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Combining Ability for Agromorphological and Physiological Traits in Different Gene Pools of Common Bean Subjected to Water Deficit

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Abstract: Water stress is one of the main limiting factors for common bean crops, negatively affecting grain yield and seed quality. Thus, the objective of this study was to evaluate the inheritance of agromorphological and physiological traits related to drought tolerance in order to identify promising combinations. The experiment was carried out in a greenhouse with a partial diallel scheme between three drought-tolerant genotypes (IAPAR 81, BAT 477, and SEA 5), and nine cultivars widely grown in Brazil (BRS Estilo, IAC Alvorada, IPR Campos Gerais, IPR Uirapuru, IPR Nhambu, BRS Esteio, IPR Garça, BRS Radiante, and DRK 18), in a randomized block design with four replicates. The plants were grown in pots with substrate under 80% of pot capacity until they reached the stage R5, when water supply was restricted to 30% for 20 days in the pots under stress treatment. A wide variability for the agromorphological and physiological traits was observed. Water deficit reduced plant performance for most agromorphological traits and altered their physiological metabolism. Additive and non-additive effects are involved in the genetic control of the majority of agromorphological and physiological traits both under water stress and control (well-watered) conditions. The parental genotypes BAT 477 (group I) and IAC Alvorada, IPR Uirapuru, and BRS Esteio (group II) may be included in breeding programs aiming at improving drought tolerance in common bean since they present high positive general combining abilities for agromorphological traits. The crosses IAPAR 81 × IPR Campos Gerais, and SEA 5 × BRS Radiante resulted in the best combinations considering grain yield per plant and total dry biomass, when cultivated under water deficit.

Keywords: *Phaseolus vulgaris* L.; drought; diallel

1. Introduction

Common bean (*Phaseolus vulgaris* L.) is considered the main legume species for human consumption and represents an important source of proteins, carbohydrates, fibers, and minerals [1,2]. Brazil is one of the largest producers and consumers of beans in the world, where it is cultivated in three seasons, with a national production of 130.3 thousand tons in 2018/2019 [3].

Despite the large production, the yield and spatial distribution of beans are severely restricted by biotic and abiotic stresses, among which drought is one of the most severe, causing reductions not only in grain yield but also in grain quality [4]. Under drought condition, the leaf water content decreases, leading to stomatal closure, and consequently, reducing CO_2 availability, net photosynthesis, and total dry biomass accumulation. In addition, water deficit causes flower abortion and pod-abortion, hampering seed yield and weight [5,6]. Finally, the impact of drought on grain yield varies depending on the frequency, duration and intensity of the stress, on the phenological stage of the crop and its interaction with other stresses.

Several studies have been carried out to identify drought-tolerant germplasm, which are found mainly in the Mesoamerican gene pool in the Durango, Mesoamerica, and Jalisco races [7,8]. From field studies, White [9] and White and Singh [10] have identified drought-tolerant bean lines, such as BAT 477, A 195, and BAT 1289. BAT 477, from the Mesoamerica race, has been widely used in studies aiming to identify mechanisms underlying plant resilience to water deficits [5,11–13] and to develop superior cultivars. The SEA 5 genotype has also been largely investigated for drought tolerance [14–16], it was derived from a cross between Mesoamerica and Durango races, in which the cultivar BAT 477 was one of the parental genotypes [17].

The selection of superior genotypes for the development of cultivars is one of the main goals of breeding programs. Among the methods of genetic analysis, the use of diallel crosses has been highlighted, providing parameter estimates that enable selection of genitors for hybridization, as well as representing a useful tool to unravel the genetic effects involved in certain agronomically desirable traits. Among the main methodologies of diallel analysis are the Griffing [18] proposals, which estimate the effects of general and specific combining abilities, the Gardner and Ebehart method [19], where the effects of variety and varietal heterosis are evaluated, and the one presented by Hayman [20], used to generate information about the basic inheritance mechanisms of the trait under study.

In view of all that has been mentioned so far, the objectives of this work were to determine, by partial diallel analysis, the inheritance of some agromorphological and physiological traits related to drought tolerance and to identify promising combinations in order to initiate a plant breeding program.

2. Materials and Methods

2.1. Plant Material and Experimental Conditions

In order to measure the combing abilities of the proposed genetic materials of beans, they were crossed among each other in a partial diallel scheme. Artificial hybridizations were performed between group I, comprised of three Mesoamerican bean genotypes considered drought-tolerant (IAPAR 81, BAT 477, and SEA 5) (Table 1) and group II, composed of nine cultivars widely used by Brazilian farmers, three carioca type from the Mesoamerican group (BRS Estilo, IPR Campos Gerais, and IAC Alvorada), three black type from the Mesoamerican group (IPR Uirapuru, IPR Nhambu, and BRS Esteio), and three belonging to the Andean group (IPR Garça, DRK 18, and BRS Radiante). All the seeds came from the gene bank of the Instituto Agronômico do Paraná (IAPAR), Londrina, Brazil.

The parental genotypes were sown in a staggered way, according to their cycle, in order to synchronize their flowering time. The hybrid seeds were obtained by artificial pollinations, performed between 8 and 11 am, in a greenhouse at IAPAR, using the crossing technique of emasculation and pollination, followed by the coverage of the stigma.

Then, the F_1 seeds from the 27 hybrids and from the 12 parental lines were pre-germinated on styrofoam trays of 128 cells with the substrate Plantmax® and after the emission of the primary leaf (stage V2) [21] the seedlings were transferred to pots containing 9 kg of substrate. The substrate was composed of 5.62 kg of soil (Red Latosol) and 3.38 kg of sand, which was sieved in a 3 mm mesh and then 50 g of the formulated fertilizer 4-30-10 (N-P_2O_5-K_2O) was added. The pots were arranged in a randomized block design, with four replicates. The cultural practices were carried out according to the technical recommendations for the crop in the region.

Table 1. Characteristics of the genitors of common bean used in the diallel crosses.

Genitors	Origin	Commercial Group	Average Cycle (days)
IAPAR 81	IAPAR	Carioca	92
BAT 477	CIAT	Brown	94
SEA 5	CIAT	Brown	90
BRS Estilo	Embrapa	Carioca	90
IPR Campos Gerais	IAPAR	Carioca	88
IAC Alvorada	Embrapa	Carioca	90
IPR Uirapuru	IAPAR	Black	86
IPR Nhambu	IAPAR	Black	90
BRS Esteio	EMBRAPA	Black	90
IPR Garça	IAPAR	White	67
DRK 18		Red	85
BRS Radiante	EMBRAPA	Cranberry	75

IAPAR: Agronomic Institute of Paraná; CIAT: International Center for Tropical Agriculture; Embrapa: Brazilian Agricultural Research Corporation.

2.2. *Water Deficit Imposition and Monitoring*

The plants were cultivated under 80% of pot capacity until they reached the stage R5 (appearance of the first floral bud) when water deficit was imposed on the plots under stress. The water regime of 30% of pot capacity was maintained for 20 days for the stress treatment, while the other plots continued to receive sufficient water supply (control treatment). This period was stipulated considering the day of maximum water stress, in which the plants showed symptoms of severe wilting, high senescence, and foliar abscission. This represents the threshold for common bean recovery from a period of drought, according to Boyer [22]. Temperature variation (maximum, minimum and average) in the greenhouse was measured using a thermohygrograph.

2.3. *Agromorphological and Physiological Evaluations*

The plants were evaluated at physiological maturity (R9) for plant height (from the shoot base to its apex, in cm), number of nodes (NN), number of pods per plant (PP), number of seeds per pod (SP), number of seeds per plant (SPL), grain yield per plant (GY, in g plant^{-1}), and total dry biomass (root, stem, leaves, and pods) (TDB, in g).

The net photosynthesis (A, in µmol CO_2 m^{-2} s^{-1}), stomatal conductance (g_s, in mol m^{-2} s^{-1}) and leaf temperature (LT, in °C) were measured in the early morning (between 8 and 10 am) of the last day of stress, on sunny periods, in order to avoid maximum transpiration and stomatal closure, using the portable system Photosynthesis LI-6400XT (LI-COR Biosciences, Lincoln, NE, USA). The leaves were placed in a measuring chamber 6400-02B of 6 cm^2, with photon flux density at 1000 µmol m^{-2} s^{-1}. The values of the intrinsic water use efficiency (iWUE, in µmol CO_2 µmol H_2O^{-1}) were obtained by the ratio A/g_s.

2.4. *Data Analysis*

The data collected were tested by analysis of variance (ANOVA), followed by the Griffing diallel analysis [18] adapted to partial diallel crosses by Geraldi and Miranda Filho [23]:

$$Y_{ijk} = m + g_i + g_j + s_{ij} + \bar{\varepsilon}_{ijk} \quad (1)$$

where: Y_{ijk} is the mean value of the hybrid combination (i ≠ i) or the parent (i = j); m is the overall mean; $\hat{g}_i$ and $\hat{g}_j$ are the general combining ability effect of the ith and jth genotype, representing group I and II, respectively; $\hat{s}_{ij}$ is the specific combining ability effect for the crosses among the ith and jth parents; and $\bar{E}_{ijk}$ is the experimental error.

The treatment effect (27 F_1 hybrids and nine parental lines), considered as a fixed effect, was decomposed into general and specific combining abilities (GCA and SCA, respectively).

2.4.1. General Combining Ability ($\hat{g}_i$):

$$\hat{g}_i = \frac{1}{p+2}[Y_{ii} + Y_{i.} - (p+1)\hat{m}] = \frac{1}{p+2}[Y_{ii} + Y_{i.} - \frac{2}{p}Y_{..}] \quad (2)$$

2.4.2. Specific Combining Ability ($\hat{s}_{ij}$):

$$\hat{s}_{ij} = Y_{ij} - \left(\hat{m} + \hat{g}_i + \hat{g}_j\right) - \frac{1}{p+2}\left[Y_{ii} + Y_{jj} + Y_{i.} + Y_{.j}\right] + \frac{2}{(p+1)(p+2)}Y_{..} \quad (3)$$

All statistical analyses were performed using Genes program [24].

3. Results

3.1. ANOVA and Diallel Analysis

When comparing the results of measurements for the different genitors and their respective F_1 hybrids grown under water deficit and control treatments, ANOVA showed significant effects ($p < 0.05$) of genotypes for all traits in both water conditions, except for LT in water deficit (Table 2). Considering the general mean, water stress dramatically reduced all evaluated characteristics, except for LT, A, and iWUE (Table 2). Most of the coefficients of variation (CV) were similar for the two water conditions, ranging from 4.24 (LT) to 46.75% (SPL) in water deficit, and from 3.78 (LT) to 45.65% (SPL) in the control treatment (well-watered) (Table 2). The decomposition of the sum of squares of genotypes for GCA (groups I and II) and SCA is presented in Table 2. The GCA of group I showed significant effects ($p < 0.05$) for PH, NN, PP, and NPS in water deficit and for PH, PP, SHL, and GY in the control condition. Regarding the GCA of group II, significant effects ($p < 0.05$) were verified for most of the characteristics in both treatments, except for PH and LT under water deficit and for PP in the control condition. Aside from SP and LT in water deficit, the other traits evaluated showed a significant effect ($p < 0.05$) of SCA in both water conditions.

3.2. General Combining Ability (GCA) Analysis

According to the GCA ($\hat{g}_i$) estimates of group I, the genitor BAT 477 presented positive values for all traits in both water conditions (Table 3). On the other hand, SEA 5 had negative results for all characteristics, with the exception of SPL in the control condition (Table 3).

Estimates of GCA ($\hat{g}_i$) of group II under water deficit and control conditions are presented in Tables 4 and 5, respectively. The parental genotypes, from Mesoamerican origin, IAC Alvorada, IPR Uirapuru, and BRS Esteio showed positive values for the majority of agromorphological characteristics in both water conditions, except for PH for BRS Esteio under water deficit. In relation to the physiological traits (A, g_s, and iWUE), the Andean genitors IPR Garça, DRK 18, and BRS Radiante showed promising results under water deficit. The estimates for IAC Alvorada, IPR Uirapuru, and BRS Esteio were positive for g_s, and negative for A and iWUE in water deficit. However, these genotypes presented values that were negative for g_s, and positive for A and iWUE in the control condition.

Table 2. Analysis of variance for agromorphological and physiological traits of the common bean genotypes under water deficit and control condition (well-watered).

Source of Variation	DF	Agromorphological and Physiological Characteristics—Water Deficit										
		PH	NN	PP	SP	SPL	GY	TDB	LT	g_s	A	iWUE
Genotypes	38	2849.45 **	12.93 **	58.38 **	1.87 **	1751.33 **	112.64 **	207.92 *	2.38	0.02 **	0.65 **	0.98 **
GCA I	2	16,351.33 **	35.02 *	147.64 **	1.35	4049.69 *	57.50	198.86	4.42	0.0001	0.16	0.25
GCA II	8	635.41	28.12 **	77.65 **	5.54 **	3583.99 **	207.28 **	278.37 *	1.51	0.04 **	0.56 **	0.70 *
SCA	27	2609.69 **	6.36 **	43.23 **	0.88	1006.44 **	90.64 **	191.50 *	2.36	0.01 **	0.67 **	1.12 **
Error	114	482.44	4.14	12.41	0.69	436.54	25.46	113.43	1.72	0.001	0.17	0.29
Mean		90.67	9.53	10.08	4.24	44.68	11.24	27.16	30.94	0.69	1.11	1.59
CV (%)		24.22	21.33	34.96	19.62	46.75	44.83	39.21	4.24	5.54	36.93	34.02
		Agromorphological and Physiological Characteristics—Control (Well-Watered)										
		PH	**NN**	**PP**	**SP**	**SPL**	**GY**	**TDB**	**LT**	g_s	**A**	**iWUE**
Genotypes	38	4915.11 **	19.19 **	72.94 **	2.24**	2971.68 **	164.32 **	655.17 **	12.19 **	0.19 **	2.22 **	2.95 **
GCA I	2	4091.31 *	0.79	114.63 *	2.24	5616.74 *	230.49 *	693.70	1.47	0.01	0.69	0.32
GCA II	8	5374.53 *	44.92 **	67.87	3.97 **	3326.34 *	218.96 **	706.28 *	24.47 **	0.39 **	4.11 **	6.15 **
SCA	27	4713.51 **	12.02 **	71.08 **	1.81 **	2633.85 **	144.73 **	650.05 *	6.30 **	0.09 **	1.47 **	1.55 **
Error	114	912.48	4.99	33.80	0.74	1250.99	69.27	264.21	1.00	0.03	0.38	0.20
Mean		119.25	11.65	15.12	4.95	77.49	19.56	41.47	26.47	0.96	3.03	3.31
CV (%)		25.33	19.17	38.44	17.3	45.65	42.55	39.22	3.78	16.97	20.22	13.62

PH: plant height (cm), NN: number of nods, PP: number of pods per plant, SP: number of seed per pod, SPL: number of seeds per plant, GY: grain yield per plant (g $plant^{-1}$), TDB: total dry biomass (g), LT: Leaf temperature (°C), g_s: stomatal conductance (mol m^{-2} s^{-1}), A: net photosynthesis (μmol CO_2 m^{-2} s^{-1}), and iWUE: intrinsic water use efficiency (μmol CO_2 μmol H_2O^{-1}); **, *: significant by *F*-test at 1% and 5% of probability, respectively.

Table 3. Estimates of general combining ability ($\hat{g}_i$) effects evaluated for drought-tolerant common bean genotypes cultivated under water deficit and control condition (well-watered).

Genitors	Water Deficit			
	PH	**NN**	**PP**	**SPL**
IAPAR 81	2.11	0.10	0.49	5.08
BAT 477	16.58	0.76	1.38	5.11
SEA 5	−18.69	−0.86	−1.87	−10.19
Genitors	**Control (Well-Watered)**			
	PH	**PP**	**SPL**	**GY**
IAPAR 81	0.41	−0.81	−6.37	−1.37
BAT 477	8.66	1.71	11.99	2.42
SEA 5	−9.07	−0.90	5.62	−1.05

PH: plant height (cm), NN: number of nods, PP: number of pods per plant, SPL: number of seeds per plant, and GY: grain yield per plant (g plant^{-1}).

Table 4. Estimates of general combining ability ($\hat{g}_i$) effects evaluated for genotypes of group II subjected to water deficit.

Genitors	Agromorphological and Physiological Traits								
	NN	**PP**	**SP**	**SPL**	**GY**	**TDB**	g_s	**A**	**iWUE**
BRS Estilo	0.74	−0.72	0.00	−3.96	−2.46	−1.85	−0.06	−0.12	−0.01
IPR Campos Gerais	0.61	−0.92	0.14	−2.72	−2.90	−3.02	−0.05	−0.11	−0.03
IAC Alvorada	0.58	1.81	0.29	10.26	0.99	3.44	0.02	−0.01	−0.04
IPR Uirapuru	0.47	0.93	0.39	7.33	1.73	1.42	0.02	−0.04	−0.10
IPR Nhambu	0.46	−1.46	0.00	−6.64	−3.75	−2.26	−0.04	−0.10	−0.07
BRS Esteio	0.95	3.16	0.58	22.01	4.69	6.05	0.04	−0.15	−0.28
IPR Garça	−1.78	−1.92	−0.75	−14.75	-0.99	−2.90	0.03	0.26	0.28
DRK 18	−0.66	0.09	0.00	−1.90	1.61	−1.58	0.02	0.13	0.12
BRS Radiante	−1.36	−0.95	−0.65	−9.61	1.08	0.70	0.03	0.13	0.12

NN: number of nods, PP: number of pods per plant, SP: number of seed per pod, SPL: number of seeds per plant, GY: grain yield per plant (g plant^{-1}), TDB: total dry biomass (g), g_s: stomatal conductance (mol m^{-2} s^{-1}), A: net photosynthesis (µmol CO_2 m^{-2} s^{-1}), and iWUE: intrinsic water use efficiency (µmol CO_2 µmol H_2O^{-1}).

Table 5. Estimates of general combining ability ($\hat{g}_i$) effects for group II cultivated under the control condition (well-watered).

Genitors	Agromorphological and Physiological Traits								
	PH	**NN**	**SP**	**SPL**	**GY**	**TDB**	**LT**	g_s	**A**	**iWUE**
BRS Estilo	−16.53	−0.22	−0.13	−15.25	−5.17	−7.72	1.10	0.16	−0.41	−0.54
IPR Campos Gerais	2.21	0.17	−0.09	−8.62	−1.74	−6.59	1.33	0.09	−0.56	−0.62
IAC Alvorada	10.99	1.40	0.40	13.45	2.66	7.76	−0.87	−0.08	0.23	0.33
IPR Uirapuru	3.15	0.91	0.31	16.73	0.32	3.22	−0.70	−0.01	0.44	0.29
IPR Nhambu	−1.22	0.48	0.33	3.93	−1.60	−2.35	1.27	0.19	−0.45	−0.69
BRS Esteio	−9.27	0.12	0.28	5.92	1.02	4.22	−0.66	−0.02	0.39	0.29
IPR Garça	−18.30	−2.50	−0.78	−9.42	−0.03	−0.85	−0.45	−0.11	0.25	0.48
DRK 18	26.42	1.13	−0.09	−6.61	3.69	2.02	−0.36	−0.12	−0.02	0.17
BRS Radiante	2.55	−1.49	−0.21	−0.12	2.88	0.30	−0.66	−0.09	0.13	0.28

PH: plant height (cm), NN: number of nods, SP: number of seeds per pod, SPL: number of seeds per plant, GY: grain yield per plant (g plant^{-1}), TDB: total dry biomass (g), LT: Leaf temperature (°C), g_s: stomatal conductance (mol m^{-2} s^{-1}), A: net photosynthesis (µmol CO_2 m^{-2} s^{-1}), and iWUE: intrinsic water use efficiency (µmol CO_2 µmol H_2O^{-1}).

3.3. Specific Combining Ability (SCA) Analysis

The crosses that presented the highest positives values of $\hat{s}_{ij}$ for GY and TDB, under water deficit, were IAPAR 81 × IPR Campos Gerais, IAPAR 81 × IPR Uirapuru, IAPAR 81 × IPR Garça, SEA 5 × BRS

Estilo, and SEA 5 × BRS Radiante (Table 6). For the physiological variables, the cross BAT 477 × BRS Radiante was highlighted by presenting positive values for A and iWUE and negative ones for g_s.

When plants were cultivated under the control condition, the combinations IAPAR 81 × BRS Esteio, IAPAR 81 × DRK 18, IAPAR 81 × BRS Radiante, BAT 477 × IAC Alvorada, BAT 477 × BRS Esteio, SEA 5 × IPR Campos Gerais, and SEA 5 × IPR Nhambu obtained the highest positive values of $\hat{s}_{ij}$ for GY and TDB (Table 7). In relation to the physiological variables, the cross IAPAR 81 × BRS Style presented positive values for A and iWUE and negative for LT and g_s. Considering only LT and g_s, the highest negative estimates were obtained between the crosses of BRS Style, IPR Campos Gerais, and IPR Nhambu with all the parental genotypes of group I (Table 7). In contrast, the highest positive effects were observed for the crosses IAPAR 81 × BRS Esteio, BAT 477 × BRS Radiant, and SEA 5 × IPR Uirapuru for LT; and SEA 5 × IPR Uirapuru, SEA 5 × DRK 18, and SEA 5 × BRS Radiant for g_s. For A, IAPAR 81 × BRS Style, BAT 477 × BRS Style, and BAT 477 × IPR Nhambu, resulted in higher values, while for iWUE the most promising results came from the combinations of IAPAR 81 × BRS Style, IAPAR 81 × BRS Radiant, BAT 477 × IAC Alvorada, and BAT 477 × DRK 18.

Table 6. Estimates of specific combining ability ($\hat{s}_{ij}$) effects resulting from the diallel crosses among the common bean genotypes cultivated under water deficit.

Genitors	Agromorphological and Physiological Traits								
	PH	NN	PP	SPL	GY	TDB	g_s	A	iWUE
P1 × P4	−0.41	−0.47	3.49	13.10	0.68	7.73	0.06	0.20	−0.18
P1 × P5	13.42	0.27	7.16	39.06	8.92	10.98	0.06	−0.04	0.20
P1 × P6	−9.64	−0.49	−0.19	−1.01	−3.06	−4.46	−0.01	0.12	−0.02
P1 × P7	5.31	0.63	0.19	6.17	3.59	3.06	−0.01	−0.04	−0.38
P1 × P8	−4.08	−0.12	5.08	18.14	4.19	1.74	0.04	−0.21	0.02
P1 × P9	2.99	0.99	−0.72	−5.53	−9.42	−0.83	−0.04	−0.03	−0.48
P1 × P10	62.52	2.38	−0.98	−5.95	5.79	6.79	−0.02	−0.39	−0.31
P1 × P11	−8.13	0.00	−3.45	−22.28	0.77	−5.73	−0.02	−0.25	0.54
P1 × P12	32.09	1.14	−5.16	−26.12	−6.54	−10.65	0.03	0.44	−0.51
P2 × P4	−7.33	1.05	2.20	5.94	4.84	−1.58	0.07	−0.26	−0.48
P2 × P5	−9.98	2.08	0.15	−1.43	−3.05	2.60	0.05	−0.05	−0.21
P2 × P6	−29.44	−0.80	0.52	3.14	3.36	0.42	−0.01	−0.38	0.33
P2 × P7	−10.15	−1.01	0.73	−1.93	−2.03	−2.60	−0.01	−0.18	−0.27
P2 × P8	−16.18	−0.53	1.68	12.99	2.13	3.83	0.04	0.28	1.43
P2 × P9	−9.67	−0.51	1.82	5.84	−2.12	−2.98	−0.04	−0.24	0.32
P2 × P10	42.39	0.05	−3.20	−16.97	−6.70	−0.45	0.03	1.18	0.82
P2 × P11	14.06	−0.10	1.32	8.86	6.25	−3.31	−0.02	0.17	−0.09
P2 × P12	27.67	−0.59	2.42	10.27	1.21	9.30	−0.01	0.56	0.05
P3 × P4	5.20	0.58	3.71	22.36	3.18	7.33	0.07	0.05	−0.16
P3 × P5	1.74	−0.37	1.06	4.29	0.70	−10.75	0.06	0.12	−0.13
P3 × P6	19.66	2.23	0.68	−1.86	0.70	7.04	−0.01	0.10	−0.02
P3 × P7	−6.88	1.35	−0.94	−0.18	0.21	1.07	−0.01	−0.14	0.46
P3 × P8	−16.90	−0.39	−0.30	−0.96	−2.59	5.24	0.05	−0.03	0.97
P3 × P9	−0.39	−0.13	−1.92	−11.48	−0.46	−3.07	−0.03	−0.05	−0.50
P3 × P10	−23.88	−1.93	−0.71	−7.33	−0.16	−9.09	−0.02	0.28	−0.18
P3 × P11	−10.69	0.46	4.78	16.07	−3.33	0.59	0.01	0.78	0.20
P3 × P12	22.90	1.11	0.21	2.65	7.78	14.02	−0.02	−0.40	−0.02

PH: plant height (cm), NN: number of nods, PP: number of pods per plant, SPL: number of seeds per plant, GY: grain yield per plant (g plant^{-1}), TDB: total dry biomass (g), g_s: stomatal conductance (mol m^{-2} s^{-1}), A: net photosynthesis (μmol CO_2 m^{-2} s^{-1}), and iWUE: intrinsic water use efficiency (μmol CO_2 μmol H_2O^{-1}). P1: IAPAR 81, P2: BAT 477, P3: SEA 5, P4: BRS Estilo, P5: IPR Campos Gerais, P6: IAC Alvorada, P7: IPR Uirapuru, P8: IPR Nhambu, P9: BRS Esteio, P10: IPR Garça, P11: DRK 18, and P12: BRS Radiante.

Table 7. Estimates of specific combining ability ($\hat{s}_{ij}$) effects resulting from the diallel crosses among the common bean genotypes cultivated under the control condition (well-watered).

Genitors	Agromorphological and Physiological Traits										
	PH	NN	PP	SP	SPL	GY	TDB	LT	g_s	A	iWUE
P1 × P4	−29.68	−1.51	−3.15	−0.49	−18.97	−4.87	−9.70	−1.86	−0.18	0.77	0.69
P1 × P5	−48.78	−0.82	−8.90	−1.05	−46.37	−3.62	−10.42	−1.10	−0.17	0.49	−0.22
P1 × P6	−15.20	1.38	−2.73	−0.14	−20.17	−4.19	−16.68	0.21	0.08	−0.04	−0.50
P1 × P7	−15.61	−2.38	−2.10	0.07	−11.69	−1.62	−4.64	0.24	−0.09	−0.84	0.61
P1 × P8	−27.49	−0.45	−0.03	−0.20	−5.60	−1.91	0.93	−0.92	−0.17	0.57	−0.24
P1 × P9	6.56	−0.59	4.65	0.85	34.37	11.50	17.36	1.06	0.02	−0.28	−0.38
P1 × P10	43.34	2.02	6.96	0.54	34.58	0.71	18.42	0.35	−0.01	−0.48	0.18
P1 × P11	22.79	1.03	−0.89	0.17	−5.20	7.02	6.64	0.46	−0.03	−0.09	0.01
P1 × P12	98.23	3.27	6.34	−0.16	24.91	3.34	8.78	0.87	−0.05	−0.28	0.77
P2 × P4	−23.18	−0.64	−0.51	0.48	0.41	−0.17	0.86	−1.43	−0.13	0.82	−0.44
P2 × P5	2.83	−0.02	−2.32	0.44	−8.47	0.76	−5.78	−1.07	−0.08	0.82	−0.23
P2 × P6	−3.96	−1.93	−1.11	0.21	−2.10	4.47	6.67	0.68	−0.05	−0.69	0.71
P2 × P7	4.64	−0.01	0.87	0.66	14.94	−2.05	3.92	0.32	−0.04	−0.45	−0.12
P2 × P8	−13.48	0.67	−2.39	−0.36	−18.01	−2.14	−3.51	−1.55	−0.12	0.82	−0.19
P2 × P9	18.32	0.53	6.37	1.07	53.75	9.40	27.92	0.44	0.08	−0.02	0.17
P2 × P10	−48.51	−3.54	−6.50	−0.77	−37.93	1.55	−18.60	0.16	0.04	−0.14	0.21
P2 × P11	−23.13	−0.99	−0.23	−0.71	−16.92	−6.62	−7.89	−0.22	0.09	0.27	0.61
P2 × P12	−3.39	0.39	3.07	−0.49	−3.09	−8.69	−7.16	1.00	−0.03	−0.06	0.53
P3 × P4	7.30	0.61	−0.32	−0.26	−3.73	−1.50	−5.93	−1.30	−0.21	0.40	0.05
P3 × P5	1.97	−0.01	5.45	0.02	26.63	3.58	11.87	−1.74	−0.23	0.13	0.46
P3 × P6	1.10	−1.51	2.84	0.31	22.51	−1.96	5.55	0.01	0.09	0.04	0.06
P3 × P7	−12.26	1.49	−3.51	−0.70	−28.58	−7.84	−11.37	0.94	0.10	0.31	0.08
P3 × P8	8.74	−0.33	2.73	0.91	28.10	6.47	13.20	−1.38	−0.10	0.45	−0.05
P3 × P9	−17.83	−0.72	−2.01	0.46	−10.52	3.32	1.62	0.69	−0.01	−0.05	−0.39
P3 × P10	47.15	2.99	4.04	0.38	21.93	−0.22	16.80	−0.30	0.00	−0.08	0.69
P3 × P11	−1.65	−0.73	0.64	−0.17	0.63	−5.30	−1.18	−0.26	0.18	0.46	−0.22
P3 × P12	17.71	1.14	−1.07	−0.93	−13.35	−6.80	−2.95	0.19	0.12	−0.04	−0.50

PH: plant height (cm), NN: number of nods, PP: number of pods per plant, SP: number of seeds per pod, SPL: number of seeds per plant, GY: grain yield per plant (g plant^{-1}), TDB: total dry biomass (g), leaf temperature (°C) g_s: stomatal conductance (mol m^{-2} s^{-1}), A: net photosynthesis (µmol CO^2 m^{-2} s^{-1}), and iWUE: intrinsic water use efficiency (µmol CO_2 µmol H_2O^{-1}). P1: IAPAR 81, P2: BAT 477, P3: SEA 5, P4: BRS Estilo, P5: IPR Campos Gerais, P6: IAC Alvorada, P7: IPR Uirapuru, P8: IPR Nhambu, P9: BRS Esteio, P10: IPR Garça, P11: DRK 18 and P12: BRS Radiante.

3.4. Principal Component Analysis (PCA)

The first principal components (PC1 and PC2) accounted for 71.85% of the total variance (Figure 1). The analysis revealed a separation among the genotypes under water deficit and the control condition (well-watered), except for the parents IPR Nhambu, IPR Campos Gerais, and BRS Estilo, which were grouped with the genotypes under drought, regardless of the treatment they were subjected. In general, the control group (well-watered) presented the highest values for agromorphological and physiological characteristics, with the exeption of LT. The agromorphological characteristics and g_s were positively associated, as well as A and iWUE; however, A and iWUE were negatively associated with LT.

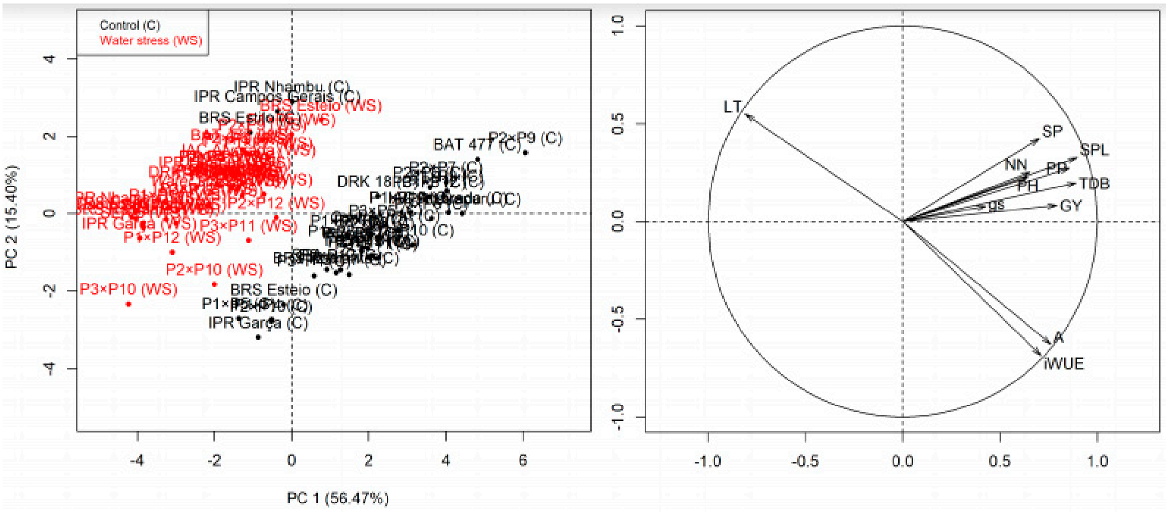

Figure 1. Principal component analysis for agromorphological and physiological traits of the common bean genotypes under water deficit and control condition (well-watered).

4. Discussion

The present study carried out a combinatorial analysis of common bean cultivars for agromorphological and physiological characteristics, in which a broad genetic variability was observed between parental genotypes and, consequently, F_1 hybrids, under water deficit and control conditions. Although water deficit is one of the main limiting factors for bean production, a wide genetic variability for water deficit tolerance has been reported in several studies [25,26]. This variability has great relevance in breeding programs aiming at drought tolerance since it can be exploited to develop adapted bean cultivars [14,27].

In this work, all agromorphological traits were negatively affected by water deficit, which was confirmed by ANOVA and PCA. Darkwa et al. [28], evaluated 64 bean genotypes under water deficit and observed reductions from 2 to 29% in yield components. Rao et al. [29] also reported that GY was reduced, on average, 31% under water deficit compared to non-stress conditions. Similarly, Nuñez et al. [30] noted that water deficit reduced PP (63.3%) and SPL (28.9%). According to Assefa et al. [31], the yield components PP and SPL are the traits most negatively affected by drought.

The agromorphological alterations are mainly a reflection of the physiological changes caused by water stress [14]. In the present study, water deficit led to lower activities of g_s, A and iWUE, in addition to increasing LT. Under drought, a cascade of physiological responses is triggered to prevent water loss and plant death [6,14], in which the first reaction is stomatal closure. Low stomatal conductance prevents water loss by transpiration, however, sequentially, it reduces the CO_2 availability in the leaves, decreasing the photosynthetic rate [32]. Moreover, high foliar temperature hinders the photosynthetic process, which becomes unable to successfully replace the carbon used in the plant respiration [33].

The general and specific combining abilities (GCA and SCA, respectively) were significant for most characteristics in both water conditions, which indicates the importance of the additive and non-additive effects in the genetic control of the agromorphological and physiological traits evaluated. Gonçalves et al. [34] also reported significance of additive and non-additive effects for the majority of the agromorphological and physiological traits of plants cultivated under water deficit and control conditions, studying the combinatorial ability of contrasting bean genotypes for drought tolerance.

The occurrence of additive genetic effects for most of the evaluated characteristics greatly facilitates breeding programs for drought tolerance in beans, since it is an autogamous species. Additive genetic effects imply that the genetic gains for these traits can be fixed over successive generations of self-fertilization. It is apparent from the CGC ($\hat{g}_i$) estimates of group I that BAT 477 presented the best results with high positive values, mainly for SPL and GY, crucial characteristics in the development of drought-tolerant cultivars.

The selection of the parental lines to form segregant populations is essential to establish a successful breeding program and the combining ability along with complementary genes are the major contributors to positive results [35]. Therefore, the genotype BAT 477 is considered a promising genitor in the development of bean cultivars not only for drought tolerance, but also for general desirable agronomic aspects. However, no significant differences were observed for GY among the genitors from group I, demonstrating that these genotypes have similar yield potential.

Among the genitors from group II, the cultivars of the Mesoamerican group IAC Alvorada, IPR Uirapuru, and BRS Esteio showed the best performance for all agromorphological traits, when subjected to water deficit. In a study of combinatorial ability among common bean genotypes, Grigolo et al. [36] verified that cultivars from Mesoamerican origin presented lower floral sensitivity compared to the ones with Andean origin, resulting in higher pod growth and, consequently, better grain yield. This characteristic may explain a greater that avoids floral abortion in Mesoamerican cultivars, improving traits related to yield.

The high CGC estimation for yield components in BRS Esteio, when subjected to water deficit, demonstrates that this genotype is a suitable genitor in breeding programs aiming at developing drought-tolerant common bean cultivars. This cultivar, released in 2012, exceeded the grain yield of the control genotype in 10% in dry and rainy seasons in Region I, comprised of the Brazilian states of Rio Grande do Sul, Santa Catarina, Paraná, São Paulo, and Mato Grosso do Sul [37].

A fact that supports the divergent evolution of the Mesoamerican and Andean beans is that when F_1 generation is viable, the segregating population generally presents inferior agronomic performance compared to both parental lines [38,39]. One of the explanations for this decrease in performance is the existence of favorable epistatic combinations for each of the gene pools which are lost in the recombinant population [40]. However, in the present study, it was observed that some Andean genitors had a good complementarity with the Mesoamerican group, which is tolerant to water deficit.

Estimates of SCA ($\hat{s}_{ij}$) effects assist the selection of the best hybrid combinations, representing results that are relatively better or worse than would be expected based on the average performance of the involved parents [41]. These measures indicate non-additive genetic effects and represent an ideal situation when the estimates are positive in hybrid combinations involving at least one parent whose GCA is favorable [35]. However, based on the $\hat{s}_{ij}$, the crosses IAPAR 81 × IPR Uirapuru and BAT 477 × IAC Alvorada presented the best results due to the participation of the genitors IPR Uirapuru and IAC Alvorada. Gonçalves et al. [34] also observed high values of $\hat{s}_{ij}$ for the combination between BAT 477 and IAC Alvorada under drought.

This study investigated the inheritance of characteristics evaluated in beans for drought tolerance and found that additive and non-additive effects are involved in the genetic control of most of the agromorphological and physiological traits under both water conditions evaluated. BAT 477 (group I) and IAC Alvorada, IPR Uirapuru, and BRS Esteio (group II) may be included in breeding programs aiming to develop drought-tolerant bean cultivars, due to their positive general combining abilities for agromorphological traits. Finally, the crosses IAPAR 81 × IPR Campos Gerais and SEA 5 × BRS Radiante resulted in the best combinations in terms of GY and TDB, when cultivated under water deficit.

5. Conclusions

A wide variability for the agromorphological and physiological traits was observed between genotypes and, consequently, F_1 hybrids, under water deficit and control conditions. Additive and non-additive effects are involved in the genetic control of the majority of agromorphological and physiological traits both under water stress and control (well-watered) conditions. The parental genotypes BAT 477 (group I) and IAC Alvorada, IPR Uirapuru and BRS Esteio (group II) may be included in breeding programs aiming at improving drought tolerance in common bean.

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