Diallelic analysis to obtain cowpea (*Vigna unguiculata* L. Walp.) populations tolerant to water deficit

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ABSTRACT. The purpose of this study was to identify parents and obtain segregating populations of cowpea (*Vigna unguiculata* L. Walp.) with the potential for tolerance to water deficit. A full diallel was performed with six cowpea genotypes, and two experiments were conducted in Teresina, PI, Brazil in 2011 to evaluate 30 F_2 populations and their parents, one under water deficit and the other under full irrigation. A triple-lattice experimental design was used, with six 2-m-long rows in each plot. Sixteen plants were sampled per plot. The data were subjected to analysis of variance, and general and specific combining ability estimates were obtained based on the means. Additive effects were more important than non-additive effects, and maternal inheritance had occurred. The genotypes BRS Xiquexique, Pingo de Ouro-1-2, and MNC99-510F-16-1 were the most promising for use in selection programs aimed at water deficit tolerance. The hybrid combinations Pingo de Ouro-1-2 x BRS Xiquexique, BRS Xiquexique x Santo Inácio, CNCx 698-128G x MNC99-510F-16-1, Santo Inácio

x CNCx 698-128G, MNC99-510F-16-1 x BRS Paraguaçu, MNC99-510F-16-1 x Pingo de Ouro-1-2, and MNC99-510F-16-1 x BRS Xiquexique have the potential to increase grain production and tolerate water deficit.

Key words: *Vigna unguiculata*; OCC; SCC; Hybrid combination; Genetic control

INTRODUCTION

The cowpea (*Vigna unguiculata* L. Walp.) is socioeconomically important, plays a key role in Brazilian agricultural production, and is a major source of dietary protein. Brazil is the third-largest cowpea producer, with 1,391,386 ha of crop that annually produce 513,619 t on average, with an average grain productivity of 369 kg/ha (Freire Filho et al., 2011). In the Brazilian Midwest, where cultivation is highly technological, the average productivity is 960 kg/ha. However, water deficit limits the productivity of this crop, particularly in the Northeast region.

Water deficit-related losses are the main challenge for grain production, particularly in semi-arid regions (Fritche-Neto and Borém, 2011). Plants are subject to adverse conditions that cause stress during their development. This term is defined as a deviation from the optimum conditions for growth, development, and survival. Water deficit tolerance is the ability of plants to tolerate water deficit in their tissues (Agbicodo et al., 2009).

Tolerance to water deficit is a complex characteristic that involves several genes and biochemical routes (Shinozaki and Yamaguchi-Shinozaki, 2007). Gene expression studies have shown that the levels of expression of hundreds of genes are altered in response to water deficit (Oztur et al., 2002; Talamè et al., 2007; Zhou et al., 2007). Despite the cowpea being regarded by farmers as a crop that is tolerant to water deficit, studies have shown that water deficit can reduce grain yield, and thus the development of water deficit-tolerant cultivars is required (Anyia and Herzog, 2004; Fatokun et al., 2009).

One of the essential steps in this process, after the selection of the parents, is the choice of promising segregating populations. There are several methodologies, including diallelic junctions, which can be used. Diallelic analysis methodologies analyze genetic design, estimate useful parameters in selecting parents for hybridization, and consider genetic effects involved in the determination of the characteristics. Therefore, the purpose of this study was to identify parents and obtain segregating populations of cowpea with the potential for tolerance to water deficit.

MATERIAL AND METHODS

The parents were six cowpea genotypes within three cultivars (BRS Paraguaçu, BRS Xiquexique, and Santo Inácio) and three lines (Pingo de Ouro-1-2, CNCx698-128G, and MNC99-510F-16-1) that had previously been selected based on studies of water deficit tolerance in the cowpea (Bastos et al., 2011; Nascimento et al., 2011).

The six parents were crossed under screenhouse conditions in a full diallelic scheme, adopting Method 1 of the model proposed by Griffing (1956). Seeds of 30 F_1 hybrids were sown under greenhouse conditions to obtain the F_2 generation. Two experiments were conducted for the assessment of 30 F_2 populations and their parents at Embrapa Mid-North, Teresina, PI,

Brazil (05°05'S, 42°48'W; 74.4 m above mean sea level) from July 26 to October 11, 2011: under water deficit during pre-flowering and under full irrigation. According to the Köppen classification, the climate of the region is the Aw type (tropical climate with wet and dry seasons). The soils in the experimental area are shallow, eutrophic yellow argisols that have a sandy texture. Soil preparation consisted of two harrowed and one ploughed grid.

The experimental design was incomplete blocks in a triple-square lattice. Each experimental plot contained six 2-m-long rows, with 1.0 m between rows and 0.50 m between plants. Three seeds were sown per hole. Fifteen days after sowing, roughing was performed, leaving one plant per hole. Hoeing and animal traction were conducted during the experiment to control weeds.

Irrigation was performed using a conventional fixed-sprinkler system, with sprinklers on side lines arranged in a 12 x 12 m manner that had an operational pressure of 250 kPa; the nozzle diameter was 3.4 x 2.6 mm and the flow rate 1.07 m^3/h. The water table was set based on the evapotranspiration rate, which was obtained from an automated meteorological station in Embrapa Mid-North, and the crop coefficient (Kc), which ranged from 0.6 to 1.1 (Ferreira et al., 2008). Four batteries of collectors were installed to monitor the water table; each battery contained 16 collectors.

Plants not under water deficit were fully irrigated throughout the experiment, and those under water deficit had no irrigation from the pre-flowering stage until the beginning of the reproductive period. Soil moisture was monitored using a Diviner 2000® capacitance probe, through 12 access tubes installed at a depth of 0.70 m; measurements were taken every 0.10 m of soil depth. A water retention curve of the soil at a depth of 0-0.4 m was generated using the Genuchten (1980) model. The field capacity and permanent wilting point values were 21.2 and 9.05 cm^3/cm^3, respectively.

Fifteen agronomic characteristics were measured in 16 individual plants. Pearson correlations were conducted in order to identify characteristics that were positively correlated with grain production. The following parameters were assessed: the number of days to maturity (NDMD), which was the number of days from sowing until the emergence of the first pod with color change, indicating the start of the drying process; the number of stems per plant (NSP), which was the number of peduncles; the number of pods per plant (NPP); the weight (g) of pods per plant (WPP); grain production (GP), which was grain weight (g) corrected for 12% moisture content; and the 100-grain weight (g) (W100G), which was the weight of 100 grains from each plant corrected for 12% moisture content.

Six parents and 30 F_2 populations were used for the diallelic analysis, including the reciprocals. The analysis of combinatorial capabilities partitioned the overall capacity of combination (OCC), the specific capacity of combination (SCC), and the reciprocal effect (RE) using the following model:

$$Y_{ij} = m + g_i + g_j + s_{ij} + r_{ij} + e_{ij} \qquad \text{Equation 1}$$

where Y_{ij} is the mean value of the hybrid combination ($i \neq j$) or parent ($i = j$); m is the general mean; g_i and g_j are the effects of the overall capacity of the ith and j^{th} parent ($i, j = 1, 2,...,6$); s_{ij} is the effect of the SCC of the crosses between parents of order i and j; r_{ij} is the RE that measured differences in the parent i or j when used as a male or female in crossing ij; and e_{ij} is the experimental medium error associated with the observation of order ij.

Quadratic components (Φ) expressed the genetic variability of the genotypes studied in terms of the OCC, SCC, and RE, and were obtained from the following expressions:

$$\Phi_g = (QM_{OCC} - QM_{Error})/2p \qquad \text{Equation 2}$$

$$\Phi_s = (QM_{SCC} - QM_{Error}) \qquad \text{Equation 3}$$

$$\Phi_{rc} = (QM_{RE} - QM_{Error})/2 \qquad \text{Equation 4}$$

where QM_{OCC} is the mean square of the OCC; QM_{SCC} is the mean square of the SCC; QM_{RE} is the mean square of the RE; and p is the number of genotypes in the diallel. All of the statistical analyses were performed using the GENES program (Cruz, 2013).

RESULTS AND DISCUSSION

The effect of genotype was highly significant ($P \leq 0.01$), indicating the existence of genetic variability in the population evaluated (Table 1). Ushakumari et al. (2010), assessing a 5 x 5 diallel, also found variability between populations in NPP and GP.

Table 1. Summary of analysis of variance of the number of days to maturity of grains (NDMD), number of stems per plant (NSP), number of pods per plant (NPP), weight of pods per plant (WPP), grain production (GP), and weight of 100 grains (W100G) obtained from a diallelic cross involving six parental cowpea (*Vigna unguiculata*) genotypes, their F_2 populations, and the reciprocals.

Sources of variation		Mean squares test with water deficit					
	d.f.	NDMD	NSP	NPP	WPP	GP	W100G
Treatment	35	1.8**	55.8**	136.0**	1,489.05**	202,057.7**	18.1**
OCC	5	0.5**	78.2**	219.0**	748.7^{ns}	79,008.8^{ns}	100.6**
SCC	15	0.7**	40.2**	94.8**	1,127.0**	165,894.5**	6.1**
RE	15	1.4**	63.9**	149.4**	2,097.8**	279,237.3**	2.6*
Error	55	0.3	11.1	24.7	316.1	41,405.0	0.8
Φ_g		0.16	5.6	16.19	36.05	3,133.65	8.31
Φ_s		0.4	29.1	70.1	810.9	124,485.5	3.5
Φ_{rc}		0.55	26.4	62.35	890.85	118,916.15	0.9
Sources of variation		Mean squares test without water deficit					
	d.f.	NDMD	NSP	NPP	WPP	GP	W100G
Treatment	35	5.1**	134.8**	241.2**	1,790.2**	188,535.7**	41.1**
OCC	5	17.5**	561.9**	1,109.4**	4,905.0**	425,038.9**	211.0**
SCC	15	4.1**	48.9*	50.8^{ns}	460.5^{ns}	42,890.8^{ns}	23.9**
RE	15	2.0*	78.4**	142.3**	2,081.6^{ns}	255,346.2**	1.7^{ns}
Error	55	1.0	16.5	40.9	447.2	50,440.5	2.9
Φ_g		1.37	45.45	89.04	371.48	31,216.53	17.34
Φ_s		3.1	32.4	9.9	13.3	-7,549.7	21.0
Φ_{rc}		0.5	30.95	50.7	817.2	102,452.85	-0.6

**,*Significant at the 1 and 5% levels, respectively, according to an F-test; ns = not significant; OCC = overall capacity of combination; SCC = specific capacity of combination; RE = reciprocal effect; Φ_g = component associated with the OCC; Φ_s = component associated with the SCC; Φ_{rc} = component associated with the RE.

The OCC, which is estimated by g_i, provides information on the concentration of additive genes and their effects, and is used to choose parents in breeding programs. The SCC, which is behavior that deviates from what would be expected based on the OCC, measures non-additive gene effects. The plant breeder is interested in hybrid combinations, with SCC estimates of the most favorable combination with at least one of the parents that has the most favorable OCC (Cruz et al., 2012). Based on this assumption, crosses with high averages are selected with at least one parent having a positive OCC value. The significant medium squares of OCC and SCC indicates that both additive and non-additive gene effects were involved in the control of NDMD, NSP, and W100G, independent of environmental conditions. NDMD, NSP, NPP, and W100G exhibited a significant effect of OCC, indicating strong additive gene effects on their expression and the greatest concentration of favorable alleles. This result corroborates that of Carvalho et al. (2012), who evaluated eight cowpea genotypes and found that additive effects were more important than non-additive effects for NGV, NPP, W100G, and GP, thereby enabling direct selection gains. Pereira et al. (2007) assessed promising segregating populations of French beans for grain production, and obtained significant medium square values for OCC and SCC, indicating additive and non-additive effects in the control of the characteristic studied. Tchiagam et al. (2011) studied the genetic control of protein content and its soluble fraction in cowpea seeds using a 5 x 5 diallel, and found that additive and non-additive effects were responsible for the genetic variation; however, non-additive effects were predominant.

The SCC was not significant for NPP, WPP, and GP under full irrigation. This result disagrees with those obtained by Ushakumari et al. (2010) when assessing a diallel cowpea population composed of parental and composite F_1 plants, who found that dominance effects were more important than additive effects. The RE was significant ($P \leq 0.01$) for most of the characteristics evaluated (NDMD, NSP, NPP, and GP), suggesting that cytoplasmic inheritance may be involved in their expression; this is of paramount importance in segregating populations.

Parents were selected based on high, positive estimates of the OCC, because they contributed to an increase in the expression of the characteristics (Table 2). However, parents with high, negative values contributed to a reduced expression of NDMD. The best genotypes were BRS Paraguaçu, BRS Xiquexique, and CNCx 698-128G.

Table 2. Estimation of the combination general capacity (OCC) and reciprocal effects for the number of days to maturity of grains (NDMD), number of stems per plant (NSP), number of pods per plant (NPP), weight of pods per plant (WPP), grain production (GP), and weight of 100 grains (W100G) obtained from a diallel involving six parental cowpea (*Vigna unguiculata*) genotypes under full irrigation and water deficit.

Parent	Water deficit					
	NDMD	NSP	NPP	WPP (g)	GP (g)	W100G (g)
BRS Paraguaçu	-0.29	-1.62	0.17	-4.10	-35.11	-0.57
Pingo de Ouro-1-2	0.29	-0.47	-2.71	-3.47	-34.26	2.99
BRS Xiquexique	-0.51	-0.28	1.6	4.64	47.35	-0.70
CNCx 698-128G	-0.28	2.45	3.68	2.24	-7.14	-2.03
Santo Inácio	0.61	-0.90	-2.61	-4.50	-39.49	0.07
MNC99-510F-16-1	0.17	-0.93	-0.13	5.25	68.65	0.24
Parent	Full irrigation					
BRS Paraguaçu	-0.78	-3.49	0.34	-10.11	73.52	-0.96
Pingo de Ouro-1-2	0.37	-2.64	-7.14	-12.75	-111.10	4.67
BRS Xiquexique	-0.39	-1.14	2.60	6.18	56.02	-1.20
CNCx 698-128G	-0.37	7.35	8.56	16.85	135.57	-2.10
Santo Inácio	1.17	-1.35	-4.76	-6.95	-102.83	0.07
MNC99-510F-16-1	0.02	1.28	0.39	6.78	95.85	-0.29

For the NPP, the values of g_i for the two treatments were negative for the same genotypes (Pingo de Ouro-1-2 and Santo Inácio), suggesting that these should not be included in crosses aimed at increasing the number of pods per plant. The CNCx 698-128G genotype stood out, with eight pods per plant. In contrast, Carvalho et al. (2012) reported low negative and positive values for this characteristic.

Regarding the WPP, the BRS Xiquexique, CNCx 698-128G, and MNC99-510F-16-1 genotypes had high and positive OCC estimates, regardless of the water treatment. Carvalho et al. (2012) also found a positive value for this characteristic when evaluating BRS Xiquexique. BRS Paraguaçu, Pingo de Ouro-1-2, and Santo Inácio should not be used for the improvement of WPP because of their high, negative values.

Xiquexique and BRS MNC99-510F-16-1 stood out for GP, as they had high, positive g_i values in both treatments. BRS Paraguaçu, Pingo de Ouro-1-2, CNCx 698-128G, and Santo Inácio reduced the expression of this characteristic, and are not recommended for GP breeding programs. Ushakumari et al. (2010) also found positive and negative effects of OCC for GP in hybrid cowpea strains. Pingo de Ouro-1-2 stood out regarding W100G, with OCC values of 2.99 and 4.67 under water deficit and fully irrigated, respectively, and is recommended for crosses that increase average grain weight. Currently, breeding programs aim to increase the W100G because of market requirements (Freire Filho et al., 2011).

The SCC, estimated by s_{ii}, indicates the deviation of a hybrid from what would be expected based on the OCC of its parents. Positive values of s_{ij} indicate that the cross is superior, and that there is a predominance of genes that exhibit dominance or epistasis effects. The parameter s_{ii} is indicative of genetic divergence; positive values indicate that the parents exhibit negative heterosis, and negative values indicate that the parents exhibit varietal heterosis with one-way negative dominance deviations, i.e., heterosis occurs in order to reduce the expression of the characteristic (Cruz et al., 2012). In this way, high SCC estimates are important in obtaining promising segregating populations because they indicate greater variability, which is essential in the selection process.

Positive and negative values of s_{ij} were observed for all of the characteristics relative to the performance of the parents (Table 3). Values of s_{ii} for the characteristics differed between the treatments. BRS Paraguaçu, Santo Inácio, and MNC99-510F-16-1 had crosses with high heterosis for GP, regardless of the water treatment.

Regarding the NDMD, which is a measure of precocity, the crosses that had favorable estimates of s_{ij} in both treatments were: Pingo de Ouro-1-2 x BRS Paraguaçu, BRS Xiquexique x CNCx 698-128G, and CNCx 698-128G x Pingo de Ouro-1-2; these had at least one parent with a negative g_i value. Both parents of the BRS Xiquexique x CNCx 698-128G cross had negative g_i values, i.e., they reduced the expression of this characteristic.

The signs of the NPP values differed between the treatments, demonstrating the influence of the environment. The crosses that stood out were Santo Inácio x CNCx 698-128G and Santo Inácio x MNC99-510F-16-1. Although Santo Inácio was repeated in these crosses with a negative OCC value, each pair had a positive g_i value.

The Santo Inácio x CNCx 698-128G cross had the highest s_{ij} value for NSP and NPP, and increased the expression of these characteristics in both treatments, indicating that these parents are ideal for these characteristics. The best crosses for the WPP were BRS Xiquexique x Pingo de Ouro-1-2, CNCx 698-128G x MNC99-510F-16-1, and Santo Inácio x CNCx 698-128G.

Regarding GP, high, positive values were obtained for the following combinations: BRS Paraguaçu x CNCx 698-128G, Pingo de Ouro-1-2 x BRS Xiquexique, CNCx 698-128G

x MNC99-510F-16-1, Santo Inácio x Pingo de Ouro-1-2, and Santo Inácio x CNCx 698-128G. However, only the parents Pingo de Ouro-1-2 and MNC99-510F-16-1 had positive OCC values in both treatments. Crosses of these parents are promising in terms of obtaining superior segregating populations.

Table 3. Estimation of the specific combination capacity (CEC) and reciprocal effects for the number of days to maturity of grains (NDMD), number of stems per plant (NSP), number of pods per plant (NPP), weight of pods per plant (WPP), grain production (GP), and weight of 100 grains (W100G) obtained from a diallel involving six parental cowpea (*Vigna unguiculata*) genotypes under full irrigation (1) and water deficit (2).

Cross	Characteristic											
	NDM		NSP		NPP		WPP (g)		GP (g)		W100G (g)	
♀ x ♂	1	2	1	2	1	2	1	2	1	2	1	2
1 x 1	0.90	0.05	-1.85	2.15	-2.70	2.15	-3.01	1.88	-59.90	-71.3	0.50	-0.45
1 x 2	-0.01	0.88	0.01	-0.12	-1.64	-0.12	-8.62	-1.92	-90.22	1.33	-1.25	-2.05
1 x 3	-0.04	-0.74	-1.53	0.64	-263	0.64	-6.25	3.39	-77.21	-0.69	-0.70	-0.16
1 x 4	-0.40	-0.46	2.68	-2.12	5.31	-2.12	12.82	-1.49	191.42	69.06	-0.18	0.91
1 x 5	-0.20	0.28	-0.12	0.78	0.25	0.78	-0.32	-0.36	-27.33	69.97	0.83	1.52
1 x 6	-0.26	-0.02	0.8	-1.32	1.40	-1.32	5.39	-1.49	63.25	-13.0	0.80	0.23
2 x 1	-0.40	-0.80	-1.37	-3.23	-1.63	-3.23	-7.45	-4.36	-54.98	-233.47	0.06	0.39
2 x 2	0.48	-0.67	4.56	-2.01	6.00	-2.01	24.63	1.33	310.00	10.05	0.63	8.32
2 x 3	0.14	0.19	1.87	1.82	3.81	1.82	15.38	0.08	178.65	36.83	-0.27	-0.6
2 x 4	-0.09	0.84	-6.36	0.16	-8.52	0.16	32.48	-1.23	-405.43	-101.57	0.42	-1.80
2 x 5	-0.11	-1.36	0.71	1.7	-0.65	1.70	-0.90	3.67	-7.19	100.07	0.86	-1.64
2 x 6	-0.40	0.11	0.62	-1.54	1.00	-1.54	1.98	-1.93	14.19	-46.72	-0.39	-0.8
3 x 1	-0.50	-0.33	-0.73	-0.03	-0.77	4.46	-10.03	1.5	-109.84	100.03	-0.36	-0.23
3 x 2	0.14	-0.83	1.9	2.93	2.40	-2.93	11.03	6.5	162.09	320.92	-1.24	-0.06
3 x 3	0.08	1.06	-4.33	4.46	-5.30	4.46	-21.09	3.37	198.63	185	-0.69	0.34
3 x 4	-0.62	-0.68	-0.41	-2.93	5.14	-2.93	10.87	-1.58	86.89	-109.94	0.37	-0.13
3 x 5	0.09	0.06	1.06	-0.35	0.42	-0.35	1.56	1.08	22.26	4.86	-0.35	0.56
3 x 6	0.36	0.11	-0.13	-3.63	-1.45	-3.63	-0.48	-4.18	-11.90	-47.97	1.63	1.39
4 x 1	-0.04	0.63	-0.9	4.23	-4.90	4.23	-5.32	5.57	-73.24	206.71	0.31	0.43
4 x 2	-0.60	-0.63	-1.07	3.43	-0.60	3.43	-6.13	4.66	-56.02	66.14	-0.63	-0.47
4 x 3	-0.10	0.6	-0.41	-7.03	-1.65	-7.03	7.05	-10.0	36.12	-353.88	0.47	-0.13
4 x 4	0.75	0.29	0.7	8.59	-2.58	8.59	-9.68	4.92	-103.48	72.88	-1.83	-0.74
4 x 5	0.16	-0.28	-0.11	-4.08	0.11	4.33	10.38	-4.21	124.61	-28.89	1.45	1.60
4 x 6	0.20	0.30	0.02	0.39	0.54	0.39	8.06	3.59	105.98	97.75	-0.23	0.14
5 x 1	0.54	0.0	1.16	-3.7	-0.17	2.06	2.11	-6.03	11.40	-315.94	-1.20	0.29
5 x 2	0.47	-0.76	5	-1.8	6.97	1.70	31.49	-0.22	390.59	64.28	-0.49	-0.95
5 x 3	-0.27	-1.1	3.36	-1.9	5.37	-1.9	17.98	0.76	174.50	87.61	0.37	-0.45
5 x 4	0.10	-0.35	6.6	4.33	10.93	4.33	39.73	6.0	476.64	309.55	0.07	0.90
5 x 5	0.09	2.45	-2.25	-1.44	-4.17	-1.44	-15.58	-1.82	-186.03	-190.92	-1.12	0.0
5 x 6	-0.03	-1.15	2.14	3.4	4.03	3.40	4.86	3.81	73.69	32.65	-1.66	-1.05
6 x 1	-0.70	-0.13	-4.57	-1.83	-5.60	-1.83	-19.38	-1.6	-199.23	-126.46	0.15	0.60
6 x 2	0.47	-0.63	-1.4	-0.4	-2.43	-0.40	-13.69	0.53	-165.12	-58.37	-1.01	0.14
6 x 3	-0.30	-0.46	-6.5	1.13	-9.77	1.13	-35.49	-1.17	-379.72	-20.59	0.40	0.79
6 x 4	-0.17	0.0	2.2	2.06	2.70	2.06	9.73	3.63	94.06	101.61	0.05	-0.03
6 x 5	-0.57	0.03	-0.73	7.03	-0.44	7.03	-5.94	7.0	-128.83	32.65	-1.13	-1.05
6 x 6	0.12	0.0	-3.45	2.7	-5.35	2.71	-19.85	0.19	-245.21	-22.63	-0.16	0.08

Additive effects were more important than non-additive effects, and cytoplasmic inheritance occurred. BRS Xiquexique, Pingo de Ouro-1-2, and MNC99-510F-16-1 are the most promising genotypes for use in selection programs for tolerance to water deficit.

The hybrid combinations Pingo de Ouro-1-2 x BRS Xiquexique, BRS Xiquexique x Santo Inácio, CNCx 698-128G x MNC99-510F-16-1, Santo Inácio x CNCx 698-128G, MNC99-510F-16-1 x BRS Paraguaçu, MNC99-510F-16-1 x Pingo de Ouro-1-2, and MNC99-510F-16-1 x BRS Xiquexique have the potential to increase grain production and tolerate water deficit.

Conflicts of interest

The authors declare no conflict of interest.

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