GY estimates. Besides, Gen TS 3-3 had beneficial effects, reducing DF (-2.44 days), DM (-2.83 days), and PH (-19.12 cm). BRS FP403, a black-seeded genotype, displayed advantageous GCA for variables like PH (-18.62 cm), LDM (0.29 g), TSDM (0.37 g), LA (318.15 cm^2), and NUP (-0.55). However, its GY and HI performance under water deficit was not interesting as a drought-tolerance parent (Table 3).

Six hybrid combinations showed significant estimates of SCA for more than one variable, namely the combinations SEA 5 × SER 16, Carioca Precoce × SER 16, BRS Majestoso × G19841, SER 16 × BRS FP403, Gen TS 3-3 × IAC Sintonia, and Gen TS 4-8 × IAC Sintonia (Table 4).

Table 4. Estimates of effects of specific combining ability ($\hat{s}_{ij}$) for the following variables: days to flowering (DF), stomatal conductance (SC), plant height (PH), leaf dry matter (LDM), total shoot dry matter (TSDM), and harvest index (HI) of the crosses of the 12 common bean parents.

$\hat{s}_{ij}$							
I	*J*	DF	SC	PH (cm)	LDM -------(g)-------	TSDM	HI
IAC Imperador	SEA 5	-0.64	2.68	4.45	0.51	0.68	0.01
IAC Imperador	Car. Precoce	1.26	-12.26	9.89	0.29	0.40	0.22
IAC Imperador	BRS Majestoso	0.26	8.05	15.41	0.38	0.54	-0.02
IAC Imperador	SER 16	-0.83	7.21	-12.94	-0.57	-0.79	0.08
IAC Imperador	G 19841	-0.74	9.26	21.11	0.61*	0.87	0.07
IAC Imperador	Wild Mex	-1.47	14.54	-26.23*	0.40	1.03	-0.09
IAC Imperador	GEN TS 3-2	0.68	11.36	-6.67	-0.08	0.01	0.18
IAC Imperador	GEN TS 3-3	-0.24	-13.53	0.73	-0.27	-0.58	0.36*
IAC Imperador	GEN TS 4-8	-0.28	-5.35	-15.76	-0.35	-0.53	-0.23
IAC Imperador	IAC Sintonia	1.17	-5.65	25.59	0.26	0.59	-0.49**
IAC Imperador	BRS FP403	0.11	0.17	12.48	-0.19	-0.26	-0.34
SEA 5	Car. Precoce	0.42	-12.63	8.59	0.18	0.26	-0.11
SEA 5	BRS Majestoso	2.75**	-7.66	-5.22	0.40	0.66	-0.10
SEA 5	SER 16	1.65*	13.54	4.10	-0.63*	-1.04	0.55**
SEA 5	G 19841	-1.25	-14.87	-10.02	0.29	0.47	0.03
SEA 5	Wild Mex	1.01	-0.47	25.64*	-0.09	-0.23	0.16
SEA 5	GEN TS 3-2	0.83	17.33	16.86	0.07	0.40	0.05
SEA 5	GEN TS 3-3	-0.58	-0.10	-4.90	-0.04	-0.02	-0.02
SEA 5	GEN TS 4-8	-1.46	-0.48	-3.72	-0.51	-0.77	0.09
SEA 5	IAC Sintonia	-2.51	6.38	-21.54	0.18	0.16	-0.34
SEA 5	BRS FP403	1.43	-0.41	-17.57	0.02	-0.20	-0.11
Car. Precoce	BRS Majestoso	0.32	0.86	27.38*	0.02	-0.01	-0.08
Car. Precoce	SER 16	-0.94	-19.53*	25.54*	0.02	0.03	-0.16
Car. Precoce	G 19841	-1.01	-10.40	-13.75	-0.22	-0.17	-0.12
Car. Precoce	Wild Mex	-0.92	19.39*	17.58	0.17	0.22	-0.21
Car. Precoce	GEN TS 3-2	-0.76	19.10*	11.97	0.55	1.05	-0.06
Car. Precoce	GEN TS 3-3	-1.01	19.25*	-10.30	-0.09	0.14	-0.10
Car. Precoce	GEN TS 4-8	0.44	-10.76	2.05	0.43	0.54	-0.26
Car. Precoce	IAC Sintonia	0.89	22.03*	-19.27	-0.04	-0.23	0.45*
Car. Precoce	BRS FP403	0.50	15.06	-0.21	-0.72*	-1.01	0.55**
BRS Majestoso	SER 16	-1.61*	-10.55	1.89	0.11	0.28	0.13
BRS Majestoso	G 19841	-0.35	18.29*	28.94*	0.01	0.33	0.05
BRS Majestoso	Wild Mex	-0.75	3.24	-15.07	-0.45	-0.81	-0.08
BRS Majestoso	GEN TS 3-2	-0.60	-4.30	-16.01	0.33	0.48	-0.12
BRS Majestoso	GEN TS 3-3	-1.18	0.92	3.89	0.02	0.32	-0.16
BRS Majestoso	GEN TS 4-8	-0.72	-3.25	7.90	0.41	0.70	0.18
BRS Majestoso	IAC Sintonia	1.22	-2.53	7.59	-0.29	-0.40	0.00
BRS Majestoso	BRS FP403	-0.50	-7.67	-3.94	0.21	0.12	0.03
SER 16	G 19841	-0.61	19.04*	0.26	-0.09	-0.24	-0.23
SER 16	Wild Mex	2.49**	-10.77	8.25	0.11	0.49	-0.11
SER 16	GEN TS 3-2	-0.69	-0.73	4.64	0.33	0.19	0.14
SER 16	GEN TS 3-3	0.56	-7.98	0.88	0.29	0.48	-0.30
SER 16	GEN TS 4-8	-1.65*	-12.24	-21.61	-0.27	-0.70	-0.12
SER 16	IAC Sintonia	0.79	-21.30*	6.24	-0.07	-0.10	-0.20
SER 16	BRS FP403	-0.43	22.74*	-6.12	0.88**	1.46**	-0.10

Continue...

Table 4. Continuation...

		$\hat{s}_{ij}$					
I	*J*	DF	SC	PH (cm)	LDM	TSDM	HI
					-------(g)-------		
G 19841	Wild Mex	2.75**	-3.27	-20.37	-0.12	-0.92	-0.11
G 19841	GEN TS 3-2	-0.43	-7.07	-5.14	-0.48	-0.78	-0.11
G 19841	GEN TS 3-3	1.99**	2.91	18.43	0.43	0.71	-0.19
G 19841	GEN TS 4-8	0.94	-14.45	-20.39	0.00	0.04	-0.26
G 19841	IAC Sintonia	-0.44	-8.57	-2.21	-0.68*	-0.98	-0.04
G 19841	BRS FP403	-1.33	12.29	-17.49	-0.32	-0.33	-0.06
Wild Mex	GEN TS 3-2	-0.50	-18.51*	20.35	-0.07	-0.32	-0.03
Wild Mex	GEN TS 3-3	-1.25	-0.92	27.59*	0.22	0.18	-0.07
Wild Mex	GEN TS 4-8	2.04**	7.42	16.77	-0.39	-0.49	0.00
Wild Mex	IAC Sintonia	-0.85	1.96	16.45	-0.44	-0.50	0.30
Wild Mex	BRS FP403	-0.90	5.16	5.42	0.04	0.17	0.14
GEN TS 3-2	GEN TS 3-3	0.40	-6.27	-5.69	-0.11	-0.14	0.11
GEN TS 3-2	GEN TS 4-8	-0.64	3.38	14.15	0.36	0.95	-0.01
GEN TS 3-2	IAC Sintonia	-0.53	-1.06	-1.66	0.11	0.04	0.23
GEN TS 3-2	BRS FP403	0.25	-11.55	8.14	-0.45	-0.78	0.06
GEN TS 3-3	GEN TS 4-8	-1.22	14.70	18.06	-0.29	-0.56	0.09
GEN TS 3-3	IAC Sintonia	-1.94*	-3.09	-22.43*	0.00	-0.16	0.03
GEN TS 3-3	BRS FP403	1.33	-6.08	-11.12	-0.17	-0.44	0.28
GEN TS 4-8	IAC Sintonia	1.01	12.00	-4.58	0.68*	1.07*	0.20
GEN TS 4-8	BRS FP403	-1.21	20.93*	13.56	0.46	0.80	-0.18
IAC Sintonia	BRS FP403	-0.10	-22.02*	11.90	0.33	0.47	0.05

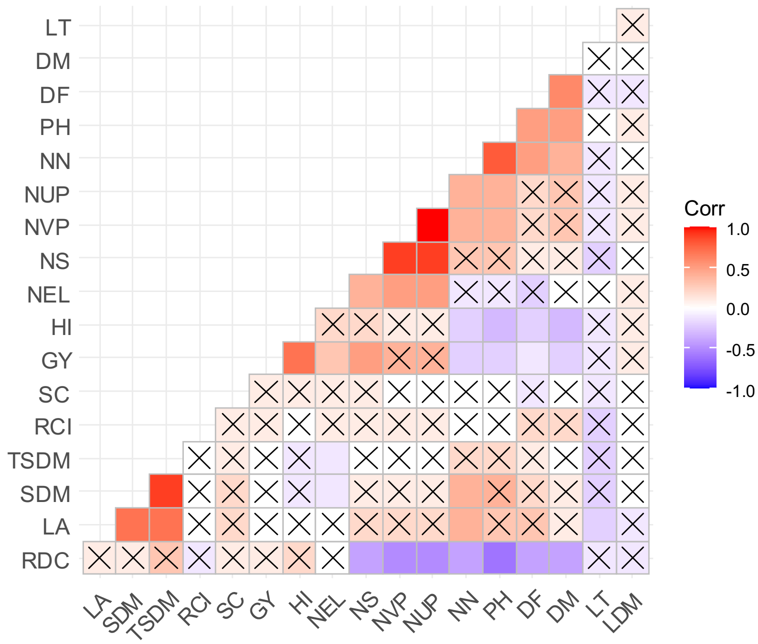
*Significant at 5% probability by the Student's t test; **significant at 1% probability by the Student's t test, I: female parent; J: male parent.

Prominent crosses for early maturity in DF were BRS Majestoso × SER 16 (-1.61 days), SER 16 × Gen TS 4-8 (-1.65 days), and Gen TS 3-3 × IAC Sintonia (-1.94 days). Optimal SC combinations included Carioca Precoce × Wild Mex, Carioca Precoce × Gen TS 3-2, Carioca Precoce × Gen TS 3-3, Carioca Precoce × IAC Sintonia, BRS Majestoso × G19841, SER 16 × G19841, SER 16 × BRS FP403, and Gen TS 4-8 × BRS FP403, with SC values of 19.39, 19.10, 19.25, 22.03, 18.29, 19.04, 22.74, and 20.93 $mmol.m^{-2}·s^{-1}$. For reduced PH, standouts were IAC Imperador × Wild Mex (-26.23 cm) and Gen TS 3-3 × IAC Sintonia (-22.43 cm). For increased dry matter, SER 16 × BRS FP403 (LDM: 0.88 g, TSDM: 1.46 g) and Gen TS 4-8 × IAC Sintonia (LDM: 0.68 g, TSDM: 1.07 g) were the best combinations.

For HI, a physiological concept that considers the ratio of grain produced in relation to total shoot dry matter of the plant, in percentage, the hybrid combinations SEA 5 × SER 16, Carioca Precoce × BRS FP403, Carioca Precoce × IAC Sintonia, and IAC Imperador × GEN TS 3-3 contributed through increases of 55, 55, 45, and 36%, respectively, for HI. HI can be used as an indirect selection criterion because it had a highly significant correlation with GY (Fig. 1) (Assefa et al. 2015, Costa et al. 1985). It is known that environmental adversities such as drought can result in lower HI. A negative index was found in the combination IAC Imperador × IAC Sintonia, with 49% reduction in the index.

When a hybrid combination has significant effect SCA for a characteristic of interest, at least one of its parents also has favorable GCA, such was the case for DF, in which the parents SER 16 and Gen TS 3-3 exhibited negative and highly significant GCA for the variable, confirming that their participation in crosses reduces the number of DF.

It was verified that the effects of SCA allowed the responses of the hybrid combinations in relation to the mean of the parents to be known, which may be greater or less than their parents. The variables LDM, TSDM, SC, DF, PH, and HI had significant effects of SCA (dominance), allowing identification of hybrid combinations that stood out from the others under water deficit. Although it was not possible to identify combinations with SCA favorable for the most desired variable, grain yield under water deficit, three combinations (SEA 5 × SER 16, Carioca Precoce × BRS FP403, and IAC Imperador × GEN TS 3-3) exhibited significant and positive SCA for HI.



LT: leaf temperature; DM: days to maturity; DF: days to flowering; PH: plant height; NN: number of nodes per plant; NUP: number of unviable pods per plant; NVP: number of viable pods per plant; NS: number of viable seeds per plant; NEL: number of empty locules; HI: harvest index; GY: grain yield; SC: stomatal conductance; RCI: relative chlorophyll index; TSDM: total shoot dry matter; SDM: stem dry matter; LA: leaf area; RCD: root collar diameter; LDM: leaf dry matter.

Figure 1. Pearson's correlation involving 18 traits evaluated under intermittent water deficit in 144 common bean genotypes originating from a diallel cross.

Reciprocal effects were noted for DF, SC, PH, LDM, TSDM, LA, and HI (Table 5). For example, in Carioca Precoce × IAC Sintonia, using IAC Sintonia as female parent resulted in negative HI (-0.22), yet positive PH (17.83 cm), LDM (0.23 g), and TSDM (0.64 g). As male parent (Table 4), IAC Sintonia had favorable, significant HI (0.45) and SC (22.03 mmol.m^{-2}·s^{-1}) estimates, not observed as pollen receptor. HI displayed 15 hybrids with positive reciprocal effects. Carioca Precoce × BRS FP403 (index 89%) and Gen TS 4-8 × IAC Sintonia (index 43%) using BRS FP403 and Gen TS 4-8 as pollen receptors stood out. Carioca Precoce × SER 16 and Carioca Precoce × BRS Majestoso also stood out (indices 39 and 37%) with SER 16 and BRS Majestoso as male parents. Significant maternal effect for PH, DF, and HI was confirmed among the seven variables.

Table 5. Estimates of reciprocal effects ($\hat{r}_{ij}$) for the following variables: days to flowering (DF), stomatal conductance (SC), plant height (PH), leaf dry matter (LDM), total shoot dry matter (TSDM), leaf area (LA), and harvest index (HI) of the reciprocal crosses of the 12 common bean parents.

		$\hat{r}_{ij}$						
I	*J*	DF	SC	PH (cm)	LDM -------(g)-------	TSDM	LA (cm^2)	HI
IAC Imperador	SEA 5	0.00	-15.50**	-9.00*	-0.09	-0.20	-207.67*	-0.13
IAC Imperador	Car. Precoce	1.17**	12.29**	16.50**	0.25*	0.36*	-156.67	-0.24**
IAC Imperador	BRS Majestoso	-0.67	6.00	35.50**	0.22*	0.66**	50.67	0.24**
IAC Imperador	SER 16	-2.00**	-21.67**	5.33	0.43**	0.85**	493.67**	-0.04
IAC Imperador	G 19841	0.00	10.25**	4.67	0.25*	0.67**	128.33	-0.08
IAC Imperador	Wild Mex	0.00	13.17**	-19.83**	0.05	0.25	135.00	-0.07
IAC Imperador	GEN TS 3-2	-0.17	1.82	22.00**	0.61**	0.66**	590.17**	0.26**
IAC Imperador	GEN TS 3-3	-1.17**	-28.35**	9.00*	-0.46**	-0.85**	-176.67	-0.24**
IAC Imperador	GEN TS 4-8	-0.83**	-15.00**	17.83**	0.00	0.18	-204.33*	-0.01
IAC Imperador	IAC Sintonia	-1.00**	4.25	31.83**	0.27*	0.71**	270.83*	-0.08
IAC Imperador	BRS FP403	1.50**	-6.47	11.75**	0.23*	0.31	484.83**	-0.15*
SEA 5	Car. Precoce	-0.33	12.73**	-4.67	-0.02	-0.06	131.33	-0.04
SEA 5	BRS Majestoso	1.50**	0.13	8.33*	-0.91**	-1.79**	-578.33**	-0.24**
SEA 5	SER 16	0.83**	15.33**	-3.83	0.20	0.28	396.67**	0.22**

Continue...

Table 5. Continuation...

				$\hat{r}_{ij}$				
I	*J*	DF	SC	PH (cm)	LDM	TSDM	LA (cm^2)	HI
					--------(g)--------			
SEA 5	G 19841	-2.17**	7.30	7.33*	0.31*	0.71**	23.67	-0.17*
SEA 5	Wild Mex	0.50	-20.17**	2.17	0.21*	0.62**	341.67**	-0.08
SEA 5	GEN TS 3-2	-1.67**	-6.00	11.00**	0.08	0.43*	-233.00*	-0.11
SEA 5	GEN TS 3-3	-0.50	14.25**	7.17	0.02	0.25	-26.33	0.11
SEA 5	GEN TS 4-8	-0.33	15.45**	-11.33**	-0.05	-0.04	-248.50*	-0.14
SEA 5	IAC Sintonia	-1.67**	-3.05	2.50	0.94**	1.48**	648.33**	-0.16*
SEA 5	BRS FP403	1.17**	-14.37**	-2.33	0.31*	0.56**	166.67	0.19**
Car. Precoce	BRS Majestoso	-0.33	-10.38**	42.33**	0.21*	0.62**	216.67*	0.37**
Car. Precoce	SER 16	3.50**	-11.83**	10.67**	0.18	0.17	2.00	0.39**
Car. Precoce	G 19841	0.33	-16.00**	-20.00**	-0.18	-0.28	-184.67	-0.08
Car. Precoce	Wild Mex	-3.50**	-3.25	-12.50**	-0.29*	-0.32	-38.33	0.08
Car. Precoce	GEN TS 3-2	3.67**	-11.33**	7.50*	0.53**	0.57**	27.17	0.21**
Car. Precoce	GEN TS 3-3	0.33	6.00	-0.50	0.20*	0.30	28.00	0.23**
Car. Precoce	GEN TS 4-8	-0.50	8.67*	-1.50	0.04	0.28	96.83	-0.20**
Car. Precoce	IAC Sintonia	-0.33	-3.50	17.83**	0.23*	0.64**	253.33*	-0.22**
Car. Precoce	BRS FP403	-1.50**	5.33	13.25**	0.03	0.41*	-418.67**	0.89**
BRS Majestoso	SER 16	0.00	4.80	-3.50	-0.53**	-0.77**	-193.33	0.07
BRS Majestoso	G 19841	-0.50	15.25**	15.83**	-0.28*	-0.09	-135.50	0.27**
BRS Majestoso	Wild Mex	-0.50	-5.83	-7.67*	-0.36**	-1.17**	-453.17**	0.02
BRS Majestoso	GEN TS 3-2	-1.67**	-8.33*	-5.00	-0.53**	-0.89**	23.33	-0.16*
BRS Majestoso	GEN TS 3-3	-1.67**	-25.27**	-9.50*	-0.62**	-0.77**	-282.50	-0.26**
BRS Majestoso	GEN TS 4-8	1.17**	-13.77**	44.50**	0.38**	0.95**	-60.83	-0.55**
BRS Majestoso	IAC Sintonia	0.17	-12.67**	-4.17	0.55**	0.77**	648.33**	0.28**
BRS Majestoso	BRS FP403	0.00	-5.00	4.83	-0.60**	-1.14**	-146.67	0.22**
SER 16	G 19841	-1.00**	8.83*	-4.00	-0.83**	-1.24**	-764.67**	0.15*
SER 16	Wild Mex	0.17	-23.83**	-10.50**	-0.22*	-0.48*	-593.33**	-0.03
SER 16	GEN TS 3-2	-3.00**	-8.90*	6.83	-0.42*	-0.39*	-326.67**	0.18**
SER 16	GEN TS 3-3	-0.50	-8.50*	7.67*	-0.40**	-0.66**	-319.00**	-0.22**
SER 16	GEN TS 4-8	-0.67*	6.25	10.17**	0.26**	0.61**	-251.83*	-0.31**
SER 16	IAC Sintonia	-0.17	6.43*	-8.67*	0.05	-0.09	528.33**	-0.09
SER 16	BRS FP403	-0.83**	16.92**	-18.50**	0.18	0.13	505.00**	0.11
G 19841	Wild Mex	3.67**	-4.37	-11.50**	-0.41**	-0.82**	-373.00**	0.10
G 19841	GEN TS 3-2	-0.50	-16.20**	36.00**	0.09	0.52*	88.33	-0.06
G 19841	GEN TS 3-3	0.50	25.57**	30.50**	0.55**	0.82**	507.33**	0.05
G 19841	GEN TS 4-8	-0.83**	-11.42**	-4.67	-0.31*	-0.52*	-462.33**	-0.16*
G 19841	IAC Sintonia	-0.17	-6.67*	-25.50**	-0.03	-0.41*	51.00	-0.31**
G 19841	BRS FP403	-0.17	32.00**	41.58**	0.09	0.63**	269.42**	0.03
Wild Mex	GEN TS 3-2	-0.17	0.03	-22.00**	-0.56**	-1.00**	-1,085.00**	0.12
Wild Mex	GEN TS 3-3	-1.67**	13.40**	12.17**	-0.31*	-0.31	-444.67**	0.00
Wild Mex	GEN TS 4-8	-1.00**	5.42	7.00*	-0.29*	-0.76**	-630.83**	-0.16*
Wild Mex	IAC Sintonia	0.83**	11.33**	-15.67**	-0.32**	-0.73**	-61.33	0.19**
Wild Mex	BRS FP403	0.33	3.67	0.83	0.23*	0.50*	652.00**	-0.14*
GEN TS 3-2	GEN TS 3-3	0.33	-25.42**	-5.83	0.01	-0.18	88.67	-0.12
GEN TS 3-2	GEN TS 4-8	-0.67*	-15.08**	-10.00**	-0.53**	-0.92**	-681.67**	0.42**
GEN TS 3-2	IAC Sintonia	-0.17	3.65	-14.50**	-0.42**	-0.67**	-306.83*	0.28**
GEN TS 3-2	BRS FP403	-0.17	4.67	-30.17**	-0.25*	-0.51*	-593.33**	-0.03
GEN TS 3-3	GEN TS 4-8	1.00**	-11.92**	5.50	0.76**	0.85**	555.00**	0.11
GEN TS 3-3	IAC Sintonia	-0.67*	0.50	14.00**	-0.49**	-1.05**	-539.17**	0.22**
GEN TS 3-3	BRS FP403	-1.50**	25.42**	3.83	-0.31*	-0.33	-773.33**	0.13
GEN TS 4-8	IAC Sintonia	0.33	14.57**	-30.83**	-0.89**	-1.10**	-214.33*	0.43**
GEN TS 4-8	BRS FP403	0.33	-9.50*	19.50**	0.20*	0.36*	311.67**	0.00
IAC Sintonia	BRS FP403	0.17	7.17*	6.83	0.39**	0.80**	299.00*	-0.19**

*Significant at 5% probability by the Student's t test; **significant at 1% probability by the Student's t test; I: female parent; J: male parent.

DISCUSSION

Significant effects were observed for the genotype source of variation for most of the variables analyzed, from which it can be inferred that the expression of these variables was affected by the water restriction imposed, which facilitates the selection of genotypes in accordance with the variability presented for determined traits (Table 2).

This result aligns with studies by Rezene et al. (2013), Asfaw and Blair (2014), Darkwa et al. (2016), Langat et al. (2019), Ribeiro et al. (2019), Papathanasiou et al. (2022) and Fogaça et al. (2023), who examined common bean responses under water deficit, revealing diverse reactions among genotypes. Beebe et al. (2008) and Beebe et al. (2013) emphasized in their research that effective breeding for drought tolerance requires considering quantitative trait inheritance. Pre-breeding is crucial to identify drought-tolerant parents, and subsequent crosses in segregating generations help incorporate additional traits. Moreover, the selecting for drought resistance not only enhances yield potential and plant efficiency, but also uncovers genes addressing inefficiencies from wild *P. vulgaris*. This insight is vital for improving common bean yield, especially in trials involving germplasm accessions, advanced bred lines, and recombinant inbred lines.

Analyzing these segregating populations boosts breeding program efficiency. Crucially, diallel crosses using GCA and SCA enable careful parent selection to transmit favorable alleles and create hybrids with desirable traits. GCA estimates reveal predominantly additive gene effects, aiding parent recommendations. SCA effects, deviations from GCA-based expectations, highlight non-additive gene effects. Breeder-favored hybrids exhibit positive SCA, often involving high-GCA parents, fostering high trait mean and genetic variability for pure line extraction (Cruz et al. 2004, Ramalho et al. 2012).

Additive and non-additive effects were observed in control of the variables, as well as a reciprocal effect for some variables. Estimates of GCA with high and positive values are desirable for the following traits: RCI; SC; RCD; NN; LDM, SDM, and TSDM; LA; NVP; NS; GY; and HI. Estimates with low or negative values would be desirable for the following traits: LT, PH, NUP, NEL, DF, and DM.

According to Cruz et al. (2004), when there is a low estimate of GCA, whether positive or negative, the value of the GCA of the parent, calculated as based on its crosses with the other parents, does not differ significantly from the overall mean of the diallel crosses. When these GCA estimates are high, whether positive or negative, the parent in question is significantly higher or lower than the other parents included in the diallel in relation to the mean response of the crosses.

Silva et al. (2011) underscored the need to include secondary traits in genetic breeding for water deficit. Despite water scarcity reducing yield variability, it amplifies the impact on secondary traits. Plants morphophysiologically adapt to withstand water stress, exhibiting features such as reduced growth, smaller leaf area, increased root growth, leaf curling, floral abscission, and changes in cuticle permeability. In water deficit, utilizing secondary traits is a common practice to identify more productive or water-efficient genotypes, enhancing precision in genotype selection beyond productivity metrics.

The shoot morphological traits (LDM, SDM, TSDM, LA, NN, PH, and RCD) showed a significant effect for GCA, and the selection of parents with effects of high and significant mean values is desirable through their exhibition of satisfactory genetic variability. Arruda et al. (2019) observed reductions in biomass, photosynthetic aspects, harvest index, and yield components in common bean grown in pots under water deficit in the reproductive stage. The authors found additive and non-additive effects acting in expression of these variables, which can be used in selection of drought-tolerant genotypes. In the case of PH, parents with negative general combining ability are sought because they contribute genes that act in reduction of the trait. In this case, the parents SEA 5, SER 16, Gen TS 3-2, Gen TS 3-3, BRS FP403, and IAC Imperador stood out reducing PH. In contrast, the parents Wild Mex and G 19841 exhibited a highly significant and positive effect, contributing to an increase in PH in the crosses in which they participated.

The DF and DM traits exhibited significant GCA (Table 3), indicating that at least one parent was superior for these additive effect traits. The aim in this case was to use parents that have negative effects of GCA for this trait as a way of reducing the plant cycle. For DF, the parents SEA 5, SER 16, and Gen TS 3-3 showed this performance. For DM, the parents SER 16, Gen TS 3-2, and Gen TS 3-3 had satisfactory results, with alleles of early maturity.

The SER 16 parent had negative GCA estimates for DF (-2.01 days), PH (-13.46 cm), and DM (-2.54 days) and may be useful when cycle reduction and determinate plant grow habit is desired, besides all these traits presenting negative correlation with GY (Fig. 1), i.e., the reduction of these traits and the increase of gain production. Even though plants of reduced size facilitate management practices and early cultivars spend a shorter time in the field, according to Cavatte et al. (2011) these cultivars possess an advantage, because they are enabled to complete their cycles before stress reaches severe levels. In addition, SER 16 led to significant and positive effects in regard to the NVP (1.75 unit) and NS (6.25 units) yield components, directly affecting the higher estimates of GCA for GY (0.76 g·plant^{-1}) and harvest index (21%). SER 16 is extracted from selections of the CIAT for drought tolerance, and its performance was confirmed in this study and in the study by Andrade et al. (2016).

The Carioca Precoce parent had the highest estimates for GY, acting with favorable alleles for an increase of 0.81 g per plant, and also for HI, with an increase of 25% in this trait. This is a useful response for breeding programs, because GY is a trait of low heritability and is highly affected by the environment. Above all, it is the main trait in selection for tolerance to water deficit since the objective is to obtain lines that yield well under drought. Evaluation of quantitative traits can be assisted by combining ability. Additive effects facilitate the process of selection for drought tolerance in common bean-breeding programs, because common bean is an autogamous species, and additive genetic effects bring about genetic gains for these traits, which can be established across generations of self-fertilization (Arruda et al. 2019, Fasahat et al. 2016).

Langat et al. (2019) identified the number of pods per plant, days to maturity, and yield per plant as the main traits for selection of drought-tolerant genotypes, and identified significant and positive correlation between the harvest index and the traits of total dry matter and number of pods per plant. According to Gonçalves et al. (2019), the number of pods per plant is one of the yield components most affected by water restriction.

The harvest index is a measure of the proportion of photoassimilation redirected to grain production, and it is used as a measure of biological efficiency. According to Assefa et al. (2015), there is a high correlation among grain yield, shoot dry mass and harvest index; they are considered to be highly discriminating and reliable traits in determination of drought tolerance in common bean. Assefa et al. (2017) found significant and positive correlation between the pod harvest index and grain yield. In agreement with these studies, the present study also showed highly significant and positive correlation between the grain yield and harvest index traits (Fig. 1), and harvest index can be used as an indirect measure of grain yield in common bean breeding. This confirms the selection of the Carioca Precoce and SER 16 parents in breeding programs for drought tolerance, because they act in increasing yield components, yield, and HI in the crosses in which they participate, showing their potential for extraction of tolerant lines from these crosses.

Other parents such as Wild Mex, Gen TS 3-3, and Gen TS 4-8 exhibited significant and negative values of GCA estimates for GY, that is, reducing grain production by -0.83 g·plant^{-1}, -0.50 g·plant^{-1}, and -0.44 g·plant^{-1}, respectively. Furthermore, Wild Mex exhibited significant and negative GCA estimates for HI (-27%) and significant and positive estimates for DM, increasing the cycle of its descendants by 4.65 days.

The advanced lines Gen TS 3-3 and Gen TS 4-8 were developed for tolerance to water deficit, proving to be efficient in experiments with exposure to water deficit under natural growing conditions and in a greenhouse using pots with soil moisture sensors when evaluated *per se* (Gonçalves et al. 2015, Ribeiro et al. 2019, Ribeiro et al. 2021, Gonçalves et al. 2022). However, when they were used as parents in these combinations, they had low values of GCA and SCA for the traits of interest, possibly due to restricted genetic variability when they are combined with the other parents. Gen TS 3-3 was developed by the hybridization of SEA 5 × IAC Carioca Tybatã, and TS 4-8 came from hybridization of SEA 5 × IAC Alvorada. That is, their parental varieties are also present in this diallel, whether as parents or in the origin of the parents.

Foolad and Bassiri (1983), evaluating a diallel between four common bean genitors regarding grain yield, yield components and days to flowering in field, found statistical significance for genitors and significant effects for GCA, SCA and reciprocal. Significant effect of GCA were observed for grain yield, numbers of pod per plant, numbers of seed per plant, a hundred seed weight and number of days to flowering; significant effect of SCA for all traits in the most hybrid combinations, and reciprocal effects except for a hundred seed weight.

Gonçalves et al. (2015), studying the combining ability in a diallel cross of four common bean cultivars under drought stress in controlled conditions regarding the physiological, morphological and yield components traits, also detected additive, dominant effects controlling these traits and reciprocal effect only for grain yield. Their results enabled the selection of the best genitors and their drought tolerant progenies.

Although SCA is useful in determination of the best hybrid combinations, it does not specify which of the parents should be used as a pollen donor or receptor in the cross (Ramalho et al. 2012, Rodrigues et al. 2018). This identification can be performed by the study of reciprocal crosses. Reciprocal effects were found for the variables DF, SC, PH, LDM, TSDM, LA, and HI, with PH, DF, and HI (Table 5), exhibiting a maternal effect, showing that there is a difference when a genotype is used as a female parent or male parent for these traits. Considering HI in relation to the variable of greatest interest in selection, GY, higher levels of significance were found in the crosses in which the genotype Carioca Precoce was used as a male parent. The combination SEA 5 × SER 16 also stood out, which exhibited a reciprocal effect for increase in HI, SC, and LA when SER 16 was used as a female parent.

For PH and DF, some specific hybrid combinations have a reciprocal effect for reduction in these variables, indicating different responses upon using the female or male as parent. In the hybrid combination Gen TS 3-3 × IAC Sintonia, when Gen TS 3-3 is used as a female parent, it acts to reduce PH in the progeny, but, when it is used as a male parent, it acts to increase PH. It is most desirable that one of the parents of the hybrid combination exhibits an effect for general combining ability, such as the result obtained by Gen TS 3-3 (Table 5).

According to Ramalho et al. (2012), if inheritance of a trait is controlled by nuclear genes, the results of a cross and of its reciprocal will be identical. However, if the results of the reciprocal crosses are different, it is due to cytoplasmic effects. This type of inheritance can be explained by two mechanisms: the maternal effect and extrachromosomal inheritance. Furthermore, according to the authors, the maternal effect is a special case of inheritance controlled by nuclear genes from the mother that can be conserved over the generations, allowing them to be exploited, in this case the variables PH, DF, and HI (Table 2). The variables with extrachromosomal inheritance arise from genes situated in organelles, and the mitochondria and plastids are the main organelles that carry these genes in eukaryotes (Ramalho et al. 2012).

It should be emphasized that in the present study the drought-tolerant parents, SER 16 and SEA 5, were prominent in GCA (additive effect), especially in regard to PH and DF, acting with alleles favorable to reduction in the two traits, in contrast with Wild Mex and G 19841, which showed an additive effect for an increase in these traits that are not desirable in commercial cultivars. The SER 16 parent stood out for increase in GY and HI, together with the cultivar Carioca Precoce, and, once more, Wild Mex had undesirable results. In accordance with SCA (non-additive effects) and RE, it can be confirmed that it is possible to identify hybrid combinations with favorable traits.

It is noteworthy that this work made it possible to carry out the indirect selection of GY using HI as a criterion. The combinations SEA 5 (pollen receptor) × SER 16 and Carioca Precoce (pollen receptor) × BRS FP403 stood out with indices of 55% for the trait, and with at least one parent also standing out for alleles of activity for HI and the reciprocals Carioca Precoce (pollen donor) × BRS FP403, with the index of 89%. Thus, the selection of parents that carry traits that lead to lower reduction in yield components, together with increase in yield under water deficit, such as Carioca Precoce and SER 16, not only contribute alleles favorable to agronomic traits essential for a cultivar with a good plant ideotype, but also to the progress of common bean breeding programs in development of segregating generations for drought tolerance.

CONCLUSION

There was predominance of additive effects on expression of the variables evaluated under water deficit conditions, and the additive effects are important for selection of parents in autogamous plants for transfer of alleles to the following generations. The parents Carioca Precoce and SER 16 had prominent favorable estimates for general combining ability in relation to GY and HI, and they can be used in breeding programs for drought tolerance. With the estimate of SCA, it was possible to select hybrid combinations based on the HI, namely: SEA 5 (pollen receptor) × SER 16; Carioca Precoce (pollen receptor) × BRS FP403; and the reciprocal Carioca Precoce × BRS FP403 (pollen receptor). The variables GY and HI showed be effective in the selection for drought-tolerance in common bean.

CONFLICT OF INTEREST

Nothing to declare.

AUTHORS' CONTRIBUTION

Conceptualization: Gonçalves, J. G. R., Silva, D. A., Chiorato, A. F., Carbonell, S. A. M. **Data curation:** Gonçalves, J. G. R., Silva, D. A., Chiorato, A. F., Rovaris, S. R. S., Carbonell, S. A. M. **Formal analysis:** Gonçalves, J. G. R., Silva, D. A., Chiorato, A. F., Rovaris, S. R. S., Gonçalves, G. M. C., Carbonell, S. A. M. **Funding acquisition:** Gonçalves, J. G. R., Chiorato, A. F., Carbonell, S. A. M. **Investigation:** Gonçalves, J. G. R., Silva, D. A., Chiorato, A. F., Carbonell, S. A. M. **Methodology:** Gonçalves, J. G. R., Silva, D. A., Chiorato, A. F., Rovaris, S. R. S., Gonçalves, G. M. C., Carbonell, S. A. M. **Project administration:** Gonçalves, J. G. R., Chiorato, A. F., Carbonell, S. A. M. **Resources:** Gonçalves, J. G. R., Chiorato, A. F., Carbonell, S. A. M. **Supervision:** Chiorato, A. F., Carbonell, S. A. M. **Validation:** Gonçalves, J. G. R., Silva, D. A., Chiorato, A. F., Rovaris, S. R. S., Gonçalves, G. M. C., Carbonell, S. A. M. **Visualization:** Gonçalves, J. G. R., Silva, D. A., Chiorato, A. F., Rovaris, S. R. S., Gonçalves, G. M. C., Carbonell, S. A. M. **Writing – original draft:** Gonçalves, J. G. R., Silva, D. A., Chiorato, A. F., Carbonell, S. A. M. **Writing – review & editing:** Gonçalves, J. G. R., Silva, D. A., Chiorato, A. F., Carbonell, S. A. M.

DATA AVAILABILITY STATEMENT

All dataset were generated and analyzed in the current study.

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