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Importance of brassinosteroids for mitigating water stress in sorghum

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Abstract

The objective of the present study was to assess the mitigating effect of brassinosteroids on water stress caused by different water supplies (water deficit and excess water) in sorghum. The experiment was conducted at the experimental farm of the State University of Goias, South Campus, in Ipameri, GO, Brazil. A completely randomized design was used, in a 2×5 factorial arrangement with 4 replications. The plants were grown under five water supplies (25%, 50%, 100%, 200%, and 400% of the evapotranspiration) and treatments with and without brassinosteroid (0.1 mg L^{-1}) application at 30.0 mL $plant^{-1}$, carried out in three moments (at 45, 47, and 49 days after emergence). The tests conducted in pots limited the root system growth by the volume of the container, but despite these conditions, sorghum plants treated with brassinosteroids presented higher root system development and plant height, denoting that the brassinosteroids have the potential for mitigation of water deficit at field level. The main mechanism of tolerance to drought of sorghum is its high stomatal sensitivity, which rapidly reduces transpiration and minimizes the plant dehydration under water deficit.

Keywords: *Sorghum bicolor*, drought, hormone, elicitor.

Abbreviations: mg_miligrama; L_litro; SPAD_índice de clorofila; DAE_days after emergence; dm^{-3}_decímetro cúbico; pH_hydrogen potential; P_phosphorus; K_Potassium; H_Hydrogen, Al_aluminium; Ca_ calcium; Mg_magnesium; Zn_zinc; Na_sodium; Kc_coefficient of culture; ETc_evapotranspiration of the crop; Reference ETo_Evapotranspiration; Cea_Electrical conductivity of water; NaCl_sodium chloride; SPAD_chlorophyll index; NL_number of leaves, PH_height of plants; E_perspiration; SWR_ stem mass ratio; TB_total biomass; RWR_root mass ratio; S/R_aerial part/root system ratio and LWR_leaf mass ratio; FW_ fresh weight; DW_dry weight; TW_ turgid weight.

Introduction

Sorghum (*Sorghum bicolor* L. Moench) has shown an expressive potential for expansion in the last years in Brazil, due to its adaptability to different regions, resilience in situations of low rainfall, and low production cost (Gomes at al*.,* 2020). Sorghum is a cereal that stands out by its use in animal feed and has been expanded to be included in human food, mainly because of its it has a high antioxidant capacity, no gluten, and considerable concentrations of vitamins, mineral, and fibers (Oliveira at al*.,* 2020).

The main sorghum crops in Brazil are planted as a second crop, with the planting beginning in March, in regions of the Cerrado biome. According to the Brazilian Institute of Geography and Statistics (Ibge, 2022), the national estimated sorghum production in 2022 is approximately 2.72 million Mg, with a mean yield of 3,178 kg ha^{-1}. In the Central-West region of Brazil, an increase of 32.5% in sorghum production is expected for the 2021-2022 crop season in relation to the 2020-2021 crop season; in the state of Goias, the sorghum area increased, the sorghum yield increased 1.7%, and an increase of of 28.7% in production is expected (Conab, 2022). Agriculture undergoes challenges, such as the selection of the crop to be planted, due to demand for plant species more productive and tolerant to water stress (Crespo-Herrera at al*.,* 2018). Sorghum is among these species; it has tropical origin and is one of the most versatile and efficient crop species, from the photosynthetic point of view and regarding maturation speed (Carcedo at al*.,* 2022). This crop requires hot climate to express its maximum genetic potential, and presents a high tolerance to frequent droughts, which is common in the second crop season and the most limiting factor for agricultural yield (Choudhary at al*.,* 2019).

Losses caused to crops due to water stress are connected to several factors, such as soil water retention capacity, evapotranspiration, and tolerance of cultivars. Damages are shown at the establishment and growth stages, between germination and beginning of panicle development, and at flowering and grain filling stages, which directly limits the final yield (Masasi at al*.,* 2019). Thus, techniques that mitigate losses are essential for overcoming low yields; application of elicitors is a functional strategy, since it increases the contents of functional compounds in the plants by activating defense mechanisms, including the production of antioxidants, which assist in mitigating stresses caused by droughts, nutritional deficiencies, and extreme temperatures and salinity (Escamilla at al*.,* 2017).

Brassinosteroids are steroids that act as plant growth regulators and can assist in this context, as they are associated with increases in biomass, adaptation to environmental factors, and stem and root growth stimulation, mainly by the development of lateral roots (Matos at al*.,* 2019). Brassinosteroids assist in the maintenance of apical dominance, vascular differentiation, growth of pollen tube, and cell elongation and division, presenting biological effects under low concentrations (Nolan, 2017; Taiz at al*.,* 2017). In addition, they act in the induction of ethylene synthesis, seed germination, and activation of antioxidants enzymes that are important for plant metabolism (Qiao at al*.,* 2017).

According to Oliveira at al*.* (2021), the use of brassinosteroids to mitigate water stress can contribute to maintain the plant turgor and growth, thus, they can be an alternative for places as the state of Goias, which undergoes water scarcity in part of the year. Therefore, studies focused on mechanisms that minimize the effect of this factor on the production of crops of economic interest are needed. In this context, the objective of the present study was to assess the mitigating effect of brassinosteroids on water stress caused by different water supplies (water deficit and excess water) in sorghum.

Results

Physiological variables

The analyses of variance for chlorophyll index (SPAD), total transpiration, relative water content, total biomass, and root weight ratio are shown in Table 1. The effect of the treatments with and without brassinosteroid application was significant ($p < 0.05$) only on root weight ratio, and the mean of plants treated with brassinosteroid was 7.7% higher than that of plants without brassinosteroid, with values of 0.56 and 0.52, respectively. The interaction between the brassinosteroid application and water supply was not significant for any of the variables evaluated.

The increase in root system is a classical function of brassinosteroids, which intensifies the development of this organ and the absorption of the soil solution. The results are consistent with those of Souza at al. (2021), who found that brassinosteroid application increased root weight ratio of papaya plants by 17.43%. Brassinosteroids are associated with higher development of lateral roots to stop water stress in plants, as reported by Matos at al. (2019).

Growth Variables

The analysis of variance for stem weight ratio, shoot to root ratio, plant height, and number of leaves are shown in Table 2. The effect of the treatments with and without application of brassinosteroids were significant for stem weight ratio, which was 21.7% higher in plants without brassinosteroid; plant height was 8.05% higher in plants with brassinosteroids. The effect of water supply was not significant only on the number of leaves.

The small differences found for some growth variables regarding the use of brassinosteroids indicate the possibility of a mitigating effect on water deficit. According to Matos at al. (2019), sorghum production significantly increases by applying brassinosteroids at the reproduction stage, which is explained by one of the functions of brassinosteroids, which is to increase the grain drain force.

Discussion

The effect of the treatments with brassinosteroid and the interaction between brassinosteroid application and water supply on chlorophyll index, total transpiration, and relative water content were not significant, thus, the mean data were processed. Plant height and root weight ratio presented differences (Figure 1). Low water availability has negative effects on production of photosynthetic pigments, which explains the low chlorophyll indexes found. However, chlorophyll indexes increased as the water availability was increased. According to Matos at al. (2019), plants minimize chlorophyll production to reduce solar radiation absorption and mitigate the oxidative stress.

Total transpiration reached the maximum point when the plants were irrigated with the water volume of 100% of the evapotranspiration, remaining constant up to the water volume of 400%; the transpiration decreased sharply under water volumes below 100% of the evapotranspiration. The relative water content slightly decreased between the water volumes of 400% and 200%, but had a pronounced decreased under water volumes below 200%.

Despite the absence of significant differences, chlorophyll index, transpiration, biomass, and number of leaves were higher in plants treated with brassinosteroids; thus denoting a possible effect of brassinosteroid application on the sorghum growth. Brassinosteroid application increased the growth in height and root weight ratio of sorghum. Brassinosteroids are important for root development and increase the absorption potential of soil solution, in addition, has an additive action to auxin in the acid growth (TAIZ at al., 2017). The results are consistent with those found by Matos at al. (2019), who evaluated sorghum plants subjected to different brassinosteroids concentrations, in the field.

Sorghum grown in the low rainfall season in the Cerrado biome in Brazil presents high stomatal sensitivity; the plants reduce transpiration to minimize dehydration as the water availability decreases (Matos et al., 2019). The results denote that the stomatal closure was so efficient that plants under water deficit (25% and 50%) presented no differences in relative water contents. According to Cruz at al. (2019), C_4 plants have the characteristics of reducing stomatal opening and osmotically regulating themselves to remain hydrated. In the present study, excess water (200% and 400%) applied to sorghum plants did not result in stress, probably due to the short period of exposure. The root weight ratio presented significant variation for both treatments; thus, the results were similar in plants irrigated with water volumes of 25% and 400%.

The root weight ratio of plants under water deficit or excess water presented growth peaks and, between water volumes of 100% and 300%, it presented intermediate values. According to Matos at al. (2019), excess water limits the activity of aquaporins and results in water deficiency in plants. It explains the root growth under excess water. Similarly, plants treated with brassinosteroids presented more intense root growth, following a test model with this type of plant growth regulator, which increases the root system growth (Matos et al., 2019).

Plant height increased as the water volume was increased, with a difference of 69.4% between plants under water volumes of 25% and 400%. Thus, the plants presented higher development under the highest water availability, and those treated with brassinosteroids stood out. Campos at al*.* (2021) found a linear growth in plant height for

Table 1. Analyses of variance for chlorophyll index (SPAD), total transpiration (E), relative water content (RWC), total biomass (TB), and root weight ratio (RWR) of sorghum (*Sorghum bicolor*) plants grown under different water supplies (25%, 50%, 100%, 200%, and 400% of the evapotranspiration), with and without brassinosteroid application. Ipameri, Goias, Brazil, 2022.

Source of Variation	Mean squares					
	DF	SPAD	E	RWC	TB	RWR
Br	1	3.6^{ns}	3150.6^{ns}	13.88^{ns}	64.66^{ns}	0.018*
WS	4	258.1*	44123.1*	145.49*	227.39 ^{ns}	0.055*
Br×WS	4	13.75^{ns}	472.76^{ns}	0.96^{ns}	158.17 ^{ns}	0.008^{ns}
Residue	30	24.77	1053.1	39.2	57.62	0.006
CV (%)	-	8.75	22.22	6.85	17.67	14.47
Brassinosteroid	Means					
With		57.18a	154.93a	90.8a	44.24a	0.56a
Without		56.58a	137.18a	91.98a	41.69a	0.52b

DF = degrees of freedom; Br = brassinosteroid treatment; WS = water supply treatment; * = significant at 5% probability; ns = not significant by the F test. Means followed by different letters in the columns are different from each other at 5% probability.

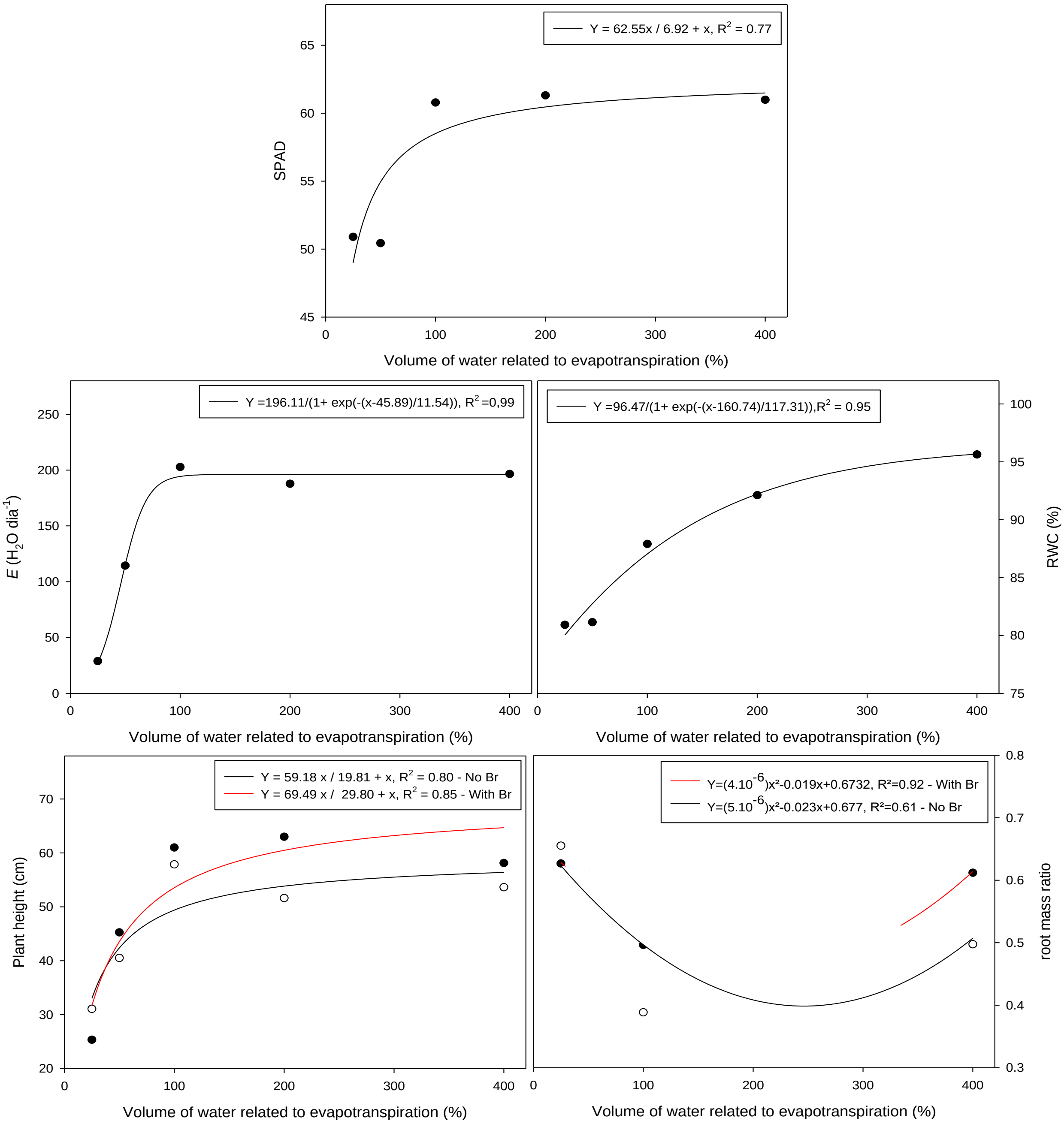

Figure 1. Regression equations for chlorophyll index (SPAD), total transpiration (E), relative water content (RWC), plant height, and root weight ratio of sorghum (*Sorghum bicolor*) plants grown under different water supplies (25%, 50%, 100%, 200%, and 400% of the evapotranspiration). Ipameri, Goias, Brazil, 2022. All models were significant at 5% probability.

Table 2. Analyses of variance for stem weight ratio (SWR), leaf weight ratio (LWR), shoot to root ratio (SRR), plant height (PH), and number of leaves (NL) of sorghum (*Sorghum bicolor*) plants grown under different water supplies (25%, 50%, 100%, 200% and 400% of the evapotranspiration), with and without brassinosteroid application. Ipameri, Goias, Brazil, 2022.

Source of Variation	Mean squares					
	DF	SWR	LWR	SRR	PH	NL
Br	1	0.016*	0^{ns}	0.202^{ns}	230.4*	1.6^{ns}
WS	4	0.03*	0.005*	0.783*	1159.1*	2.537^{ns}
Br×WS	4	0.002^{ns}	0.002^{ns}	0.241^{ns}	30.77^{ns}	1.912^{ns}
Residue	30	0.002	0.001	0.086	32.06	2.016
CV (%)	-	20.94	21.02	32.04	11.43	15.69
Brassinosteroid	Means					
With		0.23b	0.19a	0.84a	51.15a	9.25a
Without		0.28a	0.19a	0.98a	47.15b	8.85a

DF = degrees of freedom; Br = brassinosteroid treatment; WS = water supply treatment; * = significant at 5% probability; ns = not significant by the F test. Means followed by different letters in the columns are different from each other at 5% probability.

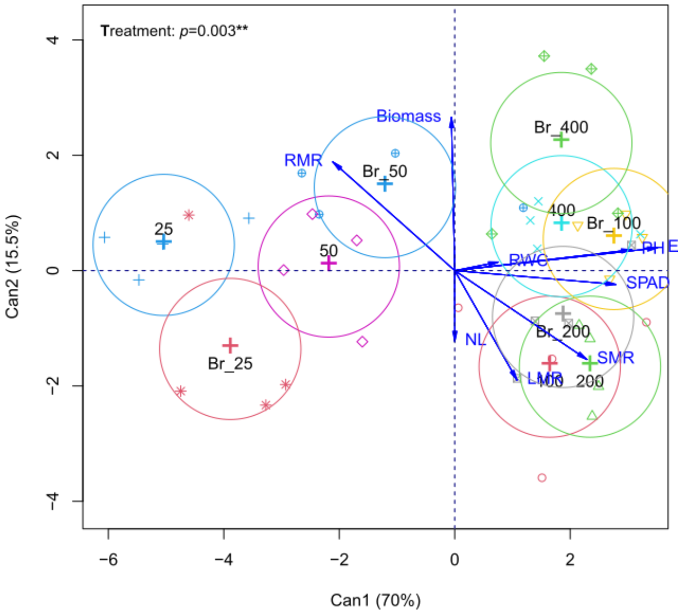

Figure 2. Analysis of canonical for variables for ordering the data for biomass, relative water content (RWC), transpiration (E), plant height (PH), chlorophyll index (SPAD), stem weight ratio (SWR), leaf weight ratio (LWR), number of leaves (NL), and root weight ratio (RWR) of sorghum (*Sorghum bicolor*) plants grown under different water supplies (25%, 50%, 100%, 200%, and 400% of the evapotranspiration), with (Br) and without brassinosteroid application. Ipameri, Goias, Brazil, 2022.

Table 3. Importance of the variables analyzed for total transpiration of sorghum (*Sorghum bicolor*) plants grown under different water supplies (25%, 50%, 100%, 200%, and 400% of the evapotranspiration), with and without brassinosteroid application. Ipameri, Goias, Brazil, 2022.

Transpiration	R^2= 0.66		F (2.37) =36.2		p<0.00005	
	Beta	Standard Error of Beta	B	Standard Error of B	t (37)	p-level
Intercept			-182.114	4.187.790	-434.870	0.0001
Plant height	0.918	0.107	5.522	0.64815	851.930	0.000
Number of leaves	0.420	0.107	5.558	142.555	389.897	0.0004

Jatropha curcas as the water volume was increased, with an increase of 43% between the lowest (25%) and the highest water volume used (175%). These results are connected to the capacity of brassinosteroids to increase growth with additive action to auxin regarding cell wall acidification and stimulation of cell division, as reported by Taiz at al. (2017).

The analysis of canonical variables shown in Figure 2 represents 85.5% of the total variation of the data.

Plants subjected to water deficit with water volumes of 25% and 50% of the evapotranspiration were on the left of the axis Can 1 (Figure 2), together with important variables for the overcoming of water stress, such as root weight ratio, whereas treatments with the highest water supplies (100%, 200%, and 400%) were on the right of Can1, together with variables connected to higher plant growth. The plants invested their resources on the increase of shoot due to the higher water availability, and increased the root weight ratio under water deficit conditions.

The lack of resources in the root environment causes, in general, changes in the biomass accumulation pattern;

consequently, changes in the pattern of reallocation of assimilates between roots and shoot are expected (Sun et al., 2019). According to Wilf at al. (2021), the initial response of plants to drought under water stress conditions is to inhibit the shoot growth and maintain root growth as an adaptive alternative to maintain water absorption and reduce loss by transpiration, which was clear in the present study.

Plant height and number of leaves were responsible for 66% of the variation of transpiration by the multiple regression evaluation, denoting that the plant architecture, together with the volume of leaves, decisively affects the water balance in sorghum plants (Table 3).

Material and methods

Search location

The experiment was conducted at the experimental farm of the State University of Goias, South Campus, in Ipameri, GO, Brazil (17°42'59.12''S, 48°08'40.49''W, and altitude of 773 m). The crop was grown in a greenhouse covered with transparent plastic film, with a 50% shade screen on the sides. The climate of the region was classified as Aw, tropical, according to the Köppen classification, with a dry winter, wet summer, and mean temperature of 20 °C (Alvares at al., 2013).

Design experimental

A completely randomized design was used, in a 2×5 factorial arrangement with 4 replications. The plants were grown under five water supplies (25%, 50%, 100%, 200%, and 400% of the evapotranspiration) applied at 30 days after emergence (DAE), and treatments with and without brassinosteroids (0.1 mg L^{-1}) application at 30.0 mL $plant^{-1}$, carried out in three moments (at 45, 47, and 49 DAE).

Three seeds of the sorghum cultivar Brevant 1G100 were sown in polyethylene pots containing 12 kg of a substrate, mixed in electrical mixer, consisted of Typic Hapludox (Latossolo Vermelho-Amarelo Distroferrico; Santos at al., 2018), sand, and bovine manure, at the proportion of 3:1:0.5, respectively. A thinning was carried out at 7 DAE, keeping one plant per pot as the experimental unit.

The chemical analysis of the substrate presented the following values: pH ($CaCl_2$) 5.7; 17 g dm^{-3} of organic matter; 28.3 mg dm^{-3} of P; 0.42 cmolc dm^{-3} of K ($Mehlich^{-1}$); 1.7 cmolc dm^{-3} (SMP Buffer) of H + Al; 2.1 cmolc dm^{-3} of Ca; 1.3 cmolc dm^{-3} of Mg; 10.1 mg dm^{-3} of Zn; 9.86 cmolc dm^{-3} of carbon; 5.52 cmolc dm^{-3} of cation exchange capacity; and 69.20% base saturation. All pots were filled with the same volume of substrate. Soil fertilizers were applied at 7 DAE, according to agronomic recommendations for sorghum crops (Prochnow at al., 2010), using 3.5 g of single superphosphate and 8 g of urea per pot.

Irrigation conditions

Initial irrigation (first 30 days) was carried out using a water volume of 100% of the evapotranspiration and, then, the plants were subjected to the treatments with water volumes of 25%, 50%, 100%, 200%, and 400% of the evapotranspiration. The crop coefficient (Kc) was not determined for sorghum crops grown in the region of Ipameri, thus, a Kc of 1.00 was used, as recommended by the FAO 56 (Allen at al., 1998) for several crops at initial developmental stages. The water volume used was calculated by determining the reference evapotranspiration and the crop coefficient, according to the equation $ETc = ETo \times Kc$, where *ETc* is the crop evapotranspiration, *Kc* is the crop coefficient, and *ETo* is the reference evapotranspiration.

The daily ETo was calculated through the Penman-Monteith method, as recommended by the FAO (Smith at al., 1991), using daily data of maximum and minimum air temperatures, relative air humidity, insolation, and wind speed collected by a meteorological station of the Brazilian National Institute of Meteorology (INMET) installed in Ipameri.

Occurrences of pests were found during the experiment period, which included fall armyworms (*Spodoptera frugiperda),* corn leafhoppers (*Dalbulus maidis*), corn leaf aphid (*Rhopalosiphum maidis*), and sugarcane aphid (*Melanaphis sacchari*). Chemical control with insecticides was carried out when they were identified; the first application was carried out at 25 DAE, using 250 mL ha^{-1} of lambda cyhalothrin and 300 mL ha^{-1} of lufenuron, and the second application was carried out at 45 DAE, using 700 mL ha^{-1} and 250 mL ha^{-1} of lambda-cyhalothrin, both carried out using a backpack sprayer. Weed management was carried out through manual weeding.

The treatment with water deficit was applied at 30 DAE, when half of the plants were subjected to brassinosteroid application. The evaluations were carried out at 50 DAE.

Growth variables

The plant height (mm) was measured from the stem base to the apex with the aid of a ruler. The number of leaves were counted. The plant parts (leaves, culm, and root) were separated, placed in paper bags, dried in a forced air circulation oven set to 70 °C for 72 hours to obtain a constant dry weight, and then weighed in a precision balance. After obtaining the dry weights

The total biomass weight was obtained by summing the weights of all plant parts; the ratios between total biomass and leaf, stem, and root weights were estimated by dividing the weight of the individual organs by the total biomass weight. The shoot to root ratio was obtained by the sum of the dry stem and leaf weights divided by the root dry weight.

Chlorophyll index (SPAD)

The chlorophyll index was determined with the aid of a portable chlorophyll meter (ClorofiLOG® model CFL 1030), which provides total chlorophyll values expressed as units called SPAD Chlorophyll Index. The measurements were carried out on the third pair of fully expanded leaves.

Leaf relative water content and transpiration

Leaf relative water contents were obtained in five leaf discs of 1.2 cm of diameter from fully expanded leaves. They were weighed in a precision balance to evaluate fresh weight (FW), placed in Petri dishes with distilled water saturated for 24 hours and weighed again to determine the turgid weight (TW), and dried for 72 hours at 70 °C to obtain the dry weight (DW). The relative water content was then calculated using the following equation: $[(FW - DW) / (TW - DW)] \times 100$.

The daily total transpiration rate of the plant was evaluated by the difference between the weights of the pots. At 49 DAE, the pots were placed in transparent plastic bags fixed with a rubber band at the plant stem, leaving only the shoot (leaves and stem) outside the bag; the pots with plant in the plastic bags were then weighed and, after 24 hours, weighed again. The total transpiration was estimated as the difference between the initial and final weights.

Statistical procedures

The variables were subjected to analysis of variance and the differences between treatments were analyzed by the Tukey's test (P≤0.05) using the statistical program Sisvar 5.6 (Ferreira, 2019). In addition, linear and quadratic regression analysis with the respective coefficients of determination (R^2) were carried out using the statistical program SigmaPlot 10.0 (Systat Software, 2006), and the program RBio (Bhering, 2017) was used for the canonical variables.

Conclusions

The application of brassinosteroids increases the growth of the root system of sorghum (*Sorghum bicolor*) plants, denoting that this plant growth regulator has potential to mitigate effects of water deficit. The main mechanism of tolerance to drought of sorghum is its high stomatal sensitivity, which rapidly reduces transpiration and minimizes dehydration of plants under water deficit. Tests conducted in pots limit the root system growth by the container volume, but despite these conditions, sorghum plants treated with brassinosteroids mitigate damages caused by water deficit; thus, the development of further studies at the field level is recommended for obtaining a reasoned practical recommendation.

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