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Can ascorbic acid induce salt tolerance in rice seeds and seedlings?

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ABSTRACT

Soil salinity is one of the abiotic stresses that affect crops. Therefore, rice seeds are susceptible to this stressor during germination, involving several physiological aspects. This study aimed to evaluate the salt tolerance induced by ascorbic acid in rice seeds and seedlings. The water content of rice seeds was determined, followed by two tests with seeds treated in ascorbic acid solution and dry powder at doses of 0 (control), 10, 20, 30, and 40 mg for 24 hours. Sowing occurred under salt stress conditions (NaCl, -0.6 MPa). Physiological quality was evaluated. The collected data were subjected to analysis of variance. Ascorbic acid doses were compared using a regression analysis, seedling length was examined under a 3x4 factorial scheme (three evaluation times x four doses of ascorbic acid), and times points were correlated using Tukey’s test. The findings indicated that the exogenous application of ascorbic acid implies salt stress tolerance. Ascorbic acid doses lower than 20 mg applied to rice seeds induce salt tolerance during germination and initial seedling development, with better physiological quality for seeds treated in the antioxidant solution.

Keywords: Attenuator, Physiological quality, Salinity, Vitamin C.

O ácido ascórbico pode induzir tolerância ao sal em sementes e plântulas de arroz?

RESUMO

A salinidade presente no solo é um dos estresses abióticos que afetam as culturas. Portanto, as sementes de arroz estão sujeitas a esse estressor durante a germinação, o que envolve diversos aspectos fisiológicos. Objetivou-se avaliar a tolerância salina induzida por ácido ascórbico em sementes e plântulas de arroz. Determinou-se o teor de água das sementes e efetuou-se dois ensaios, com sementes tratadas em solução e em pó seco de ácido ascórbico, nas doses de 0 (controle), 10, 20, 30 e 40 mg, durante 24 horas; a semeadura ocorreu em condições de estresse salino (NaCl, -0,6 MPa). Avaliou-se a qualidade fisiológica. Os dados foram submetidos à análise de variância, as doses de ácido ascórbico comparadas por análise de regressão e o comprimento de plântulas, analisado em esquema fatorial 3x4 (três épocas de avaliação x quatro doses do ácido ascórbico). As doses foram comparadas por regressão e as épocas avaliadas, confrontadas pelo teste de Tukey. Os resultados indicaram que a aplicação exógena de ácido ascórbico depreende tolerância ao estresse salino. A aplicação de doses inferiores a 20 mg de ácido ascórbico em sementes de arroz induz a tolerância salina no processo germinativo e no desenvolvimento inicial de plântulas, com melhor qualidade fisiológica para as sementes tratadas em solução do antioxidante.

Palavras-chave: Atenuador, Qualidade fisiológica, Salinidade, Vitamina C.

1. Introduction

Seeds have genetic, physical, physiological, and health attributes that ensure high germination and vigor rates, facilitating the rapid establishment of production fields (Marcos Filho, 2015). However, soil salinity is an abiotic stress that affects crop establishment and compromises agricultural success. Saline areas cover approximately 1 billion hectares, representing about 7% of the Earth's surface (Hopmans et al., 2021), and projections indicate further expansion (Omuto et al., 2020).

Salinity induced by sodium chloride (NaCl) affects various physiological and biochemical aspects of seeds and plants, reducing germination parameters, seedling height, and chlorophyll content, while increasing the production of reactive oxygen species, ultimately promoting lower crop yields (Alamri et al., 2018; Lemes et al., 2018).

Salt stress exhibits higher sensitivity during early growth stages (Kandil et al., 2017; Stefanello et al., 2018), and irrigation, combined with inadequate drainage, contributes to the accumulation of salts in the soil (Aguiar Netto et al., 2007). Therefore, integrating different management strategies in rice (*Oryza sativa* L.) cultivation may support sustainable production in saline areas and contribute to global food security (Vibhuti et al., 2015).

Research has demonstrated the effects of antioxidant compounds and exogenous applications on seed and plant performance, particularly in mitigating the impacts of salt stress (Silva et al., 2019; Fermiano et al., 2018; Melloni et al., 2012) and their biostimulant action (Alves et al., 2024).

Additionally, Ruzzi et al. (2024) highlight the potential of plant biostimulants as key components in more sustainable production systems for future agricultural practices. However, further research may elucidate the mechanisms of action and interactions of these compounds.

In this context, the antioxidant ascorbic acid (Vitamin C) modulates stress during germination, playing a key role in salt tolerance across plant species by mitigating the harmful effects of salinity and oxidative stress (Hameed et al., 2015; Athar et al., 2008). This compound also has the advantage of low acquisition costs, making it a prudent option in agricultural practices to enhance agronomic performance and sustainability by reducing stress or inducing salt tolerance.

Accordingly, this study aimed to assess the effect of ascorbic acid on the salt tolerance of rice seeds and seedlings.

2. Material and Methods

Rice seeds of the BRSMG Rubelita cultivar, produced in northern Minas Gerais, Brazil, were analyzed at the Seed Analysis Laboratory of the State University of Montes Claros (Janaúba, MG, Brazil).

Before setting up the experiments, the initial seed moisture content was determined using the oven-drying method at 105 ± 3 °C for 24 hours, with four replicates of 5 grams of seeds. The results were expressed as a percentage (Brasil, 2009).

Two experiments were conducted with different methods of ascorbic acid application to the seeds: dry powder and solution. In each test, samples of 100 grams of seeds were treated with 10, 20, 30, and 40 mg of ascorbic acid ($C_6H_8O_6$, MW: 176.13 g mol^{-1}, 99% analytical purity), as well as the control. The dry powder treatment applied the ascorbic acid directly to the rice seeds, whereas the solution treatment dissolved the acid in 200 mL of distilled water, allowing for complete seed imbibition.

During the treatment, the seeds remained in the dark inside Gerbox-type containers covered with aluminum foil to prevent oxidation. After 24 hours, sufficient time for seed imbibition, the seeds were dried under ambient laboratory conditions, and both trials were initiated under salt stress conditions. A sodium chloride (NaCl, MM: 55.44 g mol^{-1}, analytical purity ≥ 99%) solution induced salt stress, using an osmotic potential of -0.6 MPa, prepared with 8.40 g L^{-1} of NaCl, following Coelho et al. (2010).

Both experiments (dry powder and solution) presented a completely randomized design with four replicates of 50 seeds to evaluate the physiological quality of rice seeds.

The germination test was conducted on Germitest® paper rolls moistened with a sodium chloride solution (-0.6 MPa) at a volume equivalent to 2.5 times the weight of the dry paper, which remained throughout the trial (14 days) without irrigation. The rolls stayed in a germinator at a constant temperature of 25 °C. Normal seedlings (complete, developed, proportional, and healthy essential structures) were evaluated on the 5th day after test setup (first germination count) and at the end of the test, on the 14th day. The number of abnormal seedlings, hard seeds, and dead seeds was also recorded as percentages (Brasil, 2009).

Radicle protrusion was evaluated concurrently with the germination test, and the number of seeds presented a visible primary root of at least 3 mm 60 hours after test setup.

Radicle length was measured at three different time points: days 4, 8, and 12 after test setup (days after sowing). The radicle length of 10 seedlings per replicate was measured using a millimeter ruler (cm). The results were expressed in centimeters for each evaluation period across the treatment doses.

Standardized samples were collected 18 days after test setup, without any additional water supplied to the rolls. These samples included root filaments measuring 1.0 cm in length and shoot filaments measuring 1.0 x 3.0 cm (length x width) from rice seedlings.

Ten samples of roots and shoots from each replicate were weighed to determine the fresh weight and relative water content. The samples were then immersed in distilled water for 24 hours and reweighed to define the wet weight. Subsequently, they were dried in a forced-air circulation oven at 65 °C for 72 hours and weighed again to obtain the dry weight. The results were expressed as a percentage, following Equation 1 (Slavik, 1974):

$$RWC = \frac{(FW - DW)}{(WW - DW)} x\ 100$$

where: RWC = relative water content (%); FW = fresh weight (g); DW = dry weight (g); WW = wet weight (g).

Electrolyte leakage in rice seedlings was quantified in 20 shoots for each repetition of the studied treatments, following Bajji et al. (2002), and the results were reported as a percentage of membrane damage.

The data from both experiments (dry powder and solution) underwent individual analyses of variance. Ascorbic acid doses were compared using a regression analysis (t-test at 5%), seedling length was analyzed under a 3x4 factorial design (three evaluation time points x four ascorbic acid doses), and evaluation time points were correlated using Tukey's test at a 5% significance level, with statistical analyses performed in Sisvar® software (Ferreira, 2011).

3. Results and Discussion

The initial moisture content of rice seeds was below 12%, indicating no interference with the findings of the other analyses. Starchy seeds, such as those of rice, absorb more water from the environment. When relative humidity variation is low, moisture content remains at around 12% for up to one year of storage without compromising seed physiological quality (Marcos Filho, 2015; Carvalho and Nakagawa, 2012).

Germination analyses showed no significant effects in either experiment (ascorbic acid dry powder or solution) in the present study. That indicates the absence of phytotoxic effects of ascorbic acid under salt stress conditions. It is worth noting that the antioxidant promotes a species-specific action and may eliminate or mitigate salt stress (Zehra et al., 2012). Therefore, attempts to increase stress tolerance by simply raising the antioxidant dosage may not be effective; however, they suggest real germination potential under saline conditions (Khan et al., 2006), as demonstrated in the present study, where rice seed germination exceeded 70%.

Regarding radicle protrusion (Figure 1A), seeds treated with dry ascorbic acid powder showed no significant effect at different doses; however, the results remained below 30%. Conversely, the solution treatment exhibited a significant impact across ascorbic acid doses. Although 15.35 mg of ascorbic acid slightly decreased the protrusion percentage, the values remained above 69%. In this regard, rice seeds maintained in ascorbic acid solution displayed a high percentage of radicle protrusion, likely due to the higher water absorption from the solution. That promoted faster endosperm rupture and radicle emergence.

Seed soaking in water may increase germination rate and speed (Guimarães et al., 2008), as soaked seeds exhibit higher metabolic activity, a natural process driven by hydrolytic enzymes such as α-amylase, which breaks down starch reserves (Buckeridge et al., 2004).

The dry powder treatment exhibited low radicle protrusion values (Figure 1), likely due to slower water absorption, the action of the salt substrate, and the non-dissolution of the dry ascorbic acid powder. Nobre et al. (2022) state that using dry powder may restrict water uptake and create a potential water deficit, delaying the germination process.

Abnormal seedlings (Figure 1B) from seeds treated in solution showed mean values below 7%, with doses between 20 and 25 mg of ascorbic acid further reducing the number of abnormal seedlings. Seeds treated with dry powder exhibited a higher percentage of abnormalities; however, the applied doses resulted in lower mean values than the control treatment (15%), suggesting that ascorbic acid promotes normal seedling formation.

Abnormal seedlings (damaged, deformed, and deteriorated) lack the potential to continue developing into normal plants, even under favorable growth conditions (Brasil, 2009). In this study, the application of ascorbic acid helped mitigate the effects of salinity, as seeds exposed to stress conditions showed a lower incidence of abnormalities (Figure 1B).

Dry ascorbic acid powder gradually increased the percentage of hard seeds (Figure 2A), although the values do not represent interference, as they were lower than 2%. Regarding the ascorbic acid solution, although the mean percentage of hard seeds exceeded 4.5%, the evaluated doses did not show statistically significant differences. Hard seeds remain unable to absorb water longer than usual, retaining the appearance of freshly placed seeds on the substrate (Brasil, 2009). The present study shows that the higher values of hard seeds in the solution treatment were not due to challenges in water absorption, but rather the presence of salinity in the substrate, as the dry powder antioxidant may have performed better in alleviating saline conditions.

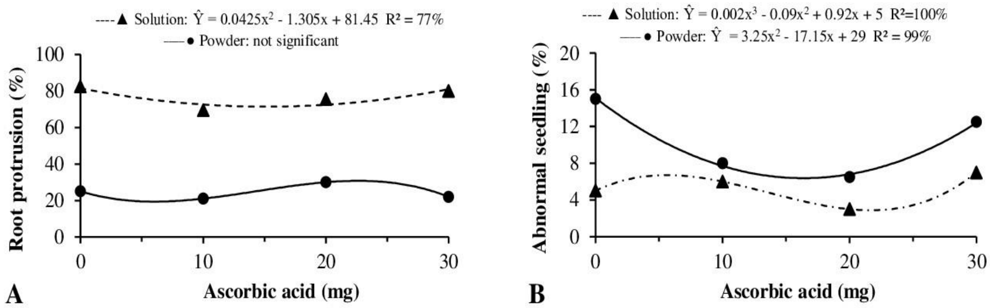

Figure 1. Root protrusion (A) and abnormal seedlings (B) from rice seeds submitted to salt stress at ascorbic acid doses applied as dry powder and solution.

Regarding membrane damage (Figure 2B), the lowest mean values occurred in rice seedlings treated with an initial dose of 10 mg of dry ascorbic acid powder applied to the seeds. The solution treatment did not present a significant effect among the evaluated doses. Membrane damage may be one of the first signs of stress. It increases electrolyte leakage due to the rupture of membrane integrity, such as the increased production of reactive oxygen species (Bajji et al., 2002; Martins et al., 2018). Thus, the findings suggest that the antioxidant attenuated the effects of salt stress.

The relative water content (RWC) of the aerial part (Figure 3A) and root of rice seedlings (Figure 3B) under ascorbic acid solution showed increasing results even under salt stress conditions. The RWC of the aerial part (Figure 3A) did not show a significant effect considering the different doses of the dry powder treatment. However, the solution doses increased the aerial part results. The dry ascorbic acid powder increased the RWC of roots (Figure 3B) up to a given dose and decreased it after 10.92 mg and the solution doses raised root RWC.

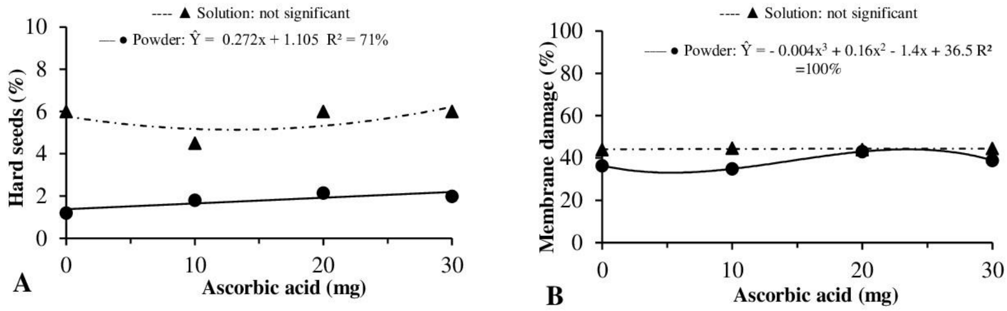

Figure 2. Hard seeds (A) and damage to the rice seedling membrane (B) subjected to salt stress under ascorbic acid doses applied as dry powder and solution.

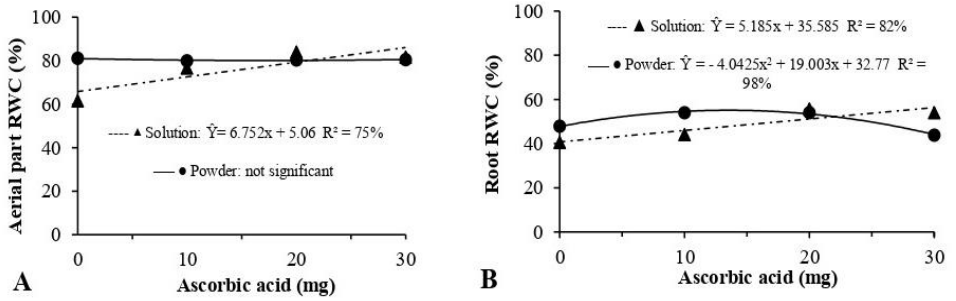

Figure 3. Relative water content (RWC) of the aerial part (A) and root (B) from rice seedlings submitted to salt stress under ascorbic acid doses applied as dry powder and solution.

The RWC analyses (Figures 3A and 3B) demonstrate that the increases in this variable suggest higher water retention in the cells, confirming the improvements induced by the antioxidant and its enhanced absorption through water when applying ascorbic acid is in a solution. Conversely, the decreases at the highest doses of the dry powder antioxidant may be due to the effects of water deficit and salt ions, which interfere with the formation of a concentration gradient that hinders water absorption by the roots, a condition that cannot be reversed even by antioxidant action.

The decrease in water availability in the substrate due to salinity, combined with the absence of irrigation in the present study, is similar to occurrences under low soil water availability. That is because the reduction in leaf water potential is related to the accumulation of sugars in the leaves and stomatal closure, which decreases transpiration and helps maintain tissue hydration (Leite et al., 2018). Seedling length, evaluated 4, 8, and 12 days after sowing (DAS) under different doses of ascorbic acid solution, showed the highest mean values for the 0, 20, and 30 mg treatments 12 DAS, differing from the measurements taken 4 DAS. For the 10mg ascorbic acid dose, all three evaluation periods differed significantly (Figure 4A).

The effects of ascorbic acid solution doses evaluated at different DAS for rice seedling length (Figure 4B) revealed a similar behavior to ascorbic acid doses 4 and 8 DAS. In contrast, at 12 DAS, longer seedlings appeared up to the 12.7mg dose, followed by a decrease.

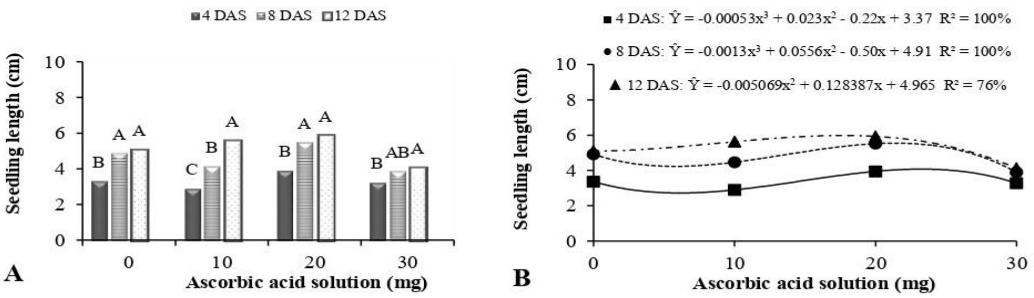

Figure 4. Seedling length evaluated 4, 8, and 12 days after sowing (DAS) for ascorbic acid solution doses (A) and ascorbic acid solution doses studied at different DAS for rice seedling length (B). Both underwent salt stress.

The longest seedlings appeared in the seed treatment with ascorbic acid solution, which required a lower ascorbic acid dose to achieve the highest average 12 DAS compared to the dry powder treatment (Figures 4 and 5A). That likely occurred due to the easier penetration of the antioxidant into the seeds through water.

Additionally, the trials were conducted under salt stress (-0.6 MPa), as salt induces water restriction, which may reduce metabolism and limit the allocation and synthesis of reserves for the embryonic axis (Bewley et al., 2013), explaining the lower vigor of rice seedlings under the present conditions. Cavalcante et al. (2019) found that salt stress conditions may compromise the length of shoots and roots from rice seedlings.

The antioxidant ascorbic acid is a key molecule that modulates the cell cycle and root growth rate, increasing root length through a pre-sowing treatment in Arabidopsis seeds (Kka et al., 2018). The rice seedling length evaluated at different DAS with ascorbic acid doses applied as dry powder showed no significant effect for the control (0 mg), which allows inferring a positive contribution of the acid to seedling growth (Figure 5A).

The different ascorbic acid doses in powder form showed no significant effect 4 DAS. However, they revealed growing seedling length increments 8 DAS, and the best results became evident for the 18.5mg dose of the acid 12 DAS, after which there were no further gains in rice seedling length (Figure 5B).

Applying ascorbic acid to rice seeds may mitigate salt stress, enhancing the physiological quality of seeds and seedlings. Doses lower than 20 mg used as dry powder or solution usually suggest some degree of salt tolerance in the early development of rice seedlings compared to those under stress that did not receive the antioxidant (control).

Although the seeds treated in solution presented higher mean values, the dry powder doses promoted satisfactory performance under the evaluated stress conditions. Salt stress may be reduced by pre-treating seeds with ascorbic acid, diminishing the harmful effects of salinity when applied immediately before sowing (Behairy et al., 2012).

In summary, the application of ascorbic acid to rice seeds plays a key role in enhancing salt stress tolerance during germination and the early stages of seedling establishment. Ascorbic acid improves the physiological quality of seeds by stimulating antioxidant defense systems, protecting cells from the excessive production of reactive oxygen species under stress conditions (Kamran et al., 2023; Barbosa et al., 2014; Ahmad et al., 2012; Athar et al., 2008).

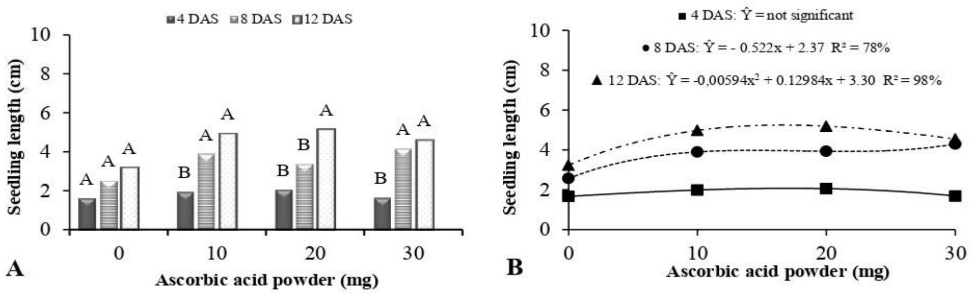

Figure 5. Seedling length evaluated 4, 8, and 12 days after sowing (DAS) for dry ascorbic acid powder doses (A) and dry ascorbic acid powder doses studied at different DAS for rice seedling length (B). Both underwent salt stress.

It also reduces ion toxicity, thereby increasing the tolerance to salt (Chen et al., 2021) and water (Silva et al., 2023) stress.

The exogenous application of ascorbic acid may also help modulate plant hormone levels, breaking dormancy and seed germination, as described by Ye et al. (2012) and Niu et al. (2024).

4. Conclusions

Applying ascorbic acid doses lower than 20 mg to rice seeds induces salt tolerance during germination and early seedling development, improving the physiological quality in seeds treated with the antioxidant solution.

Authors' Contribution

Writing - original draft, methodology, investigation, supervision, data curation and conceptualization: Danúbia Aparecida Costa Nobre. Methodology, formal analysis and data curation: Ana Clara da Silva Ribeiro. methodology, formal analysis and data curation: Jaíne Meriele Ribeiro Domingues. Methodology, formal analysis and data curation: Cleisson Dener da Silva. Supervision, review and editing: Andréia Márcia Santos de Souza David. Conceptualization, writing - review and editing: Caroline Salezzi Bonfá.

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