UNIVERSIDADE FEDERAL DE LAVRAS

MAYANA PEREIRA MAIA

ROLE OF IODINE IN ATTENUATING WATER STRESS AND TOMATO FRUIT QUALITY

LAVRAS – MG
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Dissertation presented to the Federal University of Lavras, as part of the requirements of the Graduate Program in Agronomy/Plant Physiology, to obtain the title of Master.

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Advisor

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MAYANA PEREIRA MAIA

ROLE OF IODINE IN ATTENUATING WATER STRESS AND TOMATO FRUIT QUALITY

PAPEL DO IODO NA ATENUAÇÃO DO ESTRESSE POR DÉFICIT HÍDICO E NA QUALIDADE DO FRUTO DE TOMATE

Dissertation presented to the Federal University of Lavras, as part of the requirements of the Graduate Program in Agronomy/Plant Physiology, to obtain the title of Master.

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RESUMO

O estresse por déficit hídrico representa um desafio para as plantas cultivadas em cenários de mudanças climáticas. Este estudo teve como foco o uso de diferentes fontes de iodo para atenuar os sintomas causados pelo estresse hídrico em tomate (*Solanum lycopersicum* L. cv Micro-Tom), conhecidos por sua sensibilidade a essa condição, além dos efeitos sobre a qualidade dos frutos. O delineamento foi inteiramente ao acaso em esquema fatorial 3 × 2, com duas condições hídricas (irrigado e déficit hídrico) e três condições de adubação de cobertura (ureia, ureia + iodeto de potássio (KI) e ureia + iodato de potássio (KIO_3)), com seis repetições. A adubação de cobertura foi realizada aos 15 e 30 dias após o transplantio (DAT). O estresse hídrico foi induzido de forma gradual, a partir dos 35 DAT das mudas, com duração total de 9 dias. No primeiro dia, teve uma redução de 25% no volume de água fornecido às plantas. Nos dias 2, 3, 4 e 5, a irrigação foi mantida em 60% da capacidade de campo (CC). Nos dias 6 e 7, a irrigação foi reduzida para 50% da CC. Finalmente, nos dias 8 e 9, a irrigação foi totalmente suspensa, e o estresse máximo foi observado nas plantas. Em seguida, o fornecimento de água foi restabelecido conforme a reidratação das plantas, sendo mantido até a coleta final, no fim do ciclo fenológico. Os parâmetros bioquímicos e fisiológicos foram analisados no ponto de estresse máximo e cinco dias após a reidratação, enquanto os parâmetros pós-colheita dos frutos foram avaliados ao final do ciclo (45–90 DAT). Foram analisados os parâmetros bioquímicos, fisiológicos, o estado hídrico das plantas e a qualidade pós-colheita dos frutos. O iodo modulou a alocação de biomassa, favorecendo o crescimento radicular e a absorção de água. Além disso, promoveu a resposta antioxidante, reduziu os danos oxidativos e manteve o metabolismo celular. O déficit hídrico comprometeu a fotossíntese e a produtividade, mas plantas tratadas com KI mantiveram maior taxa fotossintética. O KIO_3 contribuiu para a manutenção dos teores de proteínas e clorofila, sugerindo um papel na regulação do metabolismo do nitrogênio e dos carboidratos e no aumento da resiliência ao estresse. O iodo influenciou a qualidade dos frutos, elevando os sólidos solúveis e compostos antioxidantes, como β-caroteno e flavonoides. O tratamento com ureia + KIO_3 prolongou a vida útil pós-colheita, indicando sua eficácia na mitigação do estresse hídrico e na melhoria da qualidade nutricional e funcional dos frutos. Esses resultados destacam o potencial do KIO_3 como agente mitigador do estresse hídrico em tomateiros e seu efeito positivo na qualidade pós-colheita dos frutos.

Palavras-chave: mudanças climáticas; estresse abiótico; mitigação de estresse; metabolismo antioxidante.

ABSTRACT

Water deficit stress poses a challenge to cultivated plants during climate change. This study focused on the use of different sources of iodine to attenuate the symptoms caused by water deficit stress in tomatoes (*Solanum lycopersicum* L. cv Micro-Tom) and its effect on fruit quality are known for their sensitivity to this condition. A completely randomized 3 × 2 factorial scheme (DIC) was used with two water conditions (irrigation and water deficit) and three top-dressing conditions (urea, urea + potassium iodide (KI), and urea + potassium iodate (KIO_3)), with six replications. Cover fertilization, performed with urea enriched with different sources of iodine, was applied 15 and 30 days after transplanting. Water stress was implemented gradually 35 days after transplanting (DAT) of the seedlings for a total duration of 9 days. On the first day, a 25% reduction in the water volume was applied to the plants. On days 2, 3, 4, and 5, irrigation was maintained at 60% of CC. On days 6 and 7, irrigation was reduced to 50% of CC. Finally, on the 8th and 9th day, irrigation was completely suspended, and maximum stress was observed on the plants. Afterwards, the water supply was restored when the rehydration of the plants was considered, which was maintained until the final collection, at the end of the phenological cycle. The biochemical and physiological parameters were analyzed at maximum stress and five days after rehydration, and the postharvest parameters of the fruits were analyzed at the end of the cycle (45–90 days after transplanting). Biochemical and physiological parameters, water status, and postharvest fruit quality were analyzed. Iodine modulates biomass allocation, favoring root growth and water absorption. In addition, it improves the antioxidant response, reduces oxidative damage, and maintains cellular metabolism. Water deficits compromised photosynthesis and productivity, but plants treated with KI maintained a higher photosynthetic rate. KIO_3 contributed to the maintenance of protein and chlorophyll contents, suggesting a role in regulating nitrogen and carbohydrate metabolism and increasing resilience to stress. Iodine influences fruit quality by increasing soluble solids and antioxidant compounds, such as β-carotene and flavonoids. Treatment with urea + KIO_3 extended the postharvest shelf life, indicating its efficacy in mitigating water stress and improving the nutritional and functional quality of fruits. These results highlight the potential of KIO_3 as a mitigator of water deficit stress in tomato plants and improves fruit quality in postharvest.

Keywords: climate change; abiotic stress; stress mitigation; antioxidant metabolism.

INDICADORES DE IMPACTO

Este estudo faz contribuições significativas para agricultura ao demonstrar o potencial da ureia enriquecida com iodo na mitigação dos efeitos adversos do estresse por déficit hídrico em plantas de tomate. As mudanças climáticas impõem desafios à agricultura, especialmente devido ao aumento das temperaturas e às alterações nos padrões de precipitação, que intensificam a escassez de água nas culturas. Dado o alto consumo hídrico das plantas de tomate, o desenvolvimento de estratégias eficazes para aliviar o estresse hídrico e preservar a qualidade dos frutos é essencial. Esta pesquisa investiga a ureia enriquecida com iodo como uma abordagem inovadora para aumentar a resiliência das plantas em condições de déficit hídrico. Os resultados avançam as técnicas de fertilização mineral ao otimizar a aplicação de iodo para melhorar as respostas fisiológicas e a qualidade pós-colheita dos frutos. Ao elucidar o papel de diferentes fontes de iodo na tolerância à seca, este estudo contribui para o desenvolvimento de práticas agrícolas inteligentes para o clima, que sustentam a produtividade e aprimoram a qualidade nutricional em ambientes com disponibilidade limitada de água.

IMPACT INDICATORS

This study makes significant contributions to agriculture by demonstrating the potential of iodine-enriched urea in mitigating the detrimental effects of water deficit stress on tomato plants. Climate change imposes substantial challenges on agriculture, particularly due to rising temperatures and altered precipitation patterns, which exacerbate water scarcity in crops. Given the high water demand of tomatoes, developing effective strategies to alleviate drought stress while preserving fruit quality is essential. This research investigates iodine-enriched urea as an innovative approach to enhance plant resilience under water deficit conditions. The findings advance mineral fertilization techniques by optimizing iodine application to improve physiological responses and postharvest fruit quality. By elucidating the role of different iodine sources in drought tolerance, this study contributes to the development of climate-smart agricultural practices that sustain productivity and enhance nutritional quality in water-limited environments.

SUMMARY

FIRST PART

GENERAL INTRODUCTION

Climate change resulting from anthropogenic and geological actions has a strong influence on agriculture. Forecasts suggest that in the coming years, climate change will continue to occur, with an increase in temperature and changes in rainfall patterns expected in several regions (Medeiros et al., 2023; Yin et al., 2018). These changes expose crops to periods of water deficit, which is becoming increasingly frequent. Water deficit is one of the major causes of reduced agricultural productivity because it negatively affects the growth and development of crops (Joshi et al., 2016; Koch et al., 2019).

Water deficits in plants cause a series of changes in photosynthetic processes, resulting in significant reductions in crop growth, development, and production. Under conditions of low water availability, there is a reduction in the water potential of the plant, leading to stomatal closure. This mechanism, mediated by abscisic acid (ABA), is a crucial strategy for water conservation; however, it also limits the assimilation of CO_2 by leaves by reducing the production of photoassimilates (Pinheiro and Chaves, 2011). Consequently, partitioning of photoassimilates between plant organs is impaired, resulting in lower crop growth and yield (Kaur et al., 2021).

This impact is particularly critical in crops with a high-water demand, such as tomatoes (*Solanum lycopersicum* L.), which require irrigation during all stages of cultivation (Patanè et al., 2011). Water accounts for more than 90% of the fresh weight of many fleshy fruits (Davies et al., 1981), including tomatoes, making water deficit a challenge for their cultivation because in addition to reducing productivity, it reduces the quality of the fruits.

Tomato, especially the Micro-Tom cultivar, is widely used as a model species in physiological studies due to its well-characterized genetic profile and ease of genetic manipulation (Chaudhary et al., 2019; Martí et al., 2006). This crop is highly sensitive to water scarcity, especially during the flowering and fruit development stages, and can trigger a variety of responses at all stages of development (Chen et al., 2014; Claeys and Inzé, 2013). These responses may be mediated by reactive oxygen species (ROS) signaling, but excess ROS can cause oxidative damage (Das and Roychoudhury, 2014).

To combat this excess, plants stimulate their antioxidant defense system with enzymes such as ascorbate peroxidase (APX), superoxide dismutase (SOD), and catalase (CAT) (Altaf et al., 2022). In addition to accumulating compatible solutes, such as glutathione, flavonoids, and proline, to maintain water potential, they play a key role in signaling and mitigating stress (Ahanger et al., 2021).

Water regime during fruit formation is a determinant of tomato quality and influences sensory and nutritional attributes. Water deficiency can compromise the integrity of the fruit, accelerating its deterioration and altering the concentration of metabolites that affect flavor, color, nutritional value, shelf life, and functional potential (Chen et al., 2014; Hou et al., 2020). In addition, water restriction modifies the water content and synthesis of volatile compounds responsible for the characteristic aroma and flavor of tomatoes, directly affecting their acceptance by the consumer (Hou et al., 2020; Liu et al., 2015).

Fruit quality is defined by characteristics, such as pH, total acidity, soluble solids, firmness, vitamin C, carotenoids, flavonoids, total antioxidant activity, and phenolic compounds. These parameters are essential for defining the sensory profile and nutritional quality of tomatoes, and influence everything from taste perception to health benefits (Hou et al., 2020). The pH affects the perceived acidity and flavor balance in tomatoes and can lead to a more intense or milder flavor. Titratable acidity is directly related to the acidic taste of tomatoes. Total soluble solids are essential for the sweet taste of tomatoes, and the concentration of soluble solids can be increased under water deficit conditions, as the reduction of water content concentrates solutes. Carotenoids, including lycopene and β-carotene, are responsible for the red color of tomatoes. These compounds, along with vitamin C, contribute to the nutritional value of tomatoes and possess antioxidant properties that are important for human health. The biosynthesis of these compounds can be significantly affected by water deficit conditions (Liu et al., 2015).

Shelf life refers to the period during which the fruit maintains its commercial quality and acceptability for consumption after harvest. Firmness and respiratory activity are the determining factors in this process, directly influencing post-harvest quality. Fruits with greater firmness tend to have a lower rate of cell wall degradation, delayed softening, and senescence, which prolongs their shelf life. Firmer fruits are less susceptible to mechanical damage and infection (Beckles et al., 2012). In contrast, respiratory activity is directly related to fruit metabolism, and high rates accelerate the consumption of sugars and production of ethylene, promoting faster ripening and deterioration (Umeohia and Olapade, 2024). Thus, the interaction between these factors defines the durability of the fruit after harvest, impacting its commercialization and acceptance by consumers.

Many studies have sought to reduce the damage caused by water stress because losses can be irreversible (Seleiman et al., 2021). The strategic application of exogenous iodine could be a promising solution to mitigate the effects of water deficit stress and strengthen tomato production under unfavorable conditions. In addition to being essential for human health, iodine demonstrates beneficial properties for plants, improves resistance to stress, and stimulates plant growth (Kiferle et al., 2021). Research indicates that the application of iodine can increase the synthesis of active compounds, such as ascorbic acid and phenolic compounds, as well as increase the activity of antioxidant enzymes in several species, including soybeans (*Glycine max*), lettuce (*Lactuca sativa*), coffee (*Coffea arabica*) and tomatoes (*Solanum lycopersicum* L.) (Andrade et al., 2024; Blasco et al., 2011; Leyva et al., 2011; Lima et al., 2023a, 2023b). In addition, evidence suggests that iodine may improve the quality of tomato and strawberry fruits by promoting greater antioxidant capacity and the accumulation of phenolic compounds (Lima et al., 2023a; Medrano Macías et al., 2021). These metabolic modifications may in part be associated with protein iodination, a mechanism that influences essential physiological and biochemical processes in plants (Kiferle et al., 2021). However, little is known about the mechanisms by which iodine mitigates abiotic stress.

The limits of beneficial concentrations and toxicity of iodine vary among plant species because of the inherent variability and specific interaction of each species with edaphic, climatic, and biotic variables (Halka et al., 2018; Medrano-Macías et al., 2016). In addition to differences in the application technology, the source and dose of iodine were used. The toxicity of iodine is highly dependent on its chemical form; iodides (I^-) are better absorbed and simultaneously more toxic to plants than iodines (IO_3^-) (Hong et al., 2012; Lawson et al., 2015). When applied as iodide, especially in soil cultivation systems, where natural geochemical processes lead to alteration in iodine speciation, the sensitivity of plants to iodine toxicity increases significantly (Duborská et al., 2018).

In tomatoes (*Solanum lycopersicum*), foliar applications of potassium iodate (KIO_3) at concentrations between 10 and 50 μM improved the antioxidant activity and the content of phenolic compounds in the fruits without causing phytotoxic effects, while the application of 100 μM potassium iodide via nutrient solution conferred greater tolerance to water deficit and improved fruit quality (Blasco et al., 2011). In soybean (*Glycine max*), supplementation with 10 and 20 μM KI via nutrient solution improved tolerance to water deficit, increasing biomass and photosynthetic efficiency, whereas concentrations higher than 10 μM caused a reduction in biomass accumulation under full irrigation (Lima et al., 2023b). In coffee plants (*Coffea arabica*), foliar application of potassium iodate (KIO_3) at concentrations of 0.05% and 0.1% improved vegetative growth and chlorophyll content in leaves without causing symptoms of toxicity (Andrade et al., 2024). In addition, these doses increased the activity of antioxidant enzymes, suggesting a potential role for iodine in mitigating oxidative stress in coffee plants. In maize (*Zea mays*), the incorporation of potassium iodate (KIO_3) in enriched urea (0.2% iodine) improves nitrogen uptake and reduces volatilization losses, benefiting plant growth (Cezar et al., 2024). Therefore, the choice of dose and chemical form of iodine must consider the characteristics of the crop, cultivation environment, and route of application to maximize benefits and avoid adverse effects.

Adoption of new technologies by farmers is challenging. In this context, incorporating iodine into widely used inputs, such as urea, can facilitate their acceptance, making it possible to maximize fertilization efficiency without the need to increase application activities in field conditions. In addition, a recent study on iodine-enriched urea (0.2% I) demonstrated the potential of this combination to reduce nitrogen volatilization and improve its absorption (Cezar et al., 2024).

Therefore, it is essential to elucidate the physiological and biochemical mechanisms underlying the application of iodine as a mitigator of water deficit in tomatoes. Understanding their role in modulating oxidative stress, maintaining water homeostasis, and preserving metabolic integrity will enable the development of more effective agronomic strategies. Thus, this study will contribute to formulating innovative management practices aimed at the sustainability of agricultural production and obtaining fruits with superior quality and greater nutritional value.

REFERENCES

AHANGER, M. A. et al. Improving growth and photosynthetic performance of drought stressed tomato by application of nano-organic fertilizer involves up-regulation of nitrogen, antioxidant and osmolyte metabolism. **Ecotoxicology and Environmental Safety**, v. 216, p. 112195, 2021.

ALTAF, M. A. et al. Melatonin Improves Drought Stress Tolerance of Tomato by Modulating Plant Growth, Root Architecture, Photosynthesis, and Antioxidant Defense System. **Antioxidants**, v. 11, n. 2, 2022.

ANDRADE, O. V. S. et al. The Role of Potassium Iodate in Mitigating the Damages of Water Deficit in Coffee Plants. **Journal of Soil Science and Plant Nutrition**, 2024.

BECKLES, D. M. et al. Biochemical factors contributing to tomato fruit sugar content: a review. **Fruits**, v. 67, n. 1, p. 49–64, 2012.

BLASCO, B. et al. Does Iodine Biofortification Affect Oxidative Metabolism in Lettuce Plants? **Biological Trace Element Research**, v. 142, n. 3, p. 831–842, 2011.

CEZAR, J. V. DA C. et al. Iodine-Enriched Urea Reduces Volatilization and Improves Nitrogen Uptake in Maize Plants. **Nitrogen**, v. 5, n. 4, p. 891–902, 2 out. 2024.

CHAUDHARY, J. et al. Advances in Omics Approaches for Abiotic Stress Tolerance in Tomato. **Biology**, v. 8, n. 4, p. 90, 25 nov. 2019.

CHEN, J. et al. Modeling relations of tomato yield and fruit quality with water deficit at different growth stages under greenhouse condition. **Agricultural Water Management**, v. 146, p. 131–148, 2014.

CLAEYS, H.; INZÉ, D. The Agony of Choice: How Plants Balance Growth and Survival under Water-Limiting Conditions. **Plant Physiology**, v. 162, n. 4, p. 1768–1779, 1 ago. 2013.

DAS, K.; ROYCHOUDHURY, A. Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. **Frontiers in Environmental Science**, v. 2, 2014.

DAVIES, J. N.; HOBSON, G. E.; MCGLASSON, W. B. The constituents of tomato fruit — the influence of environment, nutrition, and genotype. **C R C Critical Reviews in Food Science and Nutrition**, v. 15, n. 3, p. 205–280, 1 nov. 1981.

DUBORSKÁ, E.; URÍK, M.; KUBOVÁ, J. Interaction with soil enhances the toxic effect of iodide and iodate on barley (Hordeum vulgare L.) compared to artificial culture media during initial growth stage. **Archives of Agronomy and Soil Science**, v. 64, n. 1, p. 46–57, 2 jan. 2018.

EMMANUEL UMEOHIA, U.; ADEKUNLE OLAPADE, A. Quality Attributes, Physiology, and Postharvest Technologies of Tomatoes (Lycopersicum Esculentum) – A Review. **American Journal of Food Science and Technology**, v. 12, n. 2, p. 42–64, 26 mar. 2024.

HALKA, M. et al. Organic iodine supply affects tomato plants differently than inorganic iodine. **Physiologia Plantarum**, v. 164, n. 3, p. 290–306, 1 nov. 2018.

HONG, C. et al. Evaluation of Iodide and Iodate for Adsorption–Desorption Characteristics and Bioavailability in Three Types of Soil. **Biological Trace Element Research**, v. 146, n. 2, p. 262–271, 2012.

HOU, X. et al. Responses of water accumulation and solute metabolism in tomato fruit to water scarcity and implications for main fruit quality variables. **Journal of Experimental Botany**, v. 71, n. 4, p. 1249–1264, 19 fev. 2020.

JOSHI, R. et al. Transcription Factors and Plants Response to Drought Stress: Current Understanding and Future Directions. **Frontiers in Plant Science**, v. 7, 14 jul. 2016.

KAUR, H. et al. Scrutinizing the impact of water deficit in plants: Transcriptional regulation, signaling, photosynthetic efficacy, and management. **Physiologia Plantarum**, v. 172, n. 2, p. 935–962, 1 jun. 2021.

KIFERLE, C. et al. Evidences for a Nutritional Role of Iodine in Plants. **Frontiers in Plant Science**, v. 12, 2021.

KOCH, G. et al. Leaf Production and Expansion: A Generalized Response to Drought Stresses from Cells to Whole Leaf Biomass—A Case Study in the Tomato Compound Leaf. **Plants**, v. 8, n. 10, p. 409, 12 out. 2019.

LAWSON, P. G. et al. Soil versus foliar iodine fertilization as a biofortification strategy for field-grown vegetables. **Frontiers in Plant Science**, v. 6, 2015.

LEYVA, R. et al. Beneficial effects of exogenous iodine in lettuce plants subjected to salinity stress. **Plant Science**, v. 181, n. 2, p. 195–202, 2011.

LIMA, J. DE S. et al. KI Increases Tomato Fruit Quality and Water Deficit Tolerance by Improving Antioxidant Enzyme Activity and Amino Acid Accumulation: A Priming Effect or Relief during Stress? **Plants**, v. 12, n. 23, 2023a.

LIMA, J. DE S. et al. Soybean Plants Exposed to Low Concentrations of Potassium Iodide Have Better Tolerance to Water Deficit through the Antioxidant Enzymatic System and Photosynthesis Modulation. **Plants**, v. 12, n. 13, 2023b.

LIU, L. et al. Regulation of Carotenoid Metabolism in Tomato. **Molecular Plant**, v. 8, n. 1, p. 28–39, 5 jan. 2015.

MARTÍ, E. et al. Genetic and physiological characterization of tomato cv. Micro-Tom. **Journal of Experimental Botany**, v. 57, n. 9, p. 2037–2047, 1 jun. 2006.

MEDEIROS, S. R. et al. **Para onde vai o clima nos próximos anos**. **Boletim Cicarne**, 2023.

MEDRANO MACÍAS, J. et al. Enhancement to Salt Stress Tolerance in Strawberry Plants by Iodine Products Application. **Agronomy**, v. 11, n. 3, 2021.

MEDRANO-MACÍAS, J. et al. Use of Iodine to Biofortify and Promote Growth and Stress Tolerance in Crops. **Frontiers in Plant Science**, v. 7, 2016.

PATANÈ, C.; TRINGALI, S.; SORTINO, O. Effects of deficit irrigation on biomass, yield, water productivity and fruit quality of processing tomato under semi-arid Mediterranean climate conditions. **Scientia Horticulturae**, v. 129, n. 4, p. 590–596, 2011.

PINHEIRO, C.; CHAVES, M. M. Photosynthesis and drought: can we make metabolic connections from available data? **Journal of Experimental Botany**, v. 62, n. 3, p. 869–882, 1 jan. 2011.

SELEIMAN, M. F. et al. Drought Stress Impacts on Plants and Different Approaches to Alleviate Its Adverse Effects. **Plants**, v. 10, n. 2, 2021.

YIN, J. et al. Large increase in global storm runoff extremes driven by climate and anthropogenic changes. **Nature Communications**, v. 9, n. 1, p. 4389, 2018.

SECOND PART – ARTICLE

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IODATE-ENRICHED UREA: AN ALLY IN MITIGATING THE EFFECTS OF WATER DEFICIT AND IMPROVING THE QUALITY OF TOMATO FRUITS

1. INTRODUCTION

Climate change, driven by anthropogenic activities, intensifies agricultural challenges, mainly due to rising temperatures and changes in rainfall patterns (Medeiros et al., 2023; Yin et al., 2018). The water deficit resulting from these changes negatively affects the growth and development of crops, as it causes significant alterations in photosynthetic processes. Initially, the water deficit is perceived by the roots, leading to a reduction in water potential, which decreases cellular turgor and triggers a series of physiological responses, among which stomatal closure mediated by abscisic acid (ABA) in plants is highlighted. This mechanism reduces CO_2 assimilation and, consequently, the production of photoassimilates, resulting in significant losses in agricultural productivity (Joshi et al., 2016; Kaur et al., 2021; Koch et al., 2019; Pinheiro and Chaves, 2011).

Crops with high water demand, such as tomatoes (*Solanum lycopersicum* L.), are very sensitive to water deficit, which affects not only their development but also the quality of the fruits, affecting attributes such as flavor, color, and nutritional value (Hou et al., 2020; Patanè et al., 2011). Among these factors, the quality of the fruit is of great interest to consumers and is strongly influenced by the water regime to which the plant is subjected (Hou et al., 2020; Liu et al., 2015). The Micro-Tom cultivar has been widely used as a model species in physiological and genetic studies because of its well-characterized genome and ease of genetic manipulation, allowing detailed investigations of the mechanisms involved in the response to water stress (Chaudhary et al., 2019; Martí et al., 2006).

Water stress leads to the accumulation of reactive oxygen species (ROS), triggering antioxidant responses mediated by enzymes such as ascorbate peroxidase (APX), superoxide dismutase (SOD), and catalase (CAT) (Altaf et al., 2022). In addition, the accumulation of compatible solutes such as glutathione, flavonoids, and proline attenuate the negative effects of water stress and preserves cellular integrity and metabolism (Ahanger et al., 2021).

Recently, the use of exogenous iodine has emerged as a promising strategy to mitigate the effects of water deficits by promoting an increase in antioxidant compounds and enzymatic activity (Andrade et al., 2024; Kiferle et al., 2021). The application of iodine has shown the potential to improve the quality of fruits from crops such as tomatoes and strawberries by increasing the antioxidant capacity and accumulation of phenolic compounds (Lima et al., 2023a; Medrano Macías et al., 2021). However, the optimal concentrations and toxicity limits vary according to the chemical form of iodine and plant species, with iodide (I-) being more toxic than iodate (IO_3-) (Hong et al., 2012; Lawson et al., 2015).

Given this scenario, it is important to determine the sources and doses of iodine to maximize the benefits of water stress management and contribute to the sustainability of agricultural production under climate change scenarios. Iodine-enriched urea has emerged as a promising approach to enable its application in the field, thereby facilitating its adoption by producers. A recent study showed that iodine-enriched urea (0.2% I) reduces nitrogen volatilization and optimizes its absorption; however, to date, only the use of KIO_3 as a source has been restricted (Cezar et al., 2024).

In this context, we hypothesize that enriching urea with different iodine sources may be an effective strategy to mitigate water deficit and improve tomato fruit quality. Thus, the study aimed to determine the most effective source of iodine (iodide or iodate), using the urea enrichment technique, to attenuate water deficit stress in tomatoes and improve postharvest fruit quality.

2. MATERIAL AND METHODS

2.1 Local

The experiment was carried out in a growth chamber with a photoperiod of 12/12 h at the Federal University of Lavras (UFLA), State of Minas Gerais (21°14′ 45" S, 44°59′59" W, 920 m above sea level), southeastern Brazil. The temperature (T, °C) and relative humidity (RH, %) inside the chambers were monitored daily using an Onset HOBO digital thermohygrometer (model UX100-003). The data were recorded every five mins and collected at the end of the experiment to obtain the RH values and the maximum and minimum temperatures. The average RH was 54.38%, with a maximum temperature of 28.45 °C, a minimum of 19.80 °C, and an average of 24.10 °C.

2.2 Plant material

Tomato plants were used *Solanum lycopersicum* cv Micro-Tom WT (Meissner et al., 1997). The seeds were placed in Petri dishes in BOD at 25ºC with a 12h photoperiod and later in the seedling stage, and then transplanted to pots with 500 g of Latossolo Vermelho distrófico (Santos et al., 2018), which corresponds to Ferralsols (IUSS, 2015) or Oxisols, in the Soil Taxonomy (Staff, 1999), a classification used as the official one in this study.

2.3 Determination of irrigation

To determine the daily irrigation, three pots containing 500 g of soil each were used. These pots were dried in an oven at 60°C until they reached a constant weight, ensuring complete moisture removal. After reaching this constant weight, soil moisture was measured using the Thetaprobe ML2x soil moisture sensor (Delta-T devices). Then, the pots were irrigated until soil saturation and remained at rest for 24 hours. After this period, the vessels were weighed again to determine the field capacity (CC), and the corresponding humidity was measured with the sensor. During the natural drying process of the soil, three additional weight measurements were carried out, associated with the sensor readings. These data were used to generate a linear regression equation ($R^2 = 0.97$), establishing the relationship between the sensor readings and soil moisture. Based on this equation, it was possible to determine the amount of water needed to restore soil moisture to field capacity, allowing irrigation to be carried out accurately at 100%. Soil moisture readings were performed daily, and water replenishment was determined by the average reading of 10 pots at random.

Water stress was implemented gradually, 35 days after transplanting (DAT) of the seedlings, with a total duration of nine days. On the first day, irrigation was reduced to 75% in relation to the treatments maintained at field capacity. On days 2, 3, 4 and 5, water replacement was adjusted to 60% of CC. On days 6 and 7, irrigation was reduced to 50% of CC. On days 8 and 9, irrigation was completely suspended, observing maximum stress on the plants, which were rehydrated after the analyses (Figure 1).

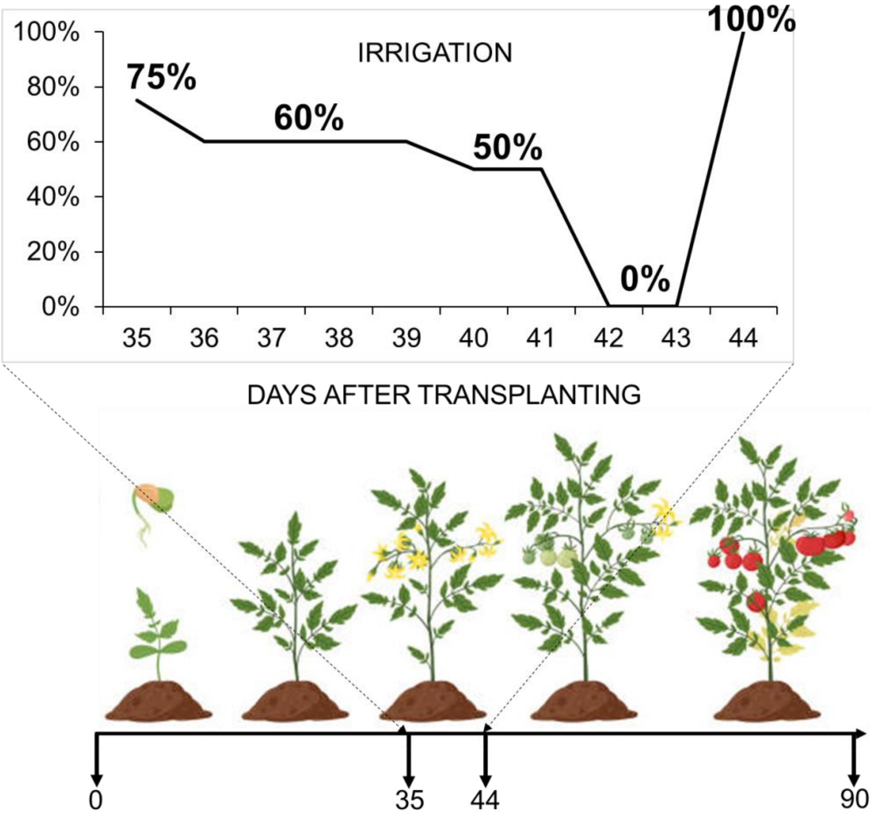


Figure 1: Irrigation percentage during the water deficit treatment period.

2.4 Synthesis of iodine-enriched urea

The synthesis of enriched urea was carried out at the Department of Soil Science of UFLA. Urea (carbamide = CH4N2O) (reagent-grade, Synth, Diadema, São Paulo, Brazil), triethanolamine, organic dye, and a source of I (Cezar et al., 2024) were used. To obtain urea enriched with potassium iodide (urea + KI), 0.147g was added, corresponding to 0.29% of the final amount. To obtain urea enriched with potassium iodate (urea + KIO_3), 0.19g of KIO_3 were added, corresponding to 0.38% of the final weight. The samples were mixed in a beaker until homogenization. After that, the samples were dried at room temperature for 24 h and stored in a cool and ventilated environment to avoid the degradation of the compounds. The final concentration of I in the enriched urea was 0.2% (2 kg ha $^{-1}$ I) in both fertilizers, calculated from the amount of I added in relation to the final weight of the urea. The application in the experiment occurred in top dressing, with a concentration of 107.2 mg of urea in each, corresponding to 100 mg kg^{-1} of nitrogen, carried out at 15 and 30 days after transplanting (Novais et al., 1991).

2.5 Experimental design

The design was completely randomized, using a double 3x2 factorial scheme, comprising the combination of three sources of top dressing, two irrigation conditions with 6 replications, totaling 72 experimental units (Table 1). The samples were collected at two times (maximum stress, rehydration and productivity).

Table 1: Representation of the experiment treatments.

Treatments	Water condition*	Fertilization
Treatment 1	Water déficit	urea
Treatment 2	Irrigated	urea
Treatment 3	Water déficit	urea + KI (0.2% I)
Treatment 4	Irrigated	urea + KI (0.2% I)
Treatment 5	Water déficit	urea + KIO_3 (0.2% I)
Treatment 6	Irrigated	urea + KIO_3 (0.2% I)

* Irrigation conditions from 35 to 44 days after transplanting (DAT).

2.6 Biomass partitioning

Biomass partitioning was evaluated by means of the dry mass of the different organs of the tomato (root, leaf, stem, inflorescence and fruit) at 44 DAT, weighed on an analytical scale (g). To obtain the dry mass, the tomato fractions were placed in paper bags and taken to the greenhouse, at 60 ºC, up to constant weight.

2.7 Physiological analyses

2.7.1 Water status

On the days of destructive collections, to measure the water status of the plants, the leaf water potential was monitored with a pressure chamber (Model 1000, PMS Instrument Company) between 12:00 and 13:00 hours to obtain the lowest water potential and between 3:00 and 5:00 hours to obtain the maximum water potential.

2.7.2 Gas exchange

Evaluations of the net rate of CO_2 (A) assimilation occurred at maximum stress and five days after rehydration. A camera was used, providing a closed system, considering the entire plant, connected to the SBA-5 CO_2 infrared gas concentration analyzer (Analyser, PP-System Inc., Amesbury, MA USA) and recorded on a computer. The chamber was composed of a transparent acrylic box 19cm x 20cm x 20cm, allowing the passage of light and the measurements were carried out with photosynthetically active radiation (PAR) around 345 μmol m^{-2} s^{-1}. The calculation of A (μmol m^{-2} s^{-1}) was performed according to the equation (Mitchell, 1992).

$$Equation\ 1{:}\ A = \frac{C1 - C2}{T1 - T2} \times V \times \frac{1}{L} \times T \times Pa$$

Where: A = CO_2 assimilation (μmol m^{-2} s^{-1}); C1 and C2 = The concentration of CO_2 (μmol mol^{-1}); T1 and T2 = time(s); V = total volume of the system (m^3); L = leaf area (m^2); T = temperature (K); and Pa = pressure (MPa). Evaluations were conducted between 9:00 and 12:00 h.

Stomatal conductance was also measured at this interval using a digital porometer (Decagon SC-1 Leaf Porometer) and expressed in mol m^{-2} s^{-1}.

2.7.3 Chlorophyll fluorescence and photosystem efficiency II

Measurements of the quantum and effective efficiency of photosystem II (Fv/Fm) were measured before water deficit stress was implemented, at maximum stress, and five days after rehydration, using a portable fluorometer MINI-PAM (Walz Inc., Effeltrich, Germany).

2.8 Biochemical analyses

After the water deficit was implemented, destructive plant collections were carried out at maximum stress (fully expanded younger leaves and roots) 44 DAT and at rehydration (fully expanded younger leaves) 49 DAT for biochemical analyses. This material was collected, immediately frozen in liquid nitrogen, and stored at -80 °C freezer until analysis. The samples were then macerated in liquid nitrogen using polyvinylpolypyrrolidone (PVPP).

2.8.1 Ethanolic extraction

Approximately 50 mg of fresh tissue was weighed and placed in 2.0 mL Eppendorf tubes. Then, 350 μL of ~90% ethanol was added, followed by stirring (vortex) and incubation in a water bath at 70-75 °C for 20 min. Subsequently, the samples were centrifuged at 14,000 RPM for 5 min at 4 °C. From that point on, all the samples were kept on ice and protected from light. The supernatant (~350 μL) was transferred to a new 1.5 mL Eppendorf tube. To the pellet in the original tube, 350 μL 80% ethanol was added, followed by stirring and incubation in a water bath at 70-75°C for 20 min. The samples were centrifuged again at 4°C and 14,000 RPM for 5 min, and the supernatant (~ 350 μL) was transferred to the second tube. Subsequently, 350 μL of 50% ethanol was added to the pellet in the first tube, followed by stirring and incubation in a water bath at 70-75°C for 20 min, with pressure removal after 1 min. The samples were centrifuged again at 4°C and 14,000 RPM for 5 min, and the supernatant (~350 μL) was transferred to the second tube. Proteins were extracted using the Bradford method (1976) and starch and sucrose were extracted using the (van Handel, 1968). An ethanolic pellet was used for starch extraction.

2.8.2 Quantification of photosynthetic pigments chlorophyll a, b and total carotenoids

For pigment analysis, Lichtenthaler and Buschmann, (2001) was used. Approximately 170 μL of ~90% ethanol was added to the first two wells of the microplate, which served as a blank. In the remaining wells, the samples were added in duplicate, with 50 μL of supernatant and 120 μL of ~90% ethanol, totaling to 170 μL. Plate readings were performed to determine the concentrations of chlorophyll a (647 nm), chlorophyll b (663 nm), and carotenoids (470 nm). The following equation was used to quantify the pigments:

$$Equation\ 2: chl\ a = 12{,}25\ A_{663}\ - 2{,}74\ A_{646}$$

$$Equation\ 3: chl\ b = 21{,}50\ A_{646}\ - 5{,}10\ A_{663}$$

$$Equation\ 4{:}\ Car = \frac{1000\ A_{470}\ -1{,}82\ chl\ a -\ 85{,}02\ chl\ b}{198}$$

2.8.3 Quantification of reducing sugars

The methodology Miller, (1959) was followed. The DNS reagent was prepared by adding 5 mL of sodium hydroxide (NaOH) 2N to 0.25 g, along with approximately 12 mL of distilled water, and stirring until completely dissolved. Subsequently, Rochelle salt (7.5 g) (sodium potassium tartrate) was added and the volume was made up to 25 mL with distilled water. The reagent was protected from light and CO_2. For the glucose curve and aliquot test, the reagents (glucose, water, and DNS) were added according to the table in test tubes, in duplicate, and left in a water bath at 100°C for 5 min. After cooling, the volume was made up to 2 mL by adding distilled water (1.5 mL). Then, 350 µL was pipetted into a microplate and the absorbance was read at 540 nm. For the samples, glucose was replaced by the extract to be analyzed, and an aliquot test was performed.

2.8.4 Quantification of total soluble sugars, starch and sucrose

For this analysis, the Yemm and Willis protocols (1954) were followed. To prepare the antrona reagent, 40 mg of antrona was added to 1 mL of distilled water, and then 20 mL of concentrated sulfuric acid (H_2SO_4) was added. This reagent was prepared in a chapel in an ice bath because of the exothermic nature of the reaction. For the glucose curve and the aliquot test, reagents were added in duplicate according to the specified table in the test tubes. The tubes were placed in a water bath at 100°C for 5 min. After cooling, 350 µL of the samples was pipetted into microplates, and the absorbance was read at 620 nm. For the samples, the glucose was replaced by the extract to be analyzed, and an aliquot test was performed.

2.8.5 Total soluble sugars

The total soluble sugar content was calculated as the sum of sucrose and reducing sugars.

2.8.6 Total non-structural carbohydrate (CTNE)

The total non-structural carbohydrate content was calculated from the sum of the total soluble sugar and starch content.

2.8.7 Amino acid quantification

Amino acids were determined according to the methodology described by Yemm et al., (1955). To prepare the reagent, a mix containing 0.2 M sodium citrate buffer pH 5.0, 5% ninhydrin (in methylcellelosolve, ethylene glycol monomethyl ether) and potassium cyanide (KCN) 2%. This mix was prepared in the proportions of 0.25 mL of buffer, 0.1 mL of nymphinin and 0.5 mL of KCN per sample, adjusting according to the number of samples. For the glycine or other amino acid curve and aliquot tests, the reagents (glycine, water, and the mixture) were added according to the table in test tubes, in duplicate, and heated in a water bath at 100°C for 20 min. After cooling, 650 µL 60% ethanol was pipetted into each tube. Then, 350 µL of each sample was pipetted into microplates, and the absorbance was read at 570 nm. For the samples, glycine was replaced by the extract to be analyzed, and an aliquot test was performed.

2.8.8 Protein quantification

The protein analysis reagent was prepared by dissolving 100 mg of coomassie blue in 50 mL of 95% ethanol. Then, 100 mL of 85% phosphoric acid (H_3PO_4) was added and the volume was completed to 1 liter with distilled water. The solution was agitated overnight and filtered. For the BSA curve (bovine albumin serum), a BSA solution (2.5 mg) was prepared by diluting BSA (12.5 mg) in 5 mL of 0.1M sodium hydroxide. The reagents were added according to the microplate table and the absorbance was read at 595 nm. For the samples, BSA was replaced by the extract to be analyzed, and an aliquot test was performed using an aliquot of 6 µL.

2.9 Evaluation of antioxidant metabolism

2.9.1 Extraction of antioxidant enzymes

The methodology described by Biemelt et al., (1998) was used to extract antioxidant enzymes. Fresh material (200 mg) was macerated in liquid nitrogen using 50% PVPP. The sample was homogenized with 1,500 µL of extraction buffer containing potassium phosphate (100 mM), EDTA (0.1 mM), and ascorbic acid (10 mM). The mixture was centrifuged at 13,000 × g (8500 rpm) for 10 min at 4°C, and the supernatant was collected for analysis.

2.9.2 Quantification of antioxidant enzyme activity

For the incubation of Catalase (CAT), The methodology of Havir and McHale, (1987) was followed for the incubation of CAT. Six microliters of the sample were pipetted in triplicate on a plate, with the first three wells being used as a blank. An incubation buffer was prepared and heated in a water bath at 30°C, containing potassium phosphate (100 mM) and water, and hydrogen peroxide (12.5 mM) was added at the time of reading. The reading was performed at 240 nm, with measurements taken every 15s for 3 min to observe the decrease in absorbance.

For the incubation of superoxide dismutase (SOD), Giannopolitis and Ries, (1977) was used to incubate SOD. In the first three wells of the plate, 10 μL of water (white) was pipetted, and in the other wells, 9 μL of the sample was added in triplicate. A mixture of hatchery buffer containing potassium phosphate (50 mM), methionine (14 mM), EDTA (0.1 μM), NBT (75 μM), riboflavin (2 μM), and water was prepared and added to each well. The plate was illuminated for 7 min, and the absorbance was measured at 560 nm. The amount of SOD was determined by inhibiting 50% of NBT photoreduction.

Incubation with ascorbate peroxidase (APX) was performed using the (Nakano and Asada, methods (1981). Nine microliters of the sample were pipetted in triplicate on a plate, with the first three wells used as the blank. Incubation buffer containing potassium phosphate (100 mM) and ascorbic acid (0.5 mM) was prepared and heated to 30°C. After incubation, hydrogen peroxide (0.1 mM) was added at the time of reading, and the absorbance was measured at 290 nm every 15 s for 3 min to observe the decrease in absorbance. The molar extinction coefficient used was 2.8 mM cm^{-1}.

2.9.3 Quantification of hydrogen peroxide and lipid peroxidation

For the quantification of hydrogen peroxide (H_2O_2) as described by Velikova et al., (2000), the material was initially stored in liquid nitrogen. Subsequently, 200 mg of fresh material (MF) was macerated in liquid nitrogen with PVPP, and the sample was homogenized in 1500 μL of 0.1% trichloroacetic acid (TCA). The mixture was centrifuged at 12,000 × g for 15 min at 4°C and the supernatant was collected. A 90 μL aliquot of the supernatant was then withdrawn and pipetted into an Eppendorf tube containing the following solutions: 10 mM potassium phosphate buffer pH 7 (final concentration: 2.5 mM) and 1M potassium iodide (0.5 M final). For the reaction, 90 μL buffer and 180 μL iodide were used, and the final volume was adjusted to 360 μL. Absorbance was measured at 390 nm using a spectrophotometer. For the standard curve of hydrogen peroxide, a solution of H_2O_2 at 250 μM was prepared, and dilutions were performed according to the specified table. The sample and pattern readings were recorded at 390 nm. The calculations were based on a standard hydrogen peroxide curve, and the reductions in the aliquot were compensated with water to reach the required volume of 90 μL.

To quantify lipid peroxidation using the thiobarbiturithiobarbituric acid Buege and Aust, (1978), the material was initially stored in liquid nitrogen. Subsequently, 200 mg of fresh material (MF) was macerated in liquid nitrogen with PVPP, and the sample was homogenized in 1500 µL of 0.1% trichloroacetic acid (TCA). The mixture was centrifuged at 12,000 × g for 15 min at 4°C and the supernatant was collected. Subsequently, a 125 µL aliquot of the supernatant was removed and pipetted into an Eppendorf tube containing 250 µL reaction medium containing 0.5% thiobarbituric acid (TBA) and 10% trichloroacetic acid (TCA). The reagents were weighed and dissolved in distilled water to obtain solutions. The mixture was then heated in a water bath at 95°C for 30 min. Each sample was prepared in duplicate, using two tubes for each sample in the bath. After heating, the reaction was stopped by rapid cooling on ice, and the absorbance was measured using a spectrophotometer at 532 and 600 nm. Calculations were performed using the following equation:

$$Equation\ 6: MDA = A535\ - A600\ (1{,}56\, X\ 10 - 5cm - 1\ \times b)$$

where b is the optical length = 1.

2.9.4 Proline determination

The proline content was determined according to the protocol established by Bates et al., (1973). To prepare the acidic ninhydrin solution, ninhydrin (2.5 g) was dissolved in a mixture of 40 mL of 6 M phosphoric acid and 60 mL of acetic acid, totaling 100 mL. The solution was stirred under heating until it was completely dissolved and then cooled for use. The proline standard solution was prepared in two steps. First, 0.050 g proline was dissolved in 100 mL distilled water to obtain a 500 µg mL^{-1} solution. Subsequently, 2 mL of this solution was diluted to 100 µg mL^{-1} with distilled water.

For the proline curve, different concentrations of proline were mixed with water, ninhydrin, and acetic acid in the test tubes. After shaking, the samples were heated to 100°C for 60 min and cooled in an ice bath. Absorbance was measured at 520 nm using a spectrophotometer.

2.10 Productivity analysis

The fresh fruit weight, yield, and number of fruits per plant in tomatoes were evaluated as follows: To determine the fresh weight, the ripe fruits were harvested directly from the plants and weighed individually on an analytical scale with a precision of 0.01 g. The weight of each fruit was then recorded. To determine the number of fruits per plant, all fruits present in each plant, including ripe and immature fruits, were counted and recorded.

2.11 Post-harvest analysis

2.11.1 Penetration resistance (firmness)

Fifty fruits were determined per treatment in the equatorial region of the fruits at a single point using a Stable Micro System texture analyzer model TA. XT2i, using a TA39 cylindrical probe (2 mm diameter). The results obtained are expressed in Newton (N).

2.11.2 Colour

Forty-two fruits per treatment were analyzed for skin color in their equatorial region, using the Konica Minolta CR-400 colorimeter, in the CIELAB color space of the International Commission of Éclairage, using the color scale system L, a* and b*, chroma (C*), and hue angle (h°).

2.11.3 Fruit respiratory rate

To measure the respiratory rate of the fruit, five grams of fruit were weighed and placed in different 50 mL glass containers. The containers were hermetically sealed with a plastic lid containing a silicone septum, through which aliquots were removed from the internal sample with the aid of the PBI Dansensor gas analyzer after 30 min of rest. The results, expressed as % CO_2, were converted into mL CO_2 kg fruit^{-1} h^{-1}, considering the volume of the container, the mass and volume of the fruits in each container, and the time that the same container remained closed.

2.11.4 Total titratable acidity, PH, Soluble solids

Samples were crushed in water at a ratio of 1:3 (m/v), filtered in an organza, and the filtrate was used for the determination of pH, titratable acidity (TA), and soluble solids (SS). The pH was determined using a TECNAL® pH meter previously calibrated using buffer solutions (pH 4.0, 7.0). Titratable acidity was determined by titration with sodium hydroxide (NaOH) solution 0.1 N, using phenolphthalein as an indicator, according to AOAC (2019). The results are expressed as 100 g of citric acid mg $^{-1}$ sample. SS was determined using an ATAGO PR-100 digital refractometer (Tokyo, Japan) with automatic temperature adjustment, and the results were expressed as %, as described by AOAC (2019).

2.11.5 Vitamin C

To determine vitamin C, 1 g of the sample was homogenized in 50 mL of 0.5% oxalic acid using a polytron. Subsequently, the homogenate was placed on a stirring table for 30 min and filtered (qualitative filter paper, 15 cm in diameter, Unifil®). The extract was then used to determine the ascorbic acid content, after oxidation of ascorbic acid and dehydroascorbic acid, by the colorimetric method, using 2,4 dinitrophenylhydrazine, according to (Strohecker and Henning, (1967), and the results were expressed in mg of ascorbic acid in 100 g^{-1} of pulp.

2.11.6 Flavonoids

The flavonoid content was determined using a method adapted from Arvouet-Grand et al., (1994). Briefly, 150 μL of 2% aluminum chloride ($AlCl_3$) in methanol was mixed with the same volume of sample solution (the same used for the determination of phenolics). The samples were incubated at room temperature for 1 h. Subsequently, the absorbance was measured at 420 nm using distilled water as white. The flavonoid content was expressed in mg 100 g^{-1} of quercetin.

2.11.7 Total phenolic compounds and antioxidant capacity

2.11.8 Obtaining extracts

This procedure was adapted from a study by Rufino et al., (2010). The sample (2 g) was weighed in a centrifuge tube, 20 mL of 95% ethanol was added, and the mixture was homogenized and left to stir (on a shaker table) for 30 min in the dark. The tubes were then placed in an ultrasound bath for 30 min, followed by filtration through filter paper (qualitative filter paper, 15 cm in diameter, Unifil®), and the filtrate was transferred to an amber flask. The obtained extract was used for further analysis. To define this extraction method, previous extraction analyses were carried out using distilled water, ethanol, and methanol as extracting agents. The extracts obtained were then used to analyze the total phenolics and antioxidant activity, and the data obtained were analyzed using the Design Expert 12 program, which provided the best combination of extractor reagents, thus optimizing the methodology.

2.11.9 Total phenolics by the Fast Blue method

Following the method described by Medina, (2011), with some adaptations, 200 μL of the extract was mixed with 20 μL of Fast Blue reagent (0.1%, v/v) and 20 μL of sodium hydroxide (5%, m/v), and the absorbance was measured at 420 nm after 1.5 h of incubation in the dark. All measurements were performed in triplicate using a 96-well microplate reader (Biochrom EZ Read, 2000). The results are reported as gallic acid equivalents in milligrams per 100 g of fresh sample weight (mg GAE 100 g FM^{-1}).

2.11.10 Antioxidant activity by the β-Carotene/linoleic acid method

The determination of antioxidant activity by the β-carotene/linoleic acid method was based on the oxidation of β-carotene (discoloration) induced by the products of the oxidative degradation of linoleic acid (Rufino et al., 2010, with modifications). The solutions were prepared by mixing 270 µl of β-carotene/linoleic acid solution and 20 µl of extract in each well of a 96-well flat-bottomed microplate. The mixture was kept in a water bath at 40 °C, and readings were taken at 470 nm in a microplate reader (EZ Read 2000, Biochrom®) after an interval of 2 h. The results were expressed as the percentage of oxidation inhibition.

2.11.11 Antioxidant activity by the ABTS method

The antioxidant activity was based on the capture of (ABTS+) by an antioxidant. Briefly, the ABTS+ solution was prepared by reacting 2,2'-azinobis diammonium salt (3-ethylbenzothiazoline-6-sulfonic acid) at a concentration of 7 mmol/L with potassium persulfate 2.45 mmol/L at room temperature for 16 h. The solution obtained was then diluted with ethanol to an absorbance of 0.70±0.05 at 734 nm. Aliquots (3 µl) of TROLOX standards (6-hydroxy-2,5,7,8-tetramethylchromano-2-carboxylic acid) and extracts were pipetted into each well of a 96-well flat-bottomed microplate. A radical solution (297 µl of radical solution was then added to each well. After a reaction time of 6 min away from light, the absorbance was measured at 734 nm using the microplate reader described above. Antioxidant activity was expressed as µmol equivalents of TROLOX per gram of fresh sample, based on a calibration curve with known concentrations of TROLOX (Auzanneau et al., 2018).

2.11.12 Antioxidant activity by the phosphomolybdenum complex method

The assay was performed as described by (Prieto et al., 1999), with some modifications. Fifty microliters of the sample extract, 450 µL of distilled water + 1.5 mL of the phosphomolybdenum complex were pipetted into tubes with screw-on caps, which were closed and shaken, placed in a water bath at 95 °C for 90 min, cooled in an ice bath, and read using a spectrophotometer at 695 nm. To determine antioxidant activity, the same process described above was performed using vitamin C to construct the curve. The results are expressed in mg of ascorbic acid per 100 g of sample.

2.12 Statistical analysis

The dataset obtained were submitted to analysis of variance (ANOVA), and since the assumptions of ANOVA were met and there was a difference according to the F test ($p \leq 0.05$), there was the comparison of means between the treatments was made by the tukey test ($p \leq$

0.05), using the R software (exp.desPT package) (Ferreira et al., 2013). The PCA and Person correlation analyses were performed using the R software (FactoMineR packages. Factoextra, Hmisc and ggcorrplot) (Harrell Jr, 2003; Husson et al., 2006; Kassambara, 2016; Kassambara and Mundt, 2016). The graphs were obtained using the SigmaPlot 15.0 software (Systat Software Ins, San Jose, CA, USA).

3. RESULTS

Plants subjected to water deficit compared with control (irrigated) showed a reduction in leaf dry mass and fruit dry mass (Figure 2), with no significant differences in the N top dressing. The dry mass of the inflorescences and stems remained unchanged between the treatments. The reference plants had the lowest root dry mass values, regardless of water availability. However, the addition of potassium iodate (KIO_3) and potassium iodide (KI) positively influenced root biomass, with different effects depending on the water conditions. Under adequate water availability, the urea + KIO_3 combination resulted in the highest accumulation of root biomass. Under water deficit conditions, the treatment that presented the best performance was urea + KI, indicating a differential effect of iodine forms on the physiological response of plants to stress.

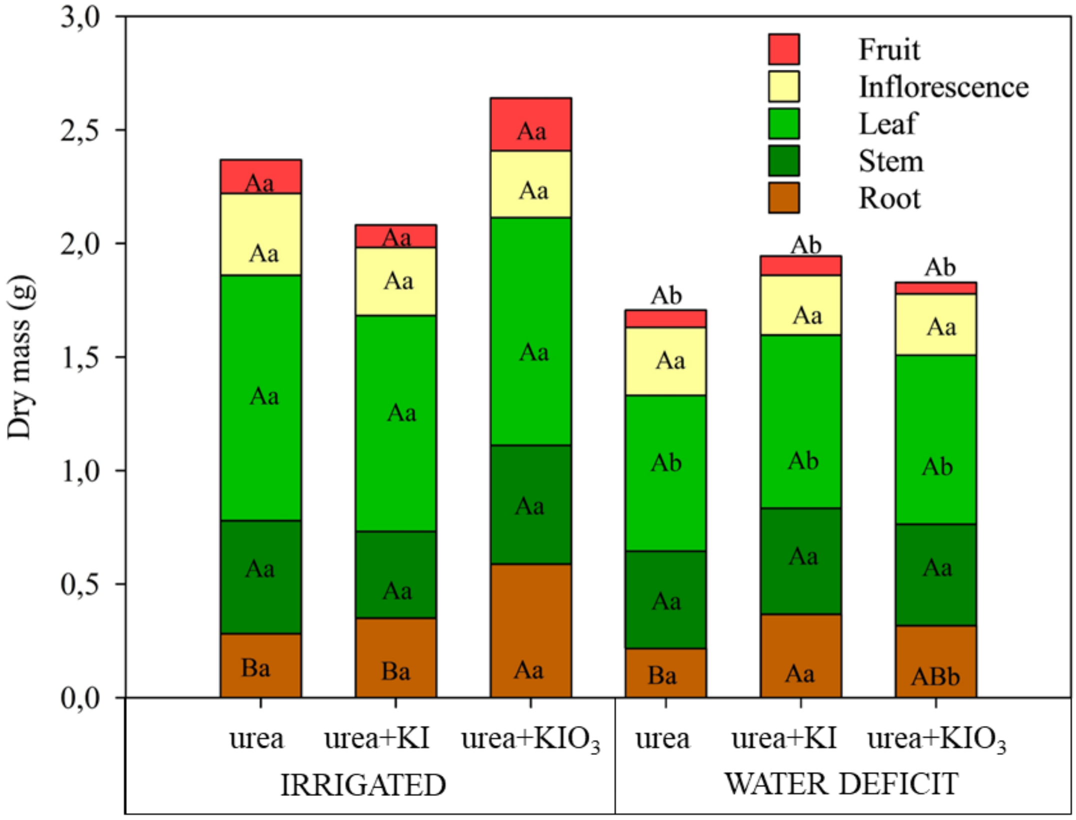


Figure 2: Total dry mass of Micro-Tom tomato plants at 44 days after transplanting (DAT). Plants were irrigated at ~90% of field capacity (IRRIGATED) or subjected to water deficit (WD) from 35 to 44 DAT and fertilized with urea enriched with potassium iodide (KI) or potassium iodate (KIO_3). Uppercase letters indicate comparisons between fertilization treatments, while lowercase letters indicate comparisons between irrigation treatments. Means followed by the same letter do not differ significantly according to Tukey's test ($p \leq 0.05$).

The number of fruits was not significantly influenced by the water conditions or the treatments applied (Figure 3). However, under water deficit conditions, a reduction in productivity was observed compared with that in plants maintained under adequate irrigation conditions.

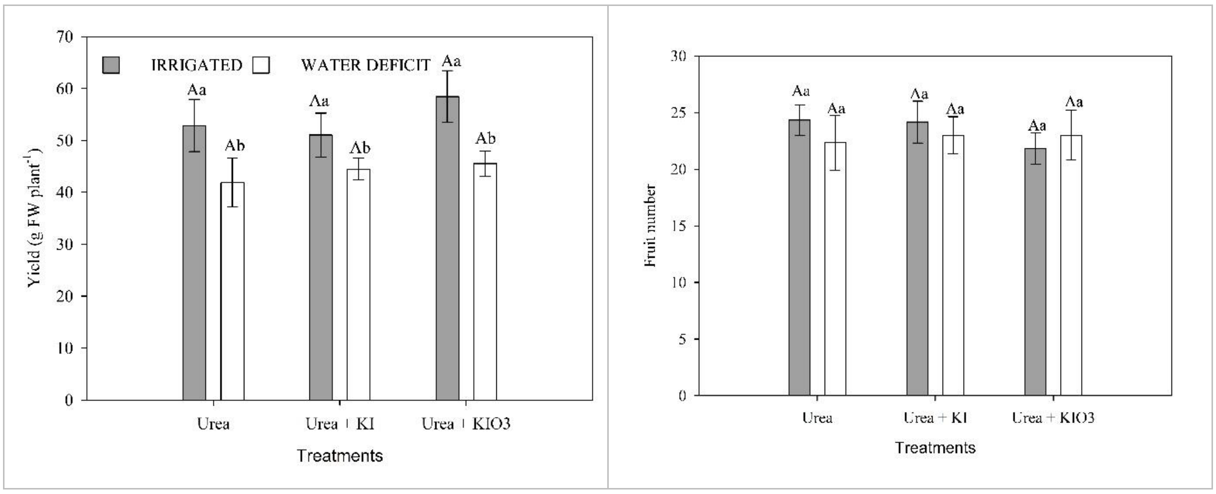


Figure 3: Yield (A) and number of fruits (B) of Micro-Tom tomato plants. Plants were irrigated at ~90% of field capacity (IRRIGATED) or subjected to water deficit (WD) from 35 to 44 DAT and fertilized with urea enriched with potassium iodide (KI) or potassium iodate (KIO_3). Uppercase letters indicate comparisons between fertilization treatments, while lowercase letters indicate comparisons between irrigation treatments. Means followed by the same letter do not differ significantly according to Tukey's test ($p \leq 0.05$). Bars represent the mean of six plants (n = 6).

The water potential of plants subjected to water deficit stress was more negative than that of the adequately hydrated plants (Table 2). By observing the water potential measured in the early morning, we noticed that the plants treated with iodine remained more hydrated than the reference plants. However, at noon, all plants subjected to water deficit showed similar levels of stress and dehydration, which correlated with the amount of water available in the soil. During the rehydration phase, we observed that the plants recovered their water potential in all treatments. The photosynthetic rate was severely reduced in plants subjected to water-deficit conditions. Plants treated with KI exhibited significantly higher net photosynthesis under both irrigation conditions. However, after rehydration, the same plants had the lowest net photosynthesis rates. During rehydration, plants that had been subjected to water deficit showed higher values of net photosynthesis than those that remained continuously hydrated.

Under water deficit conditions, the Fv/Fm ratio showed a slight reduction in all treatments. However, this decrease did not damage the photosynthetic apparatus, as the plants recovered their initial values after rehydration. Water restriction modified the pigment balance, promoting an increase in chlorophyll a and b levels in plants subjected to water deficit, which resulted in greater accumulation of total chlorophyll in reference plants (urea) and in those treated with urea + KIO_3. In contrast, plants treated with urea + KI did not show changes in chlorophyll a, b, or total chlorophyll content.

Under water deficit conditions, all treatments induced an increase in carotenoid content, although this effect was less pronounced in KI-treated plants. During rehydration, only carotenoids maintained high levels in plants previously subjected to water deficit, whereas the other pigments returned to their baseline values.

Table 2: Physiological parameters and water status of tomato plants Micro-tom wt.

Parameters		IRRIGATED			WATER DEFICIT		
		urea	urea + KI	urea + KIO_3	urea	urea + KI	urea + KIO_3
A	Maximum stress	13.18 ± 0.67 Ba	17.91 ± 0.21 Aa	11.30 ± 0.12 Ba	-0.15 ± 0.86 Bb	3.86 ± 0.36 Ab	-2.90 ± 1.60 Bb
(μmol $m^{-2}s^{-1}$)	Rehydration	12.81 ± 0.77 Ab	10.40 ± 0.16 Bb	12.25 ± 0.66 Ab	16.12 ± 0.53 Aa	12.11 ± 0.80 Ba	16.14 ± 0.35 Aa
gs	Maximum stress	0.52 ± 0.02 Aa	0.54 ± 0.06 Aa	0.50 ± 0.04 Aa	0.04 ± 0.01 Ab	0.06 ± 0.01 Ab	0.09 ± 0.01 Ab
(mol $m^{-2}s^{-1}$)	Rehydration	0.42 ± 0.03 Aa	0.46 ± 0.04 Aa	0.33 ± 0.06 Aa	0.22 ± 0.01 Bb	0.28 ± 0.02 Ba	0.40 ± 0.06 Aa
Chlo a	Maximum stress	2.88 ± 0.20 Ab	3.19 ± 0.10 Aa	3.38 ± 0.16 Ab	4.07 ± 0.18 Ba	3.41 ± 0.15 Ca	4.68 ± 0.23 Aa
(mg g^{-1} FW)	Rehydration	3.17 ± 0.22 Aa	2.81 ± 0.11 Aa	3.48 ± 0.15 Aa	3.31 ± 0.21 Aa	3.38 ± 0.09 Aa	3.56 ± 0.30 Aa
Chlo b	Maximum stress	1.06 ± 0.05 Ab	1.14 ± 0.03 Aa	1.15 ± 0.05 Ab	1.49 ± 0.05 Aa	1.23 ± 0.05 Ba	1.68 ± 0.08 Aa
(mg g^{-1} FW)	Rehydration	1.11 ± 0.07 Aa	1.03 ± 0.10 Aa	1.20 ± 0.06 Aa	1.09 ± 0.07 Aa	1.16 ± 0.05 Aa	1.33 ± 0.08 Aa
Total chlo	Maximum stress	3.94 ± 0.26 Ab	4.33 ± 0.13 Aa	4.53 ± 0.21 Ab	5.56 ± 0.23 Ba	4.64 ± 0.20 Ca	6.37 ± 0.31 Aa
(mg g^{-1} FW)	Rehydration	4.19 ± 0.24 Aa	4.12 ± 0.37 Aa	4.58 ± 0.21 Aa	4.29 ± 0.27 Aa	4.64 ± 0.17 Aa	4.75 ± 0.35 Aa
Carotenoids	Maximum stress	0.34 ± 0.02 Ab	0.36 ± 0.01 Ab	0.39 ± 0.02 Ab	0.51 ± 0.03 Aa	0.43 ± 0.02 Ba	0.59 ± 0.03 Aa
(mg g^{-1} FW)	Rehydration	0.36 ± 0.01 Ab	0.35 ± 0.01 Ab	0.35 ± 0.01 Ab	0.42 ± 0.02 Aa	0.44 ± 0.01 Aa	0.44 ± 0.05 Aa
Fv_Fm	Maximum stress	0.82 ± 0.01 Aa	0.83 ± 0.01 Aa	0.82 ± 0.01 Aa	0.81 ± 0.01 Ab	0.79 ± 0.01 Ab	0.79 ± 0.01 Ab
-	Rehydration	0.84 ± 0.01 Aa	0.84 ± 0.01 Aa	0.83 ± 0.01 Aa	0.83 ± 0.01 Aa	0.82 ± 0.01 Aa	0.83 ± 0.01 Aa
Ψw 4 A.M.	Maximum stress	-0.70 ± 0.06 Aa	-0.64 ± 0.02 Aa	-0.71 ± 0.03 Ab	-1.86 ± 0.13 Cb	-0.95 ± 0.07 Bb	-0.25 ± 0.06 Aa
(MPa)	Rehydration	-	-	-	-	-	-
Ψw 12 A.M.	Maximum stress	-0.82 ± 0.07 a	-0.58 ± 0.11 a	-0.68 ± 0.10 a	-1.50 ± 0.23 b	-1.61 ± 0.18 b	-2.16 ± 0.11 b
(MPa)	Rehydration	-0.85 ± 0.09 Aa	-0.79 ± 0.07 Aa	-0.99 ± 0.11 Aa	-0.87 ± 0.11 Aa	-0.98 ± 0.09 Aa	-0.90 ± 0.14 Aa
Soil moisture	Maximum stress	15.60 ± 3.36 a	18.43 ± 2.16 a	14.22 ± 1.57 a	5.72 ± 1.18 b	6.82 ± 0.48 b	6.03 ± 0.66 b
(%)	Rehydration	-	-	-	-	-	-

Uppercase letters indicate comparisons between fertilization treatments, while lowercase letters indicate comparisons between irrigation treatments. Means followed by the same letter do not differ significantly according to Tukey's test ($p \leq 0.05$). Abbreviations: Net photosynthesis (A), stomatal conductance (gs), maximum quantum efficiency of photosystem II (Fv/Fm), chlorophyll a (Chlo a), chlorophyll b (Chlo b), total chlorophyll (Total Chl), pre-dawn water potential (ΨW 4 A.M.), and midday water potential (ΨW 12 P.M.).

The stomatal conductance gradually decreased as irrigation decreased (Figure 4). Until the seventh day, the plants treated with iodine, especially with KI, kept their stomata more open than the reference plants under water deficit conditions. However, after this period, stomatal opening was drastically reduced in all treatments under water-deficit conditions. Full recovery of stomatal opening, five days after rehydration occurred only in plants treated with potassium iodate.

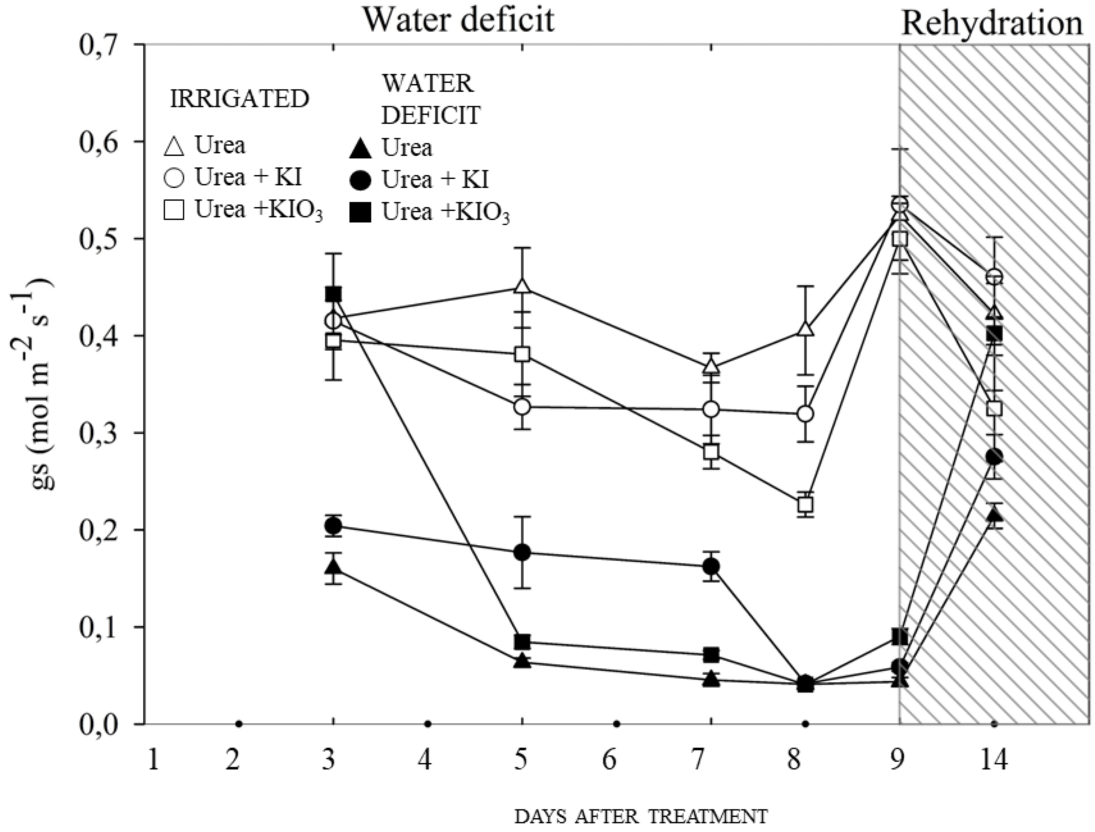


Figure 4: Stomatal conductance (gs) during the water deficit treatment period. Plants were irrigated at ~90% of field capacity (IRRIGATED) or subjected to water deficit (WD) from 35 to 44 DAT and fertilized with urea enriched with potassium iodide (KI) or potassium iodate (KIO_3).

As with the other evaluated parameters, plant development was directly influenced by the treatments. Plants subjected to water deficit and treated with KI exhibited lower levels of stress and visible damage compared to the other treatments under water restriction, suggesting a potential mitigating effect of potassium iodide on the physiological impacts of water deficit (Figure 5).

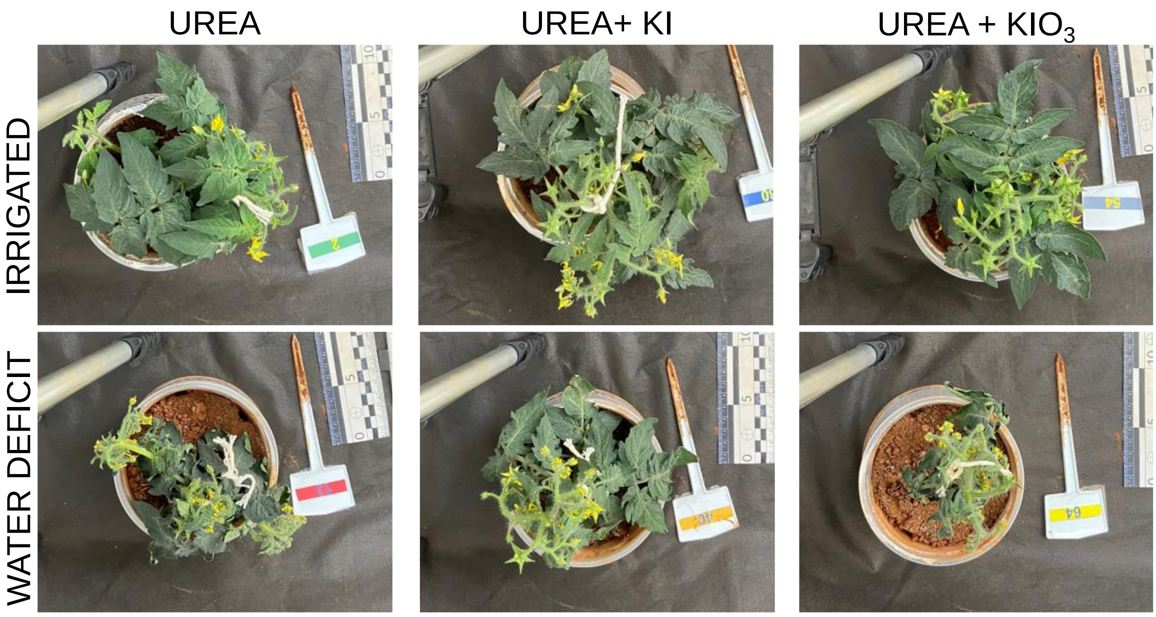
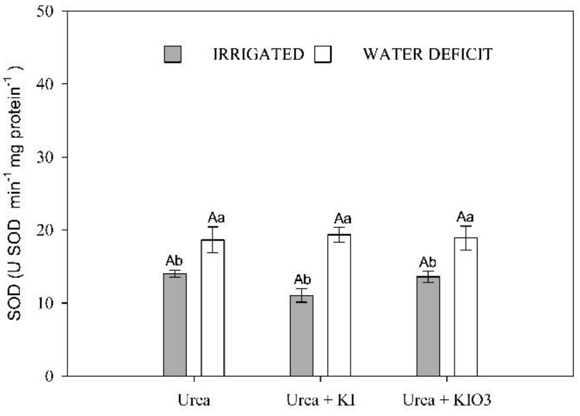


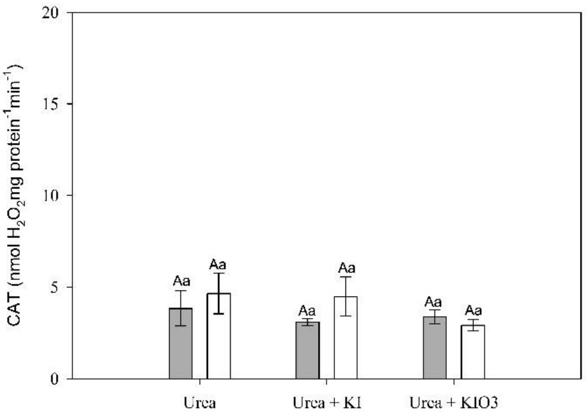
Figure 5: Effect of different irrigation and fertilization treatments on tomato plant development at maximum stress (44 DAT). Plants were irrigated at ~90% of field capacity (IRRIGATED) or subjected to water deficit (WD) between 35 and 44 DAT, and fertilized with urea enriched with potassium iodide (KI) or potassium iodate (KIO_3). Visual differences in biomass, coloration, and leaf integrity can be observed among treatments.

Water deficit stress results in increased in superoxide dismutase (SOD) activity. However, catalase activity (CAT) and malonaldehyde levels remained unchanged in all treatments, regardless of water availability. The hydrogen peroxide (H_2O_2) content increased in response to water deficit, and was highest in plants treated with KIO_3, followed by those treated with KI (Figure 6).

A



B



C

D

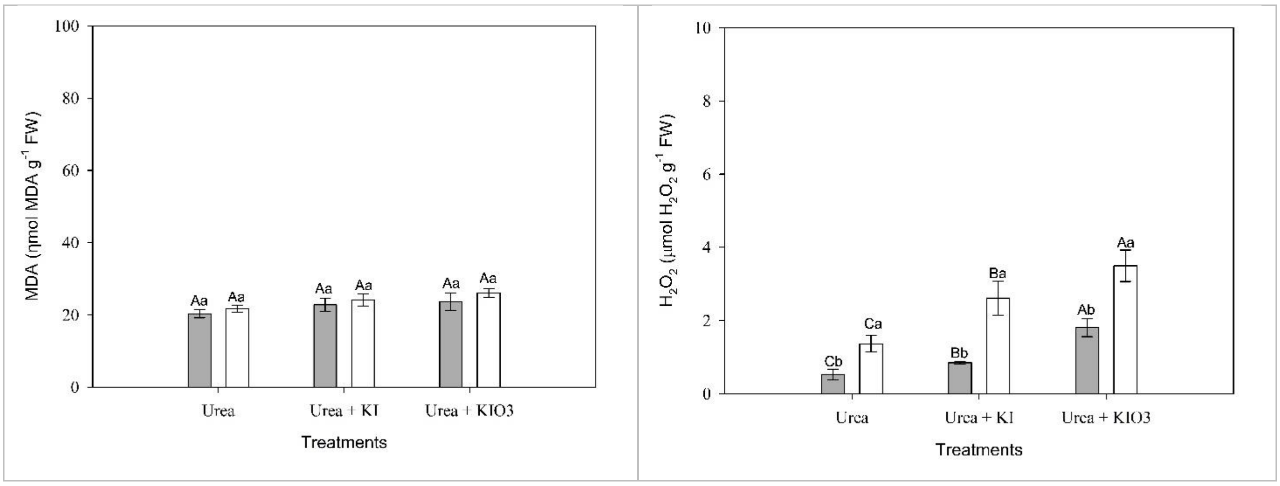
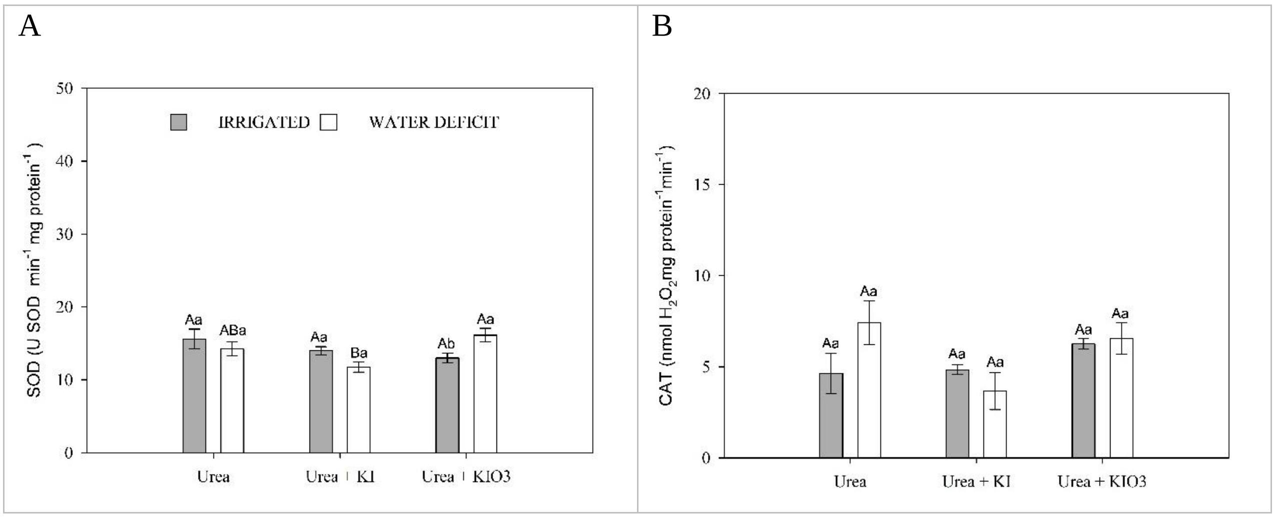


Figure 6: Activity of superoxide dismutase (SOD) (A) and catalase (CAT) (B), and contents of malondialdehyde (MDA) (C) and hydrogen peroxide (H_2O_2) (D) in Micro-Tom tomato leaves at 44 DAT (maximum stress). Plants were irrigated at ~90% of field capacity (IRRIGATED) or subjected to water deficit (WD) from 35 to 44 DAT and fertilized with urea enriched with potassium iodide (KI) or potassium iodate (KIO_3). Uppercase letters indicate comparisons between fertilization treatments, while lowercase letters indicate comparisons between irrigation treatments. Means followed by the same letter do not differ significantly according to Tukey's test ($p \leq 0.05$). Bars represent the mean (n = 4).

Five days after rehydration, plants treated with KIO_3 continued to stimulate SOD activity (Figure 7). In addition, an increase in malonaldehyde (MDA) levels was observed in plants previously subjected to water deficit and treated with iodine, regardless of the source used. Although the levels of hydrogen peroxide (H_2O_2) were reduced in relation to the stress period, they remained significantly higher compared to continuously irrigated plants.



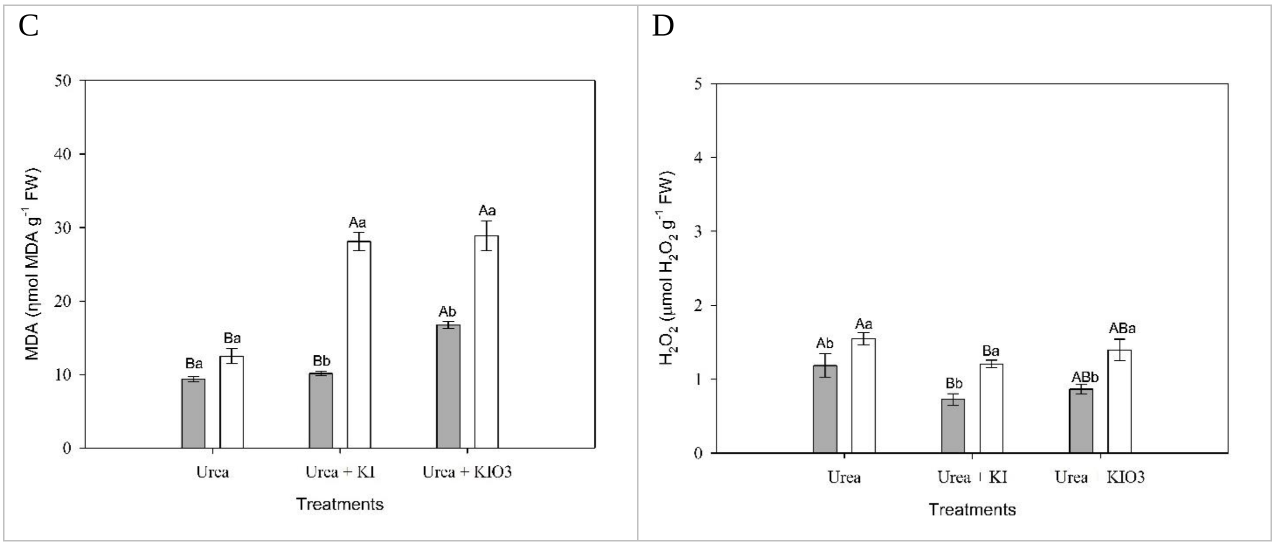


Figure 7: Activity of superoxide dismutase (SOD) (A) and catalase (CAT) (B), and contents of malondialdehyde (MDA) (C) and hydrogen peroxide (H_2O_2) (D) in Micro-Tom tomato leaves at 49 DAT (rehydration). Plants were irrigated at ~90% of field capacity (IRRIGATED) or subjected to water deficit (WD) from 35 to 44 DAT and fertilized with urea enriched with potassium iodide (KI) or potassium iodate (KIO_3). Uppercase letters indicate comparisons between fertilization treatments, while lowercase letters indicate comparisons between irrigation treatments. Means followed by the same letter do not differ significantly according to Tukey's test ($p \leq 0.05$). Bars represent the mean of four plants (n = 4).

During the period of maximum stress (44 DAT), a significant reduction in protein levels was observed in the plants, except in those treated with KIO_3, which maintained baseline protein levels (Figure 8). During rehydration, the protein content returned to values similar to the initial values, with a slight increase in previously stressed plants. The levels of free amino acids were higher in plants under water deficit, and the maximum values were recorded in plants treated with KIO_3. During the rehydration phase, plants treated with KI under water stress recovered their initial levels of free amino acids. However, the plants treated with KIO_3 and the reference (urea), despite a recovery, still showed significantly higher concentrations than the irrigated plants. The proline content followed a similar pattern, with higher concentrations observed in plants subjected to water deficit, returning to baseline levels during rehydration, and being more pronounced in plants treated with KIO_3 and the control (urea).

Maximum stress	Rehydration
A	B

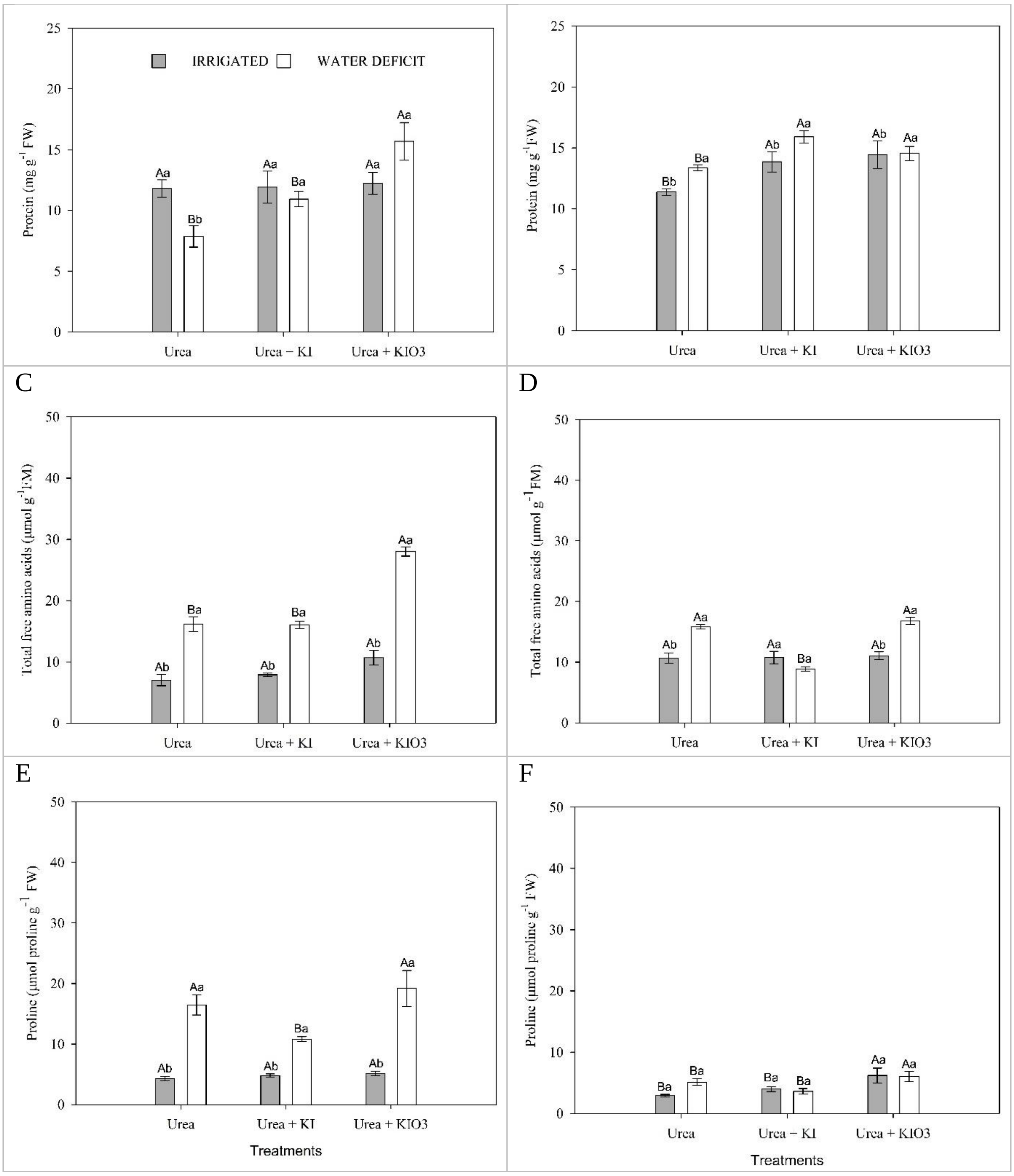


Figure 8: Protein, total free amino acids, and proline contents at peak stress (44 DAT) and after rehydration (49 DAT) in Micro-Tom tomato leaves. Plants were irrigated at ~90% of field capacity (IRRIGATED) or subjected to water deficit (WD) from 35 to 44 DAT and fertilized with urea enriched with potassium iodide (KI) or potassium iodate (KIO_3). Uppercase letters indicate comparisons between fertilization treatments, while lowercase letters indicate comparisons between irrigation treatments. Means followed by the same letter do not differ significantly according to Tukey's test ($p \leq 0.05$). Bars represent the mean of four plants (n = 4).

Plants subjected to water deficits showed similar changes in metabolism. There was an increase in the levels of reducing sugars and a reduction in starch levels, resulting in a decrease in the total non-structural carbohydrate content. Sucrose increased only in the reference plants under water deficit, which contributed to the increase in the total soluble sugar content in this treatment (Table 3).

Table 3: Non-structural carbohydrates in leaves tomatoes Micro-Tom at 44 DAT.

	Reducing sugars µmol g^{-1} FW		Starch µmol g^{-1} FW		Sucrose µmol g^{-1} FW		Total soluble sugars µmol g^{-1} FW		TNC µmol g^{-1} FW	
	Irrig.	WD	Irrig.	WD	Irrig.	WD	Irrig.	WD	Irrig.	WD
urea	0.35 ± 0.04 b	0.67 ± 0.08 a	41.00 ± 3.88 a	26.05 ± 1.50 b	21.72 ± 2.33 Ab	34.82 ± 1.22 Aa	23.57 ± 2.44 Ab	36.59 ± 0.85 Aa	64.56 ± 5.14 a	62.64 ± 0.88 b
urea + KI	0.47 ± 0.03 b	0.78 ± 0.07 a	47.84 ± 4.12 a	25.04 ± 0.56 b	26.50 ± 3.47 Aa	19.66 ± 4.46 Ba	27.26 ± 4.31 Aa	16.46 ± 3.20 Ba	75.10 ± 7.68 a	41.50 ± 3.21 b
urea + KIO_3	0.44 ± 0.03 b	0.80 ± 0.10 a	59.77 ± 9.77 a	29.47 ± 0.69 b	14.16 ± 2.27 Aa	23.22 ± 5.30 Aba	16.05 ± 2.28 Aa	27.11 ± 5.71 ABa	75.82 ± 8.38 a	56.58 ± 5.38 b

Uppercase letters indicate comparisons between fertilization treatments, while lowercase letters indicate comparisons between irrigation treatments. Means followed by the same letter do not differ significantly according to Tukey's test ($p \leq 0.05$). Abbreviations: Irrig. – Irrigated, WD – Water deficit, TNC – Total non-structural carbohydrates.

The pH of the fruit was 3.90 ± 0.03 with a °hue of 44.92 ± 1.60, chroma (C*) of 54.97 ± 3.83, and luminosity (L) of 50.01 ± 2.50, indicating a reddish-orange color with a moderately intense hue and a medium level of brightness. Titratable acidity was 0.59 ± 0.03 mg 100 g citric acid $^{-1}$, while firmness showed an overall average of 0.98 ± 0.17. These parameters showed no statistically significant differences between the treatments.

The respiratory activity of fruits was reduced in plants subjected to water scarcity and treated with KIO_3 (Figure 9). This treatment also resulted in a higher concentration of solid solubles than those that were not treated. Even under ideal irrigation conditions, an increase in the concentration of soluble solids was observed in the plants treated with KI. In addition, the concentration of phenolic compounds in the fruits increased in all treatments with iodine, in the water deficit more pronounced with KIO_3, and irrigated more pronounced with KI. Vitamin C showed an increase in iodine treatments in irrigated plants but was reduced under water deficit conditions in the KIO_3 treatment.

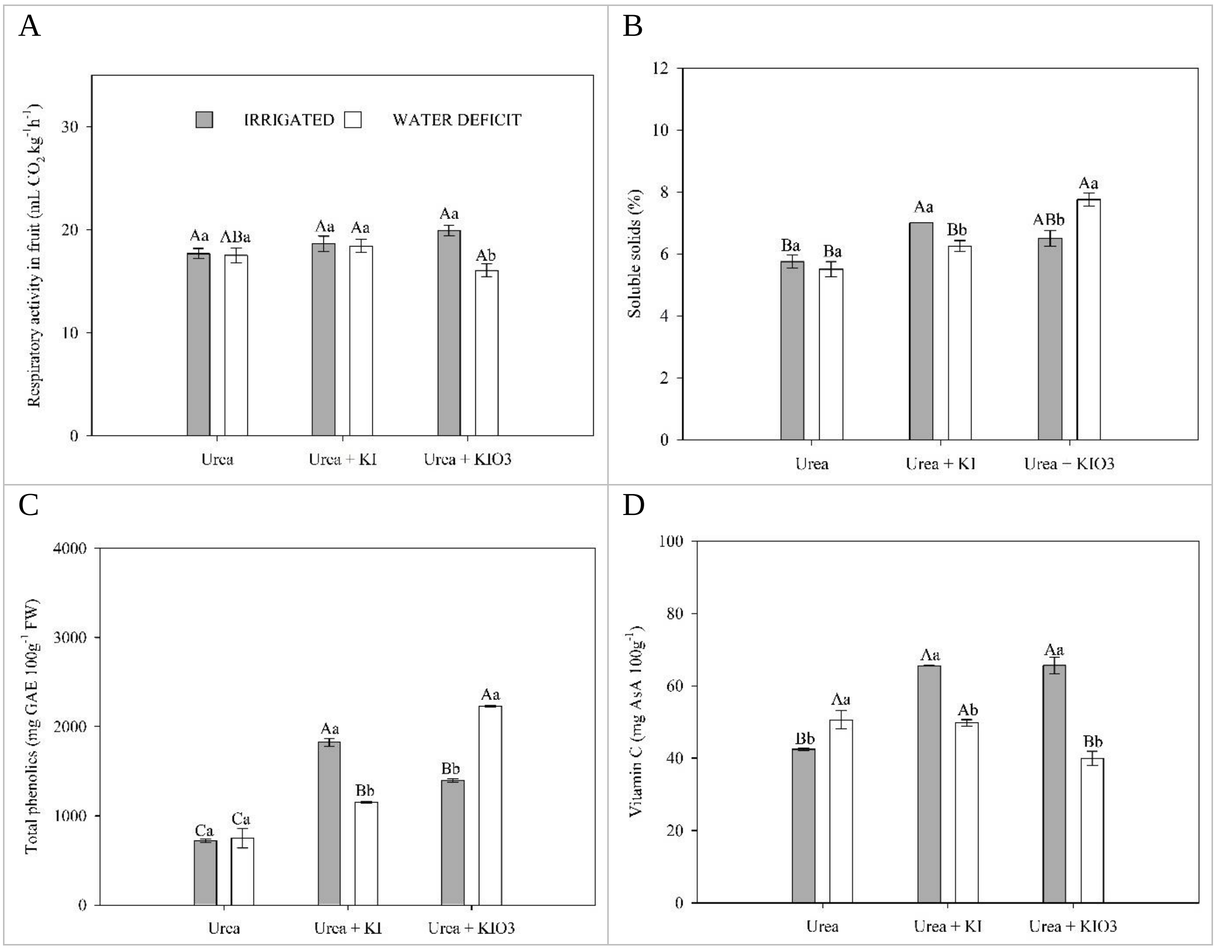


Figure 9: Respiratory activity (A), soluble solids (B), total phenolics (C), and vitamin C (D) contents in Micro-Tom tomato fruits. Plants were irrigated at ~90% of field capacity (IRRIGATED) or subjected to water deficit

(WD) from 35 to 44 DAT and fertilized with urea enriched with potassium iodide (KI) or potassium iodate (KIO_3). Uppercase letters indicate comparisons between fertilization treatments, while lowercase letters indicate comparisons between irrigation treatments. Means followed by the same letter do not differ significantly according to Tukey's test ($p \leq 0.05$). Bars represent the mean of four plants (n = 4).

In irrigated plants, both sources of iodine stimulated antioxidant activity, as evaluated using the β-carotene method (Figure 10). However, under water deficit, only the treatment with KIO_3 promoted this increase. The antioxidant activity evaluated by the ABTS method was reduced in the presence of KIO_3. In contrast, iodine treatments promoted a significant increase in flavonoid levels and antioxidant activity, as determined by the phosphomolybdenum method, regardless of the water regime.

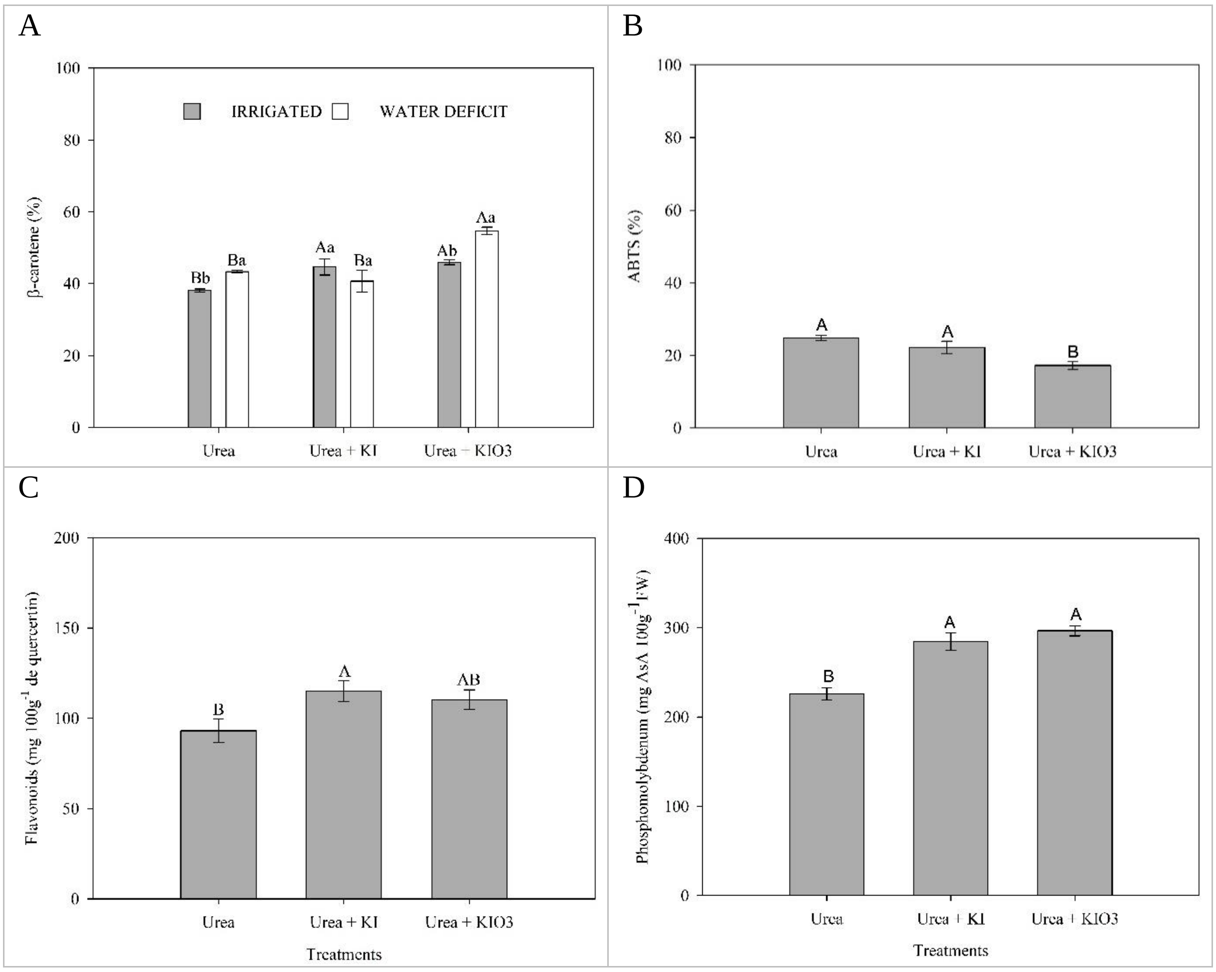


Figure 10: Antioxidant activity determined by the β-carotene bleaching method (A), ABTS reduction method (B), flavonoid content (C), and phosphomolybdenum method (D) in Micro-Tom tomato fruits. Plants were irrigated at ~90% of field capacity (IRRIGATED) or subjected to water deficit (WD) from 35 to 44 DAT and fertilized with urea enriched with potassium iodide (KI) or potassium iodate (KIO_3). Uppercase letters indicate comparisons between fertilization treatments, while lowercase letters indicate comparisons between irrigation treatments.

Means followed by the same letter do not differ significantly according to Tukey's test ($p \leq 0.05$). Bars represent the mean of four plants ($n = 4$).

Additionally, the analysis of the radar chart highlights that the urea + KIO_3 treatment significantly improved the nutritional quality and antioxidant capacity of the fruits (Figure 11). This treatment resulted in the highest levels of flavonoids, soluble solids, and total phenolic compounds, as well as superior performance in antioxidant activity assays using the phosphomolybdenum method and β-carotene bleaching. The urea + KI treatment increased vitamin C levels, while urea alone had moderate effects. In contrast, the control group exhibited the lowest values for most parameters, indicating reduced nutritional quality and antioxidant capacity.

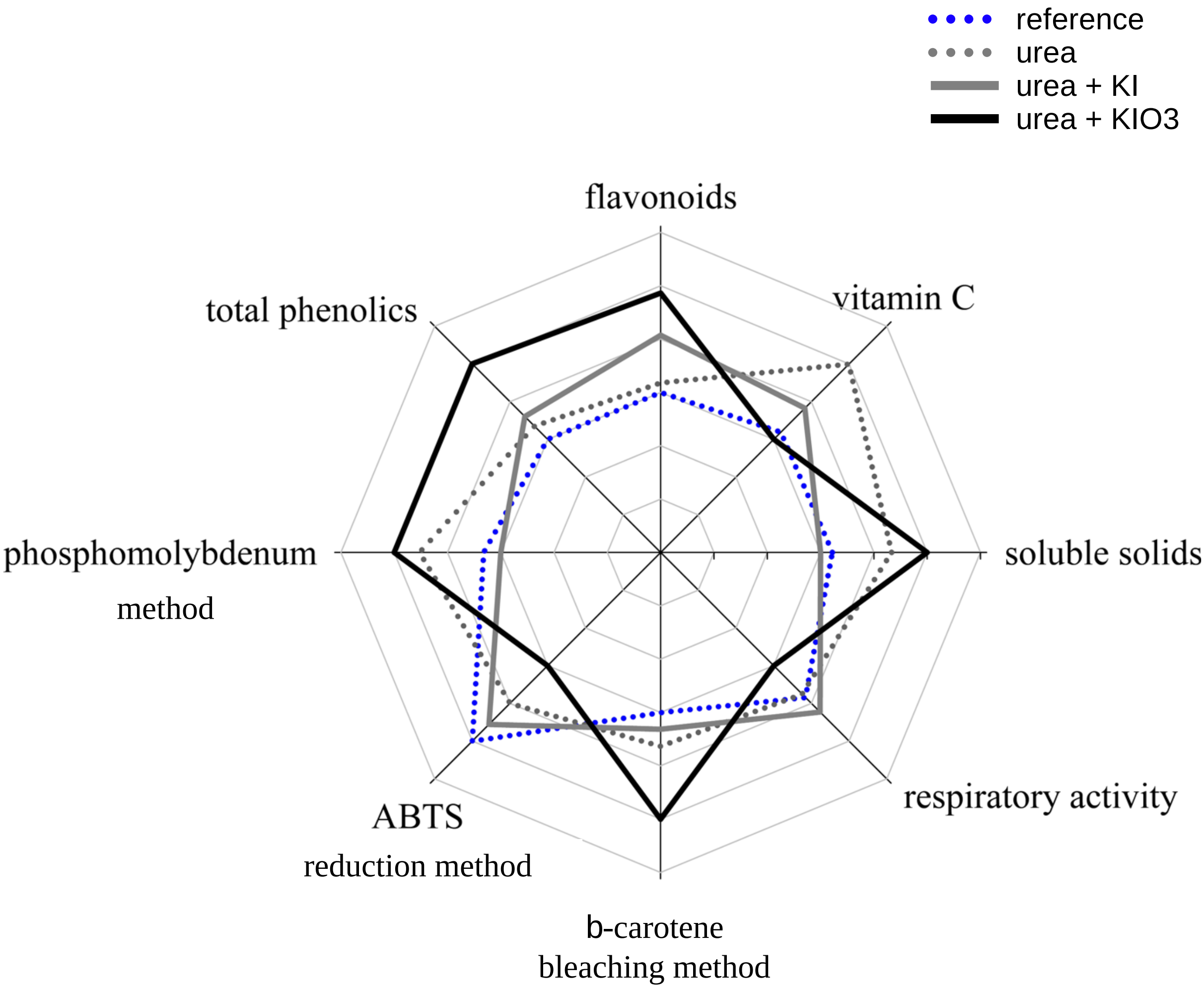


Figure 11: Radar chart of post-harvest analyses. Plants were irrigated at ~90% of field capacity (IRRIGATED) or subjected to water deficit (WD) from 35 to 44 DAT and fertilized with urea enriched with potassium iodide (KI) or potassium iodate (KIO_3). Uppercase letters indicate comparisons between fertilization treatments, while lowercase letters indicate comparisons between irrigation treatments.

Multivariate analysis

Principal component analysis (PCA) and Pearson's correlation were performed considering variables related to crop yield, fruit quality, and physiological and biochemical characteristics of tomatoes subjected to water deficit and treated with different sources of iodine (urea, urea + KI, and urea + KIO_3). The first principal components (PC1 and PC2) accounted for 63.19% of the total variance in the data (Figure 12).

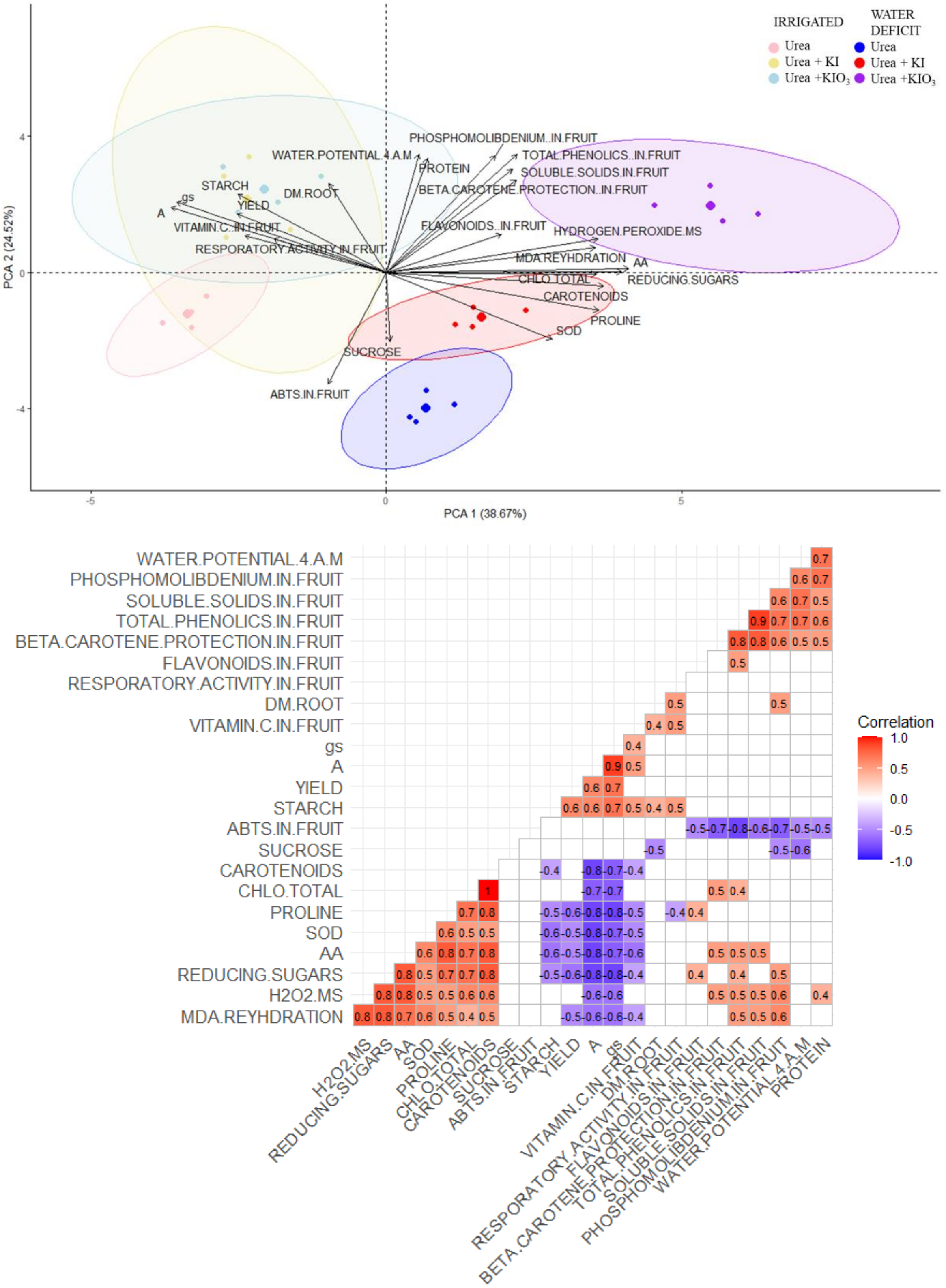


Figure 12: Principal component analysis and Pearson correlation of yield, fruit quality, and physiological and biochemical parameters of tomato plants subjected to water deficit and iodine fertilization. Significant correlations ($p < 0.05$) are highlighted in bold, with positive and negative correlations indicated in red and blue, respectively. White cells indicate non-significant correlations.

Principal component analysis (PCA) revealed a clear segregation between irrigated treatments and those subjected to water deficit, indicating distinct physiological and biochemical responses. Irrigated treatments, regardless of the iodine source, were predominantly grouped in the region associated with variables related to photosynthetic variables (A, gs, and yield) and plant water status (Ψw and dry mass root). These treatments also showed a positive correlation with the concentration of vitamin C in the fruits, suggesting that water availability favors the biosynthesis of this antioxidant compound and reduces the need for the activation of oxidative defense mechanisms.

In contrast, the treatments subjected to water deficit in the PCA biplot revealed that the treatments with urea + KIO_3 under water deficit favored most of the variables related to fruit quality, including total phenolics, flavonoids, soluble solids, and antioxidant activity, as determined by the β-carotene method.

Also, urea treatment without iodine supplementation showed a strong relationship with reducing sugars, proline, and superoxide dismutase (SOD) activity, suggesting a response to oxidative stress. Pearson's correlation reinforced this observation, indicating that the oxidative stress variables (H_2O_2 and malonaldehyde) correlated positively with each other and with MDA rehydration but negatively correlated with variables associated with yield, such as water potential and photosynthetic activity.

KI treatments showed an intermediate profile, partially favoring the accumulation of soluble sugars and carotenoids in the leaves, suggesting a regulatory effect of iodine on antioxidant metabolism.

4. DISCUSSIONS

Water deficit stress significantly affects the physiology and productivity of tomato plants, inducing stomatal closure, which results in the inhibition of photosynthesis and a reduction in fruit weight and overall productivity (Dariva et al., 2021).

Plants treated with iodine showed higher water retention capacity in the early morning, suggesting that they remained hydrated. However, at noon, a drop in water potential was observed, evidencing a severe limitation in water availability, which directly impacted photosynthesis due to stomatal closure. The reduction of the photosynthetic rate was evident in all plants subjected to water stress, however, plants treated with KI maintained a higher net photosynthesis rate compared to the other treatments under stress, a result similar to that observed in soybean and tomato under water deficit with KI application (Lima et al., 2023b, 2023a).

Biomass partitioning was also altered by water deficit, with a reduction in leaf and fruit dry mass. The decrease in net photosynthesis directly impacted the plants' ability to synthesize and redistribute photoassimilates, compromising vegetative and reproductive growth. In general, roots of plants treated with urea + KI and urea + KIO_3 showed higher biomass accumulation. These results show the role of iodine in the modulation of plant growth, particularly in the allocation of root biomass, favoring water absorption under conditions of water deficit. This influence has already been reported by Lima et al., (2023b) in soybean plants, reinforcing the hypothesis that iodine can act to mitigate the deleterious effects of water restriction through the maintenance of the root system.

The relationship between photosynthesis and photosynthetic pigments reveals a characteristic pattern. An increase in total chlorophyll and carotenoid contents was observed in plants under water deficit with severely reduced net photosynthesis. On the other hand, plants treated with KI maintained a higher photosynthetic rate even under stress and did not show significant changes in chlorophyll balance in relation to the reference, although they did exhibit differences in carotenoid content. Studies conducted by Kiferle et al., (2021) demonstrated that iodine treatment led to the iodination of several proteins, many of which are directly involved in photosynthesis, including at least 31 directly associated with chlorophyll.

Irrigated plants and plants treated with urea + KI that maintained higher photosynthetic rates even under stress showed reduced photosynthsis after rehydration. This response pattern suggests that plants subjected to more severe stress, to the point of reaching negative values of net photosynthesis, activate compensatory mechanisms to restore metabolic balance, increasing the photosynthetic rate after rehydration (Pinheiro and Chaves, 2011). The Fv/Fm ratio was slightly reduced by stress, but without impairment of the photosynthetic apparatus, evidenced by the recovery of the initial values after rehydration, indicating that the photochemical apparatus was totally preserved during the water stress.

Stomatal regulation was also influenced by iodine treatment. Plants treated with KI maintained greater stomatal opening until the seventh day of stress, favoring carbon fixation. However, from this period on, there was a drastic reduction in stomatal conductance in all treatments, evidencing a conservative response to avoid excessive water losses.

These changes in photosynthetic parameters may be related, in part, to protein iodination. Studies conducted by Kiferle et al., (2021) demonstrated that iodine treatment led to the iodination of several proteins, many of which are directly involved in photosynthesis. In addition to the proteins associated with chlorophyll, this study revealed that iodination occurred in proteins located both in the shoots and in the roots of plants. In shoots, iodinated proteins were mostly associated with the chloroplast and performed essential functions in photosynthesis. In the roots, iodination was observed mainly in peroxidases or proteins related to the action of these antioxidant enzymes.

The difference in the assimilation of the forms of iodine may explain the different effects observed between the treatments with KI and KIO_3. Because iodide (I^-) is in its reduced form, it is readily assimilated by plants, which may explain why higher photosynthetic rates were maintained in plants treated with KI under water deficit conditions. Iodate (IO_3^-), on the other hand, needs to be reduced to the iodide form in the soil before it can be absorbed by plants, a process that depends on the activity of the enzyme iodate reductase, which can slow down absorption (Duborská et al., 2018; Hong et al., 2012; Kato et al., 2013; Lawson et al., 2015; Zhang et al., 2023).

Enzymatic antioxidant metabolism is one of the mechanisms that plants have to avoid oxidative damage to cell structure and function, induced by reactive oxygen species (Das and Roychoudhury, 2014). The antioxidant response to water deficit was marked by increased superoxide dismutase (SOD) activity in all treatments. In contrast, catalase (CAT) activity remained unchanged, suggesting that other antioxidant mechanisms may be involved in hydrogen peroxide (H_2O_2) detoxification. The maintenance of malondialdehyde (MDA) and CAT levels under conditions of maximum stress indicated that the antioxidant system was efficient in preventing lipid peroxidation and severe cell damage.

Hydrogen peroxide levels also significantly increased in plants treated with water deficit, especially in plants treated with KI and KIO_3 at maximum stress, a pattern previously reported in the literature (Küpper et al., 2008; Medrano-Macías et al., 2018). Although a reduction in these levels was observed after rehydration, the levels remained higher in relation to the irrigated plants. The accumulation of H_2O_2 at controlled levels may play a role in redox signaling, acting as a secondary messenger in signal transduction owing to its relatively long half-life and high permeability across membranes. After rehydration, plants previously stressed and treated with iodine showed an increase in MDA content. However, this increase may not be related to oxidative damage, but rather to the renewal of cell membranes, as suggested by Marcos et al. (2018).

The accumulation of proline and free amino acids in plants under water stress confirms their osmoprotective role. In addition, plants treated with KIO_3 maintained their protein levels even under water deficit, suggesting a lower impairment of metabolism. These results raise the hypothesis that KIO_3 may be influencing nitrogen assimilation and redistribution, since this treatment also resulted in higher levels of proteins, free amino acids, and chlorophylls A and B.

In this context, Cezar et al., (2024) demonstrated that the application of iodate-enriched urea promoted an increase in nitrogen assimilation, which was reflected in higher levels of chlorophyll and proteins. Our findings indicate that KIO_3 can act in a similar way, enhancing nitrogen retention and favoring the synthesis of metabolites essential for tolerance to water stress. However, studies on the interaction between iodate and nitrogen metabolism are still scarce, highlighting the need for further investigations to elucidate the mechanisms involved in this response.

During a water deficit, the reallocation of sugars and non-structural carbohydrates occurs, which is an essential process for the maintenance of energy metabolism and cellular homeostasis. The limitation of photosynthetic activity under water stress reduces carbon assimilation, leading plants to mobilize their starch reserves to meet energy demands. This process results in a decrease in starch stocks and an increase in the concentration of soluble sugars derived from starch degradation.

The reduction in non-structural carbohydrates, combined with the accumulation of soluble sugars, suggests an osmotic adjustment mechanism, which is fundamental for the maintenance of cellular turgidity and for the mitigation of the deleterious effects of drought. This osmotic adjustment allows plant cells to retain water and to preserve their physiological functionality under harsh conditions. Notably, plants treated with KIO_3 showed higher starch reserves than the other treatments, indicating a possible role of iodine in regulating carbohydrate metabolism and optimizing energy storage capacity, which may confer greater resilience to water stress.

The modulation of sugars, especially starch, under conditions of maximum stress can exert a direct influence on postharvest quality and physiology. Leaves, the main tissue source of photosynthesis, play a crucial role in this process by capturing light energy and directing photoassimilates to demand organs, such as fruits (Dong et al., 2025). This transport occurs predominantly via the phloem and promotes the growth and development of fruits throughout the production cycle. Evidence indicates that foliar photosynthesis and photosynthesis share an integrated regulatory network in fruits. Photosynthetic activity in fruits can influence leaf photosynthesis through regulators, such as SlARF6A, although at a lower intensity (Dong et al., 2025; Yuan et al., 2019). However, the precise mechanisms of this interaction remain poorly understood, and further studies are required to understand its dynamics and physiological relevance.

The growing demand of consumers for foods with higher nutritional value and sensory quality reinforces the need for strategies to optimize the composition of tomato fruits (*Solanum* *lycopersicum*). In the present study, physicochemical parameters, including pH, color, and firmness, were not significantly affected by iodine treatment. However, the respiratory activity of the fruits was reduced in plants treated with KIO_3 under water deficit, indicating less metabolic degradation and a possible prolongation of the postharvest shelf life, as described by Saltveit, (2019) in the control of senescence by respiration modulation.

The concentration of soluble solids was higher in fruits of plants treated with iodine, suggesting a possible positive effect on sweetness and nutritional quality. This increase was observed in both the fruits of plants subjected to water stress, in which the best source was urea + KIO_3, and in irrigated plants, in which the most effective combination was urea + KI. These results corroborate previous findings indicating the influence of iodine on the regulation of metabolites associated with fruit flavor and nutritional value (Lima et al., 2023a; Medrano Macías et al., 2021).

Iodine also influenced the antioxidant composition of fruits, with different effects between the treatments. The β-carotene content increased in both water regimes, but under water deficit, this increase was specific to the treatment with KIO_3. Flavonoids showed higher concentrations in fruits treated with KI, regardless of water availability, whereas phenolic compounds were stimulated in both treatments, with emphasis on KI in irrigated plants and KIO_3 under water stress. These results reinforce the role of iodine in inducing specialized metabolites associated with stress response and fruit functional value, as observed in previous studies (Beckles et al., 2012; Medrano Macías et al., 2021; Riyazuddin et al., 2023).

On the other hand, vitamin C showed a response pattern dependent on water availability, increasing only in irrigated plants, while treatment with KIO_3 reduced its concentration under water deficit. Similarly, in the study by Li et al., (2017) on iodine biofortification in strawberries, an increase in vitamin C was also observed. This response can be attributed to the positive effect of iodine under adequate irrigation conditions, with water availability being a determining factor for the response observed in plants. The results obtained indicate that different sources of iodine modulate the nutritional quality and antioxidant profile of tomato fruits, both under water deficit and in irrigated plants.

5. CONCLUDING REMARKS

The growing consumer demand for foods with higher nutritional values, especially those rich in antioxidant compounds, underscores the importance of strategies that favor the accumulation of these compounds. In this context, iodine fertilization has emerged as a promising approach, not only to mitigate the effects of abiotic stress but also to improve the functional quality of fruits. Treatment with urea + KIO_3 proved to be the most efficient in attenuating the effects of water stress and promoting improvements in fruit quality and antioxidant capacity.

REFERENCES

Ahanger, M.A., Qi, M., Huang, Z., Xu, X., Begum, N., Qin, C., Zhang, C., Ahmad, N., Mustafa, N.S., Ashraf, M., Zhang, L., 2021. Improving growth and photosynthetic performance of drought stressed tomato by application of nano-organic fertilizer involves up-regulation of nitrogen, antioxidant and osmolyte metabolism. Ecotoxicol Environ Saf 216, 112195. https://doi.org/https://doi.org/10.1016/j.ecoenv.2021.112195

Altaf, M.A., Shahid, R., Ren, M.-X., Naz, S., Altaf, M.M., Khan, L.U., Tiwari, R.K., Lal, M.K., Shahid, M.A., Kumar, R., Nawaz, M.A., Jahan, M.S., Jan, B.L., Ahmad, P., 2022. Melatonin Improves Drought Stress Tolerance of Tomato by Modulating Plant Growth, Root Architecture, Photosynthesis, and Antioxidant Defense System. Antioxidants 11. https://doi.org/10.3390/antiox11020309

Andrade, O.V.S., de Sousa Lima, J., das Neves, T.T., de Morais, E.G., Benevenute, P.A.N., dos Santos, L.C., L. Nascimento, V., Guilherme, L.R.G., Marchiori, P.E.R., 2024. The Role of Potassium Iodate in Mitigating the Damages of Water Deficit in Coffee Plants. J Soil Sci Plant Nutr. https://doi.org/10.1007/s42729-024-01939-y

Arvouet-Grand, A., Vennat, B., Pourrat, A., Legret, P., 1994. [Standardization of propolis extract and identification of principal constituents]. J Pharm Belg 49, 462–8.

Auzanneau, N., Weber, P., Kosińska-Cagnazzo, A., Andlauer, W., 2018. Bioactive compounds and antioxidant capacity of Lonicera caerulea berries: Comparison of seven cultivars over three harvesting years. Journal of Food Composition and Analysis 66, 81–89. https://doi.org/10.1016/j.jfca.2017.12.006

Bates, L.S., Waldren, R.P., Teare, I.D., 1973. Rapid determination of free proline for water-stress studies. Plant Soil 39, 205–207. https://doi.org/10.1007/BF00018060

Beckles, D.M., Hong, N., Stamova, L., Luengwilai, K., 2012. Biochemical factors contributing to tomato fruit sugar content: a review. Fruits 67, 49–64. https://doi.org/DOI: 10.1051/fruits/2011066

Biemelt, S., Keetman, U., Albrecht, G., 1998. Re-Aeration following Hypoxia or Anoxia Leads to Activation of the Antioxidative Defense System in Roots of Wheat Seedlings1. Plant Physiol 116, 651–658. https://doi.org/10.1104/pp.116.2.651

Blasco, B., Ríos, J.J., Leyva, R., Cervilla, L.M., Sánchez-Rodríguez, E., Rubio-Wilhelmi, M.M., Rosales, M.A., Ruiz, J.M., Romero, L., 2011. Does Iodine Biofortification Affect Oxidative Metabolism in Lettuce Plants? Biol Trace Elem Res 142, 831–842. https://doi.org/10.1007/s12011-010-8816-9

Bradford, M.M., 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. Anal Biochem 72, 248–254. https://doi.org/10.1016/0003-2697(76)90527-3

Buege, J.A., Aust, S.D., 1978. [30] Microsomal lipid peroxidation, in: Fleischer, S., Packer, L. (Eds.), Methods in Enzymology. Academic Press, pp. 302–310. https://doi.org/https://doi.org/10.1016/S0076-6879(78)52032-6

Cezar, J.V. da C., Morais, E.G. de, Lima, J. de S., Benevenute, P.A.N., Guilherme, L.R.G., 2024. Iodine-Enriched Urea Reduces Volatilization and Improves Nitrogen Uptake in Maize Plants. Nitrogen 5, 891–902. https://doi.org/10.3390/nitrogen5040057

Chaudhary, J., Khatri, P., Singla, P., Kumawat, S., Kumari, A., R, V., Vikram, A., Jindal, S.K., Kardile, H., Kumar, R., Sonah, H., Deshmukh, R., 2019. Advances in Omics Approaches for Abiotic Stress Tolerance in Tomato. Biology (Basel) 8, 90. https://doi.org/10.3390/biology8040090

Chen, J., Kang, S., Du, T., Guo, P., Qiu, R., Chen, R., Gu, F., 2014. Modeling relations of tomato yield and fruit quality with water deficit at different growth stages under greenhouse condition. Agric Water Manag 146, 131–148. https://doi.org/https://doi.org/10.1016/j.agwat.2014.07.026

Claeys, H., Inzé, D., 2013. The Agony of Choice: How Plants Balance Growth and Survival under Water-Limiting Conditions. Plant Physiol 162, 1768–1779. https://doi.org/10.1104/pp.113.220921

Dariva, F.D., Pessoa, H.P., Copati, M.G.F., de Almeida, G.Q., de Castro Filho, M.N., Picoli, E.A. de T., da Cunha, F.F., Nick, C., 2021. Yield and fruit quality attributes of selected tomato introgression lines subjected to long-term deficit irrigation. Sci Hortic 289, 110426. https://doi.org/10.1016/J.SCIENTA.2021.110426

Das, K., Roychoudhury, A., 2014. Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. Front Environ Sci 2. https://doi.org/10.3389/fenvs.2014.00053

Davies, J.N., Hobson, G.E., McGlasson, W.B., 1981. The constituents of tomato fruit — the influence of environment, nutrition, and genotype. C R C Critical Reviews in Food Science and Nutrition 15, 205–280. https://doi.org/10.1080/10408398109527317

Dong, H., Li, F., Xuan, X., Ahiakpa, J.K., Tao, J., Zhang, X., Ge, P., Wang, Y., Gai, W., Zhang, Y., 2025. The genetic basis and improvement of photosynthesis in tomato. Hortic Plant J 11, 69–84. https://doi.org/10.1016/J.HPJ.2023.06.007

Duborská, E., Urík, M., Kubová, J., 2018. Interaction with soil enhances the toxic effect of iodide and iodate on barley (Hordeum vulgare L.) compared to artificial culture media during initial growth stage. Arch Agron Soil Sci 64, 46–57. https://doi.org/10.1080/03650340.2017.1328104

Emmanuel Umeohia, U., Adekunle Olapade, A., 2024. Quality Attributes, Physiology, and Postharvest Technologies of Tomatoes (Lycopersicum Esculentum) – A Review. American Journal of Food Science and Technology 12, 42–64. https://doi.org/10.12691/ajfst-12-2-1

Ferreira, E.B., Cavalcanti, P.P., Nogueira, D.A., 2013. ExpDes.pt: Pacote Experimental Designs (Portugues) [WWW Document]. CRAN: Contributed Packages. https://doi.org/10.32614/CRAN.package.ExpDes.pt

Giannopolitis, C.N., Ries, S.K., 1977. Superoxide Dismutases. Plant Physiol 59, 309–314. https://doi.org/10.1104/pp.59.2.309

Halka, M., Klimek-Chodacka, M., Smoleń, S., Baranski, R., Ledwożyw-Smoleń, I., Sady, W., 2018. Organic iodine supply affects tomato plants differently than inorganic iodine. Physiol Plant 164, 290–306. https://doi.org/https://doi.org/10.1111/ppl.12733

Harrell Jr, F.E., 2003. Hmisc: Harrell Miscellaneous. CRAN: Contributed Packages. https://doi.org/10.32614/CRAN.package.Hmisc

Havir, E.A., McHale, N.A., 1987. Biochemical and Developmental Characterization of Multiple Forms of Catalase in Tobacco Leaves. Plant Physiol 84, 450–455. https://doi.org/10.1104/pp.84.2.450

Hong, C., Weng, H., Jilani, G., Yan, A., Liu, H., Xue, Z., 2012. Evaluation of Iodide and Iodate for Adsorption–Desorption Characteristics and Bioavailability in Three Types of Soil. Biol Trace Elem Res 146, 262–271. https://doi.org/10.1007/s12011-011-9231-6

Hou, X., Zhang, W., Du, T., Kang, S., Davies, W.J., 2020. Responses of water accumulation and solute metabolism in tomato fruit to water scarcity and implications for main fruit quality variables. J Exp Bot 71, 1249–1264. https://doi.org/10.1093/jxb/erz526

Husson, F., Josse, J., Le, S., Mazet, J., 2006. FactoMineR: Multivariate Exploratory Data Analysis and Data Mining. CRAN: Contributed Packages. https://doi.org/10.32614/CRAN.package.FactoMineR

IUSS, W.G.W., 2015. International Soil Classification System for Naming Soils and Creating Legends for Soil Maps. World Reference Base for Soil Resources 2014, Update 2015, Rome: FAO.

Joshi, R., Wani, S.H., Singh, B., Bohra, A., Dar, Z.A., Lone, A.A., Pareek, A., Singla-Pareek, S.L., 2016. Transcription Factors and Plants Response to Drought Stress: Current Understanding and Future Directions. Front Plant Sci 7. https://doi.org/10.3389/fpls.2016.01029

Kassambara, A., 2016. ggcorrplot: Visualization of a Correlation Matrix using “ggplot2.” CRAN: Contributed Packages. https://doi.org/10.32614/CRAN.package.ggcorrplot

Kassambara, A., Mundt, F., 2016. factoextra: Extract and Visualize the Results of Multivariate Data Analyses. CRAN: Contributed Packages. https://doi.org/10.32614/CRAN.package.factoextra

Kato, S., Wachi, T., Yoshihira, K., Nakagawa, T., Ishikawa, A., Takagi, D., Tezuka, A., Yoshida, H., Yoshida, S., Sekimoto, H., Takahashi, M., 2013. Rice (Oryza sativa L.) roots have iodate reduction activity in response to iodine. Front Plant Sci 4. https://doi.org/10.3389/fpls.2013.00227

Kaur, H., Kohli, S.K., Khanna, K., Bhardwaj, R., 2021. Scrutinizing the impact of water deficit in plants: Transcriptional regulation, signaling, photosynthetic efficacy, and management. Physiol Plant 172, 935–962. https://doi.org/https://doi.org/10.1111/ppl.13389

Kiferle, C., Martinelli, M., Salzano, A.M., Gonzali, S., Beltrami, S., Salvadori, P.A., Hora, K., Holwerda, H.T., Scaloni, A., Perata, P., 2021. Evidences for a Nutritional Role of Iodine in Plants. Front Plant Sci 12. https://doi.org/10.3389/fpls.2021.616868

Koch, G., Rolland, G., Dauzat, M., Bédiée, A., Baldazzi, V., Bertin, N., Guédon, Y., Granier, C., 2019. Leaf Production and Expansion: A Generalized Response to Drought Stresses from Cells to Whole Leaf Biomass—A Case Study in the Tomato Compound Leaf. Plants 8, 409. https://doi.org/10.3390/plants8100409

Küpper, F.C., Carpenter, L.J., McFiggans, G.B., Palmer, C.J., Waite, T.J., Boneberg, E.-M., Woitsch, S., Weiller, M., Abela, R., Grolimund, D., Potin, P., Butler, A., Luther, G.W., Kroneck, P.M.H., Meyer-Klaucke, W., Feiters, M.C., 2008. Iodide accumulation provides kelp with an inorganic antioxidant impacting atmospheric chemistry. Proceedings of the National Academy of Sciences 105, 6954–6958. https://doi.org/10.1073/pnas.0709959105

Lawson, P.G., Daum, D., Czauderna, R., Meuser, H., Härtling, J.W., 2015. Soil versus foliar iodine fertilization as a biofortification strategy for field-grown vegetables. Front Plant Sci 6. https://doi.org/10.3389/fpls.2015.00450

Leyva, R., Sánchez-Rodríguez, E., Ríos, J.J., Rubio-Wilhelmi, M.M., Romero, L., Ruiz, J.M., Blasco, B., 2011. Beneficial effects of exogenous iodine in lettuce plants subjected to salinity stress. Plant Science 181, 195–202. https://doi.org/https://doi.org/10.1016/j.plantsci.2011.05.007

Li, R., Liu, H., Hong, C., Dai, Z., Liu, J., Zhou, J., Hu, C., Weng, H., 2017. Iodide and iodate effects on the growth and fruit quality of strawberry. J Sci Food Agric 97, 230–235. https://doi.org/10.1002/jsfa.7719

Lichtenthaler, H.K., Buschmann, C., 2001. Chlorophylls and Carotenoids: Measurement and Characterization by <scp>UV</scp> - <scp>VIS</scp> Spectroscopy. Current Protocols in Food Analytical Chemistry 1. https://doi.org/10.1002/0471142913.faf0403s01

Lima, J. de S., Andrade, O.V.S., Morais, E.G. de, Machado, G.G.L., Santos, L.C. dos, Andrade, E.S. de, Benevenute, P.A.N., Martins, G.S., Nascimento, V.L., Marchiori, P.E.R., Lopes, G., Vilas Boas, E.V. de B., Guilherme, L.R.G., 2023a. KI Increases Tomato Fruit Quality and Water Deficit Tolerance by Improving Antioxidant Enzyme Activity and Amino Acid Accumulation: A Priming Effect or Relief during Stress? Plants 12. https://doi.org/10.3390/plants12234023

Lima, J. de S., Andrade, O.V.S., Santos, L.C. dos, Morais, E.G. de, Martins, G.S., Mutz, Y.S., Nascimento, V.L., Marchiori, P.E.R., Lopes, G., Guilherme, L.R.G., 2023b. Soybean Plants Exposed to Low Concentrations of Potassium Iodide Have Better Tolerance to Water Deficit through the Antioxidant Enzymatic System and Photosynthesis Modulation. Plants 12. https://doi.org/10.3390/plants12132555

Liu, L., Shao, Z., Zhang, M., Wang, Q., 2015. Regulation of Carotenoid Metabolism in Tomato. Mol Plant 8, 28–39. https://doi.org/10.1016/j.molp.2014.11.006

Marcos, F.C.C., Silveira, N.M., Mokochinski, J.B., Sawaya, A.C.H.F., Marchiori, P.E.R., Machado, E.C., Souza, G.M., Landell, M.G.A., Ribeiro, R. V., 2018. Drought tolerance of sugarcane is improved by previous exposure to water deficit. J Plant Physiol 223, 9–18. https://doi.org/10.1016/J.JPLPH.2018.02.001

Martí, E., Gisbert, C., Bishop, G.J., Dixon, M.S., García-Martínez, J.L., 2006. Genetic and physiological characterization of tomato cv. Micro-Tom. J Exp Bot 57, 2037–2047. https://doi.org/10.1093/jxb/erj154

Medeiros, S.R., Feijó, G.L.D., Malafaia, G., Lampert, V., Abreu, U.G.P., 2023. Para onde vai o clima nos próximos anos. Boletim Cicarne.

Medina, M.B., 2011. Determination of the total phenolics in juices and superfruits by a novel chemical method. J Funct Foods 3, 79–87. https://doi.org/10.1016/j.jff.2011.02.007

Medrano Macías, J., López Caltzontzit, M.G., Rivas Martínez, E.N., Narváez Ortiz, W.A., Benavides Mendoza, A., Martínez Lagunes, P., 2021. Enhancement to Salt Stress Tolerance in Strawberry Plants by Iodine Products Application. Agronomy 11. https://doi.org/10.3390/agronomy11030602

Medrano-Macías, J., Leija-Martínez, P., González-Morales, S., Juárez-Maldonado, A., Benavides-Mendoza, A., 2016. Use of Iodine to Biofortify and Promote Growth and Stress Tolerance in Crops. Front Plant Sci 7. https://doi.org/10.3389/fpls.2016.01146

Medrano-Macías, J., Mendoza-Villarreal, R., Valentín Robledo-Torres, Fuentes-Lara, L.O., Ramírez- Godina, F., Pérez-Rodríguez, M.Á., Benavides- Mendoza, A., 2018. The Use of Iodine, Selenium, and Silicon in Plant Nutrition for the Increase of Antioxidants in Fruits and Vegetables, in: Shalaby, E., Azzam, G.M. (Eds.), Antioxidants in Foods and Its Applications. IntechOpen, Rijeka, p. Ch. 8. https://doi.org/10.5772/intechopen.75069

Meissner, R., Jacobson, Y., Melamed, S., Levyatuv, S., Shalev, G., Ashri, A., Elkind, Y., Levy, A., 1997. A new model system for tomato genetics. The Plant Journal 12, 1465–1472. https://doi.org/10.1046/j.1365-313x.1997.12061465.x

Miller, G.L., 1959. Use of Dinitrosalicylic Acid Reagent for Determination of Reducing Sugar. Anal Chem 31, 426–428. https://doi.org/10.1021/ac60147a030

Mitchell, C.A., 1992. Measurement of Photosynthetic Gas Exchange in Controlled Environments. HortScience HortSci 27, 764–767. https://doi.org/10.21273/HORTSCI.27.7.764

Nakano, Y., Asada, K., 1981. Hydrogen Peroxide Is Scavenged by Ascorbate-Specific Peroxidase in Spinach Chloroplasts. Plant Cell Physiol 22, 867–880.

Novais, R.F., Neves, J.C.L., Barros, N.F., 1991. Ensaio em ambiente controlado. EMBRAPA, Brasília.

Patanè, C., Tringali, S., Sortino, O., 2011. Effects of deficit irrigation on biomass, yield, water productivity and fruit quality of processing tomato under semi-arid Mediterranean climate conditions. Sci Hortic 129, 590–596. https://doi.org/https://doi.org/10.1016/j.scienta.2011.04.030

Pinheiro, C., Chaves, M.M., 2011. Photosynthesis and drought: can we make metabolic connections from available data? J Exp Bot 62, 869–882. https://doi.org/10.1093/jxb/erq340

Prieto, P., Pineda, M., Aguilar, M., 1999. Spectrophotometric Quantitation of Antioxidant Capacity through the Formation of a Phosphomolybdenum Complex: Specific Application to the Determination of Vitamin E. Anal Biochem 269, 337–341. https://doi.org/10.1006/abio.1999.4019

Riyazuddin, R., Singh, K., Iqbal, N., Nisha, N., Rani, A., Kumar, M., Khatri, N., Siddiqui, M.H., Yasheshwar, Kim, S.T., Attila, F., Gupta, R., 2023. Iodine: an emerging biostimulant of growth and stress responses in plants. Plant Soil 486, 119–133. https://doi.org/10.1007/s11104-022-05750-5

Rufino, M. do S.M., Alves, R.E., de Brito, E.S., Pérez-Jiménez, J., Saura-Calixto, F., Mancini-Filho, J., 2010. Bioactive compounds and antioxidant capacities of 18 non-traditional tropical fruits from Brazil. Food Chem 121, 996–1002. https://doi.org/10.1016/j.foodchem.2010.01.037

Saltveit, M.E., 2019. Respiratory Metabolism. Postharvest Physiology and Biochemistry of Fruits and Vegetables 73–91. https://doi.org/10.1016/B978-0-12-813278-4.00004-X

Santos, H.G. dos., Jacomine, P.K.Tito., Anjos, L.H.C. dos., Oliveira, V.Á. de., Lumbreras, J.Francisco., Coelho, M.Rizzato., Almeida, J.A. de., Filho, J.C. de Araújo., Oliveira, J.B. de., Cunha, T.J.Ferreira., 2018. Sistema brasileiro de classificação de solos, 5a. ed. Embrapa Solos, Brasilia.

Seleiman, M.F., Al-Suhaibani, N., Ali, N., Akmal, M., Alotaibi, M., Refay, Y., Dindaroglu, T., Abdul-Wajid, H.H., Battaglia, M.L., 2021. Drought Stress Impacts on Plants and Different Approaches to Alleviate Its Adverse Effects. Plants 10. https://doi.org/10.3390/plants10020259

Staff, S.S., 1999. Soil Taxonomy A Basic System of Soil Classification for Making and Interpreting Soil Surveys, 2 ed. ed. United States Department of Agriculture, Washington.

Strohecker, R., Henning, H.M., 1967. Análises de vitaminas: Métodos comprovados., Editora Paz Montalvo. ed. Madrid.

van Handel, E., 1968. Direct microdetermination of sucrose. Anal Biochem 22, 280–283. https://doi.org/10.1016/0003-2697(68)90317-5

Velikova, V., Yordanov, I., Edreva, A., 2000. Oxidative stress and some antioxidant systems in acid rain-treated bean plants: Protective role of exogenous polyamines.

Plant Science 151, 59–66. https://doi.org/https://doi.org/10.1016/S0168-9452(99)00197-1

Yemm, E.W., Cocking, E.C., Ricketts, R.E., 1955. The determination of amino-acids with ninhydrin. Analyst 80, 209. https://doi.org/10.1039/an9558000209

Yemm, E.W., Willis, A.J., 1954. The estimation of carbohydrates in plant extracts by anthrone. Biochemical Journal 57, 508–514. https://doi.org/10.1042/bj0570508

Yin, J., Gentine, P., Zhou, S., Sullivan, S.C., Wang, R., Zhang, Y., Guo, S., 2018. Large increase in global storm runoff extremes driven by climate and anthropogenic changes. Nat Commun 9, 4389. https://doi.org/10.1038/s41467-018-06765-2

Yuan, Y., Xu, X., Gong, Z., Tang, Y., Wu, M., Yan, F., Zhang, X., Zhang, Q., Yang, F., Hu, X., Yang, Q., Luo, Y., Mei, L., Zhang, W., Jiang, C.-Z., Lu, W., Li, Z., Deng, W., 2019. Auxin response factor 6A regulates photosynthesis, sugar accumulation, and fruit development in tomato. Hortic Res 6, 85. https://doi.org/10.1038/s41438-019-0167-x

Zhang, Y., Cao, H., Wang, M., Zou, Z., Zhou, P., Wang, X., Jin, J., 2023. A review of iodine in plants with biofortification: Uptake, accumulation, transportation, function, and toxicity. Science of The Total Environment 878, 163203. https://doi.org/10.1016/j.scitotenv.2023.163203

CONCLUDING REMARKS

Faced with the growing challenges posed by climate change, especially the intensification of rainfall, it is essential to develop strategies that increase the resilience of crop plants to water stress. In this context, the use of elements such as iodine has emerged as a promising approach that has not yet been explored, but it has great potential for mitigating adverse effects on plant growth and the quality of agricultural production. This study reinforces the importance of expanding research on the role of iodine in plant physiology, contributing to a scientific field that is still in its infancy. A deeper understanding of these interactions could open up new possibilities for more sustainable and adaptive agronomic practices in line with the demands of a changing agricultural scenario.