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Genetic Diversity and Morpho-Agronomic Characterization of *Vigna unguiculata* (L.) Walp Genotypes Under Heat Stress

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Abstract

Global warming poses a threat to food security, particularly for essential crops like cowpea, which exhibits sensitivity to heat stress. This study aimed to evaluate the morpho-agronomic diversity of cowpea genotypes under different daily temperature regimes. The experiment was conducted in growth chambers, and biometric and productive traits were measured to quantify genetic divergence using Mahalanobis distance and UPGMA clustering. Temperature increases markedly altered trait expression. Under the 20–26–33 °C regime, 100-grain weight, leaf dry weight, pod weight, and stem dry weight accounted for 54.44% of the total variation. Under the higher temperature regime (24.8–30.8–37.8 °C), number of pods, plant height, stem fresh weight, and leaf dry weight explained 67.27% of the diversity, evidencing the impact of heat stress on vegetative and productive traits. Cluster analysis identified five distinct groups, confirming genetic variability and temperature-dependent dissimilarity patterns. Genotypes Bico de Ouro 17-53, Bico de Ouro 17-33 and BRS Tumucumaque maintained higher grain number and grain weight under elevated temperatures, whereas others showed yield reductions of up to 65%. These findings demonstrate exploitable genetic variability for heat tolerance in cowpea and support the use of morpho-agronomic traits as effective criteria for selecting genotypes adapted to warmer environments.

Keywords: climate change; cowpea; food security; genetic improvement; heat tolerance

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1. Introduction

Modern agriculture faces the challenge of reconciling increasing food demand with the impacts of climate change on agricultural production systems. Among the elements associated with global warming, the rise in average temperature stands out as a critical factor [1], influencing plant adaptive processes and exerting direct effects on the development, productivity, and stability of agricultural systems [2].

It is estimated that the average global temperature has already risen by approximately 1.1 °C since the pre-industrial period and could exceed 2 °C in the coming decades if current greenhouse gas emission trends persist [1]. This progressive increase disrupts the thermal balance of major agricultural crops, as temperatures above the physiological optimum reduce carbon assimilation, accelerate phenological development, and compromise grain formation and filling, resulting in productivity losses [3].

In semi-arid regions, characterized by high temperatures and low water availability, further increases in temperature can exacerbate existing limitations to agricultural production. Under these conditions, food crops essential to local food security become even more vulnerable, as heat stress can compromise plant growth, reproductive development, and overall yield, thereby increasing the instability of agricultural systems [4–9]. Cowpea (*Vigna unguiculata* (L.) Walp.), widely cultivated in the Brazilian Northeast, constitutes a vital source of protein, carbohydrates, vitamins, and minerals for populations in tropical and subtropical regions and is recognized for its hardiness and its central role in regional diets [10–16]. In addition to human consumption, cowpea is also used for animal feed and as a strategic component in smallholder farming systems, playing a significant role in income generation and the sustainability of agroecosystems [17–19].

However, cowpea exhibits marked sensitivity when subjected to thermal stress, especially during the flowering stage, characterized by reduced pollen grain viability, increased floral abortion, and impaired grain filling, which result in lower yields [20–22]. Beyond the negative effects on reproductive development, heat stress can compromise vegetative growth, leaf expansion, biomass accumulation, and the balance between shoot and root systems. Elevated temperatures are also associated with reduced photosynthetic efficiency, alterations in nitrogen metabolism, and a diminished capacity for assimilate allocation to reproductive organs, ultimately leading to yield reduction. These effects depend on the intensity and duration of the stress, as well as the specific genotype, highlighting the existence of genetic variability in heat tolerance within the species [23–26].

In this scenario, studies based on biometric and yield parameters enable the identification of promising genotypes by integrating data on vegetative growth and reproductive responses to thermal stress [27]. In Brazil, such research began with performance evaluations of commercial cultivars under controlled conditions [20] and was subsequently expanded to evaluate 20 genotypes from the genetic improvement program under increased air temperatures [28]. This previous study represented an important advance in the pre-selection of heat-tolerant materials, as it evaluated a specific set of genotypes under controlled conditions of increased air temperature. Nevertheless, the approach was predominantly focused on identifying genotypes based on physiological responses and productive stability, relying on univariate analyses and direct comparisons between treatments. Therefore, further advances are required to evaluate new genotypes, including materials with different genetic backgrounds, and incorporate analyses that allow for a broader understanding of the variability among the materials used.

Analyzing the morphophysiological diversity among genotypes is essential for understanding the breadth of variability within a species and identifying differentiated response patterns to environmental conditions [29,30]. This approach allows for the recognition of groups of genotypes with similar morphophysiological behaviors, identifying characteristics associated with tolerance or sensitivity to heat. When applied to different sets of genotypes, diversity analyses expand the interpretation of phenotypic responses and reveal new adaptive patterns that may not be evident when a limited group of materials is evaluated. In addition, diversity analyses provide information on how traits interact and respond jointly to stress conditions, which is fundamental for distinguishing stable from sensitive genotypes.

Knowledge about diversity is also the basis for the efficient use of available genetic resources, favoring the selection of superior materials and directing breeding strategies aimed at adapting the crop to scenarios of increasing temperatures [21,22,27,28]. While previous studies have contributed by identifying genotypes with stable physiological and productive responses, they were restricted to specific genetic materials and did not explore in detail the structure of phenotypic variability or the patterns of genetic divergence among genotypes based on morpho-agronomic descriptors.

Therefore, the selection and characterization of genetic materials capable of maintaining the stability of biometric parameters and productive efficiency under high temperature conditions become essential for the advancement of breeding programs, assisting in the adoption of agricultural adaptation strategies through the development of cultivars adapted to future climatic conditions [28,31]. In this context, morpho-agronomic analyses play a key role by enabling the identification of traits that most contribute to variability and by supporting the differentiation of genotypes according to their adaptive responses to thermal stress, especially when applied to genetically distinct materials.

Thus, this study aimed to evaluate the morpho-agronomic diversity of cowpea genotypes subjected to different daily temperature regimes, expanding previous research by analyzing a distinct set of genotypes and emphasizing multivariate approaches to characterize genetic divergence, trait contribution, and temperature-dependent grouping patterns. This approach seeks to deepen the understanding of phenotypic variability under heat stress and to support genetic improvement aimed at selecting materials more resilient to climate change.

2. Materials and Methods

2.1. Plant Material

The genetic material consisted of 15 cowpea (*Vigna unguiculata* (L.) Walp.) genotypes, including nine superior lines and six commercial cultivars (Table 1), provided by the Embrapa Meio-Norte breeding program. The genotypes were selected to represent traditional commercial cultivars from the Brazilian semi-arid region, widely used in cowpea breeding programs in Brazil, as well as advanced breeding lines with desirable agronomic traits and high potential for use in genetic improvement programs.

Table 1. Number, name/code, and commercial subclass of the cowpea (*Vigna unguiculata*) genotypes evaluated.

Number	Name/Code	Commercial Subclass
1	Pretinho do Pará	Black
2	Pingo de Ouro 1-2	Canapu
3	BRS Aracê	Green
4	BRS Juruá	Green
5	BRS Pajeú	Brown
6	BRS Tumucumaque	White
7	Bico de Ouro—17-21	Always green
8	Bico de Ouro—17-23	Always green
9	Bico de Ouro—17-24	Always green
10	Bico de Ouro—17-33	Always green
11	Bico de Ouro—17-35	Always green
12	Bico de Ouro—17-37	Always green
13	Bico de Ouro—17-38	Always green
14	Bico de Ouro—17-43	Always green
15	Bico de Ouro—17-53	Always green

2.2. Experimental Site, Growth Conditions and Experimental Design

The experiment was conducted at Embrapa Semiárido, located in the city of Petrolina, Pernambuco, Brazil. The evaluations were carried out in the Climate Change Laboratory, in growth chambers, type Fitotron (Figure 1), with control of photoperiod, temperature (varying throughout the day, simulating the environment) and relative humidity.

Figure 1. Cowpea genotypes grown in a Fitotron-type growth chamber with controlled photoperiod, temperature, and relative humidity: one day after planting (**a**); 9 days after planting (**b**); 20 days after planting (**c**); and 33 days after planting (**d**).

The experimental design was completely randomized, in a 15 × 2 factorial scheme, with 15 cowpea genotypes and two daily temperature regimes, with four replications.

The daily temperature range of 20–26–33 °C corresponds to the average minimum, average, and maximum temperatures in the Brazilian Semi-Arid region, which vary from 18–22, 25–27, and 32–34 °C, respectively. The temperature regime of 24.8–30.8–34.8 °C considered the average temperatures of the region plus a value of 4.8 °C, based on the IPCC's temperature increase scenario [1]. The variation in temperature throughout the day can be seen in Table 2.

Table 2. Temperature regimes and variations throughout the day.

Temperature Regimes °C	**Time/Temperature (°C)**			
	8:00 PM to 6:00 AM	**6:00 AM to 10:00 AM**	**10:00 AM to 3:00 PM**	**3:00 PM to 8:00 PM**
20–26–33	18	24	30	24
24.8–30.8–34.8	22	28	34	28

2.3. Cultivation, Evaluations and Harvest

Cowpea seeds were planted in 5.5 L pots and kept in growth chambers (total area of 12 m^2) until harvest. Harvesting was carried out when all the pods had a yellowish color and a dry texture, indicating complete physiological maturity. The following were evaluated: stem diameter (mm), plant height (cm), fresh and dry mass of leaves and stem (g), and root dry biomass (g). To determine the dry matter mass, the plant parts were placed in a forced-air oven at 60 °C to dry until they reached a constant weight and were subsequently weighed.

After cutting the aerial part, the roots were separated from the soil by washing in running water, using sieves with 0.5 and 1.0 mm meshes to retain the root material. Next, they were placed in a forced-air oven at 60 °C until they reached a constant weight, and then weighed to determine the dry matter mass in all treatments.

In addition, the length and diameter of the pod, average pod weight, number of pods per plant, number of grains per pod, number of grains per plant, grain weight per plant, and weight of 100 grains were evaluated.

2.4. Statistical and Multivariate Analyses

Average data from morpho-agronomic descriptors used to quantify genetic divergence between and within species were used to obtain the distance matrix, using Mahalanobis generalized distance [32]. After obtaining the matrix, the genotypes were grouped using the unweighted group average (UPGMA) to create the dendrogram.

For comparison of averages, the data obtained were subjected to analysis of variance (ANOVA) using the Sisvar program (version 5.6), using the F-test. Student's *t*-test was used to compare the temperature regimes, and the Scott-Knott test was used to compare the genotypes.

3. Results

The morpho-agronomic descriptors were able to differentiate cowpea genotypes subjected to daily temperature regimes and to group those with greater genetic similarity (Table 3 and Figure 2). Genetic diversity among the genotypes was mainly evidenced by the following descriptors: 100-grain weight, leaf dry weight, pod weight, stem dry weight, plant height, and stem diameter.

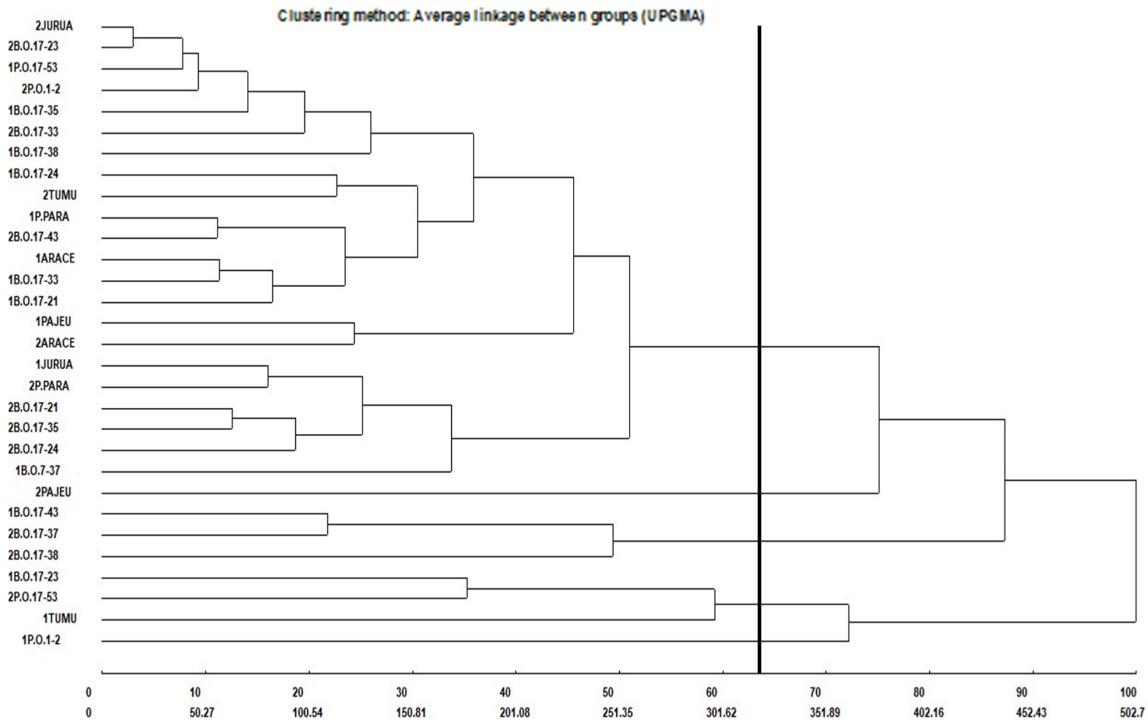

Figure 2. Dendrogram representing the genetic dissimilarity between and within cowpea genotypes subjected to temperature regimes of 20–26–33 °C and 24.8–30.8–37.8 °C, obtained by the UPGMA method, using Mahalanobis generalized distance. The horizontal line indicates the cutoff level adopted for cluster delimitation, corresponding to a cophenetic correlation coefficient (CCC) of 79%.

Table 3. Relative contribution of 15 morpho-agronomic descriptors used to evaluate the genetic dissimilarity of cowpea genotypes subjected to daily temperature regimes of 20–26–33 °C and 24.8–30.8–37.8 °C.

20–26–33 °C		24.8–30.8–37.8 °C	
Variable	**Value (%)**	**Variable**	**Value (%)**
Weight of 100 grains (g)	15.75	Number of pods per plant	21.90
Leaf dry weight (g)	13.48	Plant height (cm)	19.79
Weight of the pod (g)	12.88	Stem fresh weight (g)	13.46
Stem dry weight (g)	12.33	Leaf dry weight (g)	12.12
Plant height (cm)	10.72	Root dry weight (g)	8.07
Leaf fresh weight (g)	8.96	Weight of the pod (g)	7.92
Number of grains per pod	7.99	Stem diameter (mm)	4.79
Root dry weight (g)	4.09	Number of grains per pod	3.81
Stem diameter (mm)	4.03	Leaf fresh weight (g)	3.20
Total weight of grains per plant (g)	3.52	Pod length (cm)	2.88
Pod length (cm)	2.27	Pod width (mm)	2.05
Number of grains per plant	1.75	Total weight of grains/plant (g)	0.00
Stem fresh weight (g)	1.58	Number of grains per plant	0.00
Pod width (mm)	0.41	Weight of 100 grains (g)	0.00
Number of pods per plant	0.24	Stem dry weight (g)	0.00
Total	100		100

The relative contribution of the variables to genetic diversity showed that, under the daily temperature regime of 20–26–33 °C, the variables with the greatest contribution were 100-grain weight (15.75%), leaf dry weight (13.48%), pod weight (12.88%), and stem dry weight (12.33%), totaling 54.44% of the observed variation (Table 3). Under the daily temperature regime of 24.8–30.8–37.8 °C, the number of pods per plant (21.90%), plant height (19.79%), stem fresh weight (13.46%), and leaf dry weight (12.12%) stood out, together contributing 67.27% of the total diversity, highlighting the effect of increased temperature on the expression of productive and vegetative traits.

Genetic diversity among cowpea genotypes was also influenced by daily temperature (Figure 2). The dendrogram obtained by the UPGMA method, using the Mahalanobis generalized distance, showed a cophenetic correlation coefficient (CCC) of 79%, indicating good representativeness of the dissimilarity matrix. Five distinct groups were formed, confirming the existence of wide genetic variability among the evaluated genotypes, in which R1 represents the temperature regime of 20–26–33 °C and R2 corresponds to the temperature regime of 24.8–30.8–37.8 °C.

Group 1 comprised genotypes with greater genetic similarity, consisting of 22 components, suggesting more stable behavior in response to temperature variation. Group 2 consisted exclusively of the genotype R2.BRS Pajeú. Group 3 was formed by the genotypes R1.Bico de Ouro 17-43, R2.Bico de Ouro 17-37, and R2.Bico de Ouro 17-38. Group 4 included the genotypes R1.Bico de Ouro 17-23, R2.Bico de Ouro 17-53, and R1.BRS Tumucumaque, while Group 5 consisted of the genotype R1.Pingo de Ouro 1-2. This clustering pattern reinforces the influence of temperature on genetic dissimilarity and highlights the presence of genotypes with differentiated adaptive potential.

The range of dissimilarity values observed confirms the genetic heterogeneity among the genotypes (Table 4), allowing the identification of both highly similar genotype pairs and more genetically distant genotypes, demonstrating the significant phenotypic variability within the studied group.

Table 4. Measures of genetic dissimilarity between cowpea genotypes subjected to the daily temperature regimes—R1 (20–26–33 °C) and R2 (24.8–30.8–37.8 °C), considering 15 characteristics, based on Mahalanobis generalized distance.

Genotype	Maximum Distance	Minimum Distance
R1.Pretinho do Pará	R2.BRS Pajeú (444.02)	R2.Bico de Ouro—17-43 (55.86)
R1.Pingo de Ouro 1-2	R2.Bico de Ouro—17-33 (850.30)	R1.Bico de Ouro—17-33 (249.77)
R1.BRS Aracê	R2.BRS Pajeú (411.76)	R1.Bico de Ouro—17-33 (56.74)
R1.BRS Juruá	R1.Bico de Ouro—17-23 (618.58)	R2.Pretinho do Pará (80.43)
R1.BRS Pajeú	R1.Bico de Ouro—17-43 (844.61)	R2.BRS Aracê (122.42)
R1.BRS Tumucumaque	R1.Bico de Ouro—17-43 (696.47)	R1.Bico de Ouro—17-24 (238.05)
R1.Bico de Ouro—17-21	R1.Bico de Ouro—17-43 (438.06)	R1. BRS Aracê (67.20)
R1.Bico de Ouro—17-23	R1.BRS Pajeú (766.11)	R2.Bico de Ouro—17-53 (177.33)
R1.Bico de Ouro—17-24	R2.BRS Pajeú (656.58)	R1. BRS Aracê (89.08)
R1.Bico de Ouro—17-33	R1.Bico de Ouro—17-23 (340.21)	R1. BRS Aracê (56.74)
R1.Bico de Ouro—17-35	R1. Pingo de Ouro 1-2 (653.71)	R2.BRS Juruá (65.00)
R1.Bico de Ouro—17-37	R1.Bico de Ouro—17-23 (590.29)	R2.Bico de Ouro—17-35 (86.25)
R1.Bico de Ouro—17-38	R1.Bico de Ouro—17-23 (754.88)	R2.Bico de Ouro—17-23 (96.49)
R1.Bico de Ouro—17-43	R1.BRS Pajeú (844.61)	R2.Bico de Ouro—17-37 (109.51)
R1.Bico de Ouro—17-53	R1.Pingo de Ouro 1-2 (639.78)	R2.BRS Juruá (38.21)
R2.Pretinho do Pará	R1.Bico de Ouro—17-23 (570.33)	R1.BRS Juruá (80.43)
R2.Pingo de Ouro 1-2	R1.Pingo de Ouro 1-2 (745.81)	R2.Bico de Ouro—17-23 (43.70)
R2.BRS Aracê	R2.Bico de Ouro—17-37 (551.43)	R1.Bico de Ouro—17-53 (90.54)
R2.BRS Juruá	R1.Pingo de Ouro 1-2 (713.05)	R2.Bico de Ouro—17-23 (15.01)
R2.BRS Pajeú	R1.Pingo de Ouro 1-2 (773.28)	R2.Bico de Ouro—17-35 (182.47)
R2.BRS Tumucumaque	R1.Pingo de Ouro 1-2 (667.97)	R1. Pretinho do Pará (110.29)
R2.Bico de Ouro—17-21	R1.BRS Tumucumaque (565.73)	R2.Bico de Ouro—17-35 (62.92)
R2.Bico de Ouro—17-23	R1.Pingo de Ouro 1-2 (769.64)	R2.BRS Juruá (15.01)
R2.Bico de Ouro—17-24	R1.BRS Tumucumaque (493.49)	R2.Bico de Ouro—17-21 (64.18)
R2.Bico de Ouro—17-33	R1.Pingo de Ouro 1-2 (850.30)	R2.BRS Juruá (54.15)
R2.Bico de Ouro—17-35	R1.Pingo de Ouro 1-2 (570.91)	R2.Bico de Ouro—17-21 (62.92)
R2.Bico de Ouro—17-37	R2.BRS Pajeú (698.30)	R1.Bico de Ouro—17-43 (109.51)
R2.Bico de Ouro—17-38	R1.BRS Pajeú (823.75)	R1.Bico de Ouro—17-43 (152.94)
R2.Bico de Ouro—17-43	R1.Bico de Ouro—17-23 (526.04)	R1. Pretinho do Pará (55.86)
R2.Bico de Ouro—17-53	R2.Bico de Ouro—17-37 (658.12)	R1.Bico de Ouro—17-23 (177.33)

Genetic dissimilarity analysis highlighted the genotype pairs R2.Bico de Ouro 17-33 (850.30) and R2.Bico de Ouro 17-43 × R1.BRS Pajeú (844.61) as the most divergent, while R2.Bico de Ouro 17-23 and R2.BRS Juruá were identified as the most similar (15.01) (Table 4), where R1 represents the temperature regime of 20–26–33 °C and R2 corresponds to the temperature regime of 24.8–30.8–37.8 °C.

The evaluated genotypes showed a significant genotype × daily temperature regime interaction ($p < 0.05$) for all biometric parameters, demonstrating that temperature increase affected vegetative plant development (Table 5).

The interaction between cowpea genotypes and temperature regimes resulted in significant variation across all evaluated biometric traits, with genotypes differing significantly for all variables (Table 6).

For plant height, the highest values were observed under the temperature regime of 24.8–30.8–37.8 °C, with the genotypes BRS Juruá (237.7 cm) and BRS Aracê (233.3 cm) standing out, along with Bico de Ouro 17-53. These genotypes showed increases of 28%, 44%, and 43%, respectively, in plant height when grown under higher temperature conditions (Table 6).

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Table 5. Summary of the analysis of variance (ANOVA), using the mean square method, for the biometric values: plant height (PLH), stem diameter (STD), leaf fresh weight (LFW), stem fresh weight (SFW), leaf dry weight (LDW), stem dry weight (SDW), and root dry weight (RDW), of different cowpea genotypes, subjected to two environments with different temperatures.

Source of Variation	DF	Medium Square						
		PLH	STD	LFW	SFW	LDW	SDW	RDW
Genotype (G)	14	5049.3 **	2.7 **	2968.4 **	714.8 **	82.4 **	57.5 **	52.6 **
Temperature regime (T)	1	138.6 ns	7.4 **	62181.2 **	22685.5 **	749.2 **	1623.6 **	668.9 **
GxT	14	2561.9 **	1.2 **	548.2 **	609.8 **	12.7 **	52.1 **	10.4 **
Residue	87	40.4	0.0	40.1	24.9	0.8	9.0	0.6
CV %		4.0	4.1	7.4	7.0	8.4	18.4	11.3

DF: Degree of freedom; CV: Coefficient of variation; ns: not significant; ** Significant at 5% of probability according to Scott-Knott test.

Table 6. Mean values for plant height (PLH), stem diameter (STD), leaf fresh weight (LFW), stem fresh weight (SFW), leaf dry weight (LDW), stem dry weight (SDW), and root dry weight (RDW) of different cowpea genotypes subjected to different temperature regimes.

Regime	Genotype	PLH (cm)	STD (mm)	LFW (g)	SFW (g)	LDW (g)	SDW (g)	RDW (g)
>20–26–33 °C	Pretinho do Pará	167.7 bC	6.72 aB	85.5 bB	65.3 bB	11.5 bB	12.9 bB	7.1 bA
	Pingo de Ouro 1-2	167.0 aC	6.67 bB	79.1 bC	72.7 bA	10.6 bC	18.1 aA	7.7 bA
	BRS Aracê	162.0 bC	6.24 aC	30.1 bH	64.5 aB	3.9 bE	15.2 aA	3.5 bC
	BRS Juruá	185.0 bB	5.93 aD	59.3 bE	73.8 aA	11.9 bB	16.7 aA	5.7 bB
	BRS Pajeú	198.0 aA	6.37 aC	64.3 bE	57.1 bC	8.3 bD	12.1 bB	6.7 bB
	BRS Tumucumaque	146.3 aE	6.41 bC	64.5 bE	51.3 bC	9.4 bC	10.3 bC	2.6 bD
	Bico de Ouro 17-21	136.0 aF	6.22 aC	54.5 bF	45.1 bD	7.0 bD	8.5 bC	3.2 bC
	Bico de Ouro 17-23	130.0 bF	6.88 bB	63.2 bE	55.7 bC	7.2 bD	15.5 bA	3.7 bC
	Bico de Ouro 17-24	143.0 aE	5.49 bE	42.0 bG	45.5 bD	5.4 bE	9.5 bC	1.9 bD
	Bico de Ouro 17-33	145.3 aE	7.15 aB	53.2 bF	56.9 bC	7.4 bD	11.3 bB	2.5 bD
	Bico de Ouro 17-35	189.3 aB	6.91 bB	69.8 bD	53.1 bC	11.4 bB	13.9 bA	2.6 bD
	Bico de Ouro 17-37	133.3 aF	6.70 bB	49.6 bF	56.9 bC	6.8 bD	12.5 bB	1.7 bD
	Bico de Ouro 17-38	136.0 aF	7.77 aA	42.5 bG	40.0 bD	4.9 bE	7.4 bC	3.4 bC
	Bico de Ouro 17-43	155.0 aD	6.65 aB	95.0 bA	63.7 bB	14.2 bA	13.1 bB	8.3 bA
	Bico de Ouro 17-53	133.0 bF	7.05 aB	80.5 bC	51.5 bC	10.4 bC	12.0 bB	7.3 bA
24.8–30.8–37.8 °C	Pretinho do Pará	185.5 aB	6.22 bD	141.2 aB	97.9aB	20.1 aA	21.4 aB	16.7 aA
	Pingo de Ouro 1-2	131.8 bE	7.56 aB	105.3 aD	97.1 aB	12.1 aD	20.8 aB	12.3 aB
	BRS Aracê	233.3 aA	5.81 bD	78.4 aG	52.1 bG	8.0 aF	11.2 bD	12.6 aB
	BRS Juruá	237.7 aA	6.27 aD	125.1 aC	79.9 aD	18.5 aB	16.8 aC	9.4 aD
	BRS Pajeú	167.0 bC	6.61 aC	95.8 aE	86.1 aC	12.5 aD	20.1 aB	9.8 aD
	BRS Tumucumaque	138.3 aD	7.26 aB	88.7 aF	74.7 aE	11.0 aE	19.7 aB	7.7 aE
	Bico de Ouro 17-21	130.0 aE	6.57 aC	127.1 aC	65.2 aF	15.6 aC	12.8 aD	9.6 aD
	Bico de Ouro 17-23	140.3 aD	8.40 aA	122.3 aC	98.0 aB	13.1 aD	24.0 aB	8.7 aE
	Bico de Ouro 17-24	145.3 aD	7.20 aB	77.3 aG	82.2 aD	8.4 aF	21.2 aB	6.2 aF
	Bico de Ouro 17-33	123.8 bE	7.21 aB	83.3 aF	69.3 aE	9.0 aF	16.9 aC	5.1 aG
	Bico de Ouro 17-35	134.0 bE	8.28 aA	104.8 aD	109 aA	15.0 aC	28.3 aA	6.6 aF
	Bico de Ouro 17-37	133.0 aE	8.20 aA	102.5 aD	88.2 aC	15.4 aC	21.6 aB	7.3 aF
	Bico de Ouro 17-38	138.3 aD	8.02 aA	96.9 aE	93.5 aC	11.7 aE	22.8 aB	4.6 aG
	Bico de Ouro 17-43	130.8 bE	6.84 aC	160.8 aA	98.3 aB	19.9 aA	22.9 aB	11.2 aC
	Bico de Ouro 17-53	190.3 aB	6.17 bD	106.6 aD	74.1 aE	15.0 aC	18.8 aB	11.1 aC
standard deviation (SD)		6.28	0.29	6.34	4.99	0.95	3.01	0.78

The same lowercase letter in the column between regimes and uppercase letter between genotypes in the same regime do not differ from each other by the Scott-Knott test at 5% probability.

Under the temperature regime of 20–26–33 °C, the BRS Pajeú genotype (198.0 cm) exhibited the greatest height, surpassing the other genotypes within the same regime. However, when subjected to increased temperature, this genotype showed a 16% reduction in height. The genotypes Bico de Ouro 17-35 and Pingo de Ouro 1-2 also showed sensitivity to increased temperature, with reductions of 21% and 29%, respectively, in plant height under the higher temperature regime (Table 6).

The largest stem diameter values were observed in plants grown under the temperature regime of 24.8–30.8–37.8 °C, particularly among genotypes of the Bico de Ouro 17 group (17-23, 17-35, 17-37, and 17-38), with values exceeding 8 mm.

Leaf and stem fresh weights were influenced by increased air temperature, with most genotypes showing a significant increase in green biomass production. The genotypes Bico de Ouro 17-43 (160.8 g) and Bico de Ouro 17-35 (109 g) stood out, presenting the highest leaf fresh weight and stem fresh weight, respectively (Table 6).

Similarly, dry biomass (leaf and stem dry weight) was favored by the 4.8 °C temperature increase. The genotypes Pretinho do Pará and Bico de Ouro 17-43 were superior under the 24.8–30.8–37.8 °C regime, presenting leaf dry weights of 20.1 and 19.9 g, corresponding to increases of 75% and 40%, respectively, compared to the 20–26–33 °C regime (Table 6).

For stem dry weight, the genotype Bico de Ouro 17-35 remained superior under higher temperature conditions, with 28.3 g of stem dry biomass, representing a 104% increase (Table 6).

Increased temperature favored root biomass accumulation in all evaluated genotypes, with increases ranging from 36% to 329% in root dry weight under the 24.8–30.8–37.8 °C regime. The Pretinho do Pará genotype showed the highest root dry weight (16.7 g), outperforming the other genotypes (Table 6).

A significant genotype × daily temperature regime interaction ($p < 0.05$) was also observed for all productive parameters evaluated (Table 7), indicating distinct genotype responses across temperature regimes (Table 8).

Table 7. Summary of the analysis of variance (ANOVA), by mean squares, for the values of average pod length (APL), pod width (PWD), pod weight (PW), number of pods (NOP), number of grains per pod (NGPD), number of grains per plant (NGP), grain weight per plant (GWP) and weight of 100 grains (W100G), of different cowpea genotypes, subjected to daily temperature regimes (20–26–33 °C and 24.8–30.8–37.8 °C).

Source of Variation	DF	Medium Square							
		APL	PWD	PW	NOP	NGPD	NGP	GWP	W100G
Genotype (G)	14	26.5 **	5.1 **	1.9 **	61.2 **	15.9 **	5653.0 **	217.3 **	59.3 **
Temperature regime (T)	1	108.8 **	0.2 ns	9.4 **	108.5 **	176.1 **	80.0 ns	108.2 ns	99.4 **
GxT	14	6.9 **	1.9 **	1.0 **	33.1 **	7.1 **	2818.6 **	121.0 **	49.2 **
Residue	87	0.8	0.3	0.0	0.9	1.2	211.7	10.0	2.1
CV %		5.8	6.7	6.9	12.4	10.9	19.1	15.5	6.9

DF: Degree of freedom; CV: Coefficient of variation; ns: not significant; ** Significant at 5% of probability according to Scott-Knott test.

The genotypes showed varied responses to the productive parameters in environments with different temperature regimes (Table 8).

Under the temperature regime of 20–26–33 °C, the genotypes BRS Pajeú, BRS Tumucumaque, Bico de Ouro 17-21, and Bico de Ouro 17-43 showed the greatest pod length, with values of 20.3, 18.5, 18.9, and 19.3 cm, respectively, and did not differ statistically from each other. Among these, Bico de Ouro 17-43 also showed the highest pod width and pod weight, with averages of 10.9 mm and 4.4 g, respectively (Table 8).

Table 8. Mean values for average pod length (APL), pod width (PWD), pod weight (PW), number of pods per plant (NOP), number of grains per pod (NGPD), number of grains per plant (NGP), grain weight per plant (GWP), and weight of 100 grains (W100G) of different cowpea genotypes subjected to different temperature regimes.

Regime	Genotype	APL (cm)	PWD (mm)	PW (g)	NOP	NGPD	NGP	GWP (g)	W100G (g)
20–26–33 °C	Pretinho do Pará	17 aB	7.6 aC	2.8 aD	5 aD	12 aB	61 aC	11.5 aB	18.9 aC
	Pingo de Ouro 1-2	16 aC	9.7 aB	3.1 aC	6 aD	10 aB	56 aC	12.3 aB	22.1 bB
	BRS Aracê	17 aB	8.7 aC	2.6 aE	10 aA	12 aB	122 aA	16.5 aA	13.6 bE
	BRS Juruá	15.6 aC	9.4 aB	2.4 aF	7 bC	10 aD	66 aC	14 aB	21.3 aB
	BRS Pajeú	20.3 aA	9.9 aB	3.9 aB	6 bC	14 aA	89 aB	18.8 aA	21.2 aB
	BRS Tumucumaque	18.5 aA	8.9 aC	2.3 aF	8 bB	8 bD	67 bC	15.2 bB	22.6 bB
	Bico de Ouro 17-21	18.9 bA	8.7 bC	2.7 bE	3 bE	15 aA	52 aC	8.5 bB	16.3 bD
	Bico de Ouro 17-23	16 aC	8.5 aC	2.6 aE	8 aB	10 aD	78 aC	13.7 aB	17.4 bD
	Bico de Ouro 17-24	15.7 aC	8.1 aC	2.3 aF	7 bC	10 aD	67 bC	12.2 aB	18.2 aD
	Bico de Ouro 17-33	15.8 aC	8.4 aC	2.4 aF	7 bC	10 aD	65 bC	12.5 bB	19.2 aC
	Bico de Ouro 17-35	16 aC	8.7 aC	3 aC	8 aB	11 aC	96 aB	19.8 aA	20.6 aC
	Bico de Ouro 17-37	16.5 aB	8.2 aC	2.6 aE	5 aD	11 aC	58 aC	11.9 aB	20.5 aC
	Bico de Ouro 17-38	14.5 aC	8.3 aC	2.7 aE	10 aA	11 aC	116 aA	20.6 bA	17.7 bD
	Bico de Ouro 17-43	19.3 aA	10.9 aA	4.4 aA	3 aE	12 aB	39 aC	11.7 aB	29.9 aA
	Bico de Ouro 17-53	16.9 aB	9 aC	3.1 aC	7 bC	14 aA	98 bB	20 bA	20.4 aC
24.8–30.8–37.8 °C	Pretinho do Pará	16.9 aC	8.1 aD	2.4 bC	5 aE	12 aA	62 aD	10.9 aD	17.6 aD
	Pingo de Ouro 1-2	15.8 aD	10.1 aB	2.6 bC	6 aE	9 aB	53 aE	13.4 aC	25.3 aB
	BRS Aracê	13.7 bE	7.7 bD	2.1 bD	9 aD	8 bC	70 bD	14.1 aC	20.2 aC
	BRS Juruá	11 bF	9.3 aC	1.8 bE	10 aC	7 bC	72 aD	15.6 aC	21.7 aC
	BRS Pajeú	16.6 bC	10.1 aB	2.7 bB	8 aD	10 bB	85 aC	18.8 aC	22 aC
	BRS Tumucumaque	18.2 aB	7.7 bD	2.1 aD	13 aB	10 aB	130 aB	32.4 aA	24.9 aB
	Bico de Ouro 17-21	20.4 aA	11.3 aA	4.1 aA	5 aE	10 bB	56 aE	17 aC	30.7 aA
	Bico de Ouro 17-23	14 bE	9.1 aC	2.1 bD	3 bF	7 bC	21 bF	4.8 bE	22.5 aC
	Bico de Ouro 17-24	15.5 aD	8.8 aC	2.2 aD	10 aC	9 aC	89 aC	12.8 aC	14 bE
	Bico de Ouro 17-33	12.3 bF	8.4 aC	1.8 bE	17 aA	8 bC	130 aB	27.1 aB	21 aC
	Bico de Ouro 17-35	13.5 bE	8.6 aC	1.8 bE	6 bE	8 bC	48 bE	10.1 bD	21 aC
	Bico de Ouro 17-37	15.5 aD	8.9 aC	2.5 aC	5 aE	10 aB	47 aE	10.6 aD	22.5 aC
	Bico de Ouro 17-38	13.7 aE	8.7 aC	1.8 bE	11 aC	11 aB	118 aB	26.4 aB	22.4 aC
	Bico de Ouro 17-43	15.5 bD	10 bB	2.9 bB	3 aF	8 bC	25 aF	5.6 bE	22.8 bC
	Bico de Ouro 17-53	13 bE	7.7 bD	1.7 bE	16 aA	9 bB	149 aA	28 aB	18.8 aD
standard deviation (SD)		0.93	0.60	0.18	0.95	1.12	14.55	2.41	1.45

The same lowercase letter in the column between regimes and uppercase letter between genotypes in the same regime do not differ from each other by the Scott-Knott test at 5% probability.

Under the temperature regime of 24.8–30.8–37.8 °C, the Bico de Ouro 17-21 genotype stood out for pod length, width, and weight, with averages of 20.4 cm, 11.3 mm, and 4.1 g, respectively (Table 8).

For the number of grains per pod (NGPD), variation was observed among genotypes and temperature regimes. Cultivation under 20–26–33 °C favored grain production per pod for most genotypes, particularly BRS Pajeú, Bico de Ouro 17-21, and Bico de Ouro 17-53, which presented 14, 15, and 14 grains per pod, respectively (Table 8).

Genotypes showed distinct responses for the number and total weight of grains per plant across temperature regimes (Table 8). Under the 20–26–33 °C regime, the genotypes BRS Aracê and Bico de Ouro 17-38 were superior for the number of grains per plant (122 and 116 grains, respectively) and did not differ statistically.

Under the 24.8–30.8–37.8 °C regime, the genotypes BRS Tumucumaque and Bico de Ouro 17-33, 17-28, and 17-53 stood out for both the number and total weight of grains per plant. The genotype Bico de Ouro 17-53 presented the highest number of grains (149), while

BRS Tumucumaque showed the highest total grain weight (32.4 g) (Table 8). In contrast, the genotypes Bico de Ouro 17-23 and 17-43 showed greater sensitivity to temperature increase, with total grain weights of 4.8 and 5.6 g, corresponding to reductions of 65% and 52%, respectively, compared to the 20–26–33 °C regime (Table 8).

In the environment with temperatures of 20–26–33 °C, the genotypes BRS Aracê, BRS Pajeú, and those of the Bico de Ouro group 17-35, 17-38 and 17-53 stood out among the other genotypes for the total weight of grains per plant, presenting weights of 16.5, 18.8, 19.8, 20.6 and 20 g, respectively, and not differing statistically from each other (Table 8).

The weight of 100 grains (W100) showed little variation between temperature regimes, with only the Bico de ouro 17-24 and 17-43 genotypes showing a significant reduction in values when subjected to the temperature of 24.8–30.8–37.8 °C, both with a decrease of 23%, compared to cultivation in the 20–26–33 °C regime.

In the environment with temperatures of 20–26–33 °C, the Bico de Ouro 17-43 genotype showed the highest weight (P100) among the genotypes, with 29.9 g. On the other hand, the BRS Aracê genotype showed the lowest yield in 100-grain weight compared to the others, with only 13.6 g (Table 8). In the temperature regime of 24.8–30.8–37.8 °C, the Bico de ouro 17-21 genotype stood out, being statistically superior to the others (with 30.7 g), and the Bico de ouro 17-24 genotype (with 14 g) presented the lowest value among all genotypes in the regime with higher temperatures (Table 8).

4. Discussion

Genotype selection is a crucial step in identifying phenotypic variations of agronomic interest, contributing to the development of cultivars with stable performance adapted to heat stress conditions. Thus, it is essential to prioritize genotypes that maintain adequate vegetative growth and reproductive efficiency even under high temperatures [27].

The multivariate analyses used in this study proved fundamental for understanding the phenotypic variation among the genotypes evaluated under different daily temperature regimes. The quantitative assessment of genetic divergence, based on morpho-agronomic descriptors, made it possible to identify the traits that contributed most to the dissimilarity among genotypes. This approach is essential in cowpea breeding, as it allows the selection of genetically divergent materials with greater complementarity potential [30,33], favoring crosses that combine heat tolerance and high yield potential.

The analysis of the relative contribution of the descriptors showed that variables such as the weight of 100 grains, plant height, and the number of pods per plant had a greater impact on genetic differentiation among genotypes, varying according to the thermal regime. This indicates that these characteristics are sensitive to temperature conditions and therefore efficient in discriminating genotypes with greater adaptive capacity. Furthermore, the clustering results revealed broad genetic diversity, reflected in the formation of distinct groups, indicating the existence of sufficient variability for exploitation in hybridization programs, as reported by Belwal et al. [33], Singh et al. [34], Gupta et al. [35], and Chaudhary et al. [36]. This separation among genotypes further suggests that part of the observed variability is associated with thermal response, allowing the identification of promising materials for high-temperature environments.

The evaluated parameters contribute in a complementary manner to this process. Vegetative characteristics (height, stem diameter, fresh and dry biomass) reflect the plant's ability to sustain growth and acquire resources, while productive components (number and weight of grains per plant, weight of 100 grains, and pod characteristics) demonstrate efficiency in converting this growth into yield. These phenotypic responses are underpinned by cellular mechanisms, in which the maintenance of vegetative growth under thermal stress is intrinsically linked to the synthesis of heat shock proteins (HSPs), which act as molecular chaperones to prevent the denaturation and aggregation of essential proteins [24]. In addition, biomass accumulation depends on the preservation of thylakoid membrane fluidity and integrity, processes frequently disrupted by high temperatures but mitigated in genotypes with more efficient antioxidant systems capable of neutralizing reactive oxygen species (ROS) [37]. Thus, the biometric superiority observed in certain genotypes suggests greater internal biochemical stability against thermal damage.

The weight of 100 grains under the 20–26–33 °C regime and the number of pods per plant under the 24.8–30.8–37.8 °C regime were the variables that contributed most to genotype divergence (Table 3), indicating that the ability to maintain production under high temperatures is a key factor in genetic differentiation among materials. The balance between photoassimilate production and its partitioning to reproductive organs determines the amount of carbon available for grain filling under heat stress. In legumes, more tolerant cultivars often maintain a higher relative allocation of assimilates to reproductive structures even under stress, preserving yield and reducing seed weight loss [38,39]. Among the evaluated materials, some stood out for maintaining a balance between growth and production under high temperatures, such as the Bico de Ouro 17-53, 17-33, 17-38, and BRS Tumucumaque genotypes, which showed consistent performance across more than one parameter. These genotypes combine promising traits for direct selection or use as parents in breeding programs. In contrast, the Bico de Ouro 17-43 genotype exhibited good vegetative growth without a corresponding increase in yield under heat stress, indicating a limitation in maintaining the relationship between biomass production and grain filling. Genotypes such as BRS Pajeú and Pingo de Ouro 1-2 showed greater sensitivity to heat stress, making them less suitable for high-temperature environments and useful as references of susceptibility.

The factors underlying these patterns are associated with mechanisms already recognized as determinants of heat adaptation, including phenological adjustment (synchronization of flowering and grain filling) [21,27,40], the balance between photoassimilate production and partitioning [38,39], biomass allocation between shoot and root systems, maintenance of water transport and structural support, as well as fertility stability and pod set under high temperatures [21,41]. These mechanisms are strongly influenced by genotype × environment interactions, reinforcing the importance of evaluating lines under contrasting conditions to ensure productive stability [42].

5. Conclusions

The results demonstrated wide morpho-agronomic diversity among the cowpea genotypes evaluated under different daily temperature regimes, showing distinct responses to increasing temperature. In the scenario of increased temperature (24.8–30.8–37.8 °C), the number of pods per plant, plant height, stem fresh weight, and leaf dry weight were the traits that contributed most to the dissimilarity between genotypes. These results indicate that heat stress directly influences components of growth and production, but also reveal the existence of genotypes with greater adaptive capacity. Among them, Bico de Ouro 17-53, 17-33 and BRS Tumucumaque stand out, having shown better productive performance under high temperatures, and being potential sources for genetic improvement focused on heat tolerance and the selection of materials more resilient to climate change. Although the results play an important role in identifying phenotypic responses to heat stress, the analyses were based on morpho-agronomic traits. Therefore, future studies incorporating physiological, biochemical, and genetic approaches may contribute to a more comprehensive understanding of the mechanisms underlying heat stress adaptation in cowpea.

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