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CROP PRODUCTION

Temperature: A major climatic determinant of cowpea production

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ABSTRACT. Cowpea planting season is crucial for high yield and should comprise the period of the year that warrants the best climatic conditions for cowpea cultivation. Thus, the objective of this study was to evaluate the influence of water availability and temperature on the performance of cowpea cultivars. A greenhouse experiment was conducted using a 4 × 2 × 5 factorial arrangement, with four replications. Factors included four levels of soil moisture (25, 50, 75, and 100% of water holding capacity), two growing seasons (mild and hot), and five cowpea cultivars (Carijó, Itaim, Pujante, Rouxinol, and Tapahium). The number of pods and seeds per plant, seed production, water use efficiency, shoot dry mass, root dry mass, and physiological parameters were evaluated. Seed production was higher during the mild season than during the hot season and increased linearly with increasing soil water availability. Photosynthetic activity and transpiration were higher during the hot season than during the mild season, with their reduction under a water availability of 25% regardless of the growing season. Total chlorophyll content decreased with excess water. Regardless of water availability, temperature was the most limiting climatic factor for cowpea performance. Cultivars Carijó, Itaim, and Tapahium exhibited a lower reduction in productive potential when grown in the hot season.

Keywords: water deficit; thermal stress; seed yield; gas exchange; *Vigna unguiculata* L.

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Introduction

Plants are exposed to various environmental stress elements including water deficit and high temperature, both of which have negative effects on plant performance and prevent plants from reaching their growth and production potential (Jumrani & Bhatia, 2018). In the context of climate change, these environmental elements have become increasingly important because of the increasing frequency of extreme climate events, such as heat waves and drought periods (IPCC, 2014). Such occurrences may reduce crop water-use efficiency (Norton, Malinowski, & Volaire, 2016), owing to their direct effects on physiological processes, such as the reduction of photosynthetic activity and the increase in leaf temperature, which ultimately reduce crop yield (Perdomo, Conesa, Medrano, Ribas-Carbó, & Galmés, 2015). Additionally, an increase in air temperature may alter crop water requirements because of the concomitant increase in evaporation from the soil, thereby causing an increase in plant transpiration and consequently increasing the rate of water consumption (Taiz, Moller, & Murphy, 2017).

Cowpea (*Vigna unguiculata* L.) is a crop of high socioeconomic importance that generates employment and income for family farming. Cowpeas are widely used as food (Rocha et al., 2016) and have a lower production cost than other crops. In Brazil, cowpea production is concentrated in the north and northeast, particularly the semi-arid regions in the latter case (Melo, Melo Junior, Ferreira, Araujo Neto, & Neves, 2018). These semi-arid regions are one of the most vulnerable areas to climate change (Djanaguiraman, Perumal, Ciampitti, Gupta, & Prasad, 2018), with an average annual rainfall of 464.8 mm and an average air temperature of 26°C (Lopes, Guimarães, Melo, & Ramos, 2017; Angelotti, Barbosa, Barros, & Santos, 2020).

Understanding cowpea responses to increasing temperature under different conditions of water availability and the interaction between these two environmental factors is a challenge for research and will contribute to the development of appropriate sustainable management strategies. However, studies on cowpea water requirements (Ahmed & Suliman, 2010; Hayatu, Muhammad, & Habibu, 2014; Souza, Farias, Lima, Ramos, & Sousa, 2017; Karim, Sanoussi, Maarouhi, Falalou, & Yacoubou, 2018) have not addressed the interaction with temperature for different cultivars. Therefore, the objective of this study was to evaluate the influence of water availability and temperature on the performance of cowpea cultivars.

Material and methods

The experiment was conducted in a greenhouse during two growing seasons: from May to July 2018 (mild) and from October 2019 to January 2020 (hot). Meteorological data were obtained through an automatic weather station installed at the site. Maximum, mean, and minimum temperatures and relative humidity during the two growing seasons are shown in Figure 1.

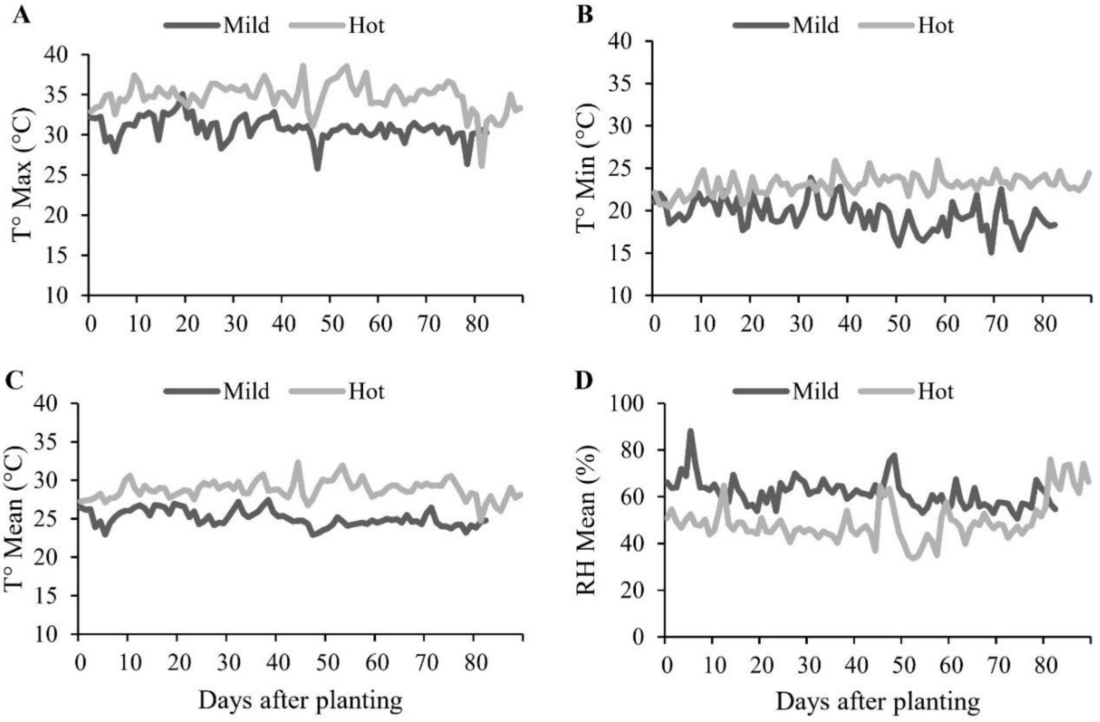

Figure 1. A: Maximum temperature (T° Max; °C), B: minimum temperature (T° Min; °C), C: mean temperature (T° Mean; °C), and D: mean relative humidity (RH Mean; %) during the hot and mild cowpea cropping seasons.

The experiment was laid in a 4 × 2 × 5 factorial arrangement, corresponding to four levels of soil moisture (25, 50, 75, and 100% of maximum water holding capacity), two growing seasons (mild and hot), and five cowpea cultivars (Carijó, Itaim, Pujante, Rouxinol, and Tapahium), with four replications for a total of 80 experimental units per growing season. Sowing was conducted in 7 L pots filled with soil collected from the topsoil layer (0 – 30 cm) of an *Argissolo Vermelho-Amarelo Eutrófico* (Ultisol), with a maximum water holding capacity of 19.5%. Basal fertilization was applied 3 days before planting, according to the results of soil chemical analyses and recommendations for the crop (Cavalcanti, 2008).

Irrigation management was planned based on the data acquired using a TDR100 (Campbell Scientific) time domain reflectometry (TDR) device using coaxial cable probes with three rods for soil water measurement. Initially, the TDR was calibrated according to Batista et al. (2016) for the soil used in the experiment. Irrigation was performed every 2 days to replenish the evapotranspiration volume of water, thus maintaining the level of soil water availability in each treatment, based on the data generated by the TDR.

The evaluation of seed yield and yield components was performed 60 days after planting according to the cultivars and growing season. The total number of days comprising the growth cycle was 83 and 90 in the mild and hot cropping seasons, respectively. Evaluated seed yield and yield components included the number of pods per plant, the number of seeds per plant, and total seed production. Water use efficiency (WUE) was calculated as the ratio of seed production to the amount of water used for irrigation throughout the crop cycle.

Shoot dry mass and root dry mass were evaluated after harvest by cutting the stem close to the soil and separating the shoots and roots. The materials were placed in paper bags and kept in an oven at 65°C until they reached a constant weight (±72h).

Physiological evaluations were performed 30 days after planting, between 09:00 and 11:00 am, when the third trifoliate leaf was completely open. Gas exchange was evaluated using a Li-Cor 6400 portable infrared gas analyzer (IRGA), under a light intensity of 2,500 μmol m^{-2} s^{-1}. The variables analyzed included photosynthesis rate (A), stomatal conductance (g_s), transpiration (E), and leaf temperature (LT). To evaluate leaf chlorophyll content, the relative chlorophyll index was determined using a portable CFL 1030 (FALKER) chlorophyll meter. An intact, fully expanded, healthy leaf in the middle third of the plant was selected to take the readings.

The results were subjected to analysis of variance using a t-test ($p < 0.05$) to determine the significance of simple and interaction effects between the two environmental factors under study. When significance was established, a regression analysis was performed to evaluate the levels of water availability tested, and Tukey's test was applied to compare planting times and cultivars using SISVAR Version 5.6 (Ferreira, 2011).

Results and discussion

The production of cowpea cultivars was affected by the environmental conditions prevalent over the growing season. The numbers of pods and seeds per plant were higher in the mild season than in the hot season (Figure 2). In the mild season, the maximum temperature ranged from 25 to 33°C and the relative humidity ranged from 70 to 90% (Figure 1A and D).

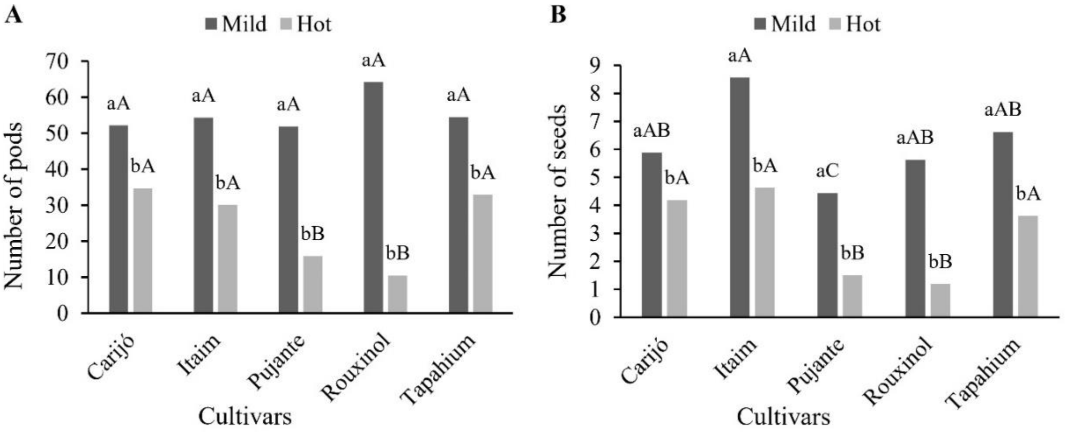

Figure 2. Number of pods and number of seeds per plant of five cowpea cultivars in two growing seasons. Lowercase letters for the growing season and uppercase letters for the cultivars.

During the hot cropping season, maximum temperature ranged from 35 to 37°C, coinciding with the flowering and pod formation stages, which explains the reduction in the number of pods and seeds per plant observed during the season (Figure 2A and B). In contrast, during the mild growing season, the maximum temperature ranged from 29 to 32°C at the same growth stages. High temperatures negatively affect the formation of flower buds, germination, and pollen tube growth, reducing the number of pollen grains released for fertilization and increasing the number of aborted flowers (Sita et al., 2017; Barros et al., 2021). Additionally, temperatures between 30 and 35°C during the seed filling stage reportedly accelerate senescence, decrease the number and weight of seeds, consequently reducing the yield of legumes (Kumar et al., 2016).

In addition to the effects described above, thermal stress causes metabolic changes that limit sucrose and starch synthesis, thereby reducing the accumulation of carbohydrates in the seeds (Kaushal et al., 2013; Sita et al., 2017). In Brazilian semi-arid regions, mean daily maximum temperatures of 37°C and nighttime temperatures of 24.8°C can noteworthily reduce cowpea yield due to high rates of flower and pod abortion (Barros et al., 2021), as observed in this study in the hot season planting. Conversely, during the mild season, days with minimum temperatures of 15°C were recorded (Figure 1B). This temperature coincided with the time of pod maturation, when temperature does not cause losses in final seed production (Ndiso, Olubayo, Chemining'wa, & Saha, 2016). Cowpea can grow within a wide temperature range (from 18 to 37°C), but the optimum temperature varies for different phenological phases (Vale, Bertini, & Borém, 2017).

The five cultivars under this study showed a reduction in the production of pods and seeds in the hot cropping season. Particularly, cultivars Pujante and Rouxinol had the lowest number of pods and seeds when planted in the hot season, with maximum temperatures between 26 and 38.60°C and a relative humidity ranging from 48.8 to 99.8% (Figure 1A and D). Specifically, in cultivar Pujante, the numbers of pods and seeds were reduced by 66.13 and 69.48% in the hot season, respectively, and in cultivar Rouxinol, the reduction in numbers of pods and seeds was 79 and 83.68%, respectively (Figure 2). Thus, despite being of the same species, the different cultivars showed distinct responses in their adaptability to the environment, indicating that they may perform differently depending on the time of planting (Matoso et al., 2018).

The highest number of pods and seeds and the maximum total seed production were obtained with increasing soil water availability during the growing season at mild temperatures (Figure 3). However, no regression model was fitted for the growing season with high temperatures, which was represented only by the mean (Figure 3C). These results reinforce the positive relationship between the amount of water applied and the production of pods and seeds per plant. Cowpeas are sensitive to water deficit, and this abiotic stress can also cause flower abortion, pod failure, and grain filling reduction (Mwale et al., 2017), as observed in the present study. An extended period of water deficit at flowering stage reduces cowpea yield by approximately 63-98% (Ndiso et al., 2016). During the flowering and grain filling stages, the abortion of young flowers occurs because of source-drain competition, causing abnormal flowers and fertilization failure, and abortion of young pods occurs because of a deficiency in photoassimilate supply (Silva, Silva, Souza, Souza, & Araújo, 2019). This deficiency is associated with a heat-induced reduction in photosynthesis that results in a low efficiency rate in energy use by the plant (Farooq et al., 2017).

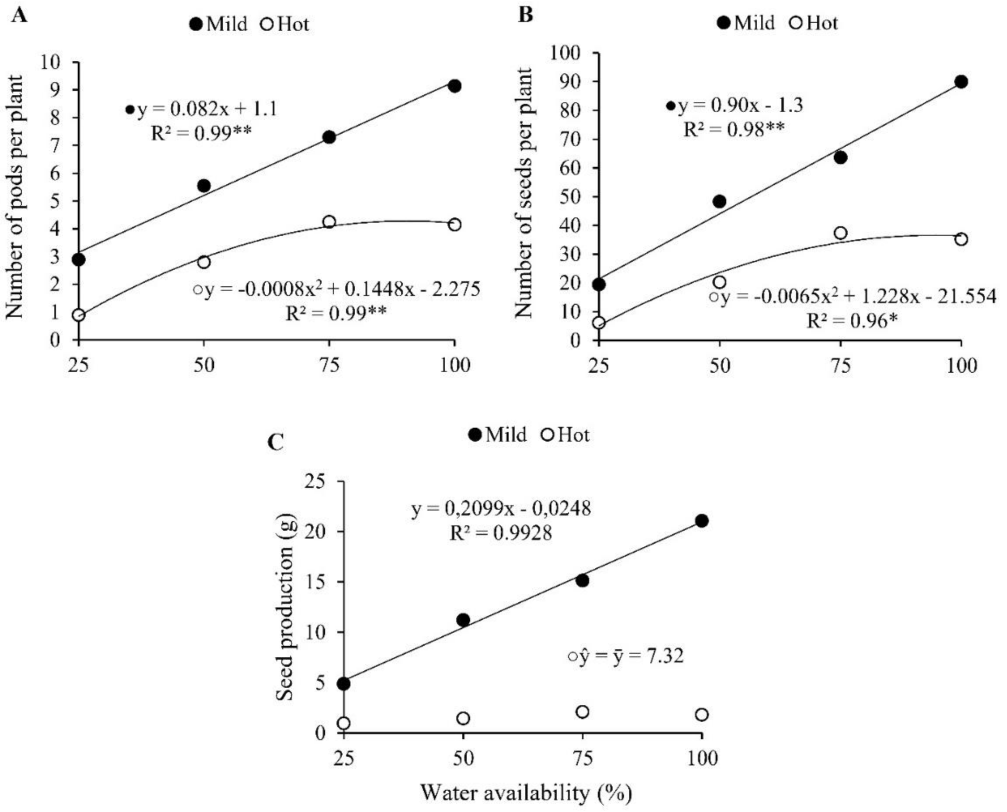

Figure 3. Number of pods per plant (A), number of seeds per plant (B), and total seed production (C) as a function of soil water availability and growing season. Regression coefficient was significant at $p < 0.01$ (**) and $p < 0.05$ (*).

Even when water availability was 100%, we recorded reductions of as much as 54 and 60% in the numbers of pods and seeds, respectively, during the hot season, relative to those in the mild cropping season (Figure 3A and B). Furthermore, we observed that seed production decreased during the hot season, with crop yield being approximately 90% lower than that observed in the mild season (Figure 3C). This finding indicated that even with irrigation, temperature was the most limiting element for cowpea production. We recorded 42 days with temperatures above 35°C during the hot season, of which 31 days occurred during the reproductive growth stage, starting at 13 days after planting. The interaction between water deficit and high temperature may delay or inhibit the development of floral buds, resulting in fewer flowers, which in turn lead to a substantial reduction in seed production (Ndiso et al., 2016) and important morphological, physiological, biochemical, and molecular changes in plants (Zandalinas, Mitler, Balfagón, Arbona, & Gómez-Cadenas, 2017).

In the mild season, a soil water availability level of 61% promoted the highest WUE, i.e., 1.28 g L-1 (Figure 4B). Thus, we conclude that the best water/grain conversion point occurred when plants were grown under a water availability of 61%. In contrast, WUE decreased at water availability levels above this value, confirming earlier finding that efficiency decreases when water availability is close to 100% (Silva et al., 2019). The reduction in WUE with the increase in water availability likely occurs because cowpea is a species capable of extracting water at lower soil potentials than soil water potential at the permanent wilting point (Coelho, Barros, Bezerra Neto, & Souza, 2014), which contributes to an increase in soil water availability. Therefore, values close to or above 100% water availability may not promote a significant increase in WUE; furthermore, they may reduce it, as observed in this study.

These results support producer decision-making aimed at sustainable irrigation management, as they clearly show that there is no need for maintaining 100% water availability; a water availability level of 61% of the maximum water holding capacity of the soil is sufficient to ensure high yield and WUE, while promoting water and energy conservation. This result is of paramount importance, especially in semi-arid regions, where water is becoming increasingly scarce.

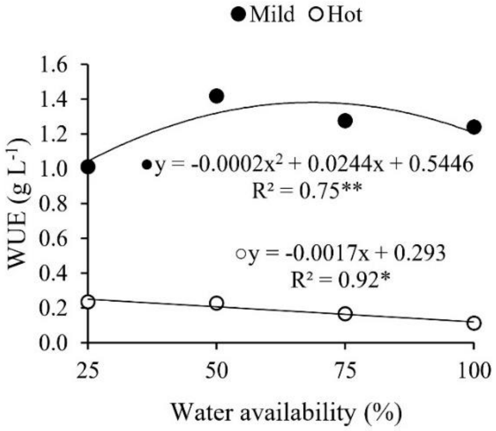

Figure 4. Water use efficiency (WUE; g L^{-1}) as a function of water availability in two growing seasons contrasting in ambient temperature. Regression coefficient significant at $p < 0.01$ (**) and $p < 0.05$ (*).

WUE was lower during the hot season than during the mild season (Figure 4). Furthermore, WUE decreased as water availability increased. This behavior is related to the reduction in seed production recorded in the hot season, because WUE holds a direct relationship with total production obtained and total plant water consumption. Consistently, Souza et al. (2017) reported high WUE under irrigation for only 75% ETo (reference evapotranspiration) while evaluating WUE in cowpeas under semi-arid conditions in December 2007.

Regarding shoot dry mass and root dry mass, the hot season favored an increase in these variables for the cultivars Pujante and Rouxinol (Figure 5); the increase in temperature directly affected their reproductive phase, consequently reducing the production of pods and seeds. This reduction prolonged the vegetative stage and ultimately resulted increased dry mass. According to Sehgal et al. (2018), leaves adapt to high ambient temperatures by regulating their temperature through transpiration. When subjected to high temperature stress, roots produce more secondary ramifications while increasing in diameter (Koevoets, Venema, Elzenga, & Testerink, 2016).

In this study, an increase in shoot dry mass and root dry mass was observed with increasing water availability in both growing seasons (Figure 6). High soil water availability contributed to water and nutrient absorption by the roots, which in turn improved photosynthetic capacity and increased the dry mass (Chen et al., 2017). Under conditions of low soil water availability, plants tend to reallocate photoassimilates from the shoots to the roots, thus interrupting their growth. This morphophysiological response is a strategy used by plants to reduce water loss through transpiration (Gray & Brady, 2016). Additionally, a prolonged water deficit causes a decrease in leaf water potential and stomatal opening, reducing leaf size and root growth (Xu, Jiang, Jia, & Zhou, 2016). This occurs because of morphological, physiological, and biochemical changes and results in increased canopy temperature, which in turn reduces chlorophyll content and ultimately reduces photosynthetic activity (Toscano, Farieri, Ferrante, & Romano, 2016; Karim et al., 2018).

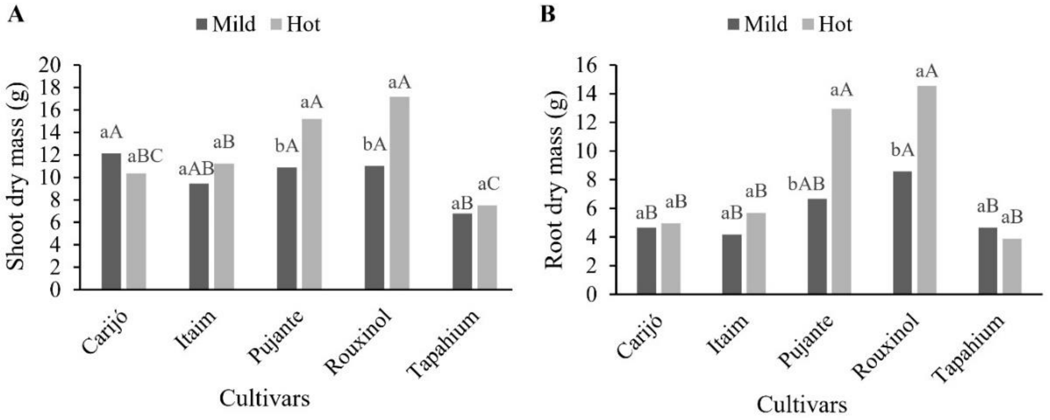

Figure 5. Shoot dry mass (A) and root dry mass (B) of five cowpea cultivars, as a function of growing season. Lowercase letters for the growing seasons, and uppercase letters for the cultivars.

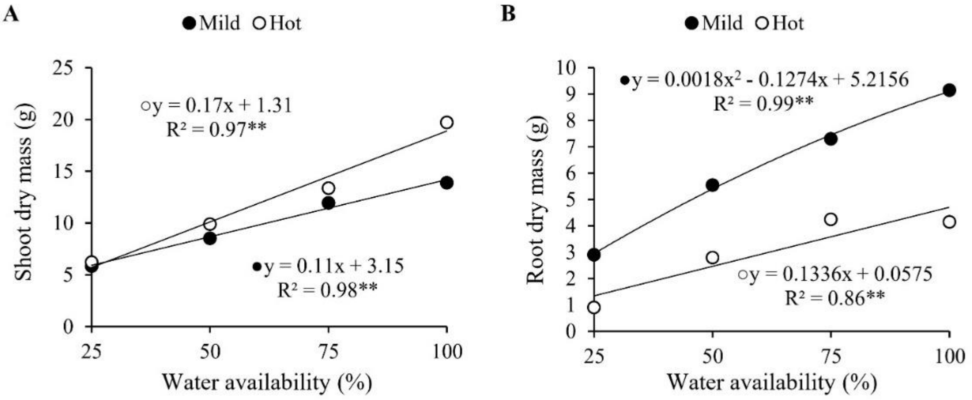

Figure 6. Shoot dry mass (A) and root dry mass (B) as a function of water availability and growing season. Regression coefficient significant at $p < 0.01$ (**).

Growing season and water availability affected photosynthesis (Figure 7A and B) and transpiration (Figure 7C and D). Photosynthetic activity was high during the hot season because of an increase in stomatal conductance and transpiration (Figure 7A, E, and C). However, low soil water availability reduced photosynthetic activity and transpiration (Figure 7B and D). Soil water availability at 84% promoted photosynthetic activity (19.10 μmol CO_2 m^{-2} s^{-1}), and that at 92% increased transpiration (6.36 mmol H_2O m^{-2} s^{-1}). During water stress, there is a reduction in tissue water content that leads to the inhibition of photosynthesis and a reduction in transpiration (Mathobo, Marais, & Steyn, 2017).

Water is an essential element regulating stomatal aperture. Thus, plants reduce stomatal opening to maintain a high internal leaf water potential under water stress at the expense of CO_2 assimilation and plant dry mass (Rivas et al., 2016). A reduction in g_s indicates the operation of adaptation mechanisms responsible for reducing water loss when plants are under water stress. Here, there was a reduction in leaf transpiration as a consequence of stomatal closure, whereby leaf temperature increased (Figure 7F). According to Buckley (2019) and Taiz et al. (2017), 97% of the water absorbed by plants is used to regulate leaf temperature through transpiration. Here, we observed a linear increase in g_s with no fit for the regression model for leaf temperature as a function of increasing water availability in the mild season (Figure 7E and F). During the hot season, a high g_s (0.33 mol H_2O m^{-2} s^{-1}) was observed at 81% water availability (Figure 7E).

Cowpea plants showed reduced g_s under limited water availability (Figure 7E). The reduction in g_s during water deficit reduces water loss (Nemeskéri & Helyes, 2019). Additionally, this promoted a reduction in photosynthesis (Figure 7B) and transpiration (Figure 7D). The reduction in photosynthetic activity resulted in reduced seed production and dry mass (Figures 4A and 6A), as photosynthesis is the main physiological process driving plant growth (Singh et al., 2014).

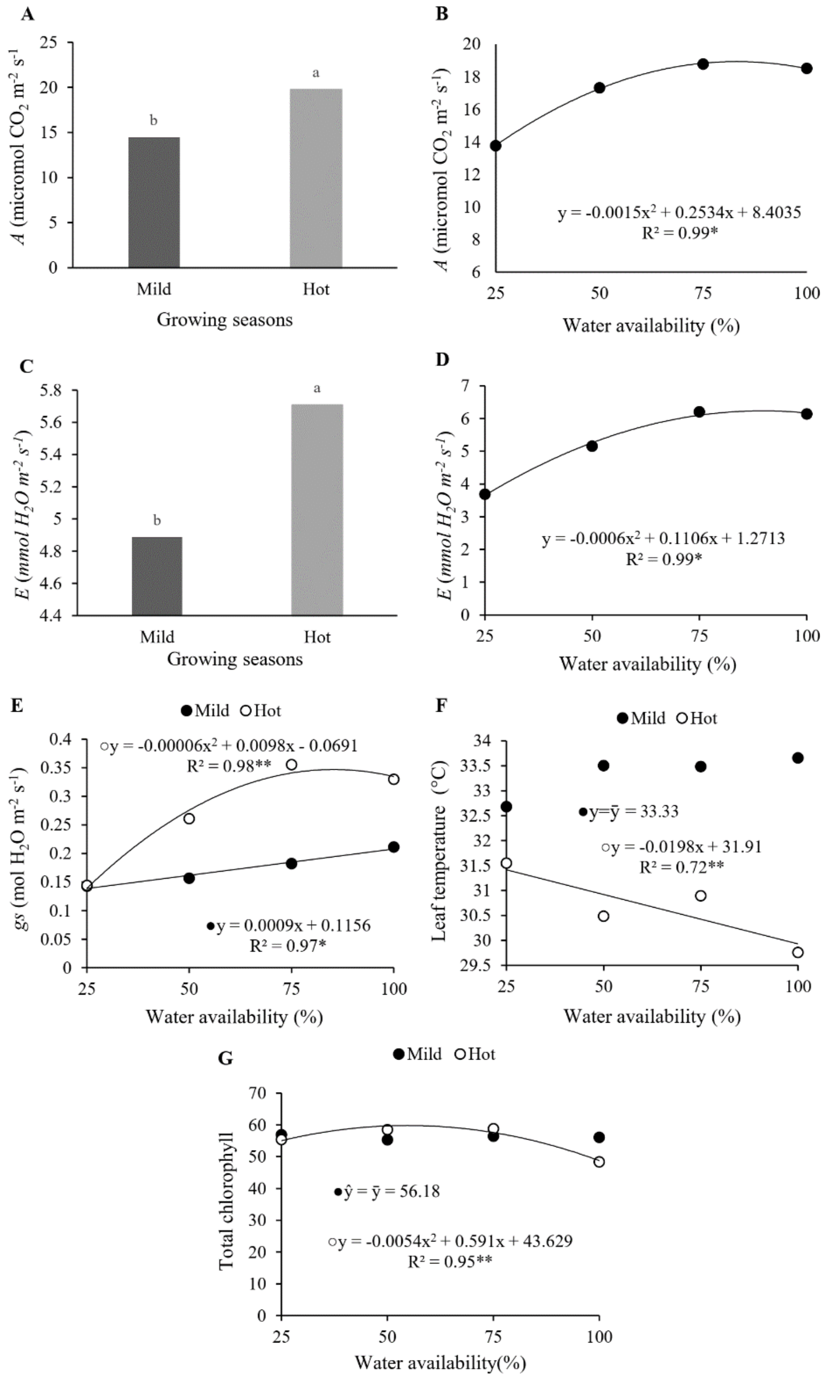

Figure 7. Gas exchange parameters in cowpea cultivars as a function of water availability and ambient temperature. Photosynthetic activity (A and B); transpiration rate (C and D); stomatal conductance (E); leaf temperature (°C) (F), and total chlorophyll index (G). Regression coefficient significant at $p < 0.01$ (**) and $p < 0.05$ (*).

During the hot season, the maximum chlorophyll index was 54.72% for plants exposed to 54.72% water availability (Figure 7G). We observed that water availability values higher than that mentioned above led to a significant reduction in chlorophyll index. Such behavior may have been caused by excess water in the soil, resulting in a lack of oxygen for the roots, which would cause the death of root tissues, whereby chlorophyll synthesis might have been impaired (Taiz et al., 2017). This reduction in chlorophyll index may account for the reduction in photosynthesis at 100% water availability (Figure 7B), because photosynthetic efficiency is linked to chlorophyll content (Taiz et al., 2017). There was no fit for the regression model for the total chlorophyll index during the mild season; therefore, it was represented by the mean (Figure 7G).

This study focused on the effects of increased temperature and water deficit on cowpea performance. From the data obtained, we inferred that, regardless of water availability, temperature is the most limiting climatic element for cowpea production. Thus, in addition to determining the ideal period for planting cowpeas to obtain high crop yields, it is necessary to adopt measures that contribute to the modification of the microclimate during hot cropping seasons, including the use of mulch, plant cocktails, and polycultures (Angelotti & Giongo, 2019). In addition to reducing the negative effects of high temperature on plant performance, these practices should contribute to optimizing WUE. Further, there is a need for studies with other cowpea cultivars to identify heat resistance genotypes.

Conclusion

Regardless of water availability, temperature is the climatic element that most restricts cowpea performance. Cowpea cultivars Carijó, Itaim, and Tapahium showed a low reduction in productive potential in the hot cropping season.

Acknowledgements

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