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MARIA ELIZIANE PANTOJA DA SILVA

DOPAMINE PROMOTES TOLERANCE IN RICE UNDER IRON EXCESS BY IMPROVING ROOT ANATOMY, IONIC BALANCE, PHOTOSYNTHETIC PERFORMANCE, AND BIOMASS

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Dissertation submitted to Universidade Federal Rural da Amazônia, as part of the requirements for obtaining the Magister Scientiae degree in Agronomy. Advisor: Prof. Dr. Allan Klynger da Silva Lobato

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Prof. Dr. Flávio José Rodrigues Cruz – 1st Examiner
UNIVERSIDADE FEDERAL DO OESTE DO PARÁ – UFOPA

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Dr.ª Talitha Soares Pereira– 3td Examiner
PURDUE UNIVERSITY

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LIST OF ILLUSTRATION

LIST OF TABLES

LIST OF ABBREVIATIONS

APX	Ascorbate peroxidase
CAR	Carotenoids
Ca	Calcium
CAT	Catalase
Chl *a*	Chlorophyll a
Chl *b*	Chlorophyll b
C_i	Intercellular CO_2 concentration
CO_2	Carbon dioxide
CP	Chlorophyll parenchyma
Cu	Copper
DOP	Dopamine
E	Transpiration rate
EL	Electrolyte leakage
ETAb	Epidermis thickness from abaxial leaf side
ETAd	Epidermis thickness from adaxial leaf side
ETR	Electron transport rate
ETR/P_N	Ratio between the apparent electron transport rate and net photosynthetic rate
EXC	Relative energy excess at the PSII level
F_0	Minimal fluorescence yield of the dark-adapted state
Fe	Iron
F_m	Maximal fluorescence yield of the dark-adapted state
F_v	Variable fluorescence
F_v/F_m	Maximal quantum yield of PSII photochemistry
g_s	Stomatal conductance
H_2O_2	Hydrogen peroxide
K	Potassium
MDA	Malondialdehyde
Mg	Magnesium
Mo	Molybdenum
NPQ	Nonphotochemical quenching
O_2^-	Superoxide

P_N	Net photosynthetic rate
P_N/C_i	Instantaneous carboxylation efficiency
POX	Peroxidase
PSII	Photosystem II
q_P	Photochemical quenching
RCT	Root cortex thickness
RDM	Root dry matter
RDT	Root endodermis thickness
RET	Root epidermis thickness
RMD	Root metaxylem diameter
ROS	Reactive oxygen species
SDM	Shoot dry matter
SOD	Superoxide dismutase
TDM	Total dry matter
Total Chl	Total Chlorophyll
VCD	Vascular cylinder diameter
WUE	Water-use efficiency
Zn	Zinc
Φ_{PSII}	Effective quantum yield of PSII photochemistry

ABSTRACT

Rice (*Oryza sativa* L.) is an essential food for more than half of the world's population, and is crucial for food security and the economy. Grown mainly in flooded soils, this crop faces challenges such as low pH and excess iron (Fe), resulting from redox conditions that favor the availability of this element. High concentrations of Fe are toxic to plants, impairing photosynthesis, gas exchange, anatomical structures, the antioxidant system, nutritional status, and biomass production. Therefore, management strategies and the use of biomolecules have been investigated to reduce these effects. Dopamine (DOP) has been studied as a neurotransmitter with a regulatory role in biotic and abiotic stresses. DOP attenuates the toxicity of heavy metals, in addition to mitigating the impacts of salinity, flooding and water stress, through the activation of antioxidant enzymes, improvement of photosynthetic efficiency, modulation of anatomical structures and increase in nutrient absorption and biomass. This study aimed to evaluate whether the exogenous application of DOP reduces oxidative damage in the photosynthetic system of rice plants exposed to excess Fe, in addition to analyzing changes in leaf structure, production of reactive oxygen species (ROS), activity of antioxidant enzymes, nutritional status and biomass. The research was conducted at the Federal Rural University of the Amazon, Paragominas Campus, in a greenhouse under controlled conditions. Ten-day-old rice seedlings were grown in a hydroponic system and subjected to four treatments: two concentrations of Fe (250 μM, control; 5000 μM, excess) and two of DOP (0 μM and 50 μM). DOP was applied to the nutrient solution from the 20th to the 40th day, while Fe was supplied from the 30th to the 40th day. On the 40th day, physiological and morphological parameters were measured, and samples were collected for anatomical, biochemical, and nutritional analyses. Data were submitted to one-way ANOVA and Scott-Knott test ($p < 0.05$). The results demonstrated that excess Fe causes significant damage to plants. However, DOP promotes nutrient accumulation in roots and leaves, providing Fe content in these structures, in addition to increasing leaf and root anatomy. DOP application minimizes oxidative damage, elevating photosynthetic pigments and increasing PSII quantum efficiency (Φ_{PSII}) and electron transport rate (ETR). In gas exchange, increases in net photosynthesis (P_N) and instantaneous carboxylation efficiency (P_N/C_i) were observed. DOP also strengthens the antioxidant defense, increasing the activities of superoxide dismutase (33%), catalase (29%), ascorbate peroxidase (75%) and peroxidase (17%), while reducing the levels of reactive oxygen species (O_2^- and H_2O_2) and oxidative stress markers (MDA and EL). Although excess Fe reduced biomass, DOP increased shoot, root and total dry matter. Therefore, DOP alleviates the effects of stress caused by excess Fe in rice plants

KEYWORDS: Antioxidant enzymes. *Oryza Sativa*. Photosynthesis. Neurotransmitter. Toxicity

RESUMO

O arroz (*Oryza sativa* L.) é um alimento essencial para mais da metade da população mundial, sendo crucial para a segurança alimentar e a economia. Cultivado principalmente em solos alagados, essa cultura enfrenta desafios como baixo pH e excesso de ferro (Fe), decorrentes das condições redox que favorecem a disponibilidade desse elemento. Concentrações elevadas de Fe são tóxicas às plantas, prejudicando a fotossíntese, as trocas gasosas, as estruturas anatômicas, o sistema antioxidante, o estado nutricional e a produção de biomassa. Diante disso, estratégias de manejo e o uso de biomoléculas têm sido investigados para reduzir esses efeitos. A dopamina (DOP) vem sendo estudada por ser um neurotransmissor com papel regulador em estresses bióticos e abióticos. A DOP atenua a toxicidade de metais pesados, além de mitigar os impactos da salinidade, alagamento e estresse hídrico, por meio da ativação de enzimas antioxidantes, melhoria da eficiência fotossintética, modulação das estruturas anatômicas e incremento na absorção de nutrientes e biomassa. Este estudo teve como objetivo avaliar se a aplicação exógena de DOP reduz os danos oxidativos no sistema fotossintético de plantas de arroz expostas ao excesso de Fe, além de analisar alterações na estrutura foliar, produção de espécies reativas de oxigênio (ROS), atividade de enzimas antioxidantes, estado nutricional e biomassa. A pesquisa foi conduzida na Universidade Federal Rural da Amazônia, *Campus* Paragominas, em estufa com condições controladas. Mudas de arroz com 10 dias foram cultivadas em sistema hidropônico e submetidas a quatro tratamentos: duas concentrações de Fe (250 μM, controle; 5000 μM, excesso) e duas de DOP (0 μM e 50 μM). A DOP foi aplicada na solução nutritiva do 20º ao 40º dia, enquanto o Fe foi fornecido do 30º ao 40º dia. No 40º dia, parâmetros fisiológicos e morfológicos foram medidos, e amostras foram coletadas para análises anatômicas, bioquímicas e nutricionais. Os dados foram submetidos à ANOVA unidirecional e ao teste de Scott-Knott ($p < 0,05$). Os resultados demonstraram que o excesso de Fe causa danos significativos às plantas. No entanto, a DOP promove o acúmulo de nutrientes nas raízes e folhas, reduzindo o teor de Fe nessas estruturas, além de aumentar a anatomia foliar e radicular. A aplicação de DOP minimiza os danos oxidativos, elevando os pigmentos fotossintéticos e aumentando a eficiência quântica do PSII (ΦPSII) e a taxa de transporte de elétrons (ETR). Nas trocas gasosas, observaram-se incrementos na fotossíntese líquida (P_N) e eficiência instantânea de carboxilação (P_N/C_i). A DOP também fortalece a defesa antioxidante, elevando as atividades da Superóxido dismutase (33%), catalase (29%), ascorbato peroxidase (75%) e peroxidase (17%), enquanto reduz os níveis de espécies reativas de oxigênio (O_2^- and H_2O_2)e os marcadores de estresse oxidativo (MDA e EL). Embora o excesso de Fe tenha reduzido a biomassa, a DOP aumentou a massa seca da parte aérea, das raízes e a massa seca total. Portanto, a DOP alivia os efeitos do estresse causado pelo excesso de Fe em plantas de arroz.

PALAVRAS-CHAVE: Enzimas antioxidantes. *Oryza sativa*. Fotossíntese. Neurotransmissor. Toxicidade.

SUMARY

1 CONTEXTUALIZATION

Rice (*Oryza sativa* L.) is one of the most widely grown cereals in the world and an important source of nutrition and food security for more than half of the global population (Carrijo; Lundy; Linquist, 2017). This crop is commonly grown in tropical and subtropical climate regions (Cheng *et al.*, 2019). The largest producers are China, India and Bangladesh. Brazil, with an annual production of 10.78 million tons, ranks 11th among the world's largest producers (FAOSTAT, 2022). Rice can be grown in a wide variety of hydrological conditions, including waterlogged soils, which provide an ideal environment for its growth due to its semi-aquatic nature (Carrijo; Lundy; Linquist, 2017; Miro; Ismail, 2013).

However, among the main challenges for cultivation in flooded systems is Fe toxicity, which negatively affects plant development and productivity (Shahid *et al.*, 2014). In flooded conditions, the reduction in available oxygen leads to a decrease in pH due to anaerobic microbial activity. It also leads to a low redox potential in the soil, which favors the reduction of Fe^{3+} to Fe^{2+}, a more soluble form that is easily absorbed by the roots (Matthus *et al.*, 2015; Pan *et al.*, 2014; Sahrawat, 2004). Fe is an essential micronutrient for processes such as photosynthesis and cellular respiration, but its excess can be highly detrimental, as it causes oxidative stress, compromises cellular functions, leading to metabolic dysfunction and cell death (Kar e Panda, 2020; Souza *et al.*, 2024). Symptoms of Fe toxicity include bronzed leaves, yellowing, reddish spots, edge necrosis, reduced growth, impaired root development, which causes lower nutrient absorption and affects the health of the plant (Wu *et al.*, 2014; Zahra *et al.*, 2021).

Agricultural practices (Fageria *et al.*, 2008), water management (Carmona *et al.*, 2021) and the use of organic molecules as plant growth regulators as 24-epibrassinolide (Tadaiesky *et al.*, 2020) and neurotransmitters, γ-aminobutyric acid (GABA) (Zhu *et al.*, 2021) and melatonin (Hoque *et al.*, 2021) have been studied to reduce Fe toxicity in rice plants in a flooded cultivation system. In this sense, dopamine (DOP) allows plant organisms to adjust their responses to biological and environmental stresses. DOP, which belongs to the catecholamine group of biogenic amines, is a natural neurotransmitter present in both the animal and plant kingdoms. Discovered in plants in 1968, its endogenous biosynthesis is influenced by some stress conditions (Kulma; Szopa, 2007; Marchiosi *et al.*, 2020).

Due to its antioxidant properties, this molecule acts directly in the neutralization of reactive oxygen species (ROS), reducing oxidative damage caused by stresses such as drought, salinity and heavy metal toxicity (Cao *et al.*, 2023; Gao *et al.*, 2020; Yildirim *et al.*, 2024).

Exogenous DOP contributes to increased photosynthetic efficiency, reduces oxidative damage and ensures the functionality of the photosynthetic machinery even under adverse conditions. This results in improved plant growth, greater carbon assimilation and, consequently, increased productivity, even in environments subject to severe stress (Abdulmajeed *et al.*, 2022; Ji *et al.*, 2022; Wang *et al.*, 2023). In this way, DOP acts to mitigate the effects of abiotic stress, improving plant growth, physiological processes and productivity (Ahammed; Li, 2023; Raza *et al.*, 2022).

In this context, the hypothesis of this study is that excess Fe causes damage to the photosynthetic apparatus, nutrient homeostasis, growth, and productivity of rice plants grown in flooded soils, which is one of the biggest problems in this cropping system (Pinto *et al.*, 2016; Wairich *et al.*, 2024). However, exogenous application of DOP mitigates stress in plants caused by heavy metals, salinity, and mineral nutrition imbalances (Li *et al.*, 2015; Liang *et al.*, 2017; Zhang *et al.*, 2023). It minimizes oxidative damage, protects the photosynthetic apparatus, and improves the anatomical structures of plants subjected to different stresses (Ji *et al.*, 2022; Jiao *et al.*, 2019; Pontes *et al.*, 2024).

Therefore, the objective of this study was to evaluate whether the exogenous application of DOP can reduce oxidative damage in the photosynthetic apparatus of rice leaves exposed to excess Fe. In addition, the anatomy of leaves and roots was analyzed to verify changes in anatomical structures, the production of reactive oxygen species (ROS), the activity of antioxidant enzymes, and the nutritional status of plants. In this sense, this research contributes to the advancement of studies on neurotransmitters as attenuators of abiotic stresses, especially in Fe toxicity in flooded rice fields, given that there are no studies on this topic.

2 LITERATURE REVIEW

2.1 Rice (*Oryza sativa* L.)

2.1.1 General aspects, cultivation and economic scenario

Rice (*Oryza sativa L.*), native to Asia, was one of the first agricultural crops cultivated by mankind, becoming an essential staple food in the daily lives of the global population (Zhou *et al.*, 2022). Rich in calories, minerals such as calcium and iron, it is a considerable source of vitamin E and B5, carbohydrates, thiamine, folate, phenolic compounds such as phytic acid and phenols and sterols such as flavonoids, terpenoids, anthocyanins, tocopherols, tocotrienols and orizanol, among other bioactive compounds (Carrijo; Lundy; Linquist, 2017) which give it antioxidant, anti-inflammatory, antidiabetic and anticancer properties (Verma; Srivastav,

2020). Its by-products, such as the husk, bran and germ, have applications in the food, cosmetics and pharmaceutical areas, as well as in the processing and production of biofuels (Colombo *et al.*, 2024).

Rice belongs to the Poaceae family and is classified into two subspecies, *O. sativa* ssp japonica adapted to more temperate climates and *O. sativa* ssp indica generally adapted to lowland tropical cultivation (Yang et al., 2014; Cheng et al., 2019). It is an annual plant that can reach 1 to 1.8 meters in height, with thin, long leaves. Its flowers grow in pendulous inflorescences, and the edible grain is a seed containing an embryo capable of germinating and forming a new plant. The grain is mainly composed of the matured ovary, the lemma and palea (which, together with other structures, form the shell), as well as the embryo located in the ventral part, next to the lemma. The edible part of the grain is the endosperm (Panesar; Kaur, 2016).

This species requires temperatures between 27°C and 35°C, high levels of humidity and an adequate distribution of rainfall, with approximately 100 cm of precipitation, to ensure its proper growth and development (Kumar; Jeena; Singh, 2019). In flooded rice crops, the formation of aerenchyma in the roots is more prominent in anaerobic conditions. In addition, it has a larger cross-sectional radius, larger vascular bundle diameter, greater root thickness and larger xylem area. These characteristics facilitate the absorption of water and nutrients (Phule *et al.*, 2019).

Around 75% of the world's rice production comes from flooded soils, corresponding to an agricultural area of approximately 85 to 90 million hectares (Datta; Ullah; Ferdous, 2017). Rice cultivated in this environment shows greater vegetative growth, higher productivity, greater plant height and more tillers, obtaining higher productivity compared to aerobic rice (Phule *et al.*, 2019; Vijayaraghavareddy *et al.*, 2020). Therefore, it plays a crucial role in meeting global food demand (Ali; Wani, 2021).

China is the world's largest rice producer with an annual production of 208.49 million tons, followed by India (196.25 million tons), Bangladesh (57.19 million tons), Indonesia (54.75 million tons), Vietnam (42.67 million tons) and Brazil in 11th place with an annual production of 10.78 million tons of rice (FAOSTAT, 2022).

In the context of agricultural production in Brazil, the main rice-growing ecosystems are flood-irrigated rice and upland rice, which encompasses all the other rice-growing systems in the country. However, most of the country's production comes from irrigated rice farming, which accounts for 93% of the total (EMBRAPA, 2024). The upland ecosystem consists of

plant development under aerobic conditions, in which rice can be grown with supplementary sprinkler irrigation or on a rainfed basis. In the flooded ecosystem, irrigated rice farming predominates, which includes systems such as traditional, minimum cultivation, no-till, pre-germinated and transplanting. This system is less dependent on climatic conditions compared to rainfed cultivation, which contributes to more stable production (Santos, 2021; Sousa *et al.*, 2021).

Rice is the third most produced grain in Brazil. The 2023/24 rice harvest estimates a planted area of 1,575,000 hectares and productivity of 6,852 kg/ha. Of the total produced, flooded rice is estimated to occupy an area of 1,254.7 thousand hectares, with productivity of 7,970 kg/ha and production of 10,000.3 tons. With regard to rainfed rice, the estimate is for a planted area of 320,300 hectares, productivity of 2,469 kg/ha and production of 790.7 tons, which are lower than those for flooded rice (CONAB, 2024). Approximately 10.0 million tons of rice are consumed in the country every year (Silva; Wander, 2023).

Rice production in Brazil is worth close to 17.76 billion reais. Rio Grande do Sul is Brazil's largest rice-producing state, with a harvest of 7.14 million tons, followed by Santa Catarina (around 1.18 million tons), Tocantins (604,000 tons), Paraná (148,92 thousand tons) and Mato Grosso (324,71 thousand tons) (IBGE, 2023).

The state of Pará ranks 10th nationally, accounting for 1.05% of Brazil's rice production, with an estimated volume of 106,023 tons. In the Northern Region, the state ranks 3rd, with 11.25% of regional production. The main producer is the municipality of Cachoeira do Arari, located in the Marajó Archipelago, responsible for 32,000 tons and a harvested area of 9,000 hectares, equivalent to 22.19% of the state's total (SEDAP, 2023).

2.2 Iron (Fe)

2.2.1 Iron in soil

Iron (Fe) is the fourth most abundant element in the Earth's crust, with approximately 5-6% by weight in sedimentary rocks. In the environment, Fe occurs mainly in two oxidation states: ferrous (Fe^{2+}), which is more soluble and bioaccessible, and ferric (Fe^{3+}), which is less soluble and less available in neutral or oxygenated environments (Huang *et al.*, 2021). Fe^{2+} can arise from sources such as chemical and physical weathering, as well as the reduction of minerals containing Fe^{3+}, including ferrihydrite, goethite, lepidocrocite, hematite and magnetite. Natural processes, such as photolysis and the action of iron-reducing bacteria, also contribute to the formation and availability of Fe^{2+} in ecosystems (Huang *et al.*, 2021; Kappler

et al., 2021).

Fe uptake in plants occurs through Strategy I and Strategy II. Strategy I, commonly in eudicots, is a reduction-based mechanism that involves the excretion of protons from the roots to the rhizosphere. Proton release requires the reduction of ferric ion to ferrous ion, which is catalyzed by ferric oxidase reductase (FRO). The Fe-regulated transport protein (IRT) transports these soluble ions across the plasma membrane to root cells (Dey *et al.*, 2020; Zhong *et al.*, 2022).

Strategy II is mainly adopted by grasses, in which ferric ion (Fe^{3+}) complexes with chemicals released by the roots, such as phytosiderophores, with mugineic acids (MA) being the most common. After the formation of the Fe (III)-MA complex, its entry into root cells occurs through specific transporters, such as *Yellow Stripe1* (YS1) and *Yellow Stripe-Like* (YSLs) (Kar; Panda, 2020; Zhang *et al.*, 2019).

Rice presents Fe absorption mechanisms characteristic of both Strategy I and Strategy II. In addition to the secretion of phytochelates (MAs), including the transporter OsYSL15, responsible for the absorption of Fe^{3+}-OS complexes, rice secretes phenolic compounds that aid in the solubilization of the Fe retained in the apoplast. Rice roots also exhibit an increased expression of the IRT-type transporter, OsIRT1, which facilitates the absorption of Fe^{2+}, predominant in the reducing environment of flooded rice fields (Kaboyashi; Nozoye; Nishizawa, 2019; Wairich *et al.*, 2019). In flooded rice paddies, the reduced and soluble form of Fe (Fe^{2+} or ferrous) predominates, which, in excess, affects productivity and, in extreme cases, can cause total crop loss (Matthus *et al.*, 2015).

2.2.2 Iron in plants and toxicity

Fe is a micronutrient involved in redox reactions in plant cells. It is a constituent of cytochromes and non-heme iron proteins that participate in photosynthesis, nitrogen fixation, and respiration (Taiz *et al.*, 2017). Fe cofactors are essential in electron transfer, oxygen and iron transport and detection, and protein stability (Gao; Dubos, 2021). In chloroplasts, they are present in iron-sulfur (FeS) proteins, such as photosystem I and ferredoxins. In mitochondria, they are part of respiratory complexes: FeS (complexes I and II), FeS and heme (complex III), and heme and copper (complex IV). Peroxisomes and the endoplasmic reticulum contain heme proteins such as peroxidases and cytochrome P450, while mono- and di-iron enzymes are in all cellular compartments (Connorton; Balk; Rodríguez-Celma, 2017).

However, ferrous ions that are absorbed by the roots and transported by the xylem

accumulate in plant tissues and cause overproduction of reactive oxygen species (ROS) by the Fenton reaction with the involvement of catalytic Fe^{2+}, since it catalyzes hydrogen peroxide (H_2O_2), generating the hydroxyl radical (HO•) (Lapaz *et al.*, 2022). ROS affect cellular structures, membranes, DNA, and proteins (Aung; Masuda, 2020), in addition to altering gas exchange and the photosynthetic apparatus such as the net photosynthetic rate, stomatal conductance, and transpiration rate (Müller *et al.*, 2017). Visual symptoms of Fe toxicity in rice plants include leaf discoloration, called bronzing, the appearance of reddish spots, and reduced shoot and root growth. Yield losses caused by Fe toxicity depend on the intensity of the stress and the stage of plant development, and in extreme cases, can result in total crop failure (Wu *et al.*, 2017).

Rice plants grown in hydroponics under Fe toxicity exhibit anatomical changes in the roots, such as a reduction in the thickness of the epidermis, exodermis, endodermis, and in the diameter of the cortex, vascular cylinder, metaxylem, as well as the aerenchyma area (Tadaiesky *et al.*, 2020). Reductions in these structures compromise root integrity, affect water and nutrient absorption and reduce oxygen transport (Yamauchi *et al.*, 2019; Enstone; Peterson; Ma, 2003). In Fe-tolerant cultivars, a more pronounced deposition of lignin is observed in the roots, in the outer layers of the cortex (exodermis and sclerenchyma ring, in the secondary deposits of the cell wall of the tertiary endodermis around the vascular cylinder, in the cells of the primary xylem parenchyma and in the cells of the medullary parenchyma. These characteristics suggest a plant tolerance mechanism to excess Fe (Stein *et al.*, 2019). As for leaf anatomy, there are significant reductions in the thickness of the epidermis on the adaxial and abaxial surfaces, the area of leaf aerenchyma and the diameter of the bulb cells (Tadaiesky *et al.*, 2020). In addition, Fe toxicity is associated with the collapse of epidermal and mesophyll cells, resulting in a reduction in leaf limb thickness (Müller *et al.*, 2015).

2.3 Dopamine (DOP)

Dopamine (DOP) (3,4-dihydroxyphenethylamine), along with adrenaline and noradrenaline, is one of the main catecholamines, a group of neurotransmitters found in animals and plants (Kulma; Szopa, 2007). DOP has the molecular formula $C_8H_{11}NO_2$ and a molecular weight of 153.18. It is an organic compound that is sensitive to light and easily undergoes oxidation in the presence of oxygen. Biotic and abiotic stresses in plants stimulate an increase in endogenous DOP levels through the upregulation of DOP biosynthetic genes (Liu *et al.*, 2020).

In higher plants, DOP is synthesized from the aromatic amino acid L-tyrosine, which originates from simple precursors derived from the glycolysis and pentose phosphate pathways (Ahammed; Li, 2023). There are two main pathways for DOP biosynthesis. In the first pathway, L-tyrosine is converted into tyramine through a decarboxylation reaction catalyzed by the enzyme tyrosine decarboxylase. Subsequently, tyramine is hydroxylated by monophenol hydroxylase, resulting in the formation of DOP. In the second pathway, L-tyrosine is initially hydroxylated by the enzyme tyrosine hydroxylase, producing levodopa (L-DOPA), which, in turn, undergoes a decarboxylation reaction catalyzed by dopa decarboxylase, forming DOP (Kulma; Szopa, 2007; Yllmaz; Gökmen, 2021).

The exogenous application of DOP in plants alleviates stress through various mechanisms of action. It plays a role in protecting against the harmful effects of heavy metals, such as cadmium, by reducing oxidative stress, regulating secondary metabolites, and promoting plant growth (Cao *et al.*, 2023). Additionally, it delays leaf senescence in *Malus hupehensis* by reducing the levels of phytohormones that promote aging through the modulation of gene expression related to hormonal pathways, as it blocks the transmission of signals that accelerate senescence (Zhang *et al.*, 2023). It enhances the resistance of *Lemna turionifera* by increasing the net photosynthesis rate and chlorophyll content while decreasing the abscission rate (Wang *et al.*, 2023). It reduces oxidative biomarker levels, increases the activity of antioxidant and non-enzymatic enzymes and osmoprotectant contents, and improves photosynthetic efficiency, polyamine accumulation, and polyamine metabolic enzyme activity in *Phaseolus vulgaris* (Abdulmajeed *et al.*, 2022). Prestes *et al.* (2025) detect that, under lead toxicity, DOP application increases root epidermis thickness and significantly enhances palisade and spongy parenchyma in leaves, as well as improves stomatal performance in *Solanum lycopersicum*.

Regarding nutrient deficiency in plants, exogenous DOP has the ability to minimize the impacts of this stress, such as nutrient deficiency in *Malus hupehensis* plants, as it significantly alleviates reductions in growth, chlorophyll concentrations, and net photosynthesis, while also mitigating disruptions in nutrient absorption, transport, and distribution. Additionally, it promotes the uptake of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), iron (Fe), manganese (Mn), zinc (Zn), and boron (B) as it alters how these nutrients are distributed throughout the plant. Furthermore, there is a positive regulation of genes induced by DOP for antioxidant enzymes involved in the ascorbate-glutathione cycle (*MdcAPX, MdcGR, MdMDHAR, MdDHAR-1,* and *MdDHAR-2*) and a negative regulation of genes

associated with senescence (*SAG12, PAO,* and *MdHXK*) (Liang *et al.*, 2017).

Under nitrogen deficiency, exogenous DOP influences root system architecture, alters the absorption, transport, and distribution of nitrogen, phosphorus, and potassium, stimulates the activity of enzymes related to nitrogen metabolism, and induces the expression of genes associated with ethylene signaling (Liu *et al.*, 2020). Treatment with 100 μM of DOP can enhance the adaptive capacity of *Lactuca sativa* under nitrogen deficiency, as it mitigates the accumulation of reactive oxygen species (ROS), enhances the activity of antioxidant enzymes, and promotes plant development, productivity, and quality (Farouk *et al.*, 2023). In cases of nitrogen excess, DOP, at concentrations of 100 to 150 μM, significantly alleviates the accumulation of nitrate nitrogen and ammoniacal nitrogen under nitrate conditions, regulates photosynthesis, carbon metabolism, and nitrogen metabolism in response to nitrate stress (Lan *et al.*, 2020).

DOP reduces the impacts of salt stress in tomato seedlings, as it helps alleviate oxidative stress and balance phytohormone levels (Yildirim *et al.*, 2024). The effects of salinity are also mitigated in *Malus hupehensis* plants, as DOP positively influences the uptake of potassium (K), nitrogen (N), phosphorus (P), manganese (Mn), sulfur (S), and copper (Cu), while inhibiting the absorption of sodium (Na) and chlorine (Cl). This neurotransmitter stimulates the activity of antioxidant enzymes and enhances the capacity of the ascorbate-glutathione cycle. Additionally, it positively regulates, in roots and leaves, the genes of the salt overly sensitive pathway under saline conditions, *MdHKT1, MdNHX1*, and *MdSOS1* (Li *et al.*, 2015).

Exogenous DOP aids in adaptation to water deficiency by inhibiting the degradation of photosynthetic pigments and increasing the net photosynthetic rate. Additionally, it stimulates antioxidant enzyme activity and carbohydrate metabolism while regulating the expression of genes related to nitrogen metabolism, secondary compounds, and amino acids. In soybean seedlings, this molecule reduces the average germination time and positively modulates the epidermal tissues, metaxylem, and vascular cylinder in root anatomy, thereby enhancing water absorption by the seedlings (Pontes *et al.*, 2024). Furthermore, it contributes to alkalinity tolerance in *Malus hupehensis* seedlings by increasing antioxidant capacity and chlorogenic acid levels, as well as promoting plant height, root length, chlorophyll levels, and photosynthetic capacity (Jiao *et al.*, 2019).

In the case of biotic stresses, such as infections caused by pathogens, exogenous DOP reduces damage to photosynthetic rates and carbohydrate metabolism by adjusting the expression of Rubisco regulatory genes (*CsrbcL* and *CsrbcS*) and decreasing the expression of

genes related to chlorophyll degradation (*CsPAO* and *CsRCCR*). Additionally, it stimulates the increase of starch, cellulose, fructose, sucrose, and glucose levels. Consequently, it significantly promotes the growth of *Cucumis sativus* under downy mildew stress and reduces the disease index, contributing to improved resistance to pathogens (Ji *et al.*, 2022). Moreover, reduced H_2O_2 levels and increased accumulation of phenolic compounds and salicylic acid have been observed in *Malus domestica* infected by *Valsa mali* and treated with DOP (Liu *et al.*, 2022).

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PAPER

Title page

Dopamine promotes tolerance in rice under iron excess by improving root anatomy, ionic balance, photosynthetic performance, and biomass

Maria Eliziane Pantoja da Silva ● Ivan Becari Viana ● Gisele Barata da Silva ● Caroline Cristine Augusto ● Bruno Lemos Batista ● Allan Klynger da Silva Lobato

M. E. P. Silva ● G. B. Silva ● A. K. S. Lobato (✉)
Núcleo de Pesquisa Vegetal Básica e Aplicada, Universidade Federal Rural da Amazônia. Paragominas, Pará, Brazil.

I. B. Viana
Departamento de Ciências Biológicas, Universidade do Estado de Minas Gerais - Unidade Carangola, Carangola, Minas Gerais, Brazil

C. C. Augusto ● B. L. Batista
Centro de Ciências Naturais e Humanas, Universidade Federal do ABC, Santo André, São Paulo, Brazil

e-mail: allanllobato@yahoo.com.br

Corresponding author: Allan Klynger da Silva Lobato
Mailing address: Rodovia PA 256, Paragominas, Pará, Brazil. Núcleo de Pesquisa Vegetal Básica e Aplicada, Universidade Federal Rural da Amazônia
Phone: +55-91-993134006

Author contribution statement
AKSL served as the advisor for this project, planned all phases of the research, and critically revised the manuscript. MEPS, GBS, and IBV conducted the experiment, performed physiological, biochemical, anatomical, and morphological determinations; they wrote and edited the manuscript. CCA and BLB nutritional analysis. All authors read and approved the final version of the manuscript.

Data availability statement
Data are available upon request to the corresponding author.

Conflict of interest
The authors declare that they have no competing interests.

Dopamine promotes tolerance in rice under iron excess by improving root anatomy, ionic balance, photosynthetic performance, and biomass

Abstract

Rice (*Oryza sativa* L.) is an essential food crop, usually grown in flooded soils. However, these environments, especially with low pH, favor iron (Fe) toxicity due to the low redox potential, which increases the Fe^{2+} availability. Excessive Fe concentrations are highly detrimental, compromising the growth, physiology, and productivity of rice plants. In this context, dopamine (DOP) has emerged as a bioactive molecule with the potential to mitigate stresses in plants. Therefore, the objective of this study was to evaluate whether the exogenous application of DOP attenuates oxidative damage in the photosynthetic apparatus of rice leaves subjected to excess Fe, as well as to analyze anatomical changes, production of reactive oxygen species (ROS), activity of antioxidant enzymes, and the nutritional status of plants. Fe excess caused the accumulation of this element in roots and leaves, reducing the uptake of other essential nutrients. However, the application of DOP significantly increased the nutritional status while reducing the accumulation of Fe in plants. In the anatomy, DOP promoted improvements in root structures, primarily in the thickness of the root epidermis (21%), as well as enhancements in leaves, including an increase in chlorophyll parenchyma (11%). DOP also minimized damage to the photosynthetic apparatus, increasing the levels of photosynthetic pigments and significantly increasing the effective quantum yield of PSII photochemistry (13%) and electron transport rate (13%). In gas exchange, the DOP application in plants under Fe excess promoted increases in the net photosynthetic rate and water use efficiency with increases of 14% and 25%, respectively. The antioxidant defense was intensified by DOP, with increases in the activities of superoxide dismutase (33%), catalase (29%), ascorbate peroxidase (75%) and peroxidase (17%). In parallel, there was a reduction in the ROS accumulation, including superoxide (14%) and hydrogen peroxide (8%), as well as malondialdehyde (37%) and electrolyte leakage (4%). Finally, the biomass was negatively impacted by excess Fe; however, DOP promoted increases in stem and root growth, proving its effectiveness in mitigating the toxic effects of Fe in rice.

Keywords: Metal toxicity; neurotransmitter; *Oryza sativa*; resilience mechanism.

Abbreviations

APX	Ascorbate peroxidase
CAR	Carotenoids
Ca	Calcium
CAT	Catalase
Chl *a*	Chlorophyll a
Chl *b*	Chlorophyll b
C_i	Intercellular CO_2 concentration
CO_2	Carbon dioxide
CP	Chlorophyll parenchyma
Cu	Copper
DOP	Dopamine
E	Transpiration rate
EL	Electrolyte leakage
ETAb	Epidermis thickness from abaxial leaf side
ETAd	Epidermis thickness from adaxial leaf side
ETR	Electron transport rate
ETR/P_N	Ratio between the apparent electron transport rate and net photosynthetic rate
EXC	Relative energy excess at the PSII level
F_0	Minimal fluorescence yield of the dark-adapted state
Fe	Iron
F_m	Maximal fluorescence yield of the dark-adapted state
F_v	Variable fluorescence
F_v/F_m	Maximal quantum yield of PSII photochemistry
g_s	Stomatal conductance
H_2O_2	Hydrogen peroxide
K	Potassium
MDA	Malondialdehyde
Mg	Magnesium
Mo	Molybdenum
NPQ	Nonphotochemical quenching
O_2^-	Superoxide
P_N	Net photosynthetic rate
P_N/C_i	Instantaneous carboxylation efficiency
POX	Peroxidase
PSII	Photosystem II
q_P	Photochemical quenching
RCT	Root cortex thickness
RDM	Root dry matter
RDT	Root endodermis thickness

RET	Root epidermis thickness
RMD	Root metaxylem diameter
ROS	Reactive oxygen species
SDM	Shoot dry matter
SOD	Superoxide dismutase
TDM	Total dry matter
Total Chl	Total Chlorophyll
VCD	Vascular cylinder diameter
WUE	Water-use efficiency
Zn	Zinc
Φ_{PSII}	Effective quantum yield of PSII photochemistry

Introduction

Rice (*Oryza sativa* L.) is an important food crop for humanity (Zhou et al. 2022). This grain is consumed daily by half of the world's population, responding to 20% of global food energy, contributing to food security (Rahman and Zhang 2022). It is widely consumed in Asia, Latin America, the Caribbean and Africa (OECD-FAO 2024). In this scenario, Brazil is the 11th largest rice producer in the world, with an annual production of 10.78 million tons (FAOSTAT 2022), being the third most produced grain (CONAB 2024). Rice cultivation can be carried out in different systems, including flooded soils. However, approximately 75% of global rice production occurs in flooded areas, promoting higher yield in this cultivation system (Datta et al. 2017).

Flooded soils with low pH can suffer from iron (Fe) toxicity due to the low redox potential of the soil, which favors the reduction of Fe^{3+} (ferric) to Fe^{2+} (ferrous). This reduction is intensified by microbial and anaerobic activities, increasing Fe solubilization and, consequently, its availability in the root zone of plants (Mahender et al. 2019). Excessive concentrations of Fe in rice fields cultivated in the flooded system are a problem, as they cause toxicity, reducing crop productivity by 10% to 100%, depending on the intensity (Mishra et al. 2022). Fe is an essential micronutrient for plant development. However, in excess, it affects hormonal homeostasis, inhibits cell division, the growth of primary and lateral roots, reduces plant height, panicle number, grain productivity, causing damage to tissue and foliar symptoms, such as tanning (Aung and Masuda 2020).

Dopamine (DOP) belongs to the group of neurotransmitters classified as catecholamines, playing important roles in regulating physiological processes and responding to biotic and abiotic stresses (Tanveer and Shabala 2020; Raza et al. 2022). This molecule has the ability to minimize the effects of nutritional deficiency in plants (Liang et al. 2017), as well as excess nutrients (Lan et al. 2020). In parallel, it plays a crucial role in reducing heavy metal toxicity (Zhang et al. 2023; Prestes et al. 2025), salinity tolerance (Jiao et al. 2019), and adaptation to water deficit (Gao et al. 2020; Pontes et al. 2024), flooding (Cao et al. 2023a) and pathogen infections (Ji et al. 2022; Liu et al. 2022), working as a relevant antioxidant against stresses in plants (Liu et al. 2020a; Ahammed and Li 2023).

In this context, rice plants subjected to Fe stress present reduced photosynthesis, deterioration of photosynthetic pigments (Pinto et al. 2016; Müller et al. 2017), increases in reactive oxygen species, lipid peroxidation markers, and cell membrane damage (Wu et al. 2017; Onyango et al. 2020), and decreased plant growth and biomass (Lubis et al. 2022). However, the exogenous application of DOP, has shown promise in maintaining photosynthesis (Abdulmajeed et al. 2022; Wang et al. 2023), increasing the activities of antioxidant enzymes (Yildirim et al. 2024), promoting nutrient uptake (Li et al. 2015), and increases biomass in plants subjected to Fe stress (Farouk et al. 2023).

This research hypothesizes that excess Fe in flooded rice is one of the most significant abiotic stresses in the cultivation system of this crop, negatively impacting the physiological processes, growth, and yield (Ullah et al. 2023). In this sense, the exogenous application of DOP acts to minimize the most diverse effects of stresses in plants (Liu et al. 2020b). The objective of this research was to investigate whether the exogenous application of dopamine can mitigate oxidative damage to the photosynthetic apparatus in rice leaves exposed to excess iron. In addition, we sought to evaluate changes in leaf

structures, stomatal variables, production of reactive oxygen species (ROS), activity of antioxidant enzymes, and nutritional status of plants.

Materials and Methods

Geographical location and growth parameters

The experiment was conducted in the Paragominas Campus of the Federal Rural University of Amazonia, Paragominas, Brazil (2°55' S, 47°34' W). The research was performed in a greenhouse with regulated temperature and humidity. The minimum, maximum, and median temperatures were 24.8 °C, 33.9 °C, and 27.1 °C, respectively. The relative humidity throughout the trial period fluctuated between 60% and 80%.

Plant material and containers

Seedlings of *O. sativa* L. cv. Puitá INTA CL™ with 10 old days were selected and placed in 700 mL pots under hydroponic conditions. These seedlings were maintained with Hoagland e Arnon (1950) solution from the 10th day after sowing, starting with 50% of the ionic force and changing to 100% after 6 days (16th day).

Experimental design

The experiment consisted of four treatments, including two with Fe supply (250 and 5000 μM Fe, representing control and excess conditions, in that order) and two concentrations of dopamine (0 and 50 μM DOP, called −DOP and +DOP, respectively).

Plant nutrition, DOP preparation, and Fe excess

Nutrients were available using a nutrient solution in agreement with Tadaiesky et al. (2020) during 24 days (16-40th day). For DOP preparation, 50 μM DOP solution (NT, Sigma-Aldrich, USA) was prepared according to the protocol described by Jiao et al. (2019). DOP was applied directly to the nutrient solution for 20 days (day 20-40 after sowing). For Fe treatments, $FeCl_2$ was prepared at concentrations of 250 μM (control, ×1 Fe) and 5000 μM (excess, ×20 Fe) and supplied for 10 days (30–40th day). Fe concentrations were chosen according to Wang et al. (2015), using pH 5.5. On day 40 of the experiment, physiological and morphological parameters were measured for all plants, and tissues were harvested for anatomical, biochemical, and nutritional analyses.

Chlorophyll fluorescence and gaseous exchange

Chlorophyll fluorescence was assessed utilizing a modulated chlorophyll fluorometer (model OS5p; Opti-Sciences), as outlined by Maia et al. (2018). Gas exchange was assessed with an infrared gas analyzer (model LCPro^{+}; ADC BioScientific), in accordance with the calibration protocols outlined by Pereira et al. (2019).

Measurements of anatomical parameters

Samples were collected from the middle region of the leaf limbs of fully expanded leaves of the third node and roots 4 cm from the root apex. Subsequently, all collected botanical material was fixed in FAA 70 (Johansen 1940) for 24 hours and dehydrated in ethanol for embedding in methacrylate resin (Leica Historesin, Nussloch/Heidelberg, Germany). Transverse sections with a thickness of 7 µm were obtained with a rotating microtome (model YD 315, American MasterTech Scientific), stained with toluidine blue, pH 4.7 (O' Brien and McCully 1981), and mounted onto slides with synthetic resin (Permount-Fischer). For stomatal characterization, the epidermal impression method (Segatto et al. 2004). The slides were observed and photomicrographed under an optical microscope (Primostar 3, Zeiss.) coupled to a digital camera (Axiocam ERc 5s, Zeiss.). The images were analysed with Image-Pro Plus previously calibrated with a micrometre slide from the manufacturer. The leaf anatomical parameters evaluated were epidermis thickness from abaxial leaf side (ETAb), epidermis thickness from adaxial leaf side (ETAd) and Chlorophyll parenchyma (CP). In the root samples, measurements of root epidermis thickness (RET), root epidermis thickness (RDT), root endodermis thickness (RCT), vascular cylinder diameter (VCD), root metaxylem diameter (RMD) were performed.

Assays of antioxidant enzymes, soluble proteins, and stress markers

Antioxidant enzymes (SOD, CAT, APX, and POX) and soluble proteins were isolated from leaf tissues (Badawi et al. 2004). Quantification of total soluble proteins was conducted (Bradford 1976). SOD assay was conducted at 560 nm (Giannopolitis and Ries 1977), and SOD activity was quantified in units per mg of protein. CAT assay was measured at 240 nm (Havir and McHale 1987), with CAT activity quantified as µmol H_2O_2 mg^{-1} protein min^{-1}. The APX experiment was conducted at 290 nm (Nakano and Asada 1981), with APX activity quantified in µmol AsA mg^{-1} protein min^{-1}. The POX assay was measured at 470 nm (Cakmak and Marschner 1992), with activity quantified in µmol tetraguaiacol mg^{-1} protein min^{-1}. The concentration of O_2^- was quantified at 530 nm (Elstner and Heupel 1976). Stress markers, specifically H_2O_2 and MDA, were isolated (Wu et al. 2006). Hydrogen peroxide (H_2O_2) was quantified (Velikova et al. 2000). The MDA concentration was calculated utilizing an attenuation value of 155 mM^{-1} cm^{-1} (Cakmak and Horst 1991). EL was assessed following the methodology outlined by Gong et al. (1998) and is computed using the formula EL (%) = $(EC_1/EC_2) \times 100$.

Assessment of photosynthetic pigments, nutritional composition, and biomass

Chlorophyll and carotenoid concentrations were assessed using 40 mg of foliar tissue. The samples were homogenized in darkness using 8 mL of 90% methanol (Sigma-Aldrich™). The homogenate underwent centrifugation at 6000 × g for 10 minutes at 5ºC. The supernatant was discarded, and the concentrations of chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), carotenoids (Car), and total chlorophyll (total Chl) were measured utilizing a spectrophotometer (model UV-M51; Bel Photonics) in accordance with the technique defined by Lichtenthaler and Buschmann (2001). Samples (100 mg) of root and leaf tissues were pre-digested in 50 mL conical tubes with 2 mL of sub-boiled HNO_3. Subsequently, 8 ml of a solution consisting of 4 ml of H_2O_2 (30% v/v) and 4 ml of ultra-pure water was added and transferred to a Teflon digestion tube (Paniz et al. 2018). Iron (Fe), calcium (Ca), magnesium (Mg), potassium (K), copper (Cu), zinc (Zn) and molybdenum (Mo) were measured using an inductively coupled plasma mass

spectrometer (model ICP-MS 7900; Agilent). The quantification of shoot and root development was conducted by measuring constant dry weights (g) after desiccation in a forced-air oven at 65°C.

Data analysis

The normality of the residuals was assessed using the Shapiro–Wilk test. The data underwent one-way ANOVA, and significant mean differences were assessed using the Scott–Knott test at a 5% probability level (Steel et al. 2006). All statistical analyses employed software R™ (Venables et al. 2021).

Results

DOP decreased Fe concentrations in plants exposed to excess

Plants subjected to Fe excess reached high Fe concentrations in root and leaf tissues (Table 1). However, DOP treatment provides significant reductions in Fe contents of 20% in root tissues and 36% in leaf tissues, when compared to the excess Fe treatment without DOP.

Benefits linked to DOP for nutrient uptake

There were significant reductions in the macro and micronutrient contents in plants exposed to excess Fe in the leaves and roots of rice plants (Table 2 and Fig. 7). However, the application of DOP contributed to a significant increase in essential nutrients in the roots, such as Ca, Mg, K, Cu, Zn and Mo of 63%, 51%, 8%, 14%, 7% and 22% respectively, in relation to plants subjected to excess Fe without DOP. In the leaves, there were also significant increases in Ca (39%), Mg (37%), K (32%), Cu (25%), Zn (12%) and Mo (144%), compared to the excess Fe treatment without DOP.

Exogenous neurotransmitter promoted protection against Fe excess Fe on anatomical structures of roots and leaves

Root structures decreased significantly in plants subjected to Fe excess (Table 3 and Figure 1). However, plants exposed to Fe stress and treated with DOP had increases of 21%, 20%, 8%, 4% and 20% in RET, RDT, RCT, VCD, RMD, in this order, when compared to the treatment of excess Fe + 0 µM DOP. In leaf structures, excess Fe caused significant decreases (Table 3 and Figura 1). However, the application of DOP provided increases in ETAd, ETAb and CP of 6%, 4% and 11%, respectively, in relation to the treatment with excess Fe and in the absence of DOP.

DOP minimized oxidative damage in the photosynthetic apparatus

Fe excess caused reductions in photosynthetic pigments Chl *a*, Chl *b*, Total Chl, and Car, but increases in Chl *a*/Chl *b*, Total/Car (Table 4). However, 50 µM of DOP in plants stressed by Fe promoted increases of 4%, 7%, 5% and 30% in Chl *a*, Chl *b*, Total Chl and Car, respectively, and a decrease of 2% and 19% in Chl *a*/Chl *b*, Total/Car, in this order, when compared to equal treatment without DOP. In chlorophyll fluorescence, plants under Fe stress had an increase in F_0 and a reduction in F_v, F_m, and F_v/F_m (Fig. 2). However, plants treated with 5000 µM Fe^{2+} + 50 µM DOP had a decrease in F_0 (2%) and an increases in F_v (6%), F_m (4%), and F_v/F_m (2%), in relation to treatment with Fe excess and without DOP (Fig. 1). High amount of Fe caused reductions in NPQ, EXC, and ETR/P_N and increases in NPQ, EXC, and ETR/P_N (Table 4 and Fig. 7). However, plants under same treatment with application of 50 µM DOP obtained increases of 13%, 11% and 13% in Φ_{PSII}, q_P, and ETR, respectively, and reductions in NPQ, EXC, and ETR/P_N of 14%, 6% and 1%, in this order, compared to the treatment of Fe excess and absence of the neurotransmitter. Gas exchange, Fe excess generated unfavorable impacts (Table 4 and Fig. 7). Plants exposed to Fe stress when treated with DOP achieved increases in P_N, WUE, and P_N/C_i of 14%, 25% and 23% respectively, and reductions of 22%, 9%, 60 in C_i, E, and g_s, sequentially compared to plants treated with 5000 µM Fe^{2+} + 0 µM DOP.

Contributions of DOP to antioxidant defense

Plants exposed to Fe excess presented increases in enzymatic activities (SOD, CAT, APX and POX) (Fig. 3 and Fig. 7). However, the application of 50 µM DOP in combination with Fe excess intensified the activities of antioxidant enzymes, resulting in significant increases of 33%, 29%, 75% and 17% for SOD, CAT, APX and POX, respectively, when compared to the same treatment without this neurotransmitter. Under Fe toxicity, plants exhibited increases in stress markers (Fig. 4 and Fig. 7). However, the treatment with 50 µM DOP to plants exposed to 5000 µM Fe caused reductions in O_2^-, H_2O_2, MDA, and EL of 14%, 8%, 37% and 4%, in that order, concerning treatment 5000 µM Fe + 0 µM DOP.

DOP reduces the negative effects caused by Fe excess in biomass

Significant decreases in biomass of plants exposed to 5000 µM de Fe were detected (Fig. 5 and Fig. 6). However, DOP utilization in plants impacted by Fe excess induced increments in SDM (6%), RDM (3%) and TDM (6%), in this order, comparing plants submitted to Fe excess without DOP.

Discussion

Fe excess in the soil solution causes accumulation of this element in both roots and leaves of rice plants. In contrast, the DOP application (50 µM) minimizes Fe stress by reducing the levels of this metal in these tissues, which highlights the role of DOP in mitigating the toxic damage caused by Fe excess. DOP reduces Fe accumulation in rice plants, possibly by regulating the expression of genes related to chelator extensions and transport, such as *OsDMAS1*, *OsYSL15*, *OsYSL2*, and *OsFRDL1*, implementing as a strategy to limit the absorption and excessive transport of Fe, contributing to the control of the accumulation of this metal (Kabir et al. 2016; Wairich et al. 2024). The *OsYSL2* gene, for example, acts in the transport of Fe via the phloem (Ishimaru et al. 2010). Thus, the possible inhibition of the expression of this gene in plants treated with DOP may have contributed to the lower concentration of Fe observed in the leaves, compared to plants exposed only to Fe excess in our study. In agreement with our study, DOP acts in the detoxification of toxic metals, such as chromium, as it decreases the absorption and transport of this metal in roots and leaves of tomato plants through phytochelatins and elimination of ROS by the action of antioxidant enzymes (Ahammed et al. 2025). In tobacco plants, the application of DOP alleviates cadmium (Cd) toxicity, since there is an increase in Cd sequestration in the root cell wall and changes in chemical forms within the cells, resulting in a significant reduction in the levels of this element and a significant increase in Mn and Zn concentrations in the roots and leaves (Zhang et al. 2025).

Fe excess affects the absorption of essential minerals, resulting in a significant reduction in Ca, Mg, K, Cu, Zn, and Mo. Fe interferes with nutrient absorption due to competition for transport (Rai et al. 2021). K^+, Ca^{2+}, and Mg^{2+} ions compete for the same transport site as Fe, decreasing the absorption of these nutrients when Fe is in excess. For micronutrients, in addition to competition between other divalent cations, such as Zn^{2+}, the formation of Fe plaques can block access to micronutrients on the surface of rice plants (Kirk et al. 2021). However, DOP treatment increases the levels of macro and micronutrients, due to the fact that DOP favors ionic homeostasis (Dehghanian et al. 2024). This is reflected in the increases in SDM, RDM and TDM found in this research, as plants absorb minerals more efficiently, such as Ca, Mg, K, Cu, Zn, Mo that are essential for plant development and growth (Saleem et al. 2022).

In the leaves of soybean seedlings under saline stress, DOP pretreatment (100 µM and 200 µM) leads to a decrease in the Na content in this tissue. In addition to the significant increase in the K and Ca ions, compared to seedlings not treated with DOP (Abo-Shanab and Diab 2024). Similarly, in Malus hupehensis under excess Na, the application of DOP (100 or 200 µM) positively influences the uptake of K, N, P, S and Mn ions. In parallel, it reduces Na uptake, alleviating saline stress in plants (Li et al. 2015).

Fe excess causes damage to the anatomical structures of roots in rice plants. However, the application of the neurotransmitter in plants stressed with Fe implies benefits for these regions. The epidermis is the first tissue to come into contact with the soil, being responsible for regulating the entry of

water and ions into the plant, as it performs a selective function. Furthermore, the epidermis immobilizes some ions, such as Fe, reducing the content of this element in the internal tissues of the plant (De-Jesús-García et al. 2020). The endodermis is located between the cortex and the vascular cylinder of the root, being a layer that contains the Casparian strip, blocking the apoplastic flow and forcing the entry of ions through the symplastic pathway, that is, inside the cells, allowing selectivity in the transport to the xylem and the homeostasis of elements such as Fe (Chao and Chao 2025). The thickening of the cell walls of the root epidermis and endodermis, especially through the accumulation of suberin and lignin, increases the selectivity and barrier capacity of these layers, acting as protection in the absorption of ions (De-Jesús-García et al. 2020). In addition, the size and number of metaxylem vessels are related to the ability of a root to transport water to the shoot (Reeger et al. 2021). Regarding leaf anatomy, DOP provides increases in CP, ETAd and ETAb in stressed plants. Fe excess damages CP in rice leaves due to the high susceptibility of these organelles to Fe toxicity, because chloroplasts located in leaf mesophyll tissues represent the leading destination of Fe in plants, storing approximately 80 to 90% of the total of this element into plant cells (Ahmed et al. 2023). CP facilitates CO_2 uptake in a leaf region where light is abundant and photosynthetic rates are high, promoting photosynthesis (Borsuk et al. 2022). This behavior is verified in this research, with significant increases in P_N. A similar result was found in study of Prestes et al. (2025), in which treatment with DOP causes a significant increase in palisade and spongy parenchyma (chlorophyll parenchyma) in tomato leaves intoxicated by Pb. Additionally, Fe toxicity is associated with the collapse of abaxial and adaxial epidermal cells and mesophyll, which results in a reduced thickness of the leaf blade (Müller et al. 2015). This behavior is in agreement with the reductions in SDM observed in our work, associated with the increase in ROS, MDA and EL, when plants are exposed to excess Fe.

DOP stimulated the activities of antioxidant enzymes (SOD, CAT, APX, and POX) in rice plants subjected to excess Fe, improving antioxidant defense and ROS elimination. The neurotransmitter amplified the activity of SOD, being an enzyme that catalyzes the dismutation of $O_2^{\cdot-}$ to form H_2O_2 and O_2. Then, CAT, APX and POX act to eliminate H_2O_2 (Rajput et al. 2021), clearly protecting the chloroplast against oxidative stress. In line with the results of our investigation, DOP at concentrations of 100 to 200 µM stimulated the activities of CAT, APX in *Cucumis sativus* plants under excess nickel (Lan et al. 2022). Zhang et al. (2023) found that there was an increase in SOD, POX and CAT activities in *Malus hupehensis* plants treated with 100 µM DOP and subjected to cadmium toxicity, demonstrating that DOP exogenous plays an important role in the elimination of ROS under stress caused by this metal.

Abiotic stresses intensify the production of ROS, causing oxidative damage to essential components, such as lipids, nucleic acids, and proteins, as well as organelles, including the chloroplast and mitochondria (Hasanuzzaman et al. 2020; Panda et al. 2024). In our research, the DOP application in plants exposed to Fe excess decreased the concentration of ROS, such as $O_2^{\cdot-}$ and H_2O_2. In parallel, reductions in MDA (marker of lipid peroxidation) and EL (indicator of damage to cell membranes) reduced the degradation of membrane lipids, revealing higher integrity of cell (Sachdev et al. 2021). In agreement with our study, the concentrations of H_2O_2 and $O_2^{\cdot-}$ significantly decreased by 20% and 21%, respectively, in *Malus hupehensis* plants under cadmium toxicity (Cao et al. 2023b). Pontes et al. (2024), when investigating the effects of DOP on soybean seedlings under water deficit, found that the application of 100 µM DOP caused significant reductions in H_2O_2, O_2, MDA, and EL.

Chloroplast pigments suffered reductions in response to stress caused by Fe. In chloroplasts, Fe is fundamental for the functioning of the photosynthetic apparatus, composing the acceptors linked to electron transport (PSII, PSI, cytochrome b6f complex and ferredoxins) and actively participating in the formation of essential cofactors such as heme and Fe-S clusters (Kroh and Pilon 2020). However, Fe accumulation in chloroplasts caused oxidative damage in chloroplasts, clearly linked to ROS overproduction (Kim et al. 2021). However, DOP application induced increases in Chl *a*, Chl *b*, Total Chl and Car. DOP contributed to protecting chloroplasts and reducing damage to the cell membrane, as identified by the reductions in MDA and EL levels found in this research. In agreement with our work, *M.*

hupehensis seedlings in hydroponic cultivation were subjected to alkaline stress and DOP utilization resulting in an increase in Chl *a*, Chl *b* and, consequently, Total Chl (Jiao et al. 2019). Li et al. (2015) studying the effects of salinity on *M. hupehensis* plants, detected that the addition of DOP to a nutrient solution caused increases in the chloroplast pigments of this species, even under salinity stress.

Treatment under Fe stress and with DOP had increases in F_v, F_m, and F_v/F_m, revealing that the neurotransmitter protected the PSII reaction center. Rice plants stressed with Fe (5000 μM) were characterized by an elevation in F_0 and reductions in F_v, F_m, and F_v/F_m. Behavior similar to our study occurred in research by Tadaiesky et al., (2020). Fe excess induced potential deteriorative activity, suggesting damage to reaction center from PSII (Xu et al. 2015). Application of 100 μM DOP increased F_v/F_m in *Malus hupehensis* conditioned to low nitrogen supplementation (Liu et al. 2020c). A study with *Lemna turionifera*, Wang et al. (2023) identified that treatment with DOP promoted increases in F_v/F_m, Φ_{PSII}, and q_P, as also found in our research.

DOP induced increases in Φ_{PSII}, q_P and ETR, being related to the positive effects on F_v, F_m and F_v/F_m described previously in this study, because the increase in these parameters indicates greater efficiency and activation of reaction centers, such as Q_A that is a molecule responsible for receiving and transferring electrons between PSII and PSI) (Pereira et al. 2019). The decrease observed in NPQ, EXC and ETR/P_N indicates that DOP contributed to a more efficient use of electrons in photochemical activity, stimulating energy absorption and electronic transport by PSII, therefore indirectly contributing to the conversion of light energy captured into biochemical energy (Melo et al. 2022). Similar to our research, the DOP treatment promoted increases in q_P and ETR of pre-treated cucumber plants under nitrate stress (Lan et al. 2020).

Rice plants under Fe stress and DOP application presented increases in P_N, WUE and P_N/C_i, these data are related to the increases in photosynthetic pigments (Chl *a*, Chl *b*, Total Chl and Car) verified in this study. Increase in P_N and reduction in C_i can be explained by the efficiency of the RuBisCO enzyme, responsible for the carboxylation of CO_2 during the photosynthesis process (Pereira et al. 2019). Decrease in E and g_s indicate that there was a decrease in water loss during transpiration process, being explained by the partial closure of the stomata, as well as water was used more efficiently, in agreement with increases in WUE values (Pereira et al. 2014). According to the literature, *Malus domestica* plants pre-treated with dopamine and exposed to drought, P_N, and gs values were significantly higher during time evaluated, comparing control treatment. In the early stages of the drought, C_i values were also higher compared to control plants, but showed lower values in the later stages of drought (Gao et al. 2020). Application of 100 μM DOP significantly increased P_N, g_s and E of *Cucumis sativus* leaves mildew-infected, while significantly reducing C_i (Ji et al. 2022).

Reduced biomass in shoot and root were observed in rice plants subjected to Fe excess. This stress causes ROS formation, resulting in cellular damage and impairing plant physiological processes, such as gas exchange and water relations, which negatively impact the development of shoot and root tissues (Dey et al. 2020). However, the DOP addition to stressed plants brought improvements in biomass, more specifically SDM, RDM, and TDM. This occurs because DOP acts as an antioxidant, contributing to reducing oxidative stress and improving the performance of the photosynthetic apparatus, with benefits on photosynthesis. Thus, plants can produce more photoassimilates, alleviating metabolic limitations and, consequently, favoring vegetative growth (Lan et al. 2020). The use of 100 Mm DOP enhanced the resilience of *Lactuca sativa* seedlings, favoring their growth (Farouk et al. 2023). Modulation of abiotic stress tolerance through antioxidant defense mechanisms directly influences the viability of plant vegetative growth (Ahammed and Li 2023). Gao et al. (2020) observed that *M. domestica* plants that received DOP treatment developed a higher biomass, compared to plants exposed to saline stress.

Conclusion

Rice plants exposed to Fe excess present accumulation of this element and decreased nutrients in

leaf and root tissues. However, DOP application alleviates the stress of this metal by reducing Fe in plant tissues and increasing nutrients, such as calcium, magnesium, potassium, copper, zinc and molybdenum, compared to the treatment with Fe excess alone. Regarding anatomical structures, DOP provides increases in the structures of root and leaf, when compared to treatment with Fe excess and without DOP. The stress caused by excess Fe in rice plants causes several damages to the photosynthetic apparatus.

However, DOP minimized the oxidative damage in the photosynthetic apparatus, promoting increases in chloroplastic pigments. Parallelly, exogenous DOP induced increases in maximal quantum yield of PSII photochemistry, effective quantum yield of PSII photochemistry and electron transport rate. Regarding gas exchange parameters, the treatment with Fe excess and DOP presents increases in net photosynthetic rate, water use efficiency, and instantaneous carboxylation efficiency, as well as reductions in intercellular CO_2 concentration, transpiration rate, and stomatal conductance, when compared to the treatment with excess Fe and DOP.

The exogenous application of DOP contributes to the antioxidant defense induced by Fe excess by enhancing the activities of the antioxidant enzymes superoxide dismutase, catalase, ascorbate peroxidase, and peroxidase. In parallel, it reduces ROS concentrations, as well as malondialdehyde and electrolyte leakage. Plants exposed to Fe excess had significant reductions in biomass. In contrast, DOP favors increases in stem dry matter, root dry matter, and total dry matter. Therefore, exogenous DOP is a molecule capable of minimizing the effects caused by Fe excess in flooded soils in rice crops, protecting the photosynthetic apparatus, promoting antioxidant defense, and stimulating the plant biomass through the intensification of nutrient uptake.

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Conflict of interest

The authors declare that they have no competing interests.

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Figure

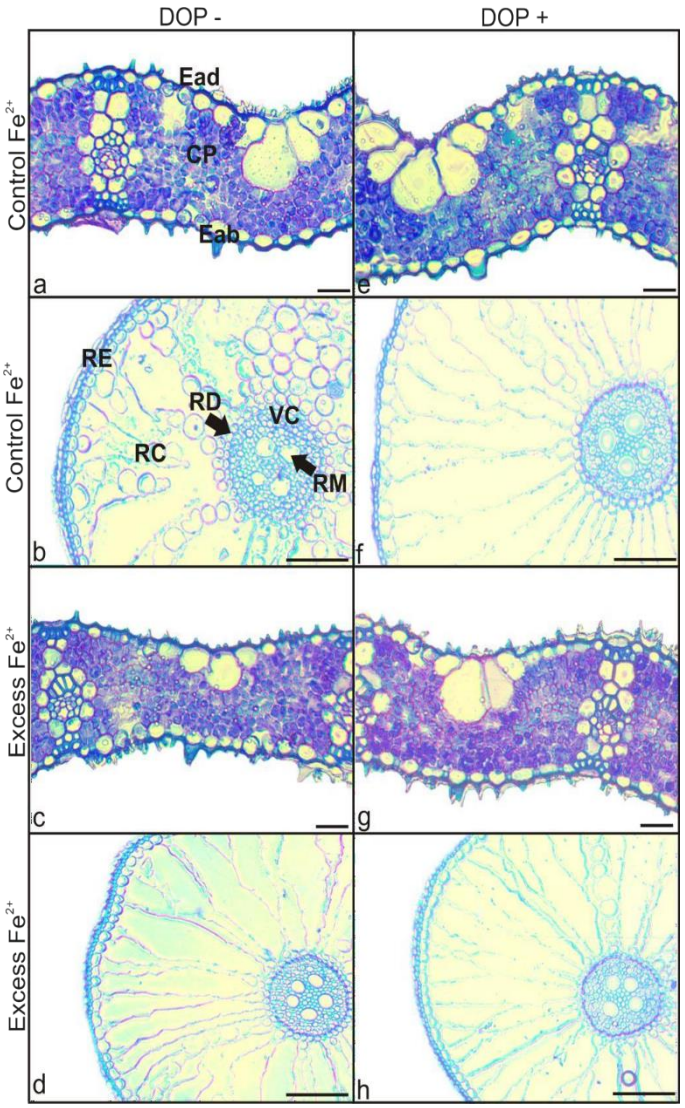

Fig. 1. Leaf and root cross sections in rice plants treated with DOP and exposed to Fe excess. Control Fe / − DOP (A and B), Control Fe / + DOP (E and F), Excess Fe / − DOP (C and D), Excess Fe / + DOP (G and H). Legends: RE = Root epidermis; RC = Root cortex; RD = Root endodermis; VC = Vascular cylinder; RM = Root metaxylem; EAd = adaxial epidermis; EAb = Adaxial epidermis; CP = Chlorophyll parenchyma. Bars (leaft) = 10 µm and bars (root) = 50 µm.

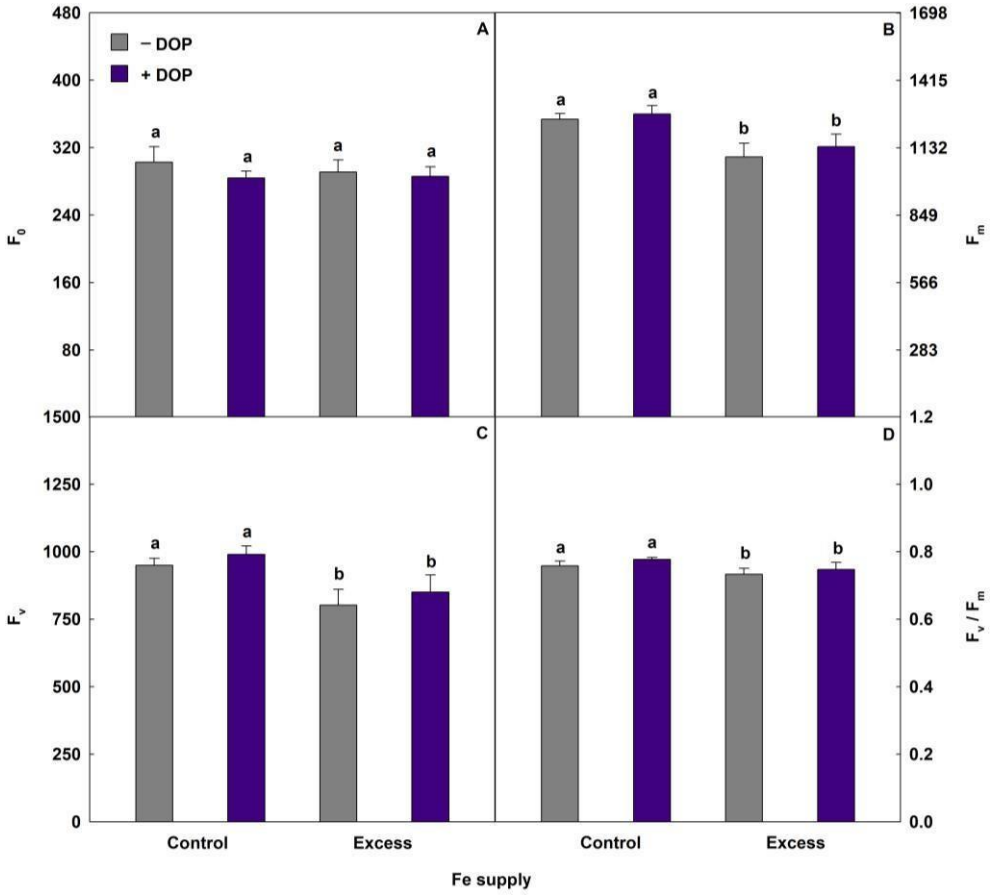

Fig. 2. Minimal fluorescence yield of the dark-adapted state (F_0), maximal fluorescence yield of the dark-adapted state (F_m), variable fluorescence (F_v) and maximal quantum yield of PSII photochemistry (F_v/F_m) in rice plants treated with dopamine and exposed to Fe excess. Bars with different letters indicate significant differences from the Scott-Knott test (P<0.05). Bars corresponding to means from five repetitions and standard deviations.

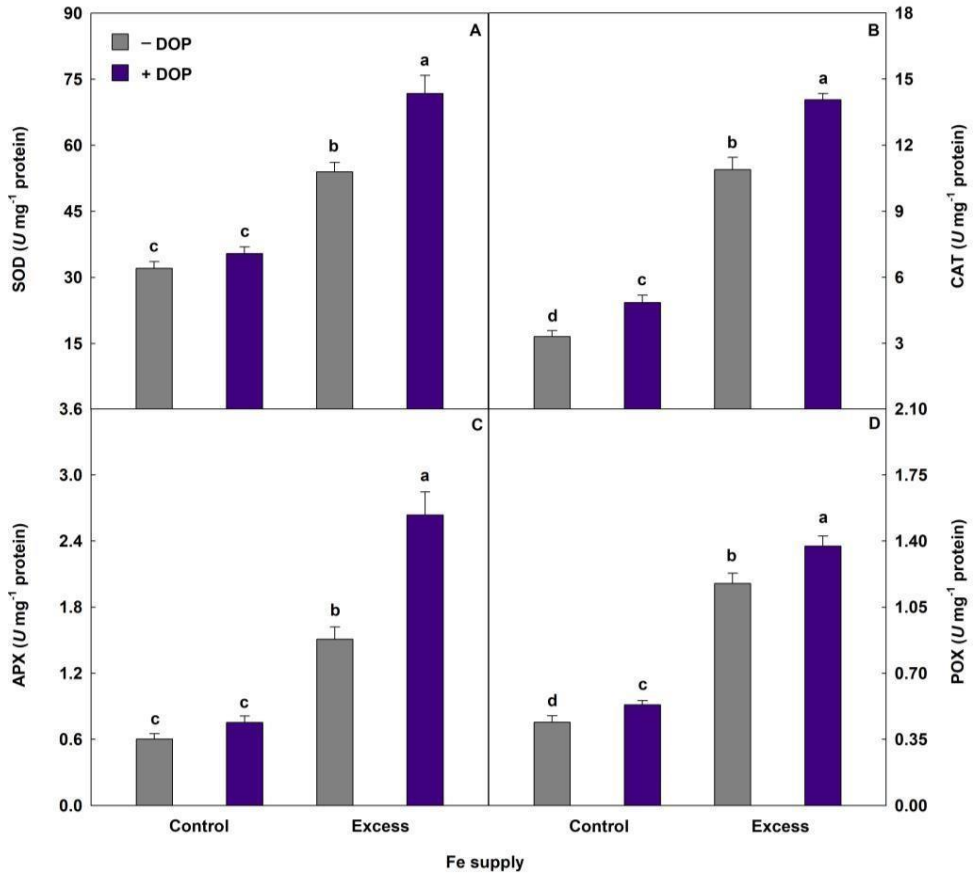

Fig. 3. Activities of superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and peroxidase (POX) in rice plants treated with dopamine and Fe excess. Columns with different letters indicate significant differences from the Scott-Knott test (P<0.05). Columns corresponding to means from five repetitions and standard deviations.

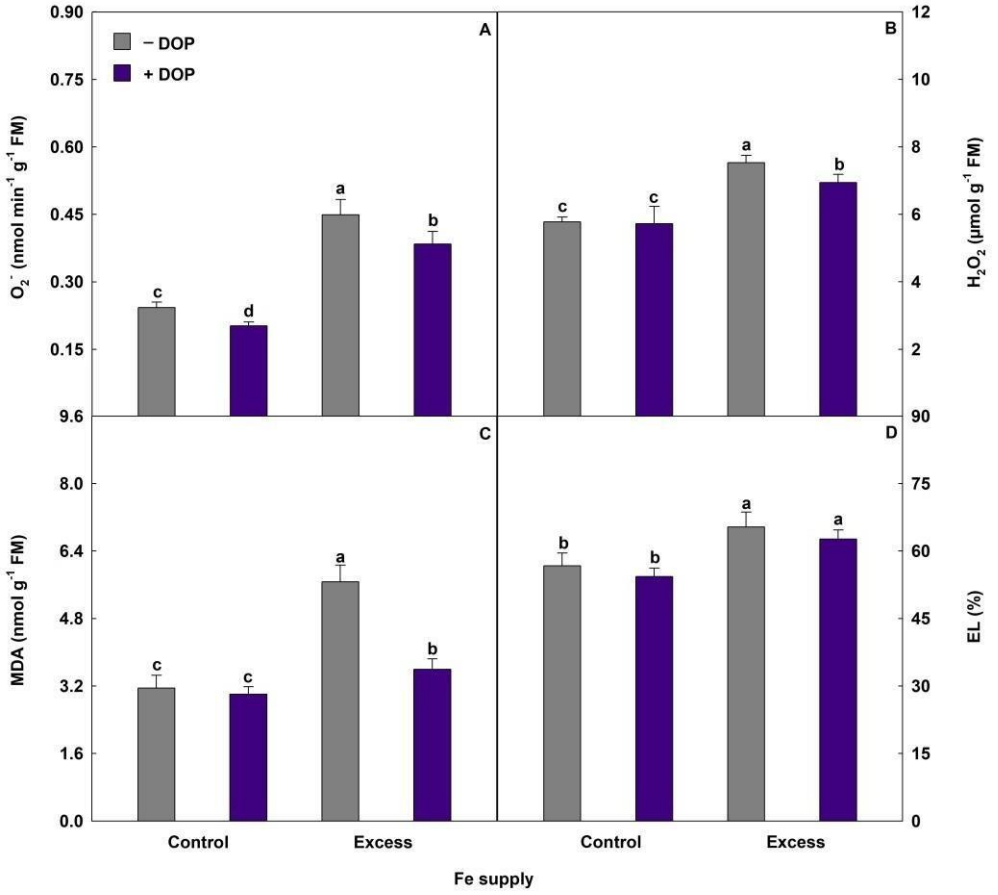

Fig. 4. Superoxide ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2), malondialdehyde (MDA) and electrolyte leakage (EL) in rice plants treated with dopamine and Fe excess. Columns with different letters indicate significant differences from the Scott-Knott test (P<0.05). Columns corresponding to means from five repetitions and standard deviations.

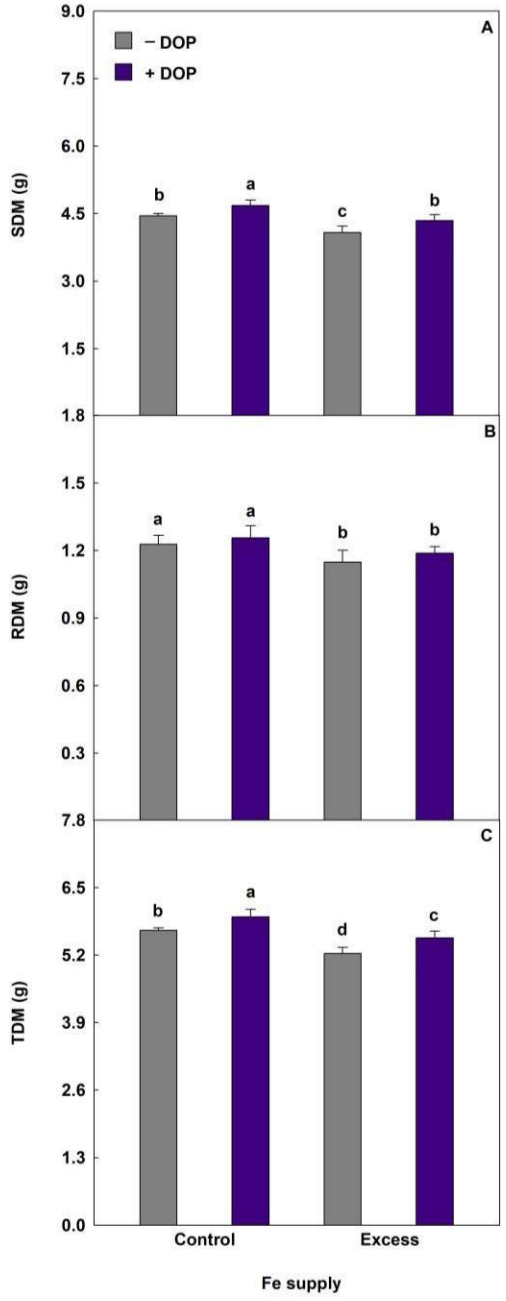

Fig. 5. Shoot dry matter (SDM), root dry matter (RDM) and total dry matter (TDM) in rice plants treated with dopamine and Fe excess. Columns with different letters indicate significant differences from the Scott-Knott test (P<0.05). Columns corresponding to means from five repetitions and standard deviations.

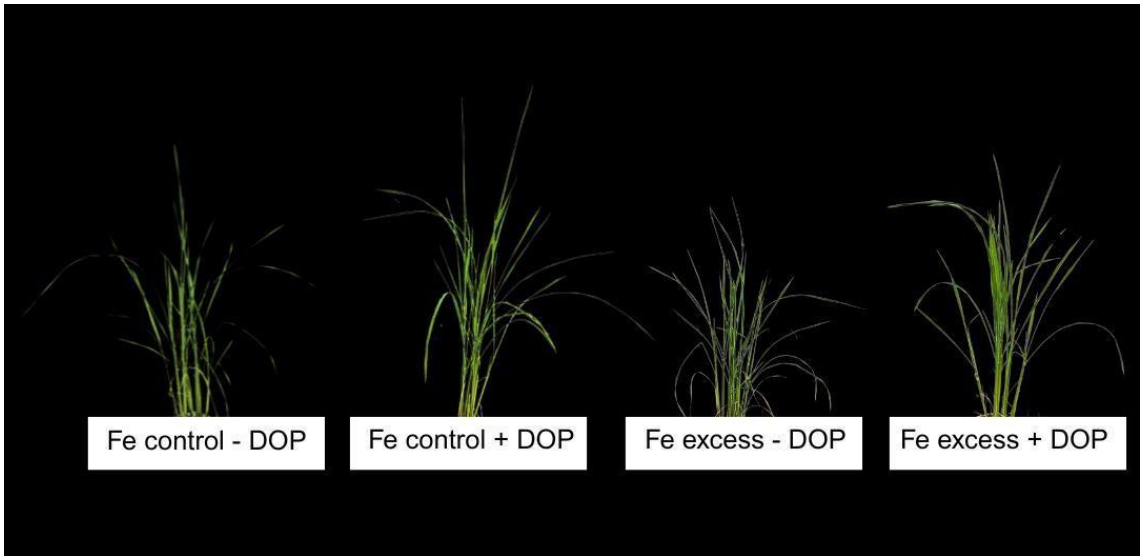

Fig. 6. Rice plants treated with dopamine and Fe excess.

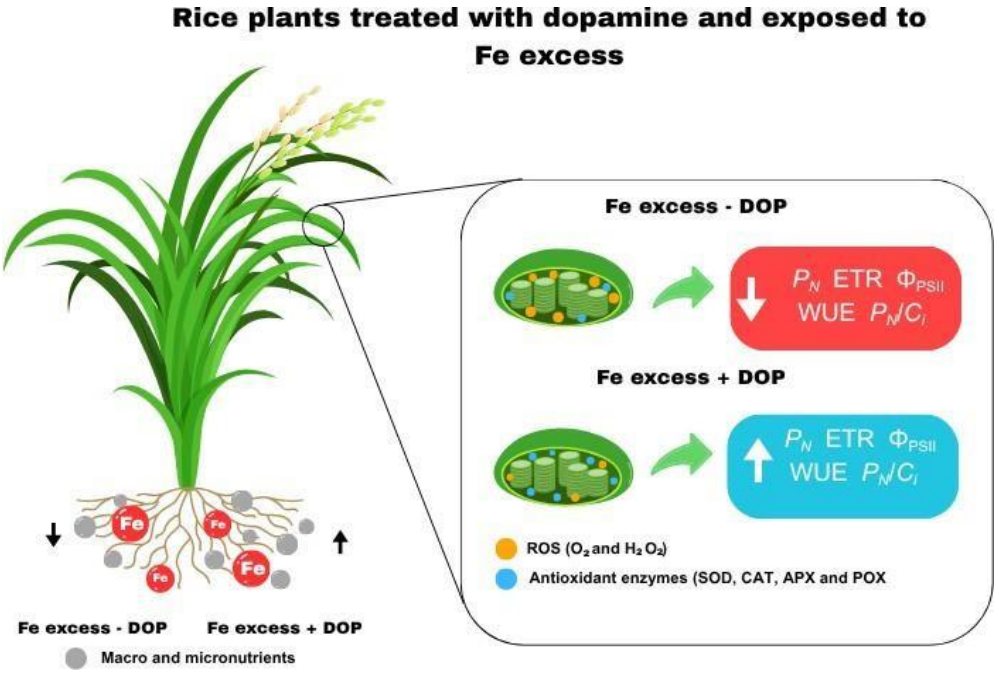

Fig. 7. Graphical representation of the main results of the research associating the antioxidant system, photosynthetic machinery and ionic balance in rice plants treated with dopamine and excess Fe

Tables

Table 1. Fe contents in rice plants treated with dopamine and Fe excess.

Fe^{2+}	DOP	Fe in root (µg g DM^{-1})	Fe in shoot (µg g DM^{-1})
Control	_	285.12 ± 1.51c	95.86 ± 0.52b
Control	+	341.85 ± 4.15c	97.95± 3.90b
Excess	_	2259.02 ± 55.26a	146.57 ± 5.07a
Excess	+	1816.14 ± 85.53b	93.70 ± 3.01b

Fe^{2+} = Iron. Columns with different letters indicate significant differences from the Scott-Knott test (P<0.05). Values described corresponding to means from five repetitions and standard deviations.

Table 2. Nutrient contents in rice plants treated with dopamine and exposed to Fe excess.

Fe^{2+}	DOP	Ca (mg g DM^{-1})	Mg (mg g DM^{-1})	K (mg g DM^{-1})	Cu (µg g DM^{-1})	Zn (µg g DM^{-1})	Mo (µg g DM^{-1})
Contents in root							
Control	_	4.47 ± 0.14b	1.89 ± 0.23b	29.42 ± 1.22b	18.61 ± 0.92b	48.57 ± 0.71b	14.41 ± 0. 43b
Control	+	5.07 ± 0.09a	2.60 ± 0.10a	37.52 ± 1.54a	25.40 ± 0.89a	59.79 ± 0.68a	15.21 ± 0.39a
Excess	_	1.71 ± 0.10d	0.80 ± 0.07d	24.31 ± 1.37d	13.79 ± 0.27d	42.11 ± 0.58d	11.23 ± 0.48d
Excess	+	2.79 ± 0.25c	1.21 ± 0.07c	26.30 ± 1.09c	15.71 ± 0.51c	45.06 ± 1.16c	13.75 ± 0.40c
Contents in shoot							
Control	_	16.20 ± 0.22a	4.99 ± 0.15b	26.30 ± 1.09b	13.73 ± 0.85b	40.37 ± 1.49b	10.62 ± 0.57a
Control	+	16.60 ± 0.25a	5.57 ± 0.18a	38.81 ± 0.57a	15.35 ± 0.98a	42.67 ± 0.67a	11.47 ±0.85a
Excess	_	5.42 ± 0.35c	2.57 ± 0.12d	18.27 ± 0.43d	10.69 ± 0.71c	33.87± 1.51d	3.19 ± 1.60c
Excess	+	7.53 ± 0.50b	3.52 ± 0.08c	24.03 ± 0.95c	13.41 ± 0.77b	37.90 ± 1.40c	7.78 ± 0.68b

Ca = Calcium; Mg = Magnesium; K= Potassium; Cu = Copper; Zn = Zinc; Mo = Molybdenum. Columns with different letters indicate significant differences from the Scott-Knott test (P<0.05). Values described corresponding to means from five repetitions and standard deviations.

Table 3. Structures of root and leaf in rice plants treated with dopamine and exposed to Fe excess.

Fe^{2+}	DOP	RET (µm)	RDT (µm)	RCT (µm)	VCD (µm)	RMD (µm)
Control	_	16.98 ± 1.39b	10.17 ± 0.72b	225.13 ± 9.76a	132.22 ± 4.82b	29.02 ± 1.50b
Control	+	21.47 ± 1.28a	11.68 ± 0.68a	233.44 ± 10.09a	148.73 ± 4.78a	31.25 ± 2.67a
Excess	_	11.69 ± 1.01d	8.28 ± 0.81c	177.41 ± 5.96b	123.66 ± 2.22b	22.48 ± 1.94c
Excess	+	14.16 ± 0.91c	9.90 ± 0.15b	191.88 ± 15.16b	128.07± 5.71b	27.00 ± 1.34b
Fe^{2+}	DOP	ETAd (µm)	ETAb (µm)	CP (µm)		
Control	_	3.56 ± 0.50b	2.92 ± 0.16b	32.22 ± 2.46b		
Control	+	3.96 ± 0.22a	3.55 ± 0.22a	38.81 ± 0.56a		
Excess	_	3.14 ± 0.17c	2.65 ± 0.17b	27.65 ± 1.73c		
Excess	+	3.31 ± 0.25c	2.77 ± 0.16b	30.71 ± 1.09b		

RET = Root epidermis thickness; RDT = Root endodermis thickness; RCT = Root cortex thickness; VCD = Vascular cylinder diameter; RMD = Root metaxylem diameter; ETAd = Epidermis thickness from adaxial leaf side; ETAb = Epidermis thickness from abaxial leaf side; CP = Chlorophyll parenchyma. Columns with different letters indicate significant differences from the Scott-Knott test (P<0.05). Values described corresponding to means from five repetitions and standard deviations.

Table 4. Photosynthetic pigments, chlorophyll fluorescence and gas exchange in rice plants treated with dopamine and exposed to Fe excess.

Fe^{2+}	DOP	Chl *a* (mg g^{-1} FM)	Chl *b* (mg g^{-1} FM)	Total Chl (mg g^{-1} FM)	Car (mg g^{-1} FM)	Ratio Chl *a*/Chl *b*	Ratio Total Chl/Car
Control	_	10.51 ± 0.78a	4.43 ± 0.22a	14.94 ± 0.88b	0.83 ± 0.02a	2.38 ± 0.18a	18.00 ± 0.97c
Control	+	10.95 ± 0.45a	4.69 ± 0.37a	15.64 ± 0.31a	0.86 ± 0.02a	2.35 ± 0.25a	18.25 ± 0.68c
Excess	_	9.69 ± 0.11b	3.88 ± 0.09b	13.57 ± 0.15d	0.46 ± 0.02c	2.50 ± 0.06a	29.77 ± 1.58a
Excess	+	10.10 ± 0.08b	4.13 ± 0.15b	14.24 ± 0.12c	0.59 ± 0.04b	2.45 ± 0.10a	24.11 ± 1.80b
Fe^{2+}	DOP	Φ_{PSII}	q_P	NPQ	ETR (µmol m^{-2} s^{-1})	EXC (µmol m^{-2} s^{-1})	ETR/P_N
Control	_	0.32 ± 0.02a	0.34 ± 0.03a	0.35 ± 0.02c	47.63 ± 3.54a	0.57 ± 0.04b	4.29 ± 0.34b
Control	+	0.34 ± 0.03a	0.39 ± 0.02a	0.31± 0.02d	50.27 ± 4.81a	0.56 ± 0.04b	4.28 ± 0.32b
Excess	_	0.24 ± 0.01c	0.25 ± 0.10b	0.49 ± 0.03a	35.87 ± 1.31c	0.67 ± 0.02a	4.92 ± 0.32a
Excess	+	0.28 ± 0.01b	0.27 ± 0.02b	0.42 ± 0.02b	40.65 ± 0.89b	0.63 ± 0.01a	4.87 ± 0.12a
Fe^{2+}	DOP	P_N (µmol m^{-2} s^{-1})	*E* (mmol m^{-2} s^{-1})	g_s (mol m^{-2} s^{-1})	C_i (µmol mol^{-1})	WUE (µmol $mmol^{-1}$)	P_N/C_i (µmol m^{-2} s^{-1} Pa^{-1})
Control	_	11.13 ± 0.94a	2.65 ± 0.12a	0.33 ± 0.03a	293 ± 4b	4.21 ± 0.29b	0.038 ± 0.003b
Control	+	11.76 ± 0.68a	2.23 ± 0.16b	0.21 ± 0.01c	277 ± 16c	5.29 ± 0.28a	0.043 ± 0.002a
Excess	_	7.30 ± 0.36c	2.77 ± 0.15a	0.28 ± 0.02b	317 ± 8a	2.64 ± 0.10d	0.023 ± 0.001d
Excess	+	8.34 ± 0.07b	2.53 ± 0.15a	0.11 ± 0.01d	296 ± 14b	3.31 ± 0.20c	0.028 ± 0.001c

Chl *a* = Chlorophyll *a*; Chl *b* = Chlorophyll *b*; Total chl = Total chlorophyll; Car = Carotenoids; Φ_{PSII} = Effective quantum yield of PSII photochemistry; q_P = Photochemical quenching coefficient; NPQ = Nonphotochemical quenching; ETR = Electron transport rate; EXC = Relative energy excess at the PSII level; ETR/P_N = Ratio between the electron transport rate and net photosynthetic rate; P_N = Net photosynthetic rate; *E* = Transpiration rate; g_s = Stomatal conductance; C_i = Intercellular CO_2 concentration; WUE = Water-use efficiency; P_N/C_i = Carboxylation instantaneous efficiency. Columns with different letters indicate significant differences from the Scott-Knott test (P<0.05). Values described corresponding to means from five repetitions and standard deviations.