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Cowpea: Prospecting for Heat-Tolerant Genotypes

Jaqueline de Almeida Silva [1], Juliane Rafaele Alves Barros [2,3], Elioenai Gomes Freire Silva [1], Maurisrael de Moura Rocha [4] and Francislene Angelotti [3,*]

[1] Postgraduate Program in Environmental Science and Technology for the Semi-Arid Region, University of Pernambuco, Petrolina 56328-900, Pernambuco, Brazil; jakyy101@hotmail.com (J.d.A.S.); elioenai.gomes@upe.br (E.G.F.S.)
[2] Foundation for the Support of Science and Technology of the State of Pernambuco, Recife 50720-001, Pernambuco, Brazil; juliane-ab@hotmail.com
[3] Embrapa Semi-arid, Petrolina 56302-970, Pernambuco, Brazil
[4] Embrapa Meio-Norte, Teresina 64008-780, Piauí, Brazil; maurisrael.rocha@embrapa.br
* Correspondence: francislene.angelotti@embrapa.br

Abstract: Selecting genotypes tolerant to high temperatures is an important measure for agricultural maintenance and production in climate change scenarios. Thus, this study aimed to select cowpea genotypes tolerant to increased air temperature. A total of 20 cowpea genotypes were used, cultivated under temperature regimes of 20–26–33 °C and 24.8–30.8–37.8 °C in a completely randomized experimental design under a 2 × 20 factorial scheme (temperature regimes × genotypes). The BRS Inhuma, Bico-de-Ouro-17-45, BRS Guariba, and BRS Imponente genotypes did not show significant differences in the analyzed physiological responses to the increase in air temperature. The BRS Inhuma, Bico-de-Oouro-17-19, Bico-de-Ouro-17-44, Bico-de-Ouro-17-45, BRS Guariba, and BRS Imponente genotypes showed increased temperature tolerance as thermal stress did not affect production. The Pingo-de-Ouro-17-48, MNC00-595F-27, MNC06-895E-1, and MNC09-981B-2 genotypes reduced water efficiency by −26.85, −25.19, −40.04, and −60.37%, respectively, due to the increase in temperature. The results obtained in this work represent a pre-selection of genotypes that are tolerant to high temperatures, with the BRS Inhuma, Bico-de-Ouro-17-45, BRS Guariba, and BRS Imponente genotypes indicated as tolerant to increased temperatures based on the interaction of physiological and productive responses. There is an urgent need to select cowpea genotypes tolerant to increased temperature to maintain production in climate change scenarios and ensure agricultural systems' sustainability and food security.

Keywords: abiotic stress; agriculture; *Vigna unguiculata* (L.) Walp

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1. Introduction

The cowpea (*Vigna unguiculata* (L.)) Walp is an important legume for food security in Brazil and other regions of the world, constituting a protein source and generating employment and income for family farming [1,2]. The cowpea is predominantly cultivated in the semi-arid region in Northeast Brazil, being planted practically throughout the year [3,4]. However, temperature and water deficit conditions can negatively affect crop productivity [5]. In addition to the region's intrinsic conditions, climate change scenarios present another challenge as they could increase the frequency of extreme temperatures with direct impacts on agricultural production. This is because temperatures above 33 °C affect cowpea production, especially in the reproductive phase, reducing the viability of pollen grains, causing floral abortion, and consequently causing a lower grain yield [6].

The demand for food will increase rapidly with the exponential growth of the world population, which could reach 10 billion by 2050 [7,8]. Given this, the search for heat-tolerant genotypes becomes crucial for food sovereignty. Barros et al. [6] analyzed different commercial cowpea cultivars and observed that they responded differently to the environments to which

they were exposed. An example was the BR 17-Gurguéia cultivar, which demonstrated tolerance to thermal stress, maintaining pollen viability, with a lower rate of flower abortion and greater production in an environment with a maximum temperature of 37.8 °C.

However, although some cowpea cultivars have been identified as heat-tolerant, progress in developing new genotypes has been limited [9]. This is partly due to imprecise phenotyping approaches that represent the main obstacle in discovering the genetic basis of stress tolerance traits, hindering advances in genetic improvement programs [10,11]. Thus, we seek to act in the pre-improvement phase through prospecting genotypes as a strategic measure to guarantee cultivation sustainability in the face of climate change. In this first phase, heat-tolerant genotypes can be selected under controlled conditions through an elucidation of their physiological responses and their interaction with productive responses [12,13]. With this as the objective, this study aimed to select cowpea genotypes tolerant to increased air temperature.

2. Materials and Methods

The experiment was conducted at the Embrapa Semi-arid facility in Fitotron-type growth chambers with controlled temperature, photoperiod, and relative humidity. A completely randomized design was used in a 2 × 20 factorial scheme (temperature regimes × genotype) with four replications. The temperature regimes were 20–26–33 °C and 24.8–30.8–37.8 °C, as shown in Table 1.

Table 1. Temperature regimes used in the experiment.

Temperature Regimes	Times for Each Temperature			
	20:00 to 6:00	**6:00 to 10:00**	**10:00 to 15:00**	**15:00 to 20:00**
T1 (20–26–33 °C)	20	26	33	26
T2 (24.8–30.8–37.8 °C)	24.8	30.8	37.8	30.8

The temperature regimes (Table 1) were determined from the minimum, average, and maximum temperatures in the ranges 18–22, 25–27, and 32–34 °C, respectively, in the sub-middle region of the São Francisco Valley over the last 30 years. An increase of 4.8 °C was used in this work based on the average temperature increase of the SSP5-8.5 scenario [14].

A total of 20 cowpea genotypes were used coming from the Embrapa Meio-Norte Cowpea Genetic Breeding Program (Table 2).

The genotypes used present genetic phenotyping, as shown in Figure 1.

Table 2. Cowpea genotypes used in the experiment (Germplasm origin: Brazil).

Genotype	Germplasm Origin	Grain Color	Grain Size	Maturity Group
GN1: BRS Inhuma	Landrace	Brown	Medium	Early
GN2: Bico-de-Ouro-17-10	Landrace	Brown	Medium	Early medium
GN3: Pingo-de-Ouro-17-18	Landrace	Brown	Medium	Early medium
GN4: Bico-de-Oouro-17-19	Landrace	Brown	Medium	Early medium
GN5: Bico-de-Ouro-17-20	Landrace	Brown	Medium	Early medium
GN6: Bico-de-Ouro-17-44	Landrace	Brown	Medium	Early medium
GN7: Bico-de-Ouro-17-45	Landrace	Brown	Medium	Early medium
GN8: Bico-de-Ouro-17-46	Landrace	Brown	Medium	Early medium
GN9: Bico-de-Ouro-17-47	Landrace	Brown	Medium	Early medium
GN10: Pingo-de-Ouro-17-48	Landrace	Brown	Medium	Early medium
GN11: Bico-de-Ouro-17-72	Landrace	Brown	Medium	Early medium
GN12: BRS Guariba	Scientific breeding	White	Medium	Early
GN13: Bico-de-Ouro-17-82	Landrace	Brown	Medium	Early medium
GN14: Bico-de-Ouro-17-86	Landrace	Brown	Medium	Early medium
GN15: MNC01-631F-20-5	Scientific breeding	Brown	Big	Early medium
GN16: MNC00-595F-27	Scientific breeding	Green	Medium	Early medium
GN17: BRS Imponente	Scientific breeding	White	Large	Early
GN18: MNC06-895E-1	Scientific breeding	White	Medium	Early
GN19: MNC09-981B-2	Scientific breeding	Black	Medium	Early
GN20: BRS Paraguaçu	Scientific breeding	White	Medium	Early medium

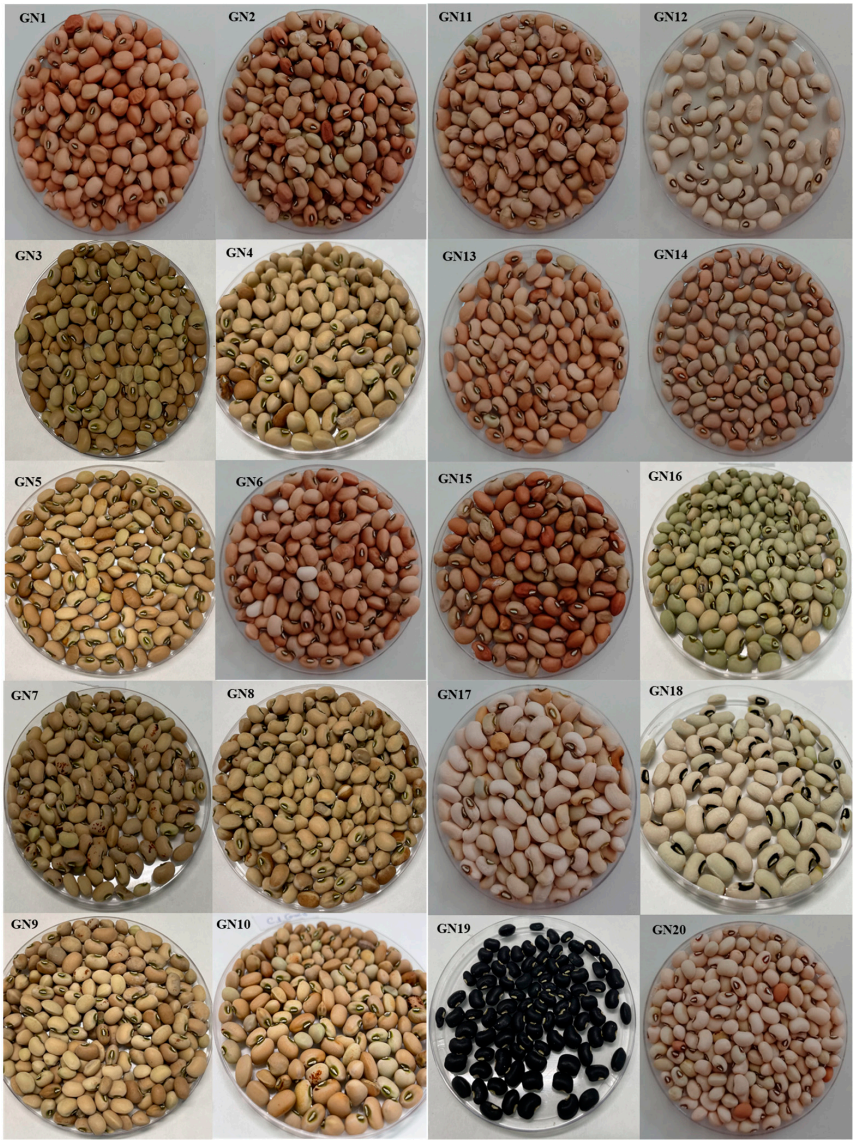

Figure 1. Genetic variability of seed morphology and size of studied cowpea genotypes. GN1: BRS Inhuma; GN2: Bico-de-Ouro-17-10; GN3: Pingo-de-Ouro-17-18; GN4: Bico-de-Oouro-17-19; GN5: Bico-de-Ouro-17-20; GN6: Bico-de-Ouro-17-44; GN7: Bico-de-Ouro-17-45; GN8: Bico-de-Ouro-17-46; GN9: Bico-de-Ouro-17-47; GN10: Pingo-de-Ouro-17-48; GN11: Bico-de-Ouro-17-72; G12: BRS Guariba; GN13: Bico-de-Ouro-17-82; GN14: Bico-de-Ouro-17-86; GN15: MNC01-631F-20-5; GN16: MNC00-595F-27; GN17: BRS Imponente; GN18: MNC06-895E-1; GN19: MNC09-981B-2; GN20: BRS Paraguaçu.

Pots with a capacity of five liters were filled with eutrophic red–yellow argisol. Ten seeds were sown per pot and thinning was carried out 15 days after sowing, leaving only one plant per pot. Fertilization was performed three days before planting with superphosphate according to the results of chemical analyses of the soil and indications for the crop [15]. Then, a second fertilization was performed 15 days after the emergence of the plants using ammonium sulfate and potassium chloride. Irrigations were performed every two days as needed by the crop.

2.1. Physiological Parameters

Physiological assessments were performed 30 days after planting at 9:00 a.m. The gas exchange was determined using a Li 6400 XT (LI-COR) Portable Infrared Gas Analyzer (Infrared Gas Analyzer—IRGA), Lincoln, Nebraska, under photosynthetically active radiation

maintained at 2500 µmol m^{-2} s^{-1}. The variables evaluated were leaf surface temperature (Lst), photosynthetic rate (A), transpiration rate (E), and stomatal conductance (gs). Fully expanded leaves of each plant were previously selected at that moment, considering uniform characteristics in terms of color, maturity, and size for periodic determination of gas exchange and the chlorophyll content of the leaves.

The chlorophyll index was determined by a portable device called a chlorophyll meter (Chlorophyll Meter model SPAD-502, Soil and Plant Analysis Development), which performs instantaneous and non-destructive measurement of a leaf by providing an absorbance value of the wavelength in the red region (peak at 650 nm), which is the region of high absorbance by chlorophyll molecules.

Water use efficiency (WUE) was calculated using the photosynthesis/transpiration ratio. The efficiencies of the genotypes were compared depending on the two temperature regimes in percentage form.

2.2. Productive Parameters

The pods were harvested and the number of pods, pod weight, total number of seeds, and weight of 100 seeds for each genotype were evaluated to determine the productive parameters. The seeds were weighed on a precision scale. The evaluations of productive parameters occurred after the pods reached the maturation point [16] according to the phenological cycle of each genotype.

2.3. Statistical Analysis

The results obtained were subjected to the Shapiro–Wilk normality test with subsequent analysis of variance (ANOVA). If statistical significance was found between the interactions, the Scott–Knott test of cluster means was applied using the SISVAR Version 5.6 program. Data that did not present normality were transformed using the square root equation Y + 1.0 − SQRT (Y + 1.0).

3. Results

3.1. Physiological Parameters

Cowpea genotypes responded differently to increased air temperature such that thermal stress caused physiological changes in different materials (Table 3).

In relation to stomatal opening, the GN2, GN5, GN9, and GN18 genotypes reduced the stomata opening of plants maintained in the temperature regime of 24.8–30.8–37.8 °C (Table 3). This reduction caused a drop in the photosynthetic rate of the GN18 genotype. It was also observed that the increase of 4.8 °C in air temperature reduced the photosynthesis of the GN3, GN8, GN 18, and GN19 genotypes (Table 3).

Increased temperature also had an impact on leaf transpiration, reducing the transpiration rate of the GN3, GN4, and GN5 genotypes. Although the 4.8 °C increase in air temperature did not reduce transpiration in most genotypes, an increase in leaf temperature was observed in the GN2, GN6, GN8, GN9, GN10, GN11, GN13, GN14, GN15, GN16, GN18, GN19, and GN20 genotypes as a function of thermal stress (Table 3).

Only the G8 genotype showed a reduction in chlorophyll content due to the increase in temperature (Table 3).

The GN1, GN7, GN12, and GN17 genotypes generally did not show significant differences in the analyzed physiological responses to the increase in air temperature (Table 3).

3.2. Productive Parameters

The productive responses of the cowpea genotypes analyzed also differed for increased temperatures (Table 4). Only the GN8 genotype showed a 52% reduction in the number of pods due to heat stress. This reduction can be explained in response to the drop-in photosynthetic rate, chlorophyll content, and increased leaf temperature (Table 3).

Table 3. Physiological parameters of different cowpea genotypes subjected to two temperature regimes (T1: 20–26–33 °C and T2: 24.8–33.8–37.8 °C).

	Genotypes																			
	Stomatal conductance (mol H_2O m^{-2} s^{-1})																			
Temperature regimes	GN1	GN2	GN3	GN4	GN5	GN6	GN7	GN8	GN9	GN10	GN11	GN12	GN13	GN14	GN15	GN16	GN17	GN18	GN19	GN20
20–26–33 °C	0.069aA ±0.0002	0.068aA ±0.0028	0.072aA ±0.0066	0.066aA ±0.0011	0.069aA ±0.0016	0.052aB ±0.0015	0.054aB ±0.0188	0.050aB ±0.0042	0.066aA ±0.0108	0.070aA ±0.0022	0.063aA ±0.0048	0.062aA ±0.0014	0.062aA ±0.0058	0.064aA ±0.0018	0.062aA ±0.0051	0.063aA ±0.0065	0.056aB ±0.0031	0.082aA ±0.0018	0.045bB ±0.01	0.065aA ±0.001
24.8–30.8–37.8 °C	0.064aB ±0.0056	0.056bC ±0.0057	0.065aB ±0.0102	0.054aC ±0.0005	0.053bC ±0.0049	0.050aC ±0.0034	0.051aC ±0.0109	0.044aC ±0.0004	0.045bC ±0.0012	0.080aA ±0.0416	0.066aB ±0.0087	0.070aB ±0.0019	0.058aC ±0.0038	0.056aC ±0.0027	0.061aB ±0.0041	0.058aC ±0.002	0.064aB ±0.0061	0.061bB ±0.0008	0.064aB ±0.0013	0.060aB ±0.005
	Photosynthesis *A* (micromol CO_2 m^{-2} s^{-1})																			
Temperature regimes	GN 1	GN2	GN3	GN4	GN5	GN6	GN7	GN8	GN9	GN10	GN11	GN12	GN13	GN14	GN15	GN16	GN17	GN18	GN19	GN20
20–26–33 °C	20.46aA ±0.76	17.86bB ±0.73	16.27aB ±1.27	13.59aC ±1.94	12.28aD ±0.23	18.32bB ±0.33	11.31aD ±0.57	14.74aC ±3.33	11.91aD ±4.52	10.24aD ±2.52	19.26aA ±0.46	18.16aB ±1.11	20.45aA ±1.24	19.77aA ±0.8	18.62aB ±0.73	12.70aD ±1.38	18.41aB ±0.91	15.05aC ±0.13	11.88aD ±2.82	20.02aA ±0.59
24.8–30.8–37.8 °C	20.60aA ±0.35	20.41aA ±0.65	10.78bB ±3.71	11.61aB ±0.4	10.44aB ±2.72	20.59aA ±0.39	12.60aB ±4.83	11.21bB ±0.37	11.20aB ±0.39	10.29aB ±2.48	19.81aA ±0.58	19.67aA ±0.27	19.93aA ±0.43	20.15aA ±0.52	20.21aA ±0.47	10.72aB ±1.93	20.14aA ±0.17	8.52bC ±0.15	8.07bC ±0.11	19.93aA ±0.2
	Leaf transpiration *E* (mmol H_2O m^{-2} s^{-1})																			
Temperature regimes	GN 1	GN2	GN3	GN4	GN5	GN6	GN7	GN8	GN9	GN10	GN11	GN12	GN13	GN14	GN15	GN16	GN17	GN18	GN19	GN20
20–26–33 °C	2.33aA ±0.03	2.14aA ±0.009	2.57aA ±0.201	2.35aA ±0.096	2.31aA ±0.043	2.16aA ±0.052	1.73aB ±0.599	1.52aC ±0.103	1.94aB ±0.299	2.06bA ±0.073	2.18aA ±0.012	2.22aA ±0.018	2.21aA ±0.032	2.27aA ±0.039	2.24aA ±0.094	1.87aB ±0.198	2.17aA ±0.005	2.31aA ±0.036	1.33aC ±0.184	2.18aA ±0.015
24.8–30.8–37.8 °C	2.32aB ±0.028	2.29aB ±0.016	1.49bC ±0.446	1.54bC ±0.037	1.57bC ±0.173	2.34aB ±0.027	1.62aC ±0.339	1.51aC ±0.019	1.58aC ±0.032	2.83aA ±1.308	2.25aB ±0.057	2.26aB ±0.047	2.31aB ±0.029	2.23aB ±0.05	2.29aB ±0.063	2.11aB ±0.062	2.29aB ±0.023	2.18aB ±0.039	2.28aB ±0.061	2.34aB ±0.087
	Leaf surface temperature																			
Temperature regimes	GN 1	GN2	GN3	GN4	GN5	GN6	GN7	GN8	GN9	GN10	GN11	GN12	GN13	GN14	GN15	GN16	GN17	GN18	GN19	GN20
20–26–33 °C	33.17aB ±0.46	33.04bB ±0.78	34.71aA ±0.25	34.17aA ±0.28	33.86aB ±0.21	35.18bA ±1.29	33.55aB ±0.14	33.20bB ±0.11	33.04bB ±0.01	33.14bB ±0.02	33.66bB ±0.8	33.81aB ±0.35	33.64bB ±1.61	33.37bB ±0.57	33.94bB ±0.9	33.20bB ±0.08	34.91aA ±0.44	33.01bB ±0.06	33.32bB ±0.92	33.15bB ±0.96
24.8–30.8–37.8 °C	33.96aC ±1.33	37.48aA ±1.09	30.71bD ±1.39	33.12aC ±0.27	33.63aC ±0.21	37.67aA ±0.72	34.10aC ±0.14	35.05aB ±0.15	35.39aB ±0.07	35.71aB ±0.05	35.29aB ±1.54	33.62aC ±0.27	35.71aB ±0.58	36.44aA ±1.08	35.18aB ±0.49	35.76aB ±0.02	34.65aB ±0.96	35.64aB ±0.07	35.63aB ±0.08	35.99aB ±0.6

Table 3. *Cont.*

	Genotypes																			
	Chlorophyll content																			
Temperature regimes	GN 1	GN2	GN3	GN4	GN5	GN6	GN7	GN8	GN9	GN10	GN11	GN12	GN13	GN14	GN15	GN16	GN17	GN18	GN19	GN20
20–26–33 °C	54.70aB ±2.5	53.47aB ±0.9	27.23aE ±1.83	24.18bE ±1.81	25.11aE ±4.25	46.86aC ±4.43	24.85aE ±1.29	25.58aE ±1.6	22.38aE ±3.73	26.18aE ±2.52	54.00aB ±1.21	55.55aB ±4.57	45.87bC ±2.59	53.55aB ±1.46	55.45aB ±2.28	33.45aD ±3.56	61.85aA ±4.81	35.30aD ±5.88	28.30aE ±0.56	55.12aB ±3.52
24.8–30.8–37.8 °C	58.40aA ±2.37	49.32aB ±2.71	28.18aD ±1.44	30.98aC ±0.6	27.83aD ±1.76	49.37aB ±4.95	28.71aD ±1.99	15.78bE ±0.35	28.25aD ±1.88	26.93aD ±3.88	55.42aA ±5.69	53.90aB ±9.99	51.49aB ±4.09	53.06aB ±4.53	51.95aB ±4.78	31.86aC ±1.93	58.25aA ±5.97	34.91aC ±0.78	33.81aC ±2.55	59.22aA ±2.06

Lowercase letters are used for temperature and capital letters are used for genotypes. GN1: BRS Inhuma; GN2: Bico-de-Ouro-17-10; GN3: Pingo-de-Ouro-17-18; GN4: Bico-de-Oouro-17-19; GN5: Bico-de-Ouro-17-20; GN6: Bico-de-Ouro-17-44; GN7: Bico-de-Ouro-17-45; GN8: Bico-de-Ouro-17-46; GN9: Bico-de-Ouro-17-47; GN10: Pingo-de-Ouro-17-48; GN11: Bico-de-Ouro-17-72; G12: BRS Guariba; GN13: Bico-de-Ouro-17-82; GN14: Bico-de-Ouro-17-86; GN15: MNC01-631F-20-5; GN16: MNC00-595F-27; GN17: BRS Imponente; GN18: MNC06-895E-1; GN19: MNC09-981B-2; GN20: BRS Paraguaçu. Values represent averages of four biological replicates. Different letters indicate significant differences ($p < 0.05$ as per Scott–Knott test).

Table 4. Productive parameters of different cowpea genotypes subjected to two temperature regimes (T1: 20–26–33 °C and T2: 24.8–33.8–37.8 °C).

	Genotypes																			
	Number of pods																			
Temperature regimes	GN1	GN2	GN3	GN4	GN5	GN6	GN7	GN8	GN9	GN10	GN11	GN12	GN13	GN14	GN15	GN16	GN17	GN18	GN19	GN20
20–26–33 °C	4.50aD ±0.58	7.25aC ±2.22	5.25aD ±1.5	5.25aD ±2.22	6.50aC ±1.00	10.50aB ±2.38	7.00aC ±2.83	10.50aB ±2.65	7.50aC ±0.58	6.00aC ±1.71	7.50aC ±3.11	10.65aB ±0.47	10.00aB ±0.82	8.50aB ±1.29	4.00aD ±1.41	3.75aD ±0.5	14.33aA ±3.37	3.25aD ±1.26	5.00aD ±1.15	7.50aC ±1.00
24.8–30.8–37.8 °C	4.25aC ±2.87	7.25aC ±1.26	6.25aC ±0.82	5.75aC ±0.96	5.25aC ±0.96	11.00aA ±2.16	5.50aC ±2.45	5.00bC ±1.5	4.75aC ±1.29	5.25aC ±0.82	8.50aB ±3.11	9.25aB ±0.5	10.25aB ±1.71	6.75aC ±1.71	5.75aC ±0.96	4.00aC ±1.83	12.60aA ±3.42	5.50aC ±3.2	3.25aC ±0.96	6.50aC ±1.73
	Pod weight																			
Temperature regimes	GN1	GN2	GN3	GN4	GN5	GN6	GN7	GN8	GN9	GN10	GN11	GN12	GN13	GN14	GN15	GN16	GN17	GN18	GN19	GN20
20–26–33 °C	15.45aC ±2.13	18.40aB ±4.13	19.02aB ±2.93	11.97aC ±5.35	14.32aC ±2.43	27.30aA ±5.55	15.75aC ±6.43	19.77aB ±3.79	15.45aC ±1.27	12.70aC ±3.44	13.52bC ±3.47	19.75aB ±4.28	23.77aA ±4.17	23.42aA ±1.76	16.45aC ±4.58	9.72aD ±1.48	23.13aA ±3.98	5.95aD ±1.67	10.72aD ±3.63	18.67aB ±3.34
24.8–30.8–37.8 °C	17.22aB ±4.29	14.92aB ±1.72	12.07bC ±2.1	11.92aC ±1.81	10.05aC ±1.74	22.40aA ±2.79	10.77aC ±3.55	19.77aD ±0.97	7.12bD ±1.51	11.65aC ±1.13	22.12aA ±6.34	14.85aB ±5.71	18.22bB ±4.71	18.55aB ±1.8	18.52aB ±3.92	7.55aD ±2.56	17.82bB ±3.09	6.11aD ±2.97	7.05aD ±2.07	12.2bC ±4.14

Table 4. *Cont.*

	Genotypes																			
	Number of seeds/pod																			
Temperature regimes	GN1	GN2	GN3	GN4	GN5	GN6	GN7	GN8	GN9	GN10	GN11	GN12	GN13	GN14	GN15	GN16	GN17	GN18	GN19	GN20
20–26–33 °C	51.75aC ±5.62	83.00aB ±13.44	64.75aC ±13.55	43.25aD ±16.11	52.50aC ±2.89	86.25aB ±16.05	47.50aD ±20.98	65.50aC ±15.76	57.75aC ±5.56	58.25aC ±13.49	47.00bD ±13.14	77.50aB ±9.00	77.25aB ±1.71	101.25aA ±5.8	44.25aD ±14.61	46.25aD ±6.13	56.66aC ±7.7	24.50aD ±4.9	39.00aD ±16.37	80.00aB ±8.64
24.8–30.8–37.8 °C	37.25aB ±8.5	50.50bB ±8.19	51.00aB ±6.16	38.25aB ±2.36	34.00bC ±6.66	74.00aA ±7.07	40.50aB ±17.15	30.50bC ±4.8	24.25bC ±6.38	41.75aB ±8.29	78.00aA ±24.12	43.25bB ±18.12	60.25aA ±15.8	80.25bA ±4.79	49.25aB ±12.53	38.75aB ±11.00	41.20aB ±13.64	27.75aC ±13.07	23.50aC ±1.63	46.00bB ±12.75
	100-seed weight																			
Temperature regimes	GN1	GN2	GN3	GN4	GN5	GN6	GN7	GN8	GN9	GN10	GN11	GN12	GN13	GN14	GN15	GN16	GN17	GN18	GN19	GN20
20–26–33 °C	25.09bB ±1.93	17.76aB ±2.78	17.98aB ±5,19	23.97aB ±6,01	20.89aB ±1.47	24.34aB ±3.75	17.86aB ±10,5	18.66aB ±3.2	19.36aB ±1.14	18.51aB ±0.45	37.60aA ±18,07	20.61aB ±4.33	23.51aB ±2.99	15.97aB ±3.37	37.99aA ±12.82	16.31aB ±1.06	26.69aB ±1.92	18.26aB ±3.42	18.41aB ±2.42	18.60aB ±3.3
24.8–30.8–37.8 °C	39.46aA ±11.79	22.39aC ±1.47	17.85aC ±5.58	23.36aC ±6.06	22.06aC ±6.9	22.06aC ±0.96	20.45aC ±2.01	22.16aC ±2.88	21.30aC ±1.1	21.24aC ±0.06	22.28bC ±0.97	28.29aB ±2.05	22.95aC ±0.82	17.06aC ±1.2	28.78bB ±0.85	14.95aC ±0.09	33.91aA ±12.38	25.64aC ±0.29	24.29aC ±8.52	20.19aC ±0.73

Lowercase letters are used for temperature and capital letters are used for genotypes. GN1: BRS Inhuma; GN2: Bico-de-Ouro-17-10; GN3: Pingo-de-Ouro-17-18; GN4: Bico-de-Oouro-17-19; GN5: Bico-de-Ouro-17-20; GN6: Bico-de-Ouro-17-44; GN7: Bico-de-Ouro-17-45; GN8: Bico-de-Ouro-17-46; GN9: Bico-de-Ouro-17-47; GN10: Pingo-de-Ouro-17-48; GN11: Bico-de-Ouro-17-72; G12: BRS Guariba; GN13: Bico-de-Ouro-17-82; GN14: Bico-de-Ouro-17-86; GN15: MNC01-631F-20-5; GN16: MNC00-595F-27; GN17: BRS Imponente; GN18: MNC06-895E-1; GN19: MNC09-981B-2; GN20: BRS Paraguaçu. Values represent averages of four biological replicates. Different letters indicate significant differences ($p < 0.05$ as per Scott–Knott test).

Reductions of 36, 54, 23, 22, and 34% of the GN3, GN9, GN13, GN17, and GN20 genotypes were observed for the pod weight, respectively, due to the 4.8 °C increase in air temperature (Table 4). Thermal stress also resulted in decreases of 39, 35, 53, 58, 44, 21, and 42% in the number of pods in the GN2, GN5, GN8, GN9, GN12, GN14, and GN20 genotypes, respectively, which contributed to reduce the pod weights of these genotypes (Table 4). The GN11 genotype showed an increase of approximately 40% in the number of seeds at higher temperatures, contributing to the increase in pod weight, as can be seen in Table 4. This can be explained due to the formation of small pods due to thermal stress (Figure 2).

Figure 2. Pods produced at temperatures of two temperature regimes: 20–26–33 °C (**a**); 24.8–30.8–37.8 °C (**b**).

The GN11 and GN15 genotypes showed reductions of 41 and 24% in the weight of 100 seeds, respectively, when the temperature increased. The GN1 genotype showed a greater weight of 100 seeds when kept at a temperature of 24.8–30.8–37.8 °C, with an increase of 36% (Table 4). This can be explained by the fact that thermal stress did not negatively affect the physiological parameters of the GN1 genotype (Table 3). There was no statistical difference when comparing the temperature regimes for the other genotypes (Table 4).

Based on the productive parameters (number of pods, pod weight, number of seeds, and weight of 100 seeds), the GN1, GN4, GN6, GN7, GN10, GN15, GN16, GN18, and GN19 genotypes were not negatively affected by the temperature increase (Table 4). However, when relating the production index and water use efficiency, the GN8, GN10, GN11, GN13, GN16, GN18, GN19, and GN20 genotypes showed reductions in water use efficiency under higher temperature conditions by 23.44%, 26.85%, 0.34%, 6.76%, 25.19%, 40.04%, 60.37%, and 7.25%, respectively (Table 5).

Table 5. Values of water use efficiency (WUE) percentages of the genotypes as a function of the 4.8 °C increase in air temperature.

WUE% of Cowpea Genotypes Due to the Increase of 4.8 °C	
GN1: 1.11	GN11: −0.34
GN2: 6.79	GN12: 6.39
GN3: 14.28	GN13: −6.76
GN4: 30.36	GN14: 3.75
GN5: 25.08	GN15: 6.16
GN6: 3.74	GN16: −25.19
GN7: 18.97	GN17: 3.66
GN8: −26.44	GN18: −40.01
GN9: 15.46	GN19: −60.37
GN10: −26.85	GN20: −7.25

Although the GN10, GN16, GN18, and GN19 genotypes do not have their productive response affected by the increase in air temperature (Table 4), greater water availability is

necessary for better water use efficiency, which can compromise production in the face of water scarcity.

4. Discussion

4.1. Physiological Parameters

The physiological activity of plants can be affected by thermal stimulation, thereby causing changes in a plant's metabolism and influencing its growth and development [17].

The physiological results indicate that the genotypes mentioned above are sensitive to increased temperature and could be negatively affected in a climate change scenario. In this context, their selection will not be interesting for pre-genetic improvement programs since thermal stress is one of the main abiotic stresses that limit plant growth and development as it alters the physiological responses of crops [18]. Plants have their photosynthetic rate affected by high temperatures due to reductions in stomatal opening and transpiration, thus favoring an increase in leaf temperature [19]. Around 90% of the water that plants absorb is used to regulate temperature through transpiration [20]. Therefore, transpiration is reduced with a decrease in stomatal conductance, and there is consequently an increase in leaf temperature, which can cause a drop in plant productivity [21].

The chlorophyll content is also affected by increased temperature, reducing the plant's ability to carry out photosynthesis, influencing its growth, development, productivity, and adaptation to different environments [22]. The reduction in the amount of chlorophyll is one of the first physiological responses of plants to thermal stress since leaves are sensitive to high temperatures [20].

However, the sensitivity of plants to increased temperature varies according to the genotype [23], as was observed in the results of this study (Table 3). The physiological responses of cowpea differed depending on the temperature and the cultivar analyzed such that the photosynthetic activity of the BRS Carijó, BRS Itaim, BRS Pujante, and BRS Tapahium cultivars was not affected by high temperature while the BRS Rouxinol cultivar showed lower photosynthetic activity in plants kept under thermal stress [12]. This shows how the impact of the physiological response can affect the productivity of different cultivars, which, despite belonging to the same species, respond differently to the environment, constituting an important parameter for selecting genotypes that are tolerant to thermal stress.

The GN1, GN7, GN12, and GN17 genotypes generally did not show significant differences in the analyzed physiological responses to the increase in air temperature (Table 3). According to Sehgal et al. [24], plants can present effective thermotolerance mechanisms through leaves adapting to high temperatures, which allows the regulation of leaf temperature through transpiration during the high-temperature period [25]. Furthermore, the antioxidant defense mechanism, changes in membrane lipid composition, ion transport, osmoprotectors, free radical scavenging, and protein increase are correlated with thermotolerance in plants [10], constituting essential mechanisms to neutralize the effects of thermal stress on plants [26]. Cowpea plants of the cultivar BRS Pajeú kept under thermal stress showed greater activity of the antioxidant enzyme superoxide dismutase, which provides the first line of defense against oxidative stress by dismutating the superoxide radical (O_2) into hydrogen peroxide (H_2O_2) and oxygen (O_2). In addition to enzymatic activity, the P5CR (proline) and αTPS6 (trehalose) genes were recently identified in cowpea plants subjected to different abiotic stresses, which suggests mechanisms of adaptation of the species in adverse environmental conditions [27].

4.2. Productive Parameters

The growth and development of plants depend on the air temperature during the growing season, with each species having a specific range represented by a minimum, a maximum, and an optimum value [28]. Cowpea develops in a wide temperature range, between 18 and 37 °C [4]. However, the optimum temperature point varies with the plant's phenological stage [29]. According to Singh et al. [30], the reproductive phase of cowpea

is more sensitive to increased temperatures, resulting in the loss of floral buds, pods, and seed production [6,12,30].

Studies have shown that temperatures above 35 °C cause flower abortion and stimulate leaf senescence, reducing photosynthetic capacity, thus affecting the productivity of cowpea pods and seeds, as this increase interferes with physiological and plant biochemicals [6,31]. This is because cowpeas are vulnerable to high temperatures during the reproductive phase, with many genotypes showing tolerance to thermal stress in the germinative and vegetative phases [9]. The negative impacts in the reproductive phase include the formation of floral components and the formation of non-viable pollen grains. With the reduction in the level of photosynthesis, the number of non-viable pollen grains may increase since the pollen grain is a significant photosynthetic sink, requiring a large accumulation of photoassimilates for its development [10].

Exposing plants to high temperatures during the grain filling phase, even for a short period, can accelerate leaf senescence and reduce the number and weight of seeds, thereby affecting crop yield, since to tolerate thermal stress, the plant uses resources that can limit photosynthesis, an essential process for reproductive development [32,33]. The drop in seed production is also associated with the impact of high temperatures during the flowering period. Some cowpea cultivars exposed to temperatures above 33 °C showed low pollen grain viability, directly influencing the structure and final retention of the pod, also affecting the number of seeds per pod [6]. High temperatures reduce pollen viability, directly impacting production [6]. In addition to the negative effect during the flowering phase of the crop, physiological changes, such as the reduction in carbon fixation and assimilation, impair the formation of floral components and the development of new flowers, reducing the number of pods and seeds [12].

This is because an increase in temperature can increase the plant's water demand, causing greater evapotranspiration and affecting water availability [34]. Thus, the water use efficiency in the plant is an important physiological indicator for ensuring productivity and sustainability in production [35].

Therefore, taking into account the physiological parameters, the weight of 100 seeds, and water use efficiency (Tables 3–5), the GN1, GN7, GN12, and GN17 genotypes presented themselves as the best genotypes when subjected to thermal stress (Tables 3–5). This group of genotypes, tolerant to increased temperature, presented genetic variability in grain morphology (Table 2, Figure 1), demonstrating that despite the phenotypic difference, the genotypes can respond in similar ways to stress. This variability is essential for genetic improvement programs as it contributes to selection and the choice of tolerant genotypes can provide better grain quality, germination performance, seedling vigor, and, consequently, greater productivity [36].

Barros et al. [6] observed that an increase of 4.8 °C in average air temperature reduced the production of commercial cowpea cultivars; however, it was noted that the BR 17-Gurguéia cultivar maintained higher production due to the synchrony of physiological and biochemical characteristics, being tolerant to an increase in temperature. Thus, the selection of thermotolerant cultivars, based on the understanding of the reproductive, physiological, and biochemical responses of plants, will be fundamental to face the challenge of reducing losses and maintaining cowpea productivity in areas with high temperatures. Future research will be essential to ensure the sustainability of cowpea cultivation and ensure food security for a rapidly growing global population.

The results obtained reinforce the potential of cowpea genotypes and provide support for the genetic improvement program and future work in the search for molecular mechanisms of tolerance, contributing to developing new cultivars.

5. Conclusions

The results obtained show that different cowpea genotypes respond differently to increased air temperature. Based on physiological productive responses and water use efficiency, the genotypes BRS Inhuma, Bico-de-Ouro-17-45 (7), BRS Guariba (12), and

BRS Imponente (17) maintained their photosynthetic rates and seed weights even in an environment with thermal stress, demonstrating tolerance to an increase of 4.8 °C in average air temperature. These genotypes can be selected for future genetic improvement work with the aim of developing tolerant cultivars and ensuring food security in the face of climate change.

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