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BIOLOGY

Morphological diversity among Brazilian *Capsicum* peppers

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ABSTRACT: *This research aimed to morphologically characterize and estimate the genetic diversity of 21 Capsicum accessions belonging to the Capsicum Germplasm Active Bank at the Universidade Federal do Piauí (BAGC–UFPI) using uni- and multivariate analysis. The experiment was carried out in a greenhouse, by completely randomized experimental design with four repetitions, with one plant per plot. Analysis of variance (ANOVA) and the comparison of means for seven quantitative variables were performed, followed by clustering the averages by the Scott-Knott test ($P < 0.05$). The analysis of the seven quantitative and thirteen qualitative descriptors was estimated based on the Gower distance. Later, it was performed the principal component analysis and the UPGMA hierarchical cluster method. Results characterized and identified a wide intra- and interspecific genetic variability related to the fruit size, colors, and shapes among the Brazilian Capsicum genotypes belonging to the BAGC–UFPI. The descriptors used in this research were effective in the discrimination of the pepper accessions, especially the closely related C. frutescens and C. chinense species.*

Key words: *Capsicum sp., genetic diversity, germplasm bank, morphological traits.*

Diversidade morfológica entre pimentas *Capsicum* brasileiras

RESUMO: *Este trabalho teve como objetivo caracterizar e estimar a diversidade genética em 21 acessos de Capsicum pertencentes ao Banco Ativo de Germoplasma da Universidade Federal do Piauí (BAGC–UFPI), por análises uni e multivariadas. O experimento foi conduzido em telado, utilizando-se o delineamento inteiramente ao acaso, com quatro repetições, sendo uma planta por parcela. Realizou-se análise de variância (ANOVA) e comparação da média para as setes variáveis quantitativas, seguidas do agrupamentos de médias pelo teste Scott-Knott ($P < 0,05$). A análise dos sete descritores quantitativos e treze qualitativos foi estimada com base na distância de Gower. Posteriormente, foi realizada a análise de componentes principais e o método de agrupamento hierárquico UPGMA. Os resultados caracterizaram e identificaram uma ampla variabilidade genética intra e interespecífica relacionada ao tamanho, cor e formato dos frutos entre os genótipos brasileiros de Capsicum do banco de germoplasma de pimentas BAGC–UFPI. Os descritores utilizados foram eficientes na discriminação dos acessos de pimentas, especialmente para espécies proximamente relacionadas C. frutescens e C. chinense.*

Palavras-chave: *Capsicum sp., diversidade genética, banco de germoplasma, descritores morfológicos.*

INTRODUCTION

Capsicum L. genus (Solanaceae Juss. family) is native to Americas and comprises about 43 species with great socioeconomic importance (ASSIS et al., 2020; BARBOZA et al., 2019, 2020). The five major domesticated and economic important species are: *C. annuum* L., *C. chinense* Jacq., *C. frutescens* L., *C. baccatum* L., and *C. pubescens* Ruiz & Pav (CARRIZO GARCÍA et al., 2016). *Capsicum* diversity is represented by a wide range of morphological features, as the fruit shape, size, weight, and color, besides pungencies, flavors and nutritional composition (COSTA et al., 2015, 2019; MACIEL et al., 2019; PESSOA et al., 2019).

Understanding the genetic variability of the plant species based on the morphological, geographical, cytogenetics and molecular traits is essential for the agronomic, genetic and evolutionary studies, especially for that poorly researched and economically under-exploited *Capsicum* species (ASSIS et al., 2020; BIANCHI et al., 2020). Moreover, the agronomic and genetic characterization is important for the conservation and the maintenance of the germplasm banks and for supplying additional knowledge for the genetic breeding programs

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(CARDOSO et al., 2018; SOARES et al., 2019). Despite of this importance, few Brazilian public institutions perform studies of genetic diversity and breeding of *Capsicum* species (REIFSCHNEIDER et al., 2016; RIBEIRO et al., 2020).

Brazil is considered a secondary center of *Capsicum* species. Aiming to preserve the genetic diversity of peppers in the country, the Universidade Federal do Piauí created a *Capsicum* Germplasm Active Bank (BAGC–UFPI). Until November 2021, the BAGC–UFPI has more than 250 peppers accessions belonging to four out of the five different Brazilian regions (Northeast, Southeast, Midwest, and South). To date, genetics, cytogenetics, agronomical and morphological studies have been performed in the pepper accessions of the BAGC–UFPI (MARTINS et al., 2018; COSTA et al., 2019).

The morphological characterization remains a classical and efficient approach to estimating the genetic diversity within and between species and/or accessions belonging to the germplasm banks (MELO et al., 2014). Pessoa et al. (2018) and Soares et al. (2019), for instance, used morphological traits to quantify and identify the genetic dissimilarity of heterotic groups of pepper accessions at BAGC–UFPI. The authors identified genotypes with potential usage in the breeding programs for ornamental peppers and with desirable agricultural characteristics for registration as cultivars, respectively.

Uni-and multivariate analysis has become routine as a research approach for genetic breeding programs, as in the divergent progenitor's studies, and methods for selection of segregation population (CRUZ et al., 2012; LEITE et al., 2018). This research aimed to morphologically characterize and estimate the genetic diversity of 21 *Capsicum* accessions belonging to the BAGC–UFPI by using uni- and multivariate analysis.

MATERIALS AND METHODS

The experiment was carried out in the greenhouse using Sombrite® 40% in the Departamento de Fitotecnia, Centro de Ciências Agrárias, Universidade Federal do Piauí (UFPI), Teresina, PI, Brazil, from May 2019 to January 2020. The 21 pepper accessions belonging to BAGC–UFPI used in research are represented in table 1.

Table 1 - Twenty-one *Capsicum* accessions belonging to the BAGC–UFPI evaluated in this research.

ID	Common name	Species	Collection site	Provenance
BAGC 81	Dedo-de-moça	*C. baccatum* var. *pendulum*	Local market	Brasília - DF
BAGC 91	Pimenta-de-cheiro (ardida)	*C. chinense*	Smallholder farm	Palmerais - PI
BAGC 110	Dedo-de-moça	*C. baccatum* var. *pendulum*	CEASA Supply Center	Teresina - PI
BAGC 114	Jalapeño mexicana	*C. annuum* var. *annuum*	Local market	Belo Horizonte - MG
BAGC 117	Malagueta preta	*C. frutescens*	Local market	Belo Horizonte - MG
BAGC 122	Dedo-de-moça	*C. baccatum* var. *pendulum*	Local fair	Brasília - DF
BAGC 130	Pimentão vermelho	*C. annuum* var. *annuum*	Local fair	Ribeirão Preto - DF
BAGC 131	Pimentão amarelo	*C. annuum* var. *annuum*	Local fair	Ribeirão Preto - DF
BAGC 156	Pimenta	*C. baccatum* var. *pendulum*	Universidade Federal de Viçosa	Jussara - GO
BAGC 157	Pimenta	*C. baccatum* var. *pendulum*	Universidade Federal de Viçosa	Inhumas - GO
BAGC 160	Murupi	*C. chinense*	Universidade Federal de Viçosa	Cáceres - MT
BAGC 163	Pimenta	*C. annuum* var. *annuum*	Universidade Federal de Viçosa	Campinas - SP
BAGC 176	Pimenta	*C. baccatum* var. *pendulum*	Universidade Federal de Viçosa	Caxias do Sul - RS
BAGC 177	Pimenta	*C. baccatum* var. *pendulum*	Universidade Federal de Viçosa	Pelotas - RS
BAGC 178	Pimenta	*C. baccatum* var. *pendulum*	Universidade Federal de Viçosa	Rio Grande - RS
BAGC 208	Pitanga	*C. baccatum* var. *pendulum*	Local fair	Montes Claros - MG
BAGC 209	Pimenta amarela	*C. chinense*	Local fair	Montes Claros - MG
BAGC 222	Dedo-de-moça	*C. baccatum* var. *pendulum*	Garden	Timon - MA
BAGC 242	Cheiro-de-laranja	*C. chinense*	Garden	Ibiapina - CE
BAGC 250	Pimenta-de-cheiro	*C. chinense*	Local market	Salvador - BA
BAGC 251	Cajarana	*C. chinense*	Local market	Salvador - BA

The experiment design was completely randomized, with four replicates, one plant per plot (14 L), 0.40 m among plants and rows.

Seeds of each accession were germinated in polystyrene seedling trays (128 cells each) with the commercial substrate Plantmax®. After two weeks, the plants were transferred to polyethylene vessels (14 L) containing substrate with vegetable soil and humus. The fertilization was performed using a mixture of 2 g of ammonium sulfate, 17 g of single superphosphate and 2.5 g of potassium chloride, as recommended by Alcântara and Ribeiro (2008). The phytosanitary treatment for pest control and irrigation was performed during all the plant cycles, by using micro-sprinkle. The low germination rate during the experiment resulted in different numbers of evaluated accessions within species.

The morphoagronomic characterization of the accessions was based on the 20 descriptors previously established by the International Plant Genetic Resources Institute for *Capsicum* genus (IPGRI, 1995), being seven quantitative and 13 qualitative multicategorical descriptors. Data were collected during reproductive development of each plant. The qualitative descriptors studied were: Calyx annular constriction (CAC); Corolla color (CC); Anther color (AC); Corolla spot color (CSP); Fruit position (PF); Fruit color at the intermediate stage (FCIS); Fruit color at the mature stage (FCMS); Fruit shape (FS); plant growth habit (PGH); Firmness and sustentation of the stem (FSS); Leaf density (LD); Fruit shape at blossom end (FSBE); and Species (SP). The quantitative descriptors studied were: Number of days to flowering (NDF); Number of days to maturation (NDM); Plant height (PH); Fruit Pedicel length (FPL), Fruit length (FL); Fruit width (FWi); Fruit weight (FWe).

Four plants were evaluated per accession, being 10 mature fruits per plant. The measurement of the plant height was performed by measuring tape, while the fruit pedicel length, fruit length and weight were obtained by digital caliper. The fruit weight was calculated using a digital scale.

Data analysis

The univariate analysis was performed by the analysis of variance (ANOVA) ($P < 0.05$) and the hierarchical Scott-Knott ($P < 0.05$) algorithm executed by GENES program (CRUZ, 2013).

For the multivariate analysis, principal component analysis (PCA) and the biplot graphic were performed by FactoMineR (HUSSON et al., 2008) and factoextra (KASSAMBARA; MUNDT, 2019) libraries. The construction of the UPGMA dendrogram was performed by adopting the Gower coefficient as dissimilarity measure (GOWER, 1971). The dendrogram validation was obtained by the cophenetic correlation by Biotools (SILVA et al., 2017) and Cluster (MAECHLER et al., 2019) packages executed in the computational and statistical environment R (R CORE TEAM, 2019).

RESULTS AND DISCUSSION

The results showed significant differences ($P < 0.05$) observed in the 21 pepper accessions for the quantitative descriptors, indicating genetic variability among them. The coefficient of variation (CV%) results for the quantitative descriptors (Table 2) ranged from 2.77% Number of days to flowering (NDF) to 23.26% Fruit weight (FWe).

The quantitative trait analysis based on the Scott-Knott test identified 10 clusters regarding the Number of days to flowering (NDF) (Table 3). The

Table 2 - Mean squares (MS) and coefficients of experimental variation (CV) obtained by the variance analysis of seven quantitative descriptors of peppers evaluated among the 21 accessions belonging to the BAGC–UFPI.

S.V.	D.F	---MS---						
		NDF	NDM	PH	FPL	FL	FWi	FWe
Genotypes	20	2364.51*	1876.91*	3781.59*	10.40*	12.73*	3.92*	218.09*
Residual	63	7.13	21.71	26.49	0.12	0.11	0.03	2.53
Total	83							
CV (%)		2.77	3.42	7.76	11.68	8.89	8.39	23.26

*5% significance by the test F; S.V – Source of variation; D.F – Degrees of freedom; NDF - Number of days to flowering; Number of days to maturation (NDF); Plant height (PH); Fruit Pedicel length (FPL), Fruit length (FL); Fruit width (FWi); Fruit weight (FWe).

Table 3 – Average of the seven quantitative descriptors evaluated among the 21 accessions belonging to the BAGC–UFPI, according to the Scott-Knott ($P < 0.05$) test.

Accession	NDF (days)	NDM (days)	PH (cm)	FPL (cm)	FL (cm)	FWi (cm)	FWe (g)
BAGC 81	92.75f	126.75f	105.2b	9.63a	5.13d	2.04f	6.13f
BAGC 91	74.5i	117.0g	39.25i	2.90c	3.74f	3.55b	14.41c
BAGC 110	127.5c	164.0b	54.95g	2.50c	3.91f	2.14f	3.13g
BAGC 114	67.75j	107.75h	59.78f	2.77c	3.90f	2.45e	9.98d
BAGC 117	72.25i	115.5g	52.48g	2.72c	3.09g	0.21k	1.12g
BAGC 122	103.0e	156.5c	63.20f	2.21d	2.59h	1.35i	2.27g
BAGC 130	75.5i	104.5h	47.50h	2.82c	6.88b	3.73a	28.48a
BAGC 131	102.0e	136.5e	32.51i	2.38c	3.94f	3.91a	23.88b
BAGC 156	73.75i	112.0g	60.33f	2.60c	3.34f	1.50h	2.11g
BAGC 157	74.5i	117.0g	68.16e	2.89c	6.05c	0.90j	1.63g
BAGC 160	108.75d	141.75d	57.15f	1.57e	5.09d	1.27i	2.11g
BAGC 163	91.0f	136.75e	37.16i	2.44c	2.89g	1.81g	5.34f
BAGC 176	105.75d	143.0d	67.73e	3.62b	2.86g	3.33b	8.16e
BAGC 177	133.0b	169.0b	90.05c	3.67b	2.37h	2.77d	5.95f
BAGC 178	107.75d	165.5b	52.0g	3.71b	1.78i	2.07f	4.38g
BAGC 208	92.0f	125.25f	78.5d	2.31d	2.35h	1.46h	1.35g
BAGC 209	166.25a	182.75a	74.25d	2.56c	2.53h	1.79g	2.65g
BAGC 222	79.25h	123.5f	75.5d	2.17d	4.35e	1.15i	1.94g
BAGC 242	107.75d	138.25e	60.6f	2.49c	8.82a	1.53h	5.76f
BAGC 250	85.5g	144.0d	176.0a	2.08d	1.32i	1.85g	1.87g
BAGC 251	79.75h	131.75e	40.0i	2.45c	4.39e	3.10c	10.91d

Different letters in the column, for the same trait, indicate significant differences at $P < 0.05$ (Scott-Knott's test). *NDF - Number of days to flowering; Number of days to maturation (NDF); Plant height (PH); Fruit Pedicel length (FPL), Fruit length (FL); Fruit width (FWi); Fruit weight (FWe).

accession BAGC 114 was the most premature, with 67 days of flowering, while the accession BAGC 209 was the latest, with 166 days to flowering. For the Number of days to maturation (NDM), we observed eight clusters, with the accession BAGC 130 the most premature (104 days for flowering), and the accession BAGC 209 the latest premature (182 days). For the Plant height (PH) descriptor, nine clusters were observed. The accession BAGC 250 showed an average height of 176.0 cm, while the accessions BAGC 91, 131, 163 and 251 were the shortest, with an average height of 40 cm. Smaller plants are suggested for being cultivated in small pots, while medium to high plants are suggested for biggest pots or landscaping (NEITZKE et al., 2010; PESSOA et al., 2018). We suggested the use of the accession BAGC 250 for the biggest pots or landscaping.

Regarding the Fruit Pedicel length (FPL) descriptor, we observed five clusters, being the accession BAGC 81 with a higher average pedicel length of 9.63 cm and the accession BAGC 160 with the shortest length of 1.57 cm. We identified nine clusters for Fruit length (FL), being the accession BAGC 242 with the higher fruit length of 8.82 cm, and the accessions BAGC 178 and 250 with an average less than 1.78 cm. The Fruit width (FWi) split the accessions into 11 clusters. We highlighted the FWi descriptor as the most important for the genetic divergence and clustering by the Scott-Knott test. The accessions BAGC 131 and 130 presented the larger fruits, with 3.91 and 3.73 cm, respectively. Conversely, the accession BAGC 117 showed smaller fruits (0.21 cm). Neitzke et al. (2010) morphologically characterized 17 pepper accessions belonging to the Active Germplasm Bank of *Capsicum* of Embrapa Clima Temperado (Brasília, Distrito Federal, Brazil). The authors reported divergences regarding the fruit width among the accessions, ranging from 0.77 to 5.63 cm in *C. baccatum* and *C. frutescens*, respectively.

For the Fruit weight (FWe) descriptor, seven clusters were observed, with higher values for BAGC 130 and 131 (28.48 g and 23.88 g, respectively). The accessions BAGC 110, 117, 122, 156, 157, 160, 178, 208, 209, 222 and 250 belong to the group with lighter fruits, with an average less than 4.38 g. The accession BAGC 130, the red bell pepper (*C. annuum*), showed a higher weight of 28.48 g. Similarly, Sudré et al. (2005) reported the weight variation in sweet pepper occurred from 25.54 g to 48.24 g. The *C. annuum* species include sweet pepper, which has larger fruits and greater weight.

The mature red bell pepper fruits can be dehydrated by heating and then ground for paprika production (food colorant). The paprika extract is one of the most consumed flavorings in worldwide cuisine (BAENAS et al., 2019). The *Capsicum* fruits owe their intense red color to different carotenoid pigments, especially capsanthin and capsorubin (KONISHI et al., 2019). Carotenoids, not naturally synthesized by humans, have a range of functions and properties in human health, such as antioxidant effects and cancer cell proliferation inhibition (KIM et al., 2016). We suggested the selection of the accession BAGC 130 for the paprika market or to be consumed *in natura*.

Our principal component analysis results indicated the variance percentage for each component, being that, 77.37% of the variance in the third component (CP3) was accumulated (Table 4). Our results corroborate with BELAY et al. (2019) research. In a study analyzing 64 hot pepper genotypes by using 19 morphoagronomical traits, the authors indicated that 69.25% of the variance in the data set was related to only three principal components.

Our *Biplot* results (Figure 1) showed the first and the second principal components, with BAGC 130 genotype the most divergent among the clusters. As we highlighted, this accession (*C. annuum*) exhibited a higher fruit weight. Moreover, the accession BAGC 130 showed prostrate plant growth habit, with no firmness nor sustentation (needed tutoring), intermediate leaf density, corolla with no spot, pallid blue anthers, no calyx annular constriction, pendants fruits with dark brown color in their intermediate maturation stage and rectangular fruits with apex sunken. Our graphic also identified the accessions BAGC 91, 131, and 251 are closely related and have a correlation with the weight and width of their fruits.

The accessions BAGC 114 and 242 created a cluster of fruit length (FL). The genotypes BAGC 122, 160, 208, 222, and 250 created a cluster for plant height (PH) (Table 3). The later accession, commonly known as "pimenta-de-cheiro" (*C. chinense*), showed the higher average, with176 cm. Similar results were obtained by Araújo et al. (2018) that analyzed 20 genotypes of peppers belonging to Peruvian, Colombian, and Brazilian Amazon Forest, and observed *C. chinense* with a greater high of 100.12 cm. The accessions BAGC 110, 177, and 209 were clustered for NDF and NDM, presenting later reproductive cycle and later days to fruiting (Table 3).

The dendrogram generated by the UPGMA method (Figure 2) using Gower distance by the qualitative and quantitative variance showed five clusters, considering a cut- off value representing 40% of dissimilarity among the analyzed accessions. Cluster 1 represents *C. baccatum* (BAGC 156) and *C. annuum* species (BAGC 163, 114, 130, and 131). Despite belonging to different species, the accessions

Table 4 - Principal component (PC), eigenvalues (EV), percentage of the variance and cumulative proportion (%) for the seven qualitative descriptors evaluated among the 21 accessions belonging to the BAGC–UFPI.

Principal component	EV	CP (%)	Accumulated %
PC1	1.5885	36.05	36.05
PC2	1.3071	24.41	60.45
PC3	1.0882	16.92	77.37
PC4	0.9514	12.93	90.30
PC5	0.7289	7.59	97.89
PC6	0.3026	1.30	99.20
PC7	0.2365	7.99	100.0

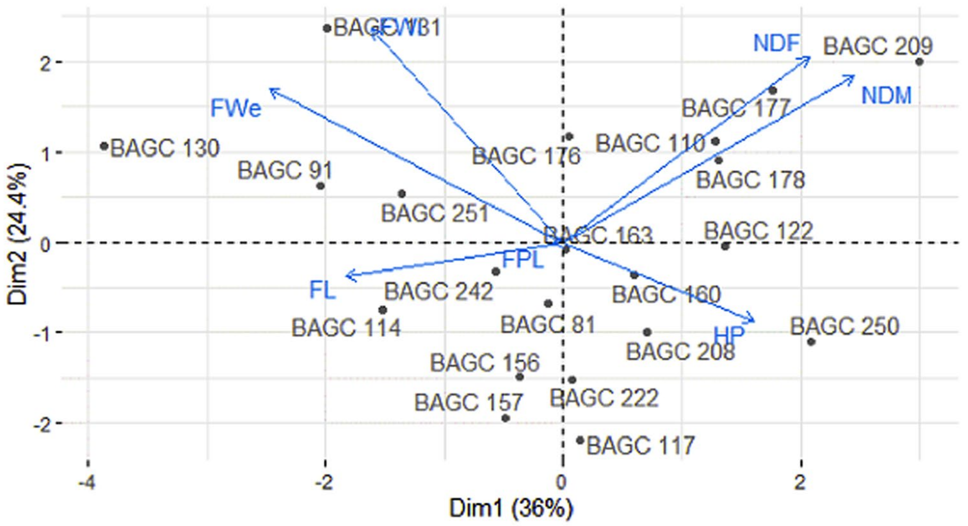

Figure 1 - Graphical dispersion based on the principal component analysis (PCA), considering the seven quantitative traits of the 21 pepper accessions belonging to the *Capsicum* Germplasm Active Bank at the Universidade Federal do Piauí (BAGC–UFPI).

share similar traits, such as plant prostrate growth habit, intermediate and sparse leaves, white corolla, and pendants fruits.

Cluster 2 was represented by only one accession of *C. frutescens* (BAGC 117), which presented plants with stem and pubescence leaves, besides erect and black fruits in the immature stage (Figure 2). These peppers, known as “malaguetas”, are one of the most consumed peppers in Brazil, especially in Zona da Mata Mineira, which are consumed *in natura* or as in hot pickled sauce production (CARVALHO et al., 2006).

The domesticated *C. annuum*, *C. chinense, C. frutescens* and the wild *C. galapagoense* species belong to *Annuum* clade, previously known as the “white flower group” (CARRIZO GARCÍA et al., 2016). The closely related *C. frutescens* and *C. chinense* are easily confused regarding their morphological features. The presence of the calyx annular constriction with no geniculate pedicel in *C. chinense* is the main morphological difference between these species (CARVALHO et al., 2014). In our research, the quantitative and qualitative multi-categorical descriptors showed to be effective in the discrimination and identification of *C. chinense* and *C. frutescens* accessions.

Cluster 3 presented a higher number of accessions: BAGC 176, 177, 208, 157, 81, 222, 178, 110 and 122, all belonging to *C. baccatum* (Figure 2). These peppers, known as “dedo-de-moça” (BAGC 81, 110, 122, 156 and 157) are commonly used in sauce and jelly production (CARVALHO et al., 2006; LIMA et al., 2017). Within this cluster, we noted phenotype similarity between the accessions BAGC 110 and 122. No differences were observed in the qualitative variance, regardless of the different provenance of the accessions.

Cluster 4 is represented by *C. chinense* genotypes (BAGC 160, 242, 91 and 251) (Figure 2). We highlighted the accession BAGC 160 (murupi pepper), with elongated and yellow fruits, besides a wrinkled surface. Murupi pepper is widely used in the North of Brazil as seasoning because it exhibits characteristic flavor and chili taste. Its pepper commercialization usually occurs in marketplaces as *in natura* or as homemade sauces (NASCIMENTO FILHO et al., 2007). The accessions belonging to cluster 4 show a wide range of shapes, sizes, and color of their fruits. Similarly, Moreira et al. (2018) reported wide differences in 65 *C. chinense* accessions belonging to different Brazilian regions, in terms of color, shape, size, and pungency of their fruits, being widely used in the Brazilian cuisine

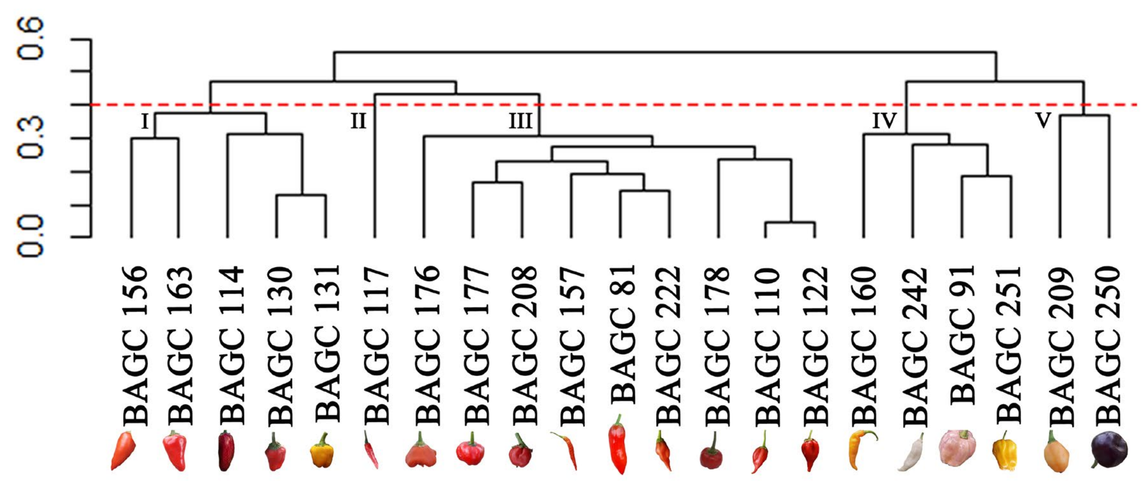

Figure 2 - Dendrogram of the 21 pepper accessions by the combinatory analysis of the quantitative and qualitative descriptors, based on the Gower distance and the UPGMA hierarchical clustering. The dissimilarity cut-off of 40% generated five clusters (represented by roman numerals) and cophenetic correlation coefficient (r) = 0.82.

(NASCIMENTO FILHO et al., 2007; ARAÚJO et al., 2018). The authors highlighted the importance of understanding the genetic variability of *C. chinense* for its current conservation and future status in the genetic breeding programs.

Cluster 5 is composed by two *C. chinense* accessions, BAGC 209 and 250, being the later with the higher average plant height, besides the purple fruits in the immature stages (Figure 2). “Cheiro” pepper fruits (BAGC 91, 242, 209, and 250) are known because of their strong flavor and sweet pungency. They are mostly commercialized as *in natura* and used as rice, salads, and fish seasoning (CARVALHO et al., 2006). These accessions have the potential to be used in several breeding programs or be commercialized as fresh vegetables for gastronomic usage.

Our results confirmed the high morphological diversity among *Capsicum* species and varieties. The continued development of the genetic diversity exploration among peppers, including accessions belonging to germplasm banks, is fundamental for understanding the genetic diversity of this genus. Additionally, morphological data are essential for the germplasm characterization and provide aids for current and future efficient strategies of the genetic breeders for usage and conservation of the genetic resources of this socioeconomic important *Capsicum* genus.

CONCLUSION

Quantitative and qualitative descriptors showed high intra- and interspecific genetic variability among the genotype collection of *Capsicum* accessions at BAGC–UFPI. The descriptors used in this research showed to be effective to differentiate the analyzed pepper accessions, especially the closely related *C. frutescens* and *C. chinense* species. The evaluated genotypes have economic potential and usage in breeding programs.

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DECLARATION OF CONFLICT OF INTEREST

The authors declare no conflict of interest. The founding sponsors had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, and in the decision to publish the results.

AUTHORS’ CONTRIBUTIONS

All authors contributed equally for the conception and writing of the manuscript. All authors critically revised and approved the final version of the manuscript.

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