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Agronomic performance and genetic divergence between genotypes of *Manihot esculenta*

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ABSTRACT

The morphoagronomic characterization of 12 genotypes of *M. esculenta* was performed during the 2013/2014 and 2014/2015 crop years. The 12 genotypes were planted in a randomized block design, with four replicates per genotype. Number of tuberous roots per plant, weight of tuberous roots, root yield, total plant weight, harvest index, plant height, height of first branch, number of shoots, stem diameter, number of buds, leaf dry weight and petiole length were evaluated. Genotypes "Camuquem" and "Goiás" were the most productive, and "Amarela" and "Gema de Ovo" were the most divergent. Seventy percent of genetic diversity was due to petiole length (22.86%), root yield (19.20%), weight of tuberous roots (14.89%) and number of buds (13.72%). Overall, the present results indicate a broad genetic basis for the evaluated genotypes, so that such genetic variation benefits the plant breeding for future scenarios Further studies of the evaluated genotypes should be performed under environmental limitations, using biochemical and molecular tools to identify markers for genetic improvement.

Key words: Cassava, plant breeding, dissimilarity, multivariate analysis.

INTRODUCTION

The genus *Manihot* belongs to the family Euphorbiaceae and includes 98 species. It is native to the American continent, being distributed from the USA to Argentina (Rogers and Appan 1973). Brazil is considered its main diversity center, possessing at least 78 species, approximately 80% of the total number of species (Nassar 2000, Reflora 2017). *M. esculenta* ssp. is its only domesticated species (Brown et al. 2013).

Cassava (*M. esculenta* Crantz) is one of the main sources of carbohydrates in tropical and subtropical regions of Africa, Asia and Latin America, playing an essential part in the food safety of millions of families, especially in developing regions, where

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it is grown as subsistence crop (Pootakham et al. 2014, Silva et al. 2014a, Vidal et al. 2015, Schmitz et al. 2016, Boas et al. 2017, Morais et al. 2017). Cassava is also an important raw material for starch extraction, which has several applications in the food, chemical, cosmetic and pharmaceutical industries. In 2014, 268.28 million tons of cassava were produced globally, grown on 23.87 million hectares, with an average yield of 11.24 t ha^{-1} (FAO 2017). In Brazil, 1.5 million hectares were occupied by cassava plantations, and 23.1 million tons of cassava root were harvested in 2015, with an average yield of 15.2 t ha^{-1}, 35% higher than the global productivity (IBGE 2016).

Cassava is a diploid (2n=36 chromosomes) and monoicous species, with predominantly allogamous fertilization, making it highly heterozygotic (Pootakhan et al. 2014) and giving it high genetic diversity, even though it propagates vegetatively (Costa et al. 2013, Silva et al. 2014a). It can therefore adapt to different edaphoclimatic conditions, such as drought and low-fertility soils (Vidal et al. 2015, Schmitz et al. 2016). Because of these characteristics, cassava cultivation is attractive to farmers with limited resources. Small-farm cultivation is of great importance to the conservation of genetic resources used in improvement programmes (Silva et al. 2014a, Delaquis et al. 2018).

Knowing and characterizing the genetic variability of a given population, manifested through morphological and agronomic traits, is fundamental to guide its conservation and management and to help improvement programmes by identifying superior genotypes that are better adapted to new production systems (Dias et al. 2015, Zerbielli et al. 2016). Multivariate statistics allows for the simultaneous integration of data for multiple traits and has been widely used to quantify genetic divergence in several crops, such as cassava (Mehouenou et al. 2016, Moura et al. 2016, Ortiz et al. 2016, Agre et al. 2017), coffee (Dalcomo et al. 2015, Rodrigues et al. 2016, Machado et al. 2017), jabuticaba (Zerbielli et al. 2016), banana (Koukouma et al. 2016), sorghum (Almeida Filho et al. 2016), soybean (Ferreira Júnior et al. 2015) and many others. The aim of the present study was to evaluate the genetic divergence of 12 genotypes of *M. esculenta* based on their morphoagronomic characterization.

MATERIALS AND METHODS

PLANT MATERIAL AND EXPERIMENTAL DESIGN

The experiment was conducted during the 2013/2014 and 2014/2015 crop years, in the municipality of Vila Valério, state of Espírito Santo (ES), Brazil (latitude 18° 57' 01'' S, longitude 40° 18' 35" W; 140 m altitude; 23 °C mean annual temperature). The region's climate is Aw according to the Köppen climate classification, tropical with hot and humid summers and dry winters (Alvares et al. 2013), and a mean annual rainfall of 1200 mm (ANA 2015).

Twelve genotypes of *M. esculenta* were evaluated (Table I). The genotypes were obtained from the germplasm bank of Embrapa Cassava and Fruticulture (Embrapa Mandioca e Fruticultura) and regional farmers. The 12 genotypes were planted in a randomized block design, with four replicates per genotype. The experimental units consisted of four rows with seven plants. The two lateral rows and the two plants in each end of the central rows were used as the border.

The soil was prepared using a microtractor rotary disk plough, followed by furrowing. Cassava roots with 15-20 cm, collected from mature and healthy plants, were planted manually at approximately 10 cm depth, in October 2013 and 2014, with 1 m spacing between furrows and 0.6 m between plants. For both plantations, soil acidity was corrected and fertilization was performed based on the soil chemical analysis, according to the technical recommendations for cassava (Prezotti

TABLE I
Evaluated *Manihot esculenta* genotypes, in a municipality located in the north of the state of Espírito Santo, Brazil.

Identification	Name	Identification	Name
1	Gema de Ovo	7	Saracura
2	Eucalipto	8	São Rafael
3	Camuquem	9	Cacau
4	Aipim do Sol	10	Amarela
5	Paraguai	11	Goiás
6	Cacauzinho	12	Cassava Grande

Note: Genotypes 1 to 9 were supplied by Embrapa Cassava and Fruticulture; Genotypes 10 to 12 are traditionally grown in the study region.

et al. 2007, Partelli et al. 2010). Lime application was not necessary. Fertilization was applied at planting, with the equivalent of 330 kg ha^{-1} single superphosphate and 100 kg ha^{-1} potassium chloride. Cover fertilizations were performed 50 days after planting with application of 65 kg ha^{-1} urea. Basic management practices were performed during cultivation, especially during the initial stage, such as manual weeding, sprinkler irrigation and plant health control.

MORPHOAGRONOMIC CHARACTERIZATION

The plants in the useful area were collected 12 months after planting, and the following morphoagronomic traits were evaluated: number of tuberous roots per plant (NTR); weight of tuberous roots (WTR, kg), calculated as the ratio between total root weight and number of roots; root yield (RY, t ha^{-1}), calculated by multiplying the weight of root per plant and the number of plants per hectare; total plant weight (TPW, kg), calculated as the sum of root weight, stump weight and shoot weight for each plant; harvest index (HI, %), calculated as the ratio between WTR and TPW; plant height (PH, m), measured from the ground to the terminal bud; height of first branch (HFB, m), measured from the ground to the first branch; number of shoots (NS), measured by counting the number of shoots in each plant; stem diameter (SD, mm), measured at 20 cm from the ground using a digital calliper; number of buds (NB), measured in a 20 cm segment in the middle third of the stem; leaf dry weight (LDW, g), measured after placing the leaves in forced-air circulation oven at 60 °C until constant weight was achieved, using an analytical balance; and petiole length (PL, cm), measured in fully developed leaves using a graduated ruler. NTR, WTR and RY refer to the mean of the two plantations; the remaining traits (morphological) were only evaluated in the second plantation.

STATISTICAL ANALYSIS

Analysis of variance (ANOVA) was performed, and homogeneity of variance was tested using the F test. Means were grouped using the Scott-Knott test ($p<0.05$). Genetic divergence was analysed using the generalized Mahalanobis distance (D^2). Genotype cluster analysis was performed using Tocher's optimization method and the hierarchical method unweighted pair group method using arithmetic averages (UPGMA), with the generalized Mahalanobis distance as the dissimilarity measure. The relative contribution of each trait to genetic divergence between *M. esculenta* genotypes was evaluated using Singh's method (Singh 1981). All statistical analyses were performed using Genes software (Cruz 2013).

RESULTS AND DISCUSSION

Except for TPW, all morphoagronomic traits evaluated differed according to *M. esculenta* genotype (Table II). This shows the genetic heterogeneity of the studied *M. esculenta* population, which is important to genetic divergence analyses and favorable to genetic improvement because it indicates the possibility of identifying superior and divergent individuals.

TABLE II
Summary of variance analysis for 12 morphoagronomic traits evaluated for 12 genotypes of *Manihot esculenta*. Vila Valério, Espírito Santo, Brazil.

SV	d.f.	Mean squares					
		NTR	WTR	RY	TPW	HI	PH
Blocks	3	11.1410	0.0005	17.4176	6.1532	84.5596	0.8311
Genotypes	11	14.8181**	0.0057**	263.4025**	1.6654^{ns}	374.0109**	0.6095**
Residual	33	1.3462	0.0009	29.5897	0.9553	76.9305	0.0633
Mean		7.95	0.19	26.28	3.67	29.95	2.80
CV (%)		14.59	15.54	20.7	26.66	29.29	8.98
SV	**d.f.**	**Mean squares**					
		HFB	NS	SD	NB	LDW	PL
Blocks	3	0.1189	0.3957	4.4877	9.7326	0.0084	12.5396
Genotypes	11	0.2231**	0.9329**	27.833**	20.0824**	0.0973*	68.0157**
Residual	33	0.0703	0.1887	2.2052	1.6843	0.0395	6.2871
Mean		0.89	2.15	23.42	8.94	1.08	28.14
CV (%)		29.67	20.19	6.34	14.52	18.38	8.91

^{ns}, ** and *: not significant, significant at p≤0.01, and significant at p≤0.05, respectively, according to the F test. SV: Source of Variation; d.f.: degrees of freedom; CV: C*oefficient of Variation;* NTR: number of tuberous roots per plant; WTR: weight of tuberous roots; RY: root yield; TPW: total plant weight; HI: harvest index; PH: plant height; HFB: height of first branch; NS: number of shoots; SD: stem diameter; NB: number of buds; LDW: leaf dry weight; PL: petiole length.

Most traits presented a low (CV<10%) or medium coefficient of variation (CV<20%) (Pimentel-Gomes 2009), indicating good experimental accuracy (Cruz et al. 2014). The Scott-Knott test for morphoagronomic traits grouped the genotypes into up to four groups (Table III).

Three groups were formed for NTR and WTR. NTR varied between 4.91 and 10.63 (mean=7.95 kg), and WTR between 0.14 and 0.25 kg (mean=0.19 kg). The group with the highest NTR was formed by five genotypes (3, 8, 11, 6 and 7), all presenting NTR higher than 9.02, with a mean of 9.92 roots per plant. The group with highest WTR was formed by four genotypes (10, 11, 4 and 3), of which only two were also included in the group with highest NTR, and one belonged to the group with lowest NTR. The same was observed for the group with the highest mean NTR, indicating no correlation between these traits.

The highest variability was observed for root yield (RY), which varied between 15.38 and 42.31 t ha^{-1}, and the genotypes were divided into four groups. The group with the highest mean RY was composed of genotypes 11 and 3 and presented a mean RY of 40.94 t ha^{-1}, 55.78% higher than the overall mean (26.28 t ha^{-1}) (Table III). This indicates that the most productive plants presented a higher number of tuberous roots and root weight. On the other hand, the lowest RY was observed for genotypes 1 (16.63 t ha^{-1}) and 12 (15.38 t ha^{-1}). Previous studies also observed a positive correlation between RY and number of roots per plant (Rós and São João 2016, Tumuhimbise et al. 2015, Silva et al. 2016).

HI is the ratio between WTR and TPW. HI varied between 15.94 and 46.06 (mean 29.95), and only two groups were formed for this trait. The group presenting the highest HI was formed by seven genotypes (3, 11, 10, 8, 7, 9 and 2), all with HI higher than 30.8. HI higher than 50% is considered ideal. However, varieties with higher HI do not always present higher root production because plants with both low root and low shoot production also present high HI (Silva et al. 2002, Gomes et al.

TABLE III
Morphoagronomic traits evaluated in 12 genotypes of *Manihot esculenta*. Vila Valério, Espírito Santo, Brazil.

Genotype	NTR	WTR	RY	TPW	HI	PH	HFB	NS	SD	NB	LDW	PL
1	6.89^{b}	0.14^{c}	16.63^{d}	4.35^{a}	15.94^{b}	2.74^{b}	0.81^{b}	1.88^{b}	28.21^{a}	10.25^{b}	1.21^{a}	36.18^{a}
2	7.30^{b}	0.20^{b}	25.15^{c}	3.50^{a}	30.80^{a}	2.79^{b}	1.01^{a}	2.25^{a}	21.53^{b}	8.44^{c}	1.35^{a}	28.76^{b}
3	10.63^{a}	0.22^{a}	39.57^{a}	4.32^{a}	46.06^{a}	2.68^{b}	0.66^{b}	2.88^{a}	22.02^{b}	8.31^{c}	1.19^{a}	28.24^{b}
4	5.35^{c}	0.24^{a}	22.33^{c}	2.87^{a}	20.20^{b}	3.24^{a}	1.00^{a}	1.75^{b}	25.38^{a}	8.13^{c}	1.11^{a}	32.08^{a}
5	7.28^{b}	0.19^{b}	23.62^{c}	3.63^{a}	25.76^{b}	3.46^{a}	1.19^{a}	1.53^{b}	25.96^{a}	7.13^{c}	0.97^{b}	24.15^{c}
6	9.63^{a}	0.14^{c}	22.86^{c}	3.15^{a}	23.33^{b}	2.86^{b}	1.23^{a}	2.79^{a}	21.38^{b}	6.88^{c}	1.04^{b}	23.49^{c}
7	9.02^{a}	0.17^{b}	26.92^{c}	2.91^{a}	34.29^{a}	2.50^{b}	0.59^{b}	2.54^{a}	19.53^{b}	10.63^{b}	0.87^{b}	27.81^{b}
8	10.20^{a}	0.18^{b}	31.04^{b}	4.57^{a}	34.38^{a}	2.65^{b}	0.66^{b}	1.34^{b}	26.83^{a}	8.25^{c}	1.25^{a}	29.38^{b}
9	7.57^{b}	0.18^{b}	21.96^{c}	3.81^{a}	33.93^{a}	2.91^{b}	1.15^{a}	2.00^{b}	23.78^{b}	7.56^{c}	1.01^{b}	24.30^{c}
10	6.59^{b}	0.25^{a}	27.56^{c}	2.69^{a}	35.79^{a}	1.89^{c}	0.60^{b}	2.46^{a}	21.12^{b}	14.94^{a}	1.17^{a}	33.61^{a}
11	10.10^{a}	0.25^{a}	42.31^{a}	4.21^{a}	42.23^{a}	2.82^{b}	0.81^{b}	2.37^{a}	22.32^{b}	9.56^{b}	0.84^{b}	25.62^{c}
12	4.91^{c}	0.19^{b}	15.38^{d}	3.99^{a}	16.68^{b}	3.08^{a}	1.04^{a}	2.04^{b}	22.99^{b}	7.19^{c}	0.99^{b}	24.10^{c}
Mean	7.95	0.19	26.28	3.67	29.95	2.80	0.89	2.15	23.42	8.94	1.08	28.14
$F_{11;33}$	11.01	6.29	8.90	1.74	4.86	9.63	3.17	4.94	12.62	11.92	2.46	10.82
CV%	14.59	15.54	20.7	26.66	29.29	8.98	29.67	20.19	6.34	14.52	18.38	8.91

Means followed by the same letter within the same column belong to the same group, according to the Scott-Knott test, at p≤05. NTR: number of tuberous roots per plant; WTR: weight of tuberous roots (kg); RY: root yield (t ha^{-1}); TPW: total plant weight (kg); HI: harvest index; PH: plant height (m); HFB: height of first branch (m); NS: number of shoots; SD: stem diameter (mm); NB: number of buds; LDW: leaf dry weight (g); PL: petiole length (cm).

2007). In fact, genotype 9 presented relatively high HI but low root and shoot production. Lower HI is usually due to diversion of carbohydrates from roots to the emission of new shoots.

Three groups were formed for plant height (PH), which ranged between 1.89 m (genotype 10) and 3.46 m (genotype 5). The group with the highest PH was formed by genotypes 5, 4 and 12. The second group was formed by 8 genotypes, with PH between 2.50 and 2.91 m. The third group was formed only by genotype 10. The ideal height for cassava plants has not been established. Taller plants may be beneficial for some crop management practices, but they are also more prone to stalk lodging. On the other hand, investment in shoot growth may compromise root production by unbalancing sink-source relationships (Lambers et al. 2008), thereby compromising the production of tuberous roots (Gomes et al. 2007) and resulting in lower HI. In fact, the three genotypes that formed the group with higher PH (genotypes 5, 4 and 12) presented lower-than-average productivity and lower HI.

Two groups were formed for HFB. The group with the highest HFB was formed by genotypes 6, 5, 9, 12, 2 and 4, with a mean HFB of 1.10 m. The second group was also formed by six genotypes (1, 11, 3, 8, 10 and 7) and presented a mean HFB of 0.69 m. In general, higher HFB tends to facilitate crop management practices, especially those related to harvest and weed management and intercropping (Vidigal Filho et al. 2000, Gomes et al. 2007).

The maximum and minimum dissimilarity for each of the 12 genotypes of *M. esculenta*, based on the generalized Mahalanobis distance (D^2), varied between 12.279 and 222.372, indicating wide genetic diversity between individuals (Table IV).

The genetic divergence analysis, based on the generalized Mahalanobis distance (D^2), showed lower dissimilarity between genotypes 6 and 9 (12.28) and genotypes 2 and 9 (13.22) and higher dissimilarity between genotypes 10 and 12 (222.37)

TABLE IV
Mean, maximum and minimum dissimilarity for 12 genotypes of *Manihot esculenta* based on the generalized Mahalanobis distance (D^2), considering 12 morphoagronomic traits[1]. Vila Valério, Espírito Santo, Brazil.

Genotype	Average dissimilarity	More dissimilar		Less dissimilar	
		Genotype	Distance	Genotype	Distance
1	126.26150	12	208.634067	8	51.782532
2	51.10381	1	131.758819	9	13.223786
3	67.68456	12	143.259622	11	20.836267
4	61.17200	1	112.669245	5	31.145170
5	65.88590	10	167.893705	9	13.998441
6	63.35243	10	144.985400	9	12.279067
7	57.05195	12	124.419137	11	23.925858
8	68.56685	12	154.162333	3	35.480786
9	61.70703	10	158.086828	6	12.279067
10	123.09394	12	222.372449	7	54.543594
11	65.80012	12	135.781810	3	20.836267
12	110.12085	10	222.372449	9	26.234547

[1]Number of tuberous roots per plant; mean tuberous root weight; root yield; total plant weight; harvest index; plant height; height of first branch; number of shoots; stem diameter; number of buds; leaf dry weight; petiole length.

and genotypes 1 and 12 (208.63). These genotype combinations should result in higher heterosis and therefore in a higher probability of recovering superior genotypes in segregating generations (Falconer 1983).

Grouping by the Tocher's optimization method is based on group formation and uses the generalized Mahalanobis distance (D^2) as a measure of genetic dissimilarity. This method grouped the 12 genotypes into four different groups (Table V). This shows the genetic variability between the evaluated genotypes because this method tries to minimize the distance within groups and maximize the distance between groups.

Four different groups were formed by Tocher's method, with group III (genotype 10) and group IV (genotype 1) being formed by only one genotype (Table V). The fact that these genotypes were grouped alone indicates that they were more divergent. The first group was formed by half of the genotypes evaluated (5, 9, 12, 4, 2 and 6), and the second by four genotypes (3, 11, 7 and 8). Nick et al. (2010) studied 100 subsamples of cassava and Zuin et al. (2009) 43 cassava accessions collected in the northwest region of the state of Paraná, and both observed the formation of nine groups. Those authors reported that the first group included more than half of the studied population, similarly to the present study.

Grouping by UPGMA was performed using the generalized Mahalanobis distance (D^2) as the genetic dissimilarity measure, and a dendrogram was constructed showing the genetic distance between the studied genotypes. An upper threshold

TABLE V
Grouping by the Tocher method, based on the generalized Mahalanobis distance (D^2), of 12 genotypes of *Manihot esculenta*, considering 12 morphoagronomic traits[1]. Vila Valério, Espírito Santo, Brazil.

Groups	Genotypes
1	5 9 12 4 2 6
2	3 11 7 8
3	10
4	1

[1]Number of tuberous roots per plant; weight of tuberous roots; root yield; total plant weight; harvest index; plant height; height of first branch; number of shoots; stem diameter; number of buds; leaf dry weight; petiole length.

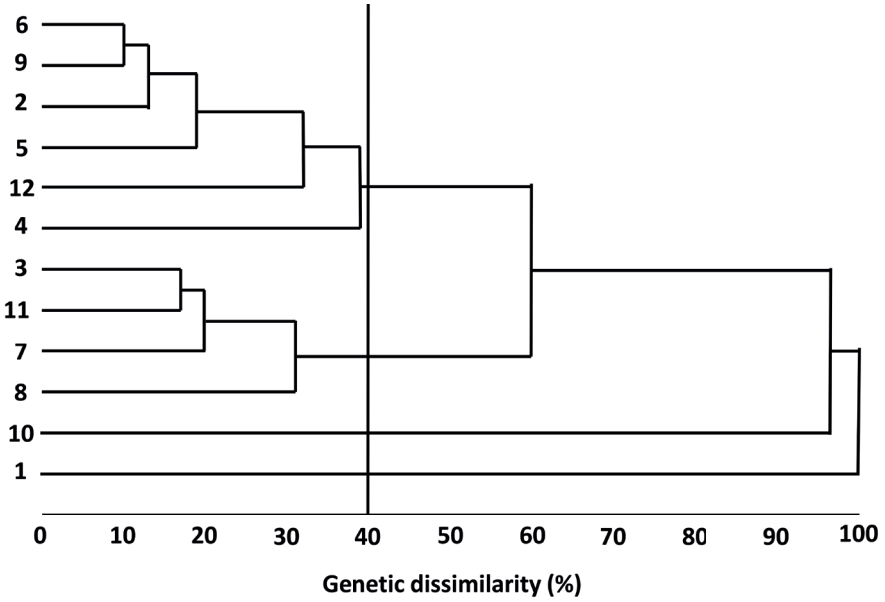

Figure 1 - Dendrogram showing genetic dissimilarity between 12 genotypes of *Manihot esculenta*, determined by UPGMA, based on the generalized Mahalanobis distance (D^2), considering 12 morphoagronomic traits. Note: cophenetic correlation coefficient (CCC): 76.27%.

of 40% dissimilarity between genotypes was established for genotypes to be included in the same group. Four groups were formed using this method (Figure 1).

The groups formed by UPGMA were similar to those formed using Tocher's method. Zuin et al. (2009) observed a similar grouping of cassava accessions using Tocher's method and hierarchical neighbor joining, with an upper threshold of 70% dissimilarity between genotypes. Similar grouping using optimization and hierarchical methods was also reported for robusta coffee (*Coffea canephora*) (Covre et al. 2016), bean (*Phaseolus vulgaris*) (Gonçalves et al. 2016), peach trees (*Prunus persica*) (Silva et al. 2014b), and *Byrsonima dealbata* (Lourenço et al. 2013). It should be highlighted that all genotypes constituting the most divergent pairs based on the generalized Mahalanobis distance (D^2) (Table IV) were placed into four different groups by both Tocher's optimization method (Table V) and UPGMA when the upper threshold of dissimilarity between genotypes was set at 40% (Figure 1).

The relative contributions of the 12 morphoagronomic traits to the genetic distance between the 12 genotypes of *M. esculenta*, analysed using the Singh method (1981), varied between 0.14% and 22.86% (Table VI).

The traits that most contributed to genetic divergence between genotypes were PL (22.86%), RY (19.20%), average WTR (14.89%) and NB (13.72%), together being responsible for approximately 70.64% of the genetic divergence between genotypes. Zuin et al. (2009) also observed PL (18.04%) to be one of the traits that most contributed to genetic divergence between table cassava accessions. On the other hand, HI (0.14%), average LDW (0.67%) and NTR (0.77%) were the traits that least contributed to genetic divergence. However, their omission from the analysis resulted in significant changes to grouping, indicating that trait omission is not desirable.

CONCLUSIONS

There is considerable genetic divergence between the *M. esculenta* genotypes evaluated, indicating

TABLE VI
Relative contributions of 12 morphoagronomic traits to genetic divergence between 12 genotypes of *Manihot esculenta*, according to the Singh method (1981), based on the generalized Mahalanobis distance (D^2). Vila Valério, Espírito Santo, Brazil.

Traits	*S.j*	Value (%)
PL	1174.828929	22.8629
RY	986.839186	19.2045
WTR	765.177762	14.8909
NB	704.850428	13.7169
SD	476.110292	9.2654
PH	459.479573	8.9418
HFB	253.473312	4.9328
NS	129.615579	2.5224
TPW	106.630121	2.0751
NTR	39.939368	0.7772
LDW	34.333452	0.6682
HI	7.294092	0.1419

PL: petiole length; RY: root yield; WTR: weight of tuberous roots; NB: number of buds; SD: stem diameter; PH: plant height; HFB: height of first branch; NS: number of shoots; TPW: total plant weight; NTR: number of tuberous roots per plant; LDW: leaf dry weight; HI: harvest index.

that this population can be potentially used in future genetic improvement programmes. Genotypes "Camuquem" and "Goiás" were the most productive, and genotypes "Amarela" and "Gema de Ovo" were the most divergent. The genotypes were similarly grouped into four groups by Tocher's optimization and hierarchical UPGMA. Of the analysed traits, PL, RY, WTR and NB were the most efficient in explaining the dissimilarity between genotypes. Future studies should evaluate the studied genotypes under different environmental conditions (e.g., drought and salinity) and identify molecular markers for the selection of elite genotypes.

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