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Research Article

Exogenous superoxide dismutase alleviates drought stress in cotton genotypes[1]

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ABSTRACT

In drought-tolerant plants, adverse effects caused by water deficit can be mitigated by antioxidant enzymes, which activate the plant's defense mechanisms. This study aimed to evaluate the mitigating effect of exogenous superoxide dismutase (SOD) supplementation on cotton plants subjected to drought stress. Four cotton genotypes (BRS Seridó, FM 966, FMT 705 and CNPA 7MH) were grown in a greenhouse and evaluated under the following treatments: control (daily irrigation), drought stress (plants subjected to 6 days without irrigation) and drought stress with exogenous SOD supplementation at concentrations of 11, 22 and 33 μg mL^{-1}. The experimental design was a randomized block arrangement, in a 4 × 5 factorial scheme, with four replications. Plant growth, biomass accumulation and gas exchange parameters were evaluated. Overall, the exogenous SOD supplementation at 33 μg mL^{-1} effectively mitigated the adverse effects of drought stress on cotton growth and gas exchange, with a more pronounced response observed for the drought-sensitive genotypes.

KEYWORDS: *Gossypium hirsutum*, water deficit, drought tolerance, antioxidant defense.

RESUMO

Superóxido dismutase exógena alivia o estresse por seca em genótipos de algodão

Em plantas tolerantes à seca, os efeitos adversos causados pelo déficit hídrico podem ser mitigados por enzimas antioxidantes, que ativam os mecanismos de defesa da planta. Objetivou-se avaliar o efeito mitigador da suplementação exógena de superóxido dismutase (SOD) em plantas de algodão submetidas a estresse hídrico. Quatro genótipos de algodão (BRS Seridó, FM 966, FMT 705 e CNPA 7MH) foram cultivados em casa-de-vegetação e avaliados sob os seguintes tratamentos: controle (irrigação diária), estresse hídrico (plantas submetidas a 6 dias sem irrigação) e estresse hídrico com suplementação exógena de SOD nas concentrações de 11, 22 e 33 μg mL^{-1}. O delineamento experimental foi em blocos ao acaso, em esquema fatorial 4 × 5, com quatro repetições. Foram avaliados o crescimento das plantas, acúmulo de biomassa e parâmetros de troca gasosa. De modo geral, a suplementação exógena de SOD a 33 μg mL^{-1} mitigou efetivamente os efeitos adversos do estresse hídrico sobre o crescimento e a troca gasosa das plantas de algodão, com resposta mais pronunciada observada nos genótipos sensíveis à seca.

PALAVRAS-CHAVE: *Gossypium hirsutum*, déficit hídrico, tolerância à seca, defesa antioxidante.

INTRODUCTION

Drought stress is one of the primary environmental factors contributing significantly to crop yield losses. At the cellular level, water shortage disrupts homeostasis, adversely affecting nutrient uptake and cell turgor (Khan et al. 2018). Such disruptions impair essential physiological processes, including cell expansion, division, enzyme activity, gas exchange and the synthesis of compatible solutes, culminating in an imbalance between photochemical reactions in the photosystem II (PSII) and carbon assimilation due to reduced CO_2 diffusion (Chaves et al. 2009, Dutra et al. 2018).

Consequently, the electron transport chain's activity in chloroplasts and mitochondria decreases,

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leading to the generation of reactive-oxygen species (ROS) such as superoxide anion ($O_2 \bullet^-$), hydrogen peroxide (H_2O_2), hydroxyl radical (OH•) and singlet oxygen ($^1O_2$), which collectively damage cellular metabolism (Yi et al. 2016, Foyer 2018).

Plants employ enzymatic and non-enzymatic antioxidant systems to detoxify these species, with their activity levels determining the plant's tolerance or sensitivity to stress (Gill & Tuteja 2010, Barbosa et al. 2014). Within the enzymatic pathway, superoxide dismutase (SOD; EC 1.15.1.1) catalyzes the dismutation of $O_2 \bullet^-$ into H_2O_2 and O_2 (Apel & Hirt 2004). Superoxide dismutase, a metalloenzyme, constitutes the primary antioxidant defense in various subcellular compartments (Gill & Tuteja 2010).

Studies have reported the crucial role of SOD in antioxidant defense mechanisms across both C_3 and C_4 plant species (Pereira et al. 2012, Sharma et al. 2019, Barbosa et al. 2023). Under drought conditions, plants typically upregulate the SOD activity to mitigate oxidative damage from ROS. In general, enzymatic and non-enzymatic organic compounds act synergistically to minimize cellular damage under environmental stress. The literature highlights promising outcomes from exogenous supplementation of organic solutes to alleviate environmental stresses, particularly drought, such as ascorbic acid in quinoa (Aziz et al. 2018), salicylic acid in cowpea (Dutra et al. 2017), tocopherol in mung bean (Sadiq et al. 2017) and pyruvate in peanut and cotton (Barbosa et al. 2021, Silva et al. 2023). Notably, Barbosa et al. (2023) demonstrated that peanut plants supplemented with SOD at 22 μg mL^{-1} under drought conditions exhibited enhanced leaf relative water content by 40 % and increased the endogenous SOD activity by 50 %, significantly improving gas exchange.

The present study evaluated four contrasting cotton (*Gossypium hirsutum* L.) cultivars to determine whether the exogenous supplementation of SOD at low concentrations can mitigate growth and physiological impairments induced by drought stress. Cotton, characterized by C_3 photosynthesis and elevated photorespiration rates, undergoes significant molecular and physiological changes under low CO_2 availability due to the RuBisCO oxygenase activity (Santos et al. 2022). Silva et al. (2023) observed that drought-stressed cotton plants supplemented with exogenous pyruvic acid exhibited improved gas exchange, water relations and compatible solute synthesis, particularly in drought-sensitive cultivars.

Although cotton cultivars exhibit varying tolerance levels to drought stress, drought episodes occurring before the flowering stage typically negatively impact plant growth and fiber yield (Chiavegato et al. 2009). Thus, this study aimed to provide critical insights into the potential benefits of organic compound supplementation in crop management strategies to reduce the detrimental effects of drought stress.

MATERIAL AND METHODS

Four cotton cultivars exhibiting contrasting levels of drought tolerance (BRS Seridó, FM 966, FMT 705 and CNPA 7MH; Table 1) were used in this study. The experiment was conducted in a greenhouse located in Campina Grande, Paraíba state, Brazil (07º13'50"S, 35º52'52"W and 551 m of altitude), between November and December 2019. Seeds were planted in 0.6-L pots filled with organic substrate (Basaplant Base Agro, Brazil). At 5 days after emergence, the seedlings were thinned to 1 plant pot^{-1}, representing the experimental unit. The leaf water potential was adopted as an indicator of plant water status.

Water stress was initiated at 21 days after emergence, corresponding to the stage with four fully expanded leaves (Marur & Ruano 2001), and continued for six days. The following treatments were established: control - plants received adequate

Table 1. Agronomic traits of the cotton cultivars used in this study.

Cultivar	Cycle	Environmental adaptation	Drought tolerance
BRS Seridó	Medium (135-150 days)	Semiarid/Cerrado	Tolerant
FM 966	Late (150-160 days)	Cerrado	Sensitive
FMT 705	Late (150-160 days)	Cerrado	Moderate
CNPA 7MH[1]	Early (120-130 days)	Semiarid	Tolerant

[1] Obtained from crossing between 'Mocó' and Latifolium subspecies. Sources: Rodrigues et al. (2016) and Vasconcelos et al. (2018).

irrigation, with water volume determined by drainage-based lysimetry (i.e., the volume applied minus the volume drained from the previous irrigation); water stress - plants subjected to water suppression for six days; water stress combined with supplementation of exogenous SOD (Merck/Sigma Aldrich) at the concentrations of 11, 22 and 33 µg mL^{-1}. Three successive foliar applications of SOD (1 mL) were administered to stressed plants, beginning at 3 days after the onset of water stress. To prevent spray drift, the pot bases were protected with a waterproof covering.

The experiment followed a randomized block design, with a 4 × 5 factorial arrangement and four replications. Growth and physiological parameters were evaluated. The growth parameters included plant height, leaf area, root length, root and shoot dry weight. The leaf area (La) was determined using the equation La = L x W x f, where L is the leaf length, W the leaf width and f a correction factor obtained by simple regression analysis between the leaf area of a sample and the product of its linear dimensions (Monteiro et al. 2005).

The roots were carefully washed to remove substrate particles, gently dried on paper towels and then measured for length. To determine the shoot and root dry weights, the tissues were oven-dried at 65 ºC, for 72 hours, and weighed using an analytical scale (0.1 mg resolution).

The physiological parameters included gas exchange measurements on young leaves (approximately 5 cm in length) located in the upper canopy, measuring stomatal conductance (*gs*), transpiration rate (*E*), CO_2 assimilation rate (*A*) and internal CO_2 concentration (*Ci*), using an infrared gas analyzer (IRGA; ADC LC-Pro). Measurements were taken between 7:00 and 8:00 a.m., with the chamber irradiance set at 1,200 µmol m^{-2} s^{-1}. The instantaneous carboxylation efficiency (*CEi*) was estimated using the *A/Ci* ratio.

Statistical analyses were performed using the Sisvar software version 5.8 (Ferreira 2019). The Lilliefors test was applied to assess data normality. Analysis of variance (Anova) was conducted using the F test, and mean comparisons were performed using the Tukey test at $p < 0.05$.

RESULTS AND DISCUSSION

The summary of Anova for the growth traits of cotton cultivars subjected to water stress and treated with exogenous superoxide dismutase (SOD) is presented in Table 2. Significant effects of cultivar and treatment ($p < 0.05$) were observed for all evaluated traits. The interaction effect between cultivar and treatment (C × T) was significant for all traits, except for root dry weight, indicating that the mitigating effects of exogenous SOD supplementation were cultivar-dependent.

Overall, the exogenous SOD supplementation exhibited limited beneficial effects on the growth of drought-tolerant cultivars under water-stress conditions (Figures 1, 2 and 3). For BRS Seridó and CNPA 7MH, beneficial effects of SOD supplementation were observed in leaf area from 22 µg mL^{-1} (Figure 1A) and shoot dry weight at 33 µg mL^{-1} (Figure 3), approaching control conditions. For plant height and root length, although statistical differences among treatments within cultivars were noted, the mean values remained within the same statistical group. No significant improvement was observed for root dry weight following SOD supplementation (Figure 2B). These findings can be attributed to the inherent drought tolerance of these cultivars, allowing them to use internal physiological adjustments and organic

Table 2. Summary of Anova for growth traits of cotton plants under water stress and exogenous superoxide dismutase application.

Source of variation	DF	Mean square				
		LA	PH	RL	RDW	SDW
Cultivar (C)	3	36,782.09**	127.93**	77.19**	0.0296**	0.3077**
Treatment (T)	4	48,934.46**	74.67**	206.33**	0.0202**	0.3777**
C × T	12	1,432.28**	8.92*	20.37**	0.0014^{ns}	0.0107**
Replication	3	346.16	0.42	0.48	0.0007	0.0006
Error	57	288.84	4.15	7.09	0.0008	0.0040
CV (%)		8.12	8.28	11.39	13.97	5.69

DF: degree of freedom; LA: leaf area; PH: plant height; RL: root length; RDW: root dry weight; SDW: shoot dry weight; CV: coefficient of variation. **, * and ^{ns}: significant at 1 % and 5 % and not significant, respectively.

resources to maintain growth under water-limited conditions (Rodrigues et al. 2016, Vasconcelos et al. 2018). Macedo et al. (2019) demonstrated that both cultivars maintained their growth under 14 days of water suppression through efficient osmotic adjustment, reflected in lower variations for water potential.

Conversely, the drought-sensitive cultivars exhibited a more pronounced beneficial effect of exogenous SOD supplementation, particularly at the concentration of 33 μg mL^{-1} (Figures 1, 2 and 3). FM 966 and FMT 705, although robust and high-yielding cultivars, typically display limited adaptation to environments characterized by irregular water availability, such as semi-arid conditions (Rodrigues et al. 2016, Vasconcelos et al. 2018). The present findings suggest that exogenous SOD supplementation in stressed plant tissues potentially reduced the accumulated ROS, enhancing leaf expansion, plant growth balance and dry matter production (Figure 3). The likely mitigation of oxidative stress also reduced the moisture demand of the root system (Figure 2), indicating that the SOD supplementation at 33 μg mL^{-1} effectively restored the physiological homeostasis in stressed plants. This inference aligns with results reported by Rodrigues et al. (2016), who found no increase in endogenous SOD activity for these cultivars after 7 days of water stress, thereby limiting their capacity for ROS neutralization.

Table 3 summarizes the Anova results for gas exchange parameters of cotton cultivars subjected to water stress and exogenous SOD supplementation. Significant differences were identified among the treatments for all parameters. Genotype and cultivar × treatment (C x T) interaction effects were

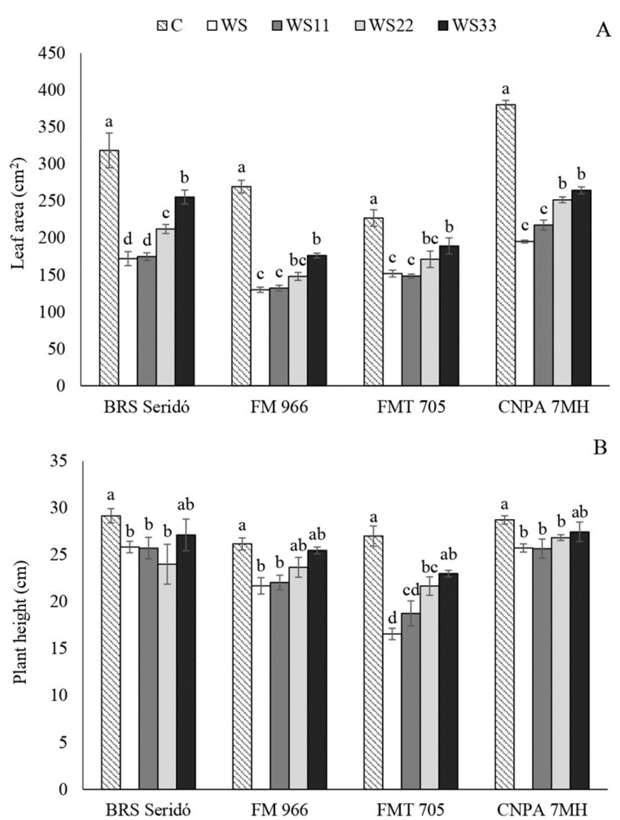

Figure 1. Leaf area (A) and plant height (B) of cotton genotypes under water stress and exogenous superoxide dismutase (SOD) treatment. C: control; WS: water stress; WS11, WS22 and WS33: water stress supplemented with SOD at 11, 22 and 33 μg mL^{-1}, respectively. Means followed by the same letter within each genotype do not differ significantly according to the Tukey test ($p < 0.05$). Bars represent standard errors.

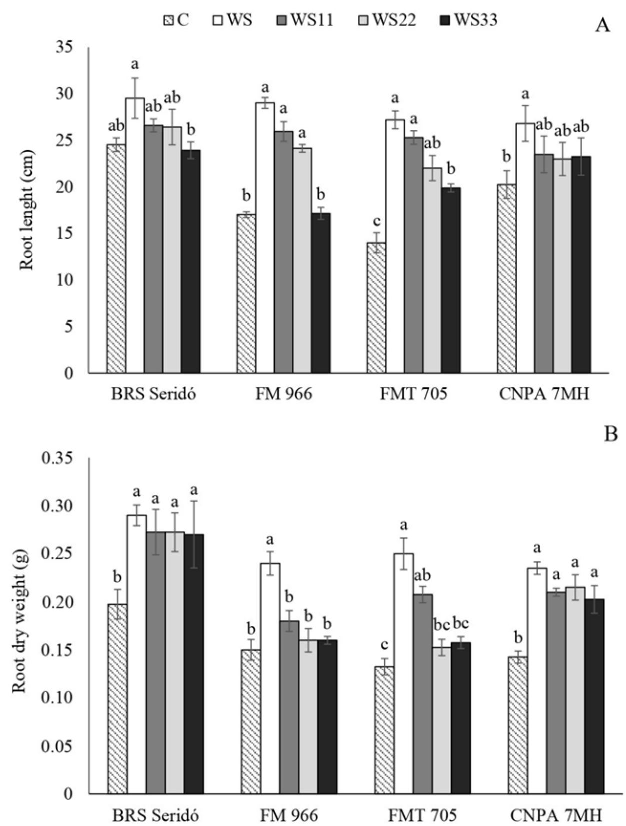

Figure 2. Root length (A) and root dry weight (B) of cotton genotypes under water stress and exogenous superoxide dismutase (SOD) treatment. C: control; WS: water stress; WS11, WS22 and WS33: water stress supplemented with SOD at 11, 22 and 33 μg mL^{-1}, respectively. Means followed by the same letter within each genotype do not differ significantly according to the Tukey test ($p < 0.05$). Bars represent standard errors.

Table 3. Summary of Anova for gas exchange parameters of cotton plants under water stress and exogenous superoxide dismutase application.

Source of variation	DF	Mean square				
		gs	*A*	*Ci*	*E*	*CEi*
Cultivars (C)	3	0.0003^{ns}	205.17**	556.76^{ns}	220.59**	0.0057**
Treatment (T)	4	0.0375**	110.93**	1,655.84**	32.89**	0.0023**
C × T	12	0.0012^{ns}	11.03**	301.61^{ns}	11.25**	0.0000**
Replication	3	0.00004	1.49	1,213.53	1.27	0.0001
Error	57	0.0007	3.32	264.18	0.92	0.0001
CV (%)		25.27	23.46	8.15	24.25	24.18

DF: degree of freedom; *gs*: stomatal conductance; *A*: CO_2 assimilation rate; *Ci*: internal CO_2 concentration; *E*: transpiration; *CEi*: instantaneous carboxylation efficiency; CV: coefficient of variation. ** Significant at 1 %; ^{ns} non-significant.

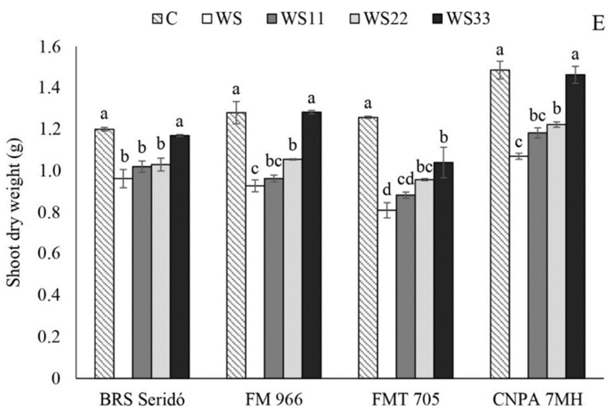

Figure 3. Shoot dry weight of cotton genotypes under water stress and exogenous superoxide dismutase (SOD) treatment. C: control; WS: water stress; WS11, WS22 and WS33: water stress supplemented with SOD at 11, 22 and 33 μg mL^{-1}, respectively. Means followed by the same letter within each genotype do not differ significantly according to the Tukey test ($p < 0.05$). Bars represent standard errors.

significant for CO_2 assimilation rate (*A*), transpiration rate (*E*) and instantaneous carboxylation efficiency (*CEi*).

Figure 4 presents the means of gas exchange parameters in cotton cultivars. Unlike growth traits, where stress effects manifest visually through plant phenotype, gas exchange parameters reflect earlier metabolic disturbances at the cellular level (Jiménez et al. 2013, Ferrari et al. 2015, Taiz et al. 2017). Although most growth traits demonstrated beneficial effects at the concentration of 33 μg mL^{-1} of SOD, gas exchange parameters exhibited optimal responses primarily at 22 μg mL^{-1}. A pronounced alleviation of water stress due to SOD supplementation was observed, particularly in the sensitive cultivars FM 966 and FMT 705, which experienced significant reductions in stomatal conductance (*gs*), photosynthetic rate (*A*) and transpiration rate (*E*).

The CNPA 7MH cultivar efficiently used exogenous SOD to restore cellular homeostasis in stressed tissues. Recovery in *gs* was achieved at the lowest SOD concentration (11 μg mL^{-1}) (Figure 4A), facilitating the increased CO_2 influx into the substomatal cavity (Figure 4C), reduced water loss via transpiration (Figure 4D) and restored photosynthetic rate at 22 μg mL^{-1} (Figure 4B).

Figure 5 illustrates the means for instantaneous carboxylation efficiency (*CEi*), an indicator of photosynthetic efficiency relative to CO_2 concentration in the substomatal chamber. A complete recovery was observed for BRS Seridó and FMT 705 at the concentration of 22 μg mL^{-1}, whereas FM 966 required SOD supplementation at 33 μg mL^{1} to fully restore the *CEi* levels.

The recovery of *CEi* in CNPA 7MH was limited to 27% at 22 μg mL^{-1}, in relation to the water-stressed treatment. This response may be related to its canopy architecture, characterized by fewer and smaller leaves, resulting in reduced photosynthetic activity, but less vulnerability to water stress (Silva et al. 2023). CNPA 7MH, renowned for its broad drought tolerance, originated from the cross between *Gossypium gossypium* var. *latifolium* and Marie-Galante, inheriting morphological and physiological traits that confer resilience to dry environments (Vasconcelos et al. 2018, Macedo et al. 2019, Silva et al. 2023). Rodrigues et al. (2016) noted this cultivar's intrinsic capability for adaptive adjustments under moderate to severe drought, making it an invaluable genetic resource for drought-tolerance breeding programs.

Drought adverse effects significantly influence crop management, directly affecting growth and yield. While genetic traits and gene transfer strategies are

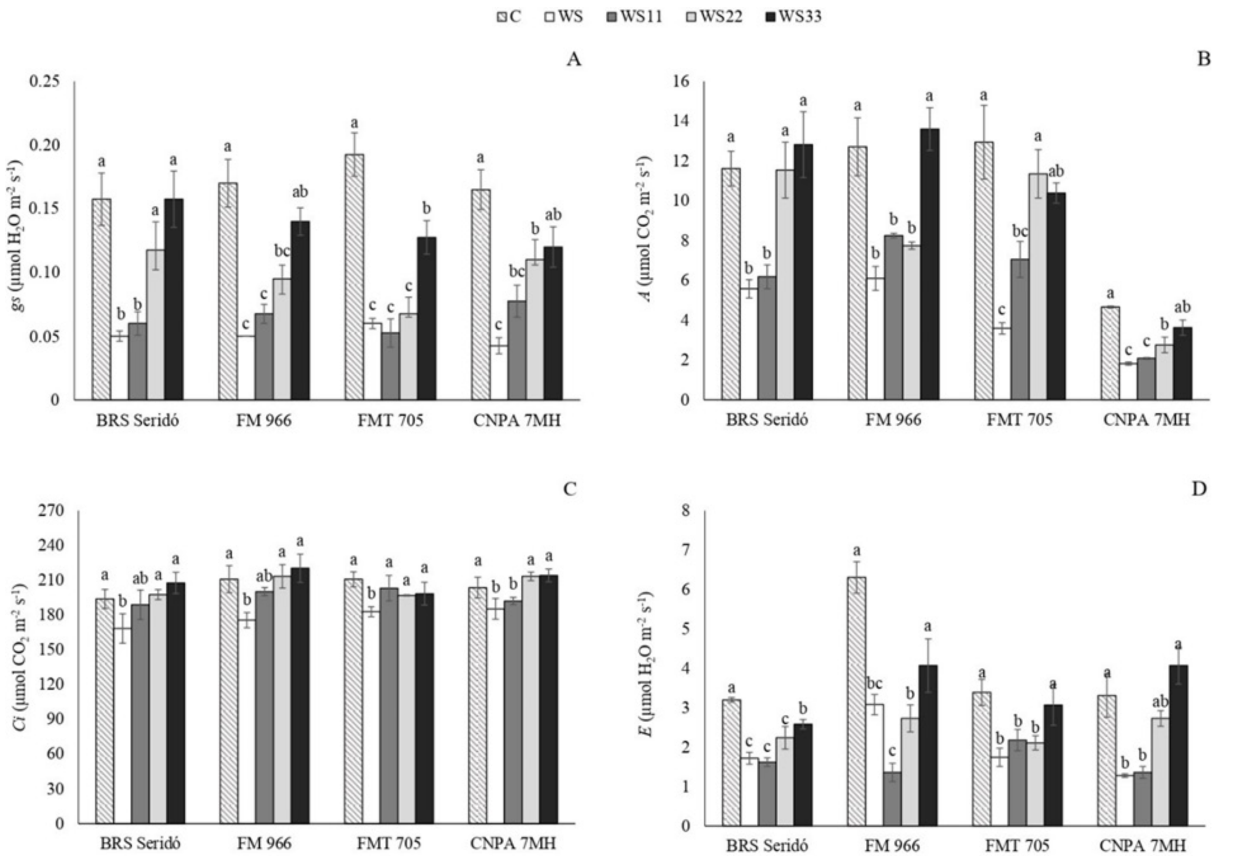

Figure 4. Stomatal conductance (*gs*; A); CO_2 assimilation rate (*A*; B); internal CO_2 concentration (*Ci*; C) and transpiration rate (*E*; D) of cotton cultivars subjected to water stress and exogenous superoxide dismutase (SOD) supplementation. C: control; WS: water stress; WS11, WS22 and WS33: water stress supplemented with SOD at concentrations of 11, 22 and 33 µg mL^{-1}, respectively. Means followed by the same letter within each genotype do not differ significantly according to the Tukey test ($p < 0.05$). Bars represent standard errors.

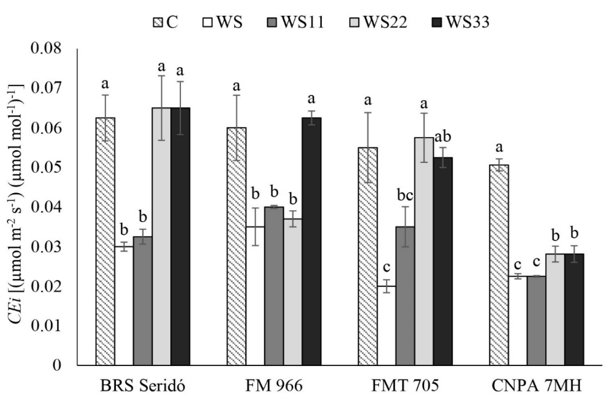

Figure 5. Instantaneous carboxylation efficiency (*CEi*) of cotton genotypes under water stress and treated with exogenous superoxide dismutase (SOD). C: control; WS: water stress; WS11, WS22 and WS33: water stress supplemented with SOD at concentrations of 11, 22 and 33 µg mL^{-1}, respectively. Means followed by the same letter within each genotype do not differ significantly according to the Tukey test ($p < 0.05$). Bars represent standard errors.

commonly employed to enhance drought tolerance in commercial cultivars, these cultivars, despite their robust productivity, often exhibit vulnerability under prolonged water deficits (Rodrigues et al. 2016, Silva et al. 2023).

Although drought tolerance has a genetic basis, maintaining a minimum water supply throughout the crop cycle is crucial, especially during critical periods such as the onset of flowering and cotton square formation (Chiavegato et al. 2009). Water scarcity during these phases results in the abscission of reproductive structures, ultimately leading to yield reduction (Bezerra et al. 2010, Aquino et al. 2012, Silva et al. 2023). This adverse impact is particularly pronounced in drought-sensitive cultivars, limiting their suitability to more favorable environmental conditions (Silva et al. 2023).

The exogenous application of organic compounds to mitigate drought stress offers potential to broaden the adaptation range of sensitive yet high-yielding cultivars to areas with irregular rainfall (Barbosa et al. 2023, Silva et al. 2023). While various organic compounds have been tested for alleviating plant stress damage, the role of exogenous SOD remains relatively underexplored, despite its critical involvement in cellular defense against oxidative stress. As an initial enzyme in detoxification pathways, exogenous SOD supplementation may confer additional physiological benefits to stress-sensitive plants.

Barbosa et al. (2023) treated two peanut cultivars with contrasting drought tolerances with exogenous SOD after a week of drought stress. Their results demonstrated an effective mitigation of drought stress through improved gas exchange and antioxidant enzyme activity, with the sensitive cultivar exhibiting more pronounced recovery at lower SOD concentrations (11 μg mL^{-1}), likely due to its more responsive stress-coping mechanisms.

Building upon these findings, the present study, employing contrasting cotton cultivars, underscores the potential of exogenous SOD supplementation to alleviate drought-induced physiological impairments, particularly in sensitive genotypes. Notably, FMT 705 exhibited a significant gas exchange recovery at a relatively low SOD concentration (33 μg mL^{-1}). Although FMT 705 is highly productive and recommended for the Cerrado (Brazilian Savanna) region, its susceptibility to irregular rainfall limits its use.

Despite the modest outcomes observed herein, this research highlights promising directions for future studies investigating low-concentration antioxidant supplementation as a strategy to mitigate drought-induced physiological disruptions in short-cycle commercial crops.

CONCLUSIONS

1. The exogenous supplementation of superoxide dismutase (SOD) at the concentration of 33 μg mL^{-1} effectively mitigates the adverse effects of drought stress on the growth of cotton cultivars during the vegetative phase;
2. Drought-sensitive cultivars exhibit pronounced benefits from exogenous SOD supplementation, significantly restoring gas exchange parameters starting from a concentration of 22 μg mL^{-1}.

REFERENCES

APEL, K.; HIRT, H. Reactive oxygen species: metabolism oxidative stress, and signal transduction. *Annual Review of Plant Biology*, v. 55, n. 1, p. 373-399, 2004.

AQUINO, L. A.; AQUINO, R. F. B. A.; SILVA, T. C.; SANTOS, D. F.; BERGER, P. G. Aplicação do fósforo e da irrigação na absorção e exportação de nutrientes pelo algodoeiro. *Revista Brasileira de Engenharia Agrícola e Ambiental*, v. 16, n. 4, p. 355-361, 2012.

AZIZ, A.; AKRAM, N. A.; ASHRAF, M. Influence of natural and synthetic vitamin C (ascorbic acid) on primary and secondary metabolites and associated metabolism in quinoa (*Chenopodium quinoa* Willd.) plants under water deficit regimes. *Plant Physiology and Biochemistry*, v. 123, n. 1, p. 192-203, 2018.

BARBOSA, D. D.; FERNANDES, P. D.; MARCELINO, A. D. A. L.; SILVA, F. A.; DIAS, M. S.; SILVA, C. R. C.; SANTOS, R. C. Exogenous pyruvate mitigates the detrimental effects of water stress in contrasting peanut genotypes. *Genetics and Molecular Research*, v. 20, n. 3, egmr18907, 2021.

BARBOSA, D. D.; MARCELINO, A. D. A. L.; FERNANDES, P. D.; SILVA, F. A.; FERRAZ, R. L. S.; SANTOS, R. C. Exogenous superoxide dismutase mitigates cell damage in drought-sensitive peanuts. *Genetics and Molecular Research*, v. 22, n. 3, egmr19115, 2023.

BARBOSA, M. R.; SILVA, M. M. A.; WILLADINO, L.; ULISSES, C.; CÂMARA, T. R. Geração e desintoxicação enzimática de espécies reativas de oxigênio em plantas. *Ciência Rural*, v. 44, n. 3, p. 453-460, 2014.

BEZERRA, J. R. C.; AZEVEDO, P. V.; SILVA, B. B.; DIAS, J. M. Evapotranspiração e coeficiente de cultivo do algodoeiro BRS-200 Marrom, irrigado. *Revista Brasileira de Engenharia Agrícola e Ambiental*, v. 14, n. 6, p. 625-632, 2010.

CHAVES, M. M.; FLEXAS, J.; PINHEIRO, C. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. *Annals of Botany*, v. 103, n. 4, p. 551-560, 2009.

CHIAVEGATO, E. J.; SALVATIERRA, D. K.; GOTTARDO, L. C. B. Cultivos temporários: algodão. *In*: MONTEIRO, J. E. (ed.). *Agrometeorologia dos cultivos*: o fator meteorológico na produção agrícola. Brasília, DF: INMET, 2009. p. 35-49.

DUTRA, W. F.; GUERRA, Y. L.; RAMOS, J. P. C.; FERNANDES, P. D.; SILVA, C. R. C.; BERTIOLI, D. J.; LEAL-BERTIOLI, S. C. M.; SANTOS, R. C. Introgression of wild alleles into the tetraploid peanut crop to improve water use efficiency, earliness and yield. *Plos One*, v. 13, n. 6, e0198776, 2018.

DUTRA, W. F.; MELO, A. S.; SUASSUNA, J. F.; DUTRA, A. F.; SILVA, D. C.; MAIA, J. M. Antioxidative responses of cowpea cultivars to water deficit and salicylic acid treatment. *Agronomy Journal*, v. 109, n. 3, p. 895-905, 2017.

FERRARI, E.; PAZ, A.; SILVA, A. C. Déficit hídrico no metabolismo da soja em semeaduras antecipadas no Mato Grosso. *Nativa*, v. 3, n. 1, p. 67-77, 2015.

FERREIRA, D. F. Sisvar: a computer analysis system to fixed effects split plot type designs. *Revista Brasileira de Biometria*, v. 37, n. 4, p. 529-535, 2019.

FOYER, C. H. Reactive oxygen species, oxidative signaling and the regulation of photosynthesis. *Environmental and Experimental Botany*, v. 154, n. 1, p. 134-142, 2018.

GILL, S. S.; TUTEJA, N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiology and Biochemistry*, v. 48, n. 12, p. 909-930, 2010.

JIMÉNEZ, S.; DRIDI, J.; GUTIÉRREZ, D.; MORET, D.; IRIGOYEN, J. J.; MORENO, M. A.; GOGORCENA, Y. Physiological, biochemical and molecular responses in four Prunus rootstocks submitted to drought stress. *Tree Physiology*, v. 33, n. 10, p. 1061-1075, 2013.

KHAN, A.; PAN, X.; NAJEEB, U.; TAN, D. K. Y.; FAHAD, S.; ZAHOOR, R.; LUO, H. Coping with drought: stress and adaptive mechanisms, and management through cultural and molecular alternatives in cotton as vital constituents for plant stress resilience and fitness. *Biological Research*, v. 51, n. 1, e47, 2018.

MACEDO, E. C. F.; ZONTA, J. H.; MELO, Y. L.; MELO, A. S.; SILVA, D. C.; ANDRADE, W. L. Changes in osmoregulatory metabolism of cotton genotypes during water deficit and recovery period. *Revista Brasileira de Engenharia Agrícola e Ambiental,* v. 23, n. 8, p. 607-613, 2019.

MARUR, C. J.; RUANO, O. A reference system for determination of cotton plant development. *Revista de Oleaginosas e Fibrosas*, v. 5, n. 2, p. 243-247, 2001.

MONTEIRO, J. E. B. A.; SENTELHAS, P. C.; CHIAVEGATO, E. J.; GUISELINE, C.; SANTIAGO, A. V.; PRELA, A. Estimação da área foliar do algodoeiro por meio de dimensões e massa das folhas. *Bragantia*, v. 64, n. 1, p. 15-24, 2005.

PEREIRA, J. W. L.; MELO FILHO, P. A.; ALBUQUERQUE, M. B.; NOGUEIRA, R. J. M. C.; SANTOS, R. C. Mudanças bioquímicas em genótipos de amendoim submetidos a déficit hídrico moderado. *Ciência Agronômica*, v. 43, n. 4, p. 766-773, 2012.

RODRIGUES, J. D.; SILVA, C. R. C.; PEREIRA, R. F.; RAMOS, J. P. C.; MELO FILHO, P. A.; CAVALCANTI, J. J. V.; SANTOS, R. C. Characterization of water-stress tolerant cotton cultivars based on plant growth and in activity of antioxidant enzymes. *African Journal of Agricultural Research*, v. 11, n. 39, p. 3763-3770, 2016.

SADIQ, M.; AKRAM, N. A.; ASHRAF, M. Foliar applications of alpha-tocopherol improves the composition of fresh pods of *Vigna radiata* subjected to water deficiency. *Turkish Journal of Botany*, v. 41, n. 3, p. 244-252, 2017.

SANTOS, T. B.; RIBAS, A. F.; SOUZA, S. G. H.; BUDZINSKI, I. G. F.; DOMINGUES, D. S. Physiological responses to drought, salinity, and heat stress in plants: a review. *Stresses*, v. 2, n. 1, p. 113-135, 2022.

SHARMA, P.; SHARMA, P.; ARORA, P.; VERMA, V.; KHANNA, K.; SAINI, P.; BHARDWAJ, R. Role and regulation of ROS and antioxidants as signaling molecules in response to abiotic stresses. *In*: KHAN, M. I. R.; REDDY, P. S.; FERRANTE, A.; KHAN, N. A. (ed.). *Plant signaling molecule*: role and regulation under stressful environments. Cambridge: Woodhead Publishing, 2019. p. 141-156.

SILVA, F. A.; DIAS, M. S.; FERNANDES, P. D.; MARCELINO, A. D. A. L.; LIMA, A. M.; PEREIRA, R. F.; BARBOSA, D. D.; SILVA, M. F. C. S.; SILVA, A. A. R.; SANTOS, R. C. Pyruvic acid as attenuator of water deficit in cotton plants varying the phenological stage. *Brazilian Journal of Biology*, v. 83, e272003, 2023.

TAIZ, L.; ZEIGER, E.; MOLLER, I. M.; MURPHY, A. *Fisiologia e desenvolvimento vegetal*. 6. ed. Porto Alegre: Artmed, 2017.

VASCONCELOS, U. A. A.; CAVALCANTI, J. J. V.; FARIAS, F. J. C.; VASCONCELOS, W. S.; SANTOS, R. C. Diallel analysis in cotton (*Gossypium hirsutum* L.) for water stress tolerance. *Crop Breeding and Applied Biotechnology*, v. 18, n. 1, p. 24-30, 2018.

YI, X-P.; ZHANG, Y-L.; YAO, H-S.; LUO, H-H.; GOU, L.; CHOW, W. S.; ZHANG, W-F. Rapid recovery of photosynthetic rate following soil water deficit and re-watering in cotton plants (*Gossypium herbaceum* L.) is related to the stability of the photosystems. *Journal of Plant Physiology*, v. 194, n. 1, p. 23-34, 2016.