Genetic parameters for drought-tolerance in cassava

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Abstract – The objective of this work was to evaluate the effect of drought on genetic parameters and breeding values of cassava. The experiments were carried out in a completely randomized block design with three replicates, under field conditions with (WD) or without (FI) water deficit. Yield of storage roots (RoY), shoot (ShY), and starch (StY), as well as the number of roots (NR), and root dry matter content (DMC) were evaluated in 47 cassava accessions. Significant differences were observed among accessions; according to heritability, these differences had mostly a genetic nature. Heritability estimates for genotypic effects (h_g^2) ranged from 0.25±0.12 (NR) to 0.60±0.18 (DMC), and from 0.51±0.17 (NR) to 0.80±0.21 (RoY and StY) for WD and FI, respectively, as a consequence of greater environmental influence on WD. Selective accuracy was lower in WD, and ranged from 0.71 (NR) to 0.89 (RoY, DMC, and StY). However, genetic gains were quite high and ranged from 24.43% (DMC) to 113.41% (StY), in WD, and from 8.5% (DMC) to 75.70% (StY) in FI. These genetic parameters may be useful for defining which selection strategies, breeding methods, and experimental designs are more suitable to obtain cassava genetic gains for tolerance to drought.

Index terms: *Manihot esculenta*, breeding, drought stress, germplasm.

Parâmetros genéticos da mandioca quanto à tolerância ao deficit hídrico

Resumo – O objetivo deste trabalho foi avaliar o efeito do deficit hídrico sobre os parâmetros e os valores genéticos da mandioca. Os experimentos foram realizados em delineamento de blocos ao acaso com três repetições, em campo com (CD) ou sem deficit hídrico (SD). A produtividade de raízes (PR), da parte aérea (PA) e de amido (PAM), assim como o número de raízes (NR) e a massa de matéria seca das raízes (MS) foram avaliados em 47 acessos de mandioca. Observaram-se diferenças significativas entre os acessos; conforme a herdabilidade, estas diferenças foram em sua maioria de natureza genética. As estimativas de herdabilidade dos efeitos genotípicos (h_g^2) variaram de 0,25±0,12 (NR) a 0,60±0,18 (MS) e de 0,51±0,17 (NR) a 0,80±0,21 (PR e PAM) para CD e SD, respectivamente, em decorrência da maior influência ambiental sobre o CD. A acurácia seletiva foi menor no CD, com variação de 0,71 (NR) a 0,89 (PR, MS e PAM). No entanto, os ganhos genéticos foram elevados, de 24,43% (MS) a 113,41% (PAM) no CD, e de 8,5% (MS) a 75,70% (PAM) no SD. Estes parâmetros genéticos podem ser úteis para definir estratégias de seleção, métodos de melhoramento e delineamentos experimentais mais apropriados, para a obtenção de ganhos genéticos em mandioca quanto à tolerância à seca.

Termos para indexação: *Manihot esculenta*, melhoramento, estresse hídrico, germoplasma.

Introduction

Cassava (*Manihot esculenta* Crantz) is a widely cultivated crop in many tropical countries in Africa, Latin America, and Asia, between 30ºN and 30ºS, whose coordinates coincide with the boundaries of many developing countries. Cassava is worldwide considered a staple food for over one billion people (The world cassava economy, 2000), so it has great importance for food security. Moreover, it is a multi-purpose, highly adaptable crop to different agricultural production systems. Although cassava is adaptable to marginal soils with low fertility, and to irregular rainfall conditions, and as it holds a relatively stable productivity and flexibility for the harvesting process, the challenges posed by global climate change (both temperature and drought severity increasing) have caused negative impacts on this crop productivity. For instance, the severe and widespread drought in Northeast Brazil over the past five years

led to 20% decrease in root yield (10.08 to 8.41 Mg ha^{-1}) and 36% decrease in overall production compared to other regions (8.18 to 6.01 million tons) (Instituto Brasileiro de Geografia e Estatística, 2014). Therefore, in 2012 the average root yield of Northeastern Brazil was about 10 times lower than the crop's potential, estimated at 90 Mg ha^{-1} under experimental conditions (El-Sharkawy, 2005). The main factors contributing to this low productivity is the use of traditional varieties with low tolerance to drought and the use of marginal soils with low fertility.

Increased incidence and severity of drought have directed the efforts to cassava breeding programs for the selection of drought-tolerant genotypes and to the understanding of the mechanisms associated with this abiotic stress. This is necessary because the development of improved varieties can result in major increases in crop yield in marginal growing regions. Moreover, the selection of drought-tolerant genotypes has been a challenge for many crops, depending on their quantitative nature of trait complexity (El-Sharkawy, 2005, 2007; Budak et al., 2013; Okogbenin et al., 2013).

The availability and use of cassava varieties with high yield and tolerance to water stress may contribute to help the product offer, particularly in more sensitive environments to climate change as Brazilian Northeast. One of the bottlenecks in developing these varieties is to identify germplasm with known and proven, effective tolerance against drought stress. This has become increasingly difficult, considering that the species domestication usually limits genetic diversity, since accessions adapt to artificial environments and, consequently, lose tolerance to water stress.

Even with the methodological breakthrough for selection of drought-tolerant genotypes (controlled conditions or molecular marker-assisted selection), many authors reported that research under field conditions, using genotypes of broad genetic base, is the most appropriate way to study productivity patterns in response to drought (Long et al., 2006; El-Sharkawy, 2007). However, before starting the breeding activities, it is necessary to know the genetic parameters of drought tolerance, because they allow to know the structure and the potential for selecting superior genotypes. Although several studies have reported the identification of drought-resistance sources in cassava (Lenis et al., 2006; Long et al., 2006; El-Sharkawy, 2007; Laban et al., 2013; Okogbenin et al., 2013), there are no reports on the estimation of genetic parameters for yield traits under irrigated and water deficit conditions.

As genetic parameters guide the selection process and genetic gains in the different selection cycles, knowledge of population genetic parameters effectively allows the discrimination between genetic and environmental effects, thus contributing to the efficient selection of the best genotypes based on their merits (Espitia et al., 2010).

The objective of this work was to evaluate the effect of drought on the genetic parameters and breeding values of cassava.

Materials and Methods

The experiment was carried out at Bebedouro Experimental Station, Embrapa Semiarid, Petrolina, PE (9º22'S, 40º22'W, at 376 m altitude), Brazil, from December 2012 to December 2013. with an average of 164 mm annual rainfall, whose distribution was 71, 49, 16, and 27 mm for the 1st, 2nd, 3rd and 4th quarter of the experiment, respectively. The genotype (47) group included local and improved varieties with a history of tolerance to drought, either because they have been collected in semiarid regions, or because they have been selected under these conditions, in which case improved varieties were used (Table 1).

The cassava varieties were analyzed under normal irrigation (FI) and under drought stress (WD). In both conditions, a completely randomized block design with three replicates was used with 10 plants per plot (two rows with five plants), 0.90 m spacing between rows, and 0.80 m between plants. For planting, 16 cm cuttings were used and all cultural practices recommended for the crop were followed.

All six blocks were irrigated up to four months after planting (MAP), with water supply by inline dripping (4 L h^{-1}) according to plant evapotranspiration, which was estimated by using meteorological data provided by meteorological station close to experimental area. From this period, the irrigation of the three blocks for drought assessment of the 47 genotypes was suspended until harvest, and irrigation was maintained in the other three blocks.

Plants were harvested at 12 MAP, and the following traits were evaluated: number of storage roots (NR); root yield (RoY), expressed in Mg ha^{-1}; shoot yield (ShY), expressed in Mg ha^{-1}; dry matter content of

roots (DMC), measured by hydrostatic balance and expressed in %; starch yield (StY), expressed in Mg ha^{-1}, considering the productivity and the root dry matter.

Table 1. Cassava varieties used to obtain estimates of genetic parameters for yield and root quality traits under water deficit conditions.

Genotypes	Types	Drought reaction	Selection reason
9624-09	Improved	Unknown	High leaf retention
BGM0089	Local variety	Unknown	High leaf retention
BGM0096	Local variety	Unknown	Semiarid collection
BGM0116	Local variety	Tolerant	Semiarid collection
BGM0163	Local variety	Unknown	Semiarid collection
BGM0279	Local variety	Unknown	High leaf retention
BGM0331	Improved	Unknown	High leaf retention
BGM0360	Improved	Unknown	High leaf retention
BGM0541	Local variety	Unknown	High leaf retention
BGM0598	Local variety	Tolerant	High leaf retention
BGM0785	Local variety	Unknown	High leaf retention
BGM0815	Local variety	Unknown	Semiarid collection
BGM0856	Local variety	Unknown	Semiarid collection
BGM0876	Local variety	Susceptible	High leaf retention
BGM0908	Local variety	Susceptible	High leaf retention
BGM1171	Local variety	Unknown	High leaf retention
BGM1195	Local variety	Unknown	High leaf retention
BGM2020	Local variety	Unknown	High leaf retention
Branquinha	Local variety	Unknown	Productive variety
BRS Amansa Burro	Improved	Tolerant	Tolerant to drought
BRS Dourada	Improved	Unknown	Productive variety
BRS Formosa	Improved	Tolerant	Tolerant to drought
BRS Gema de Ovo	Improved	Tolerant	Tolerant to drought
BRS Kiriris	Improved	Tolerant	Tolerant to drought
Cacau	Local variety	Susceptible	High leaf retention
Cachimbo	Local variety	Susceptible	High leaf retention
Do Céu	Local variety	Tolerant	Tolerant to drought
Engana Ladrão	Local variety	Tolerant	Tolerant to drought
Eucalipto	Local variety	Unknown	High leaf retention
GCP-001	Improved	Tolerant	Tolerant to drought
GCP-009	Improved	Tolerant	Tolerant to drought
GCP-014	Improved	Tolerant	Tolerant to drought
GCP-020	Improved	Tolerant	Tolerant to drought
GCP-025	Improved	Tolerant	Tolerant to drought
GCP-043	Improved	Tolerant	Tolerant to drought
GCP-046	Improved	Tolerant	Tolerant to drought
GCP-095	Improved	Tolerant	Tolerant to drought
GCP-128	Improved	Tolerant	Tolerant to drought
GCP-179	Improved	Tolerant	Tolerant to drought
GCP-190	Improved	Tolerant	Tolerant to drought
GCP-194	Improved	Tolerant	Tolerant to drought
GCP-227	Improved	Tolerant	Tolerant to drought
GCP-374	Improved	Tolerant	Tolerant to drought
Mani Branca	Improved	Unknown	High leaf retention
NG310	Improved	Unknown	High leaf retention
Paulo Rosa	Local variety	Susceptible	High leaf retention
Sacai	Local variety	Tolerant	Tolerant to drought

Genetic value prediction for each trait was performed by the best linear unbiased prediction method (BLUP), and the estimation of variance components was performed through the restricted maximum likelihood (REML). The employed statistical model was $y = Xr + Zg + \varepsilon$, in which: y is a vector data; r is a replicate effect vector (assumed to be fixed) added to the overall average; g is a vector of genotypic effects (assumed to be random); ε is a vector of errors and residues (random); X is an incidence matrix for replicate effect; and Z is an incidence matrix for genotypic affects. The variance components (individual REML) estimates were the following equations below describe: the heritability of individual plots in the broad sense $\hat{h}_g^2 = \hat{\sigma}_g^2 / \hat{\sigma}_g^2 + \hat{\sigma}_e^2 = \hat{\sigma}_g^2 / \hat{\sigma}_f^2$, in which $\hat{\sigma}_g^2$ is the genotypic variance among genotypes, $\hat{\sigma}_e^2$ is the residual and environment variance among plots, and $\hat{\sigma}_f^2$ is the individual phenotypic variance; and the heritability of average genotypes assuming full stand

$$\hat{h}_m^2 = \hat{\sigma}_g^2 \Big/ \hat{\sigma}_g^2 + \frac{\hat{\sigma}_e^2}{b}, \text{for which } \left(\hat{h}_m^2\right)^{0.5}$$

is the genotype selection accuracy (Acclon). The REML/BLUP analyses were performed using the software Selegen-REML/BLUP (Resende, 2007).

Results and Discussion

For all analysed traits, there were significant differences between treatments, and between irrigated and drought conditions (Table 2). This result is an indication of a high genetic variation among the cassava accessions.

A reduction of about 42 and 41% was observed for NR and DMC, respectively, when the cassava accessions were subjected to water deficit (WD). Reductions for RoY and StY were about there and four times higher, respectively, in comparison to the experiments without drought stress (FI) (Table 3).

Low coefficients of genotypic variation (CVg) were observed for DMC (17.54 and 8.21 for WD and FI, respectively). In contrast to the other traits, the CVg was indicative of the presence of high genotypic variability among accessions, whose CVg ranged from 27.78 to 87.47% for ShY and StY, respectively, under water deficit conditions, and 33.60 to 54.64% for NR and StY, respectively, in the absence of water deficit (Table 3). Although CVg estimates have been greater under WD, this genetic variability is a prerequisite for performing selection in both situations.

The residual variation coefficient (CVe) also showed less variation for DMC (14.37 and 6.20%, WD and FI, respectively). For ShY and StY, CVe ranged from 42.45 to 75.83% respectively for the other traits, in WD, and from 26.97 to 33.05% for RoY and NR, respectively, in FI (Table 3). In general, in the FI, the CVe estimates were lower than CVg for all traits, whereas, in the WD, this situation occurred only for RoY, DMC and StY. As a result, the relative variation coefficient (CVr = CVg/CVe) was lower than the unity only for NR and ShY under WD, indicating an unfavorable situation for selecting these traits under this environmental condition. For other traits under WD conditions, the CVr was greater than the unity, which indicates that environmental variation among the genotypes was lower than the genetic variation from the average.

The CVe is consistent with the quantitative and polygenic nature of NR, RoY, ShY, and StY, with great influence from environmental characteristics. CVe high values (> 50%) have been observed in other cassava studies for traits like shoot weight, and yield per plant and per area (Aina et al., 2007). Furthermore, according to Borges et al. (2010), high values for the variation coefficient (> 50%), as observed for shoot weight and average unmarketable root weight in sweet potato (*Ipomoea batatas* L.), are common when the evaluated trait is a structure located underground, where the environmental control is difficult.

Table 2. Estimates of deviance for yield and root quality traits evaluated in cassava accessions, with (WD) or without (FI) water deficit.

Characteristic[1]	Treatment/ index	Deviance		LRT (Chi-square)	Significance
		Genotype	Complete model		
DMC	FI	421.41	476.84	55.43	0.000
	WD	551.73	599.45	47.72	0.000
NR	FI	939.16	972.20	33.04	0.000
	WD	897.75	904.66	6.91	0.009
ShY	FI	645.74	709.14	63.40	0.000
	WD	507.20	518.38	11.18	0.001
StY	FI	454.67	559.96	105.29	0.000
	WD	219.01	261.82	42.81	0.000
RoY	FI	810.87	914.63	103.76	0.000
	WD	586.64	624.88	38.24	0.000

[1]DMC, dry matter content; NR, number of roots; ShY, shoot yield; StY, starch yield; RoY, root yield.

Estimates of genetic variance (σ_g^2) among accessions, both in WD and in FI, showed that the variance component estimates for all traits, except for DMC, were higher in the FI. The σ_g^2 estimates for NR, ShY, RoY, and StY in the FI were about 3, 9, 10, and 12 times higher, respectively, than those obtained in the WD. The σ_g^2 highest estimates in the FI can be explained by the presence of very susceptible genotypes that, under strong water stress, greatly reduced their root and starch productive potential, causing the genetic variability for these traits to be decreased. Reports on cereals also indicated the presence of low genotypic variance and large genotype x environment interaction in plant selection for yield traits under water stress (Kőszegi et al., 1996; Farshadfar et al., 2014).

Table 3. Estimates of variance components, heritability, accuracy, and variance coefficients for number of roots (NR), root yield (RoY), shoot yield (ShY), dry matter content (DMC), and starch yield (StY) of cassava accessions, in the presence or absence of water deficit.

Parameter[(1)]	NR	RoY	ShY	DMC	StY
			Experiment with water deficit		
$\hat{\sigma}_g^2$	72.26	20.23	4.34	15.59	1.29
$\hat{\sigma}_e^2$	217.47	15.80	10.14	10.46	0.97
$\hat{\sigma}_f^2$	289.73	36.03	14.48	26.05	2.26
h_g^2	0.25±0.12	0.56±0.18	0.30±0.13	0.60±0.18	0.57±0.18
h_m^2	0.50	0.79	0.56	0.80	0.80
Ac	0.71	0.89	0.75	0.89	0.89
CVg (%)	28.94	71.28	27.78	17.54	87.47
CVe (%)	50.20	63.00	42.45	14.37	75.83
CVr	0.58	1.13	0.65	1.22	1.15
$\bar{X}_f$	29.37	6.31	7.50	22.51	1.30
			Experiment without water deficit		
σ_g^2	197.23	204.35	38.77	6.82	15.71
σ_e^2	190.84	51.36	18.91	3.89	3.86
σ_f^2	388.08	255.71	57.69	10.72	19.57
h_g^2	0.51±0.17	0.80±0.21	0.67±0.19	0.64±0.19	0.80±0.21
h_m^2	0.76	0.92	0.86	0.84	0.92
Ac	0.87	0.96	0.93	0.92	0.96
CVg (%)	33.60	53.80	44.21	8.21	54.64
CVe (%)	33.05	26.97	30.88	6.20	27.08
CVr	1.02	1.99	1.43	1.32	2.02
$\bar{X}_f$	41.80	26.57	14.09	31.80	7.25

[(1)] $\hat{\sigma}_g^2$, genotype variance; $\hat{\sigma}_e^2$, residual variance; $\hat{\sigma}_f^2$, phenotypic individual variance; h_g^2, total genotypic heritability effects; h_m^2, heritability adjusted for average genotype; Ac, genotype selection accuracy; CVg, genotypic coefficient of variation; CVe, residual variation coefficient; CVr, relative variation coefficient (CVg/CVe); $\bar{X}_f$, experiment overall average.

The values of heritability coefficient of total genotypic effects (h_g^2) were low or medium in the WD, and medium to high in the FI (Table 3). The h_g^2 ranged from 0.25±0.12 (NR) to 0.60±0.18 (DMC) in the WD, while in the FI it ranged from 0.51±0.17 (NR) to 0.80±0.21 (RoY and StY). Similarly, the heritability coefficient estimates adjusted for genotype average (h_m^2) were higher in the FI (Table 3). In the WD, h_m^2 ranged from 0.50 for NR to 0.80 for DMC and StY, while in the FI it ranged from 0.76 for NR to 0.92 for RoY and StY (Table 3). The h_g^2 and h_m^2 estimates for NR, RoY, ShY, and StY were significantly improved in the FI. Similarly, high h_g^2 estimates have been reported for various morpho-physiological traits in common bean (Hinkossa et al., 2013) and chickpeas (Farshadfar et al., 2008), both under water-stress and no water-stress conditions, in which the heritability estimates were lower in water deficit conditions.

Heritability estimates in broad sense for DMC in cassava roots have been reported in the literature, ranging from 0.42 (Kizito et al., 2007) to 0.80 (Aina et al., 2007). This discrepancy in heritability values for certain characteristics is mainly due to differences in the methods used for their determination, genetic materials, locations, and age assessment. In the present work, the results for DMC are in agreement with these previous reports, even in the presence of water deficit.

The highest h_g^2 and h_m^2 estimates obtained for RoY, DMC, and StY under both water stress conditions are possibly due to the greater genetic variability of these traits. High magnitude heritability estimates may indicate fewer genes controlling the character, and low environmental influence on the expression of the phenotype (Flint-Garcia et al., 2005). Concerns on the homogenization of environmental conditions, in the experiments on drought resistance, may have contributed to a greater stability of genotypes upon environmental changes, and have resulted in a lower complexity for RoY, DMC, and StY traits. High heritability estimates show that the additive effects are more effective than the dominance ones, and simple selection methods can be effective for the improvement of these traits under water stress condition (Farshadfar et al., 2014).

Heritability estimates help the breeder to define the most appropriate selection strategies for each trait, breeding methods and type of experimental design, in order to minimize experimental errors and maximize

genetic gains per selection cycle. Furthermore, heritability estimates indicate the precision in average genotypic values that can be used to analyse the mapping of quantitative trait loci (QTL).

Accuracy values or genotypic correlation between predicted and actual values were above 0.90 for RoY, ShY, DMC and StY only in the FI, and are considered high according to Resende & Duarte (2007). Moreover, under water deficit conditions, the selective accuracy was lower for all traits, although the median values could be considered for plant selection, mainly for RoY, DMC, and StY (0.89) (Table 3). An important observation was the increase of about 7 and 14% in the selective accuracy for NR and ShY characteristics, respectively, in comparison to the experiment without water deficit conditions.

In the WD experiment, six out of the 10 best genotypes with higher NR bear the GCP code, which refers to segregating populations derived from the crossing of tolerant and susceptible MCol1734 x MVen77, respectively. In contrast, in the FI experiment, only four genotypes of GCP population were observed. In addition, only four genotypes (BGM0815, BRS Formosa, GCP-046 and GCP-190) were sorted in both treatments (Table 4). This may indicate that one of the drought-tolerance mechanisms refers to the maintenance of the number of roots per plant, whereas most of drought-sensitive genotypes showed low NR. The average NR values for WD and FI were 29.37 and 41.80, respectively (Table 3). In contrast, selection and recombination of the 10 best genotypes for NR in WD and FI allow to obtain selection gains of 27.86 and 38.48%, respectively. Thus, the predicted average for NR after one selection cycle would reach 37.6 and 57.9 roots per plot, in the WD and in the FI treatments, respectively (Table 4).

Regarding root yield (RoY), the average was 6.31 and 26.57 Mg ha^{-1} in WD and FI, respectively (Table 3). Instead, the genotypes BGM0279, BGM0163, BGM0815, BGM0116, GCP-020, GCP-009, and the varieties BRS Formosa, Engana Ladrão, 9624-09, and Cacau stood out due to their higher genotypic value than other materials. These genotype selections have the potential to increase RoY in upland conditions to 11.9 Mg ha^{-1} (88.45%) and 46.5 Mg ha^{-1} (75.09%) under irrigated conditions. In an experiment for drought-tolerance in Colombia, El-Sharkawy (2007) reported an average cassava yield much higher than the observed in the present study (ranging from 15.0 to 27.0 Mg ha^{-1}) when analyzing 16 cassava accessions. However, comparisons to these results show a bias related to the different experimental conditions and climate, particularly regarding pluvial precipitation, which was about 800 mm higher those of the present experiment.

A similar situation can be observed for ShY, in which the predicted genetic values with the selection of the 10 best genotypes is 30.79% (new average of 9.8 Mg ha^{-1}) and 59.28% (new average of 22.4 Mg ha^{-1}) for WD and FI, respectively (Table 4). Although the potential of genetic gain was higher in the irrigated treatment for ShY, half of the accessions (BGM0116, BGM0360, BGM0541, BGM0598 and BGM0815) are common to the different treatments.

The average root dry matter (DMC) was lower in the WD experiment (22.51%) compared to the 31.80% observed in FI experiment. Observations of this nature have been reported for drought-tolerance in cassava experiments, in which the DMC was below 25% (El-Sharkawy, 2007). In contrast, some studies reported DMC levels above 33% under water stress (Laban et al., 2013). Possibly, the low DMC contents in the present experiment can be associated with the occurrence of heavy rainfalls before harvest (27 mm for the 4th quarter of the experiment) which stimulated the assimilate translocation for shoot recovery, which was severely lost during the water stress period. However, the possibility for genetic improvement from selecting the best genotypes is quite high, mainly under water stress conditions (24.43% gain, with the new predicted average of 28.00% for DMC). However, the DMC increase under irrigated conditions is only 8.5% (the new average is 34.5%). In this case, only four genotypes are common to the two hydric treatments: BGM0876, GCP-194, GCP-374, and Sacai (Table 4).

The average starch yield (StY) in the WD and FI was 1.30 and 7.25 Mg ha^{-1}, respectively (Table 3). The StY variation in WD was 0.32 to 5.89 Mg ha^{-1}, which was considered superior to those reported by El-Sharkawy (2007) – 0.40 to 3.3 Mg ha^{-1} – in an experiment evaluated in Guajira Department (560 mm rainfall), in Colombia. The predicted genetic gains by the selection of the best genotypes under WD was high (113.41%) in comparison to FI (75.70%). However, the predicted average under WD (2.8 Mg ha^{-1}) would be even lower than under FI (12.7 Mg ha^{-1}) (Table 4). However,

Table 4. Classification of sorted cassava accessions, based on predicted breeding values (μ+g), and their genetic gains (GG) and improved averages (IA) in experiments with or without water deficit.

Genotype	NR			Genotype	RoY			Genotype	ShY			Genotype	DMC			Genotype	StY		
	u+g	GG	IA		u+g	GG	IA		u+g	GG	IA		u+g	GG	IA		u+g	GG	IA
		(nº)				(Mg ha^{-1})				(Mg ha^{-1})				(%)				(Mg ha^{-1})	
Experiment with water deficit																			
GCP-001	43.0	13.6	43.0	BRS Formosa	23.6	17.3	23.6	BGM0541	11.4	3.9	11.4	BGM0116	30.6	8.1	30.6	BRS Formosa	5.9	4.6	5.9
GCP-020	42.2	13.2	42.6	GCP-020	14.3	12.6	19.0	BGM1195	10.6	3.5	11.0	BGM0815	29.4	7.5	30.0	BGM0163	2.9	3.1	4.4
GCP-190	40.5	12.5	41.9	BGM0279	11.6	10.2	16.5	GCP-009	10.5	3.3	10.8	BGM0163	29.3	7.3	29.8	BGM0815	2.8	2.6	3.9
BRS Formosa	39.3	11.9	41.2	BGM0163	11.2	8.9	15.2	BGM0815	10.4	3.2	10.7	GCP-128	28.6	7.0	29.5	GCP-020	2.6	2.2	3.5
BGM0360	36.2	10.9	40.2	BGM0815	10.6	8.0	14.3	BGM0279	10.1	3.1	10.6	GCP-374	28.5	6.8	29.3	BGM0116	2.5	2.0	3.3
GCP-374	35.2	10.0	39.4	BGM0116	10.0	7.3	13.6	BGM0598	9.8	3.0	10.5	Sacai	28.4	6.6	29.1	BGM1195	2.4	1.9	3.2
Branquinha	35.2	9.4	38.8	E. Ladrão[1]	10.0	6.7	13.1	BGM0116	9.0	2.8	10.3	BRS Formosa	28.0	6.5	29.0	BGM0279	2.4	1.8	3.1
BGM0815	35.0	8.9	38.3	9624-09	9.7	6.3	12.6	E. Ladrão	8.9	2.6	10.1	BGM0876	26.1	6.1	28.6	E. Ladrão	2.2	1.7	3.0
GCP-046	34.6	8.5	37.9	GCP-009	9.0	5.9	12.2	BGM0360	8.8	2.4	9.9	Cacau	25.7	5.8	28.3	GCP-374	2.0	1.6	2.9
GCP-179	34.4	8.2	37.6	Cacau	8.8	5.6	11.9	BGM0163	8.6	2.3	9.8	GCP-194	25.5	5.5	28.0	Sacai	2.0	1.5	2.8
Experiment without water deficit																			
BRS Formosa	75.6	33.8	75.6	BRS Formosa	73.2	46.6	73.2	BGM0541	34.5	20.4	34.5	Sacai	36.8	5.0	36.8	BRS Formosa	20.5	13.2	20.5
BRS Dourada	67.1	29.5	71.3	GCP-001	54.1	37.1	63.6	Sacai	23.4	14.9	29.0	GCP-374	35.6	4.4	36.2	GCP-001	15.7	10.8	18.1
BGM0815	57.0	24.8	66.6	BRS Dourada	52.8	33.4	60.0	BGM0116	23.3	13.0	27.1	A. Burro[2]	35.2	4.1	35.9	BRS Kiriris	14.5	9.6	16.9
GCP-190	55.9	22.1	63.9	BRS Kiriris	49.7	30.9	57.4	BGM0815	22.6	11.9	26.0	GCP-194	35.0	3.9	35.7	BRS Dourada	12.1	8.4	15.7
BRS Kiriris	55.7	20.5	62.3	GCP-009	42.9	28.0	54.5	BRS Dourada	21.5	11.0	25.1	BGM2020	34.2	3.6	35.4	GCP-009	11.8	7.7	14.9
GCP-046	54.4	19.2	61.0	BGM0163	40.3	25.6	52.2	BGM0360	21.0	10.3	24.4	BGM1171	33.8	3.3	35.1	BGM0163	11.6	7.1	14.4
BGM0279	53.8	18.1	59.9	BGM0785	39.0	23.7	50.3	GCP-194	20.3	9.7	23.8	GCP-046	33.7	3.1	34.9	Mani Branca	11.1	6.6	13.9
BGM0163	53.5	17.3	59.1	Mani Branca	38.8	22.3	48.8	BRS Formosa	20.1	9.3	23.3	BGM0876	33.6	2.9	34.7	BGM0815	10.7	6.2	13.5
GCP-095	53.1	16.7	58.5	BGM0815	38.1	21.1	47.6	BGM0598	18.8	8.8	22.8	GCP-043	33.6	2.8	34.6	GCP-190	9.9	5.8	13.1
GCP-009	52.7	16.1	57.9	BGM0360	36.4	19.9	46.5	Mani Branca	18.8	8.4	22.4	BRS Kiriris	33.5	2.7	34.5	BGM0360	9.5	5.5	12.7

[1]E. Ladrão, Engana Ladrão; [2] A. Burro, Amansa Burro.

these yield levels under strong water-stress conditions illustrate the great potential of cassava to withstand very harsh weather conditions, whereas other crops of great importance as food grains are possibly not able to produce this amount of energy/starch by area under the same adverse condition.

Taking into account a higher selection intensity – for instance 10% (selection of the top five genotypes) –, the predicted genetic gains can be 30% higher for all traits, regardless of water deficit presence or absence. However, as the number of individuals and kinship directly affect the magnitude of the remaining genetic variance in subsequent generations, it is necessary to be aware of these parameters to avoid the improvement reduction in few generations. In this case, the mildest selection of the best individuals (20%) makes early gains relatively minor, but the new improved population may have an increased genetic variance retention, and a lower risk of inbreeding, which likely ensures its sustainability in long-term.

Despite being recognized as a crop with tolerance to drought, low-water availability is still among the most significant abiotic constraints to cassava. There are important differences between cassava genotypes for drought tolerance (Lenis et al., 2006; El-Sharkawy, 2007; Laban et al., 2013; Okogbenin et al., 2013). Therefore, improving the attributes for root and starch yield under water deficit has become a goal for breeding programs. One of the basic points in developing an efficient breeding program for drought-tolerant varieties is knowing the inheritance of the main interest traits. Genetic parameters related to the yield of root and starch in cassava under water deficit, obtained in the present study, may provide practical information for breeders to develop varieties. Despite the high magnitude for h_g^2 and h_m^2 estimates, a strong environmental influence was observed on the expression of most traits under water deficit, whose heritability and selective estimate accuracies were much lower than those calculated on the basis of experiments without water stress.

In addition to obtaining estimates of genetic parameters, the present work identified germplasm accessions and cassava varieties with high production potential in extreme drought. One of these genotypes focusing on starch production is the BRS Formosa with a genotypic value of 23.6 Mg ha^{-1} for root yield, 28% for dry matter, and 5.9 Mg ha^{-1} for starch yield. Additionally, BGM0541, BGM1195, GCP-009, BGM0815, and BGM0279 accessions showed a great potential for use in animal feed, whose main selection criterion is shoot mass, which was over 10.1 Mg ha^{-1} (Table 4). From the results, these genotypes could be used into the cassava crop system or even in breeding programs for high-yielding cassava production under drought stress.

Conclusions

1. Estimates of genetic variances are higher in the absence of water deficit for most agronomic traits of cassava.

2. Estimates of heritability coefficients are from low to medium in the presence of water deficit, and medium to high in the absence of water deficit, for most agronomic traits of cassava.

3. Accuracy estimates of about 0.89 for root yield, dry matter content, and starch yield are considered suitable for the selection of top accessions under water deficit conditions.

4. The predicted values with the selection of 20% of accessions allow to obtain high-genetic gains, mainly for root and starch yield, with or without water deficit.

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