

Physiological performance of ‘Swingle’ citrumelo seeds inoculated with *Azospirillum brasilense* under salt stress

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ABSTRACT

Soil and substrate salinity interferes with plant development. Understanding the salinity tolerance of plant species and adopting strategies to mitigate its negative effects, such as inoculation with the rhizobacterium *Azospirillum brasilense*, may promote more efficient plant development under saline conditions. This study aimed to evaluate the germination and vigor of ‘Swingle’ citrumelo rootstock seeds under different sodium chloride (NaCl) concentrations, using *A. brasilense* as a potential mitigator of salt stress. The treatments were arranged in a 5 × 2 factorial scheme consisting of five NaCl concentrations (0, 30, 60, 90, and 120 mM), with distilled water used as the control, combined with the absence or presence of *A. brasilense* applied by pre-sowing seed immersion. Evaluated parameters included germination speed index, mean germination time, germination percentage, and percentages of abnormal seedlings, viable ungerminated seeds, and dead seeds. Primary root and shoot lengths were also measured, along with root, shoot, and total dry mass. Salt stress impaired the germination process, delaying germination and reducing seed germination and vigor. The rootstock was sensitive to salinity, and seed treatment with the rhizobacterium was ineffective in mitigating the deleterious effects of salt stress.

Keywords: Citrus; Sodium chloride, Abiotic stress, Rhizobacteria.

Desempenho fisiológico de sementes de citrumeleiro ‘Swingle’ inoculadas com *Azospirillum brasilense* sob estresse salino

RESUMO

A ocorrência de salinidade no solo e em substratos é um fator que interfere no desenvolvimento das plantas. Compreender os níveis de tolerância das espécies à salinidade e adotar estratégias para reduzir os impactos negativos, como a aplicação da rizobactéria *Azospirillum brasilense*, constitui uma alternativa para promover um desenvolvimento mais eficiente das plantas em ambientes salinizados. Objetivou-se avaliar a germinação e o vigor de sementes do porta-enxerto citrumeleiro ‘Swingle’ em diferentes concentrações salinas de cloreto de sódio (NaCl), utilizando *A. brasilense*, como possível atenuante do estresse salino. Os tratamentos foram arranjados em esquema fatorial 5 x 2, sendo, quatro concentrações salinas de NaCl: 30, 60, 90 e 120 mM, adicionado do tratamento controle (somente água destilada), combinadas com ausência ou presença (imersão em solução pré-semeadura) de *A. brasilense*. Foram avaliados: o índice de velocidade de germinação, o tempo médio de germinação, a porcentagem de germinação, de plântulas anormais, de sementes vivas não germinadas e de sementes mortas. Também foram mensurados o comprimento da raiz principal e da parte aérea das plântulas, bem como a massa seca de raízes, da parte aérea e total. O estresse salino compromete o processo germinativo, ocasionando atraso e redução da germinação e do vigor das sementes. O porta-enxerto mostrou-se sensível à

salinidade, e o tratamento das sementes com a rizobactéria não apresentou eficiência na atenuação dos efeitos deletérios desse estresse.

Palavras-chave: Citros, Cloreto de sódio, Estresse abiótico, Rizobactéria.

1. Introduction

Brazilian citrus farming is notable for its socioeconomic importance because it generates direct and indirect employment and income while contributing to regional development (Martins et al., 2022). Citrus plants are cultivated under diverse soil and climatic conditions (Almeida et al., 2018a), particularly in arid and semi-arid regions, where water sources often contain high ion concentrations (Brito et al., 2018). In these environments, the use of salinity-tolerant rootstocks is a key strategy for ensuring the viability and success of citrus production in Brazil.

Salinity is a major environmental factor limiting plant growth and development (Fontes et al., 2022). Salt stress inactivates genes associated with gibberellin synthesis, and these phytohormones are essential for seed germination and proper seedling growth (Liu et al., 2018). In citrus genotypes used as rootstocks, this stress impairs growth and productive performance (Brito et al., 2014; Martins et al., 2022). However, responses vary among genotypes, allowing the selection of those best adapted to specific growing conditions and thereby contributing to the sustainability of the production system (Martins et al., 2022).

Studies examining the germination responses of seeds exposed to artificially induced stress are crucial for understanding the survival and adaptive capacity of plant species under natural stress conditions (Fontes et al., 2022). In this context, inoculating plants with plant growth-promoting bacteria (PGPB) is a promising strategy because these microorganisms establish beneficial interactions with plants that can mitigate the harmful effects of salt stress (Gupta and Pandey, 2019). They also promote plant development through various physiological and biochemical mechanisms (Barros et al., 2025; Nascimento et al., 2023; Oliveira et al., 2020).

Among these bacteria, the genus *Azospirillum* is one of the most extensively studied (Morais et al., 2015). In addition to fixing atmospheric N_2 , *Azospirillum brasilense* promotes plant development through several mechanisms, including the synthesis of growth-promoting substances such as auxins, gibberellins, and cytokinins; increased nitrate reductase activity; induction of plant resistance to abiotic and biotic stresses; and phosphate solubilization (Fukami et al., 2018).

The 'Swingle' citrumelo is one of the most important rootstocks used in the Brazilian citrus belt (Girardi et al., 2021). Despite its widespread use, limited information is available regarding its tolerance

to salt stress or potential strategies to mitigate the effects of this stress. Therefore, research evaluating these conditions is essential, particularly during seed germination, a critical stage in the production of high-quality seedlings. Accordingly, this study aimed to evaluate the germination and vigor of 'Swingle' citrumelo rootstock seeds under different salinity levels induced by sodium chloride (NaCl) and investigate the potential of the rhizobacterium *A. brasilense* to mitigate the adverse effects of salt stress.

2. Material and Methods

The study was initiated on April 22, 2025, and conducted at the Horticultural Plant Seed Laboratory of the Department of Crop Production, School of Agricultural and Veterinary Sciences (UNESP/FCAV), Jaboticabal Campus, São Paulo, Brazil. Seeds of the 'Swingle' citrumelo rootstock were obtained from the citrus seedling nursery of José Salomão Gibran Agropecuária S/A, located in Viradouro, São Paulo, Brazil.

A completely randomized experimental design was used. The experiment followed a 5×2 factorial scheme comprising five NaCl concentrations: 0 mM (control; distilled water only), 30, 60, 90, and 120 mM. The latter four concentrations corresponded to electrical conductivities of 3.32, 5.70, 7.80, and 9.70 $dS\ m^{-1}$, respectively. These treatments were combined with the absence or presence of *Azospirillum brasilense* applied by seed immersion. The experiment consisted of four replicates of 25 seeds, with each experimental unit comprising a Gerbox-type acrylic box.

To remove the seed coat, the seeds were pretreated with an aqueous sodium hydroxide (NaOH) solution (5 $g\ L^{-1}$) for 60 min. They were then washed under running water for 60 s to remove NaOH residue and subsequently air-dried in the shade for 30 min.

After surface drying, two subsamples of 50 seeds each were used to determine the initial water content according to the Rules for Seed Analysis (Brazil, 2025). The results were expressed as a percentage, and the initial water content was 51%.

Based on Oliveira et al. (2024), seeds assigned to treatments with *A. brasilense* strains AbV5 and AbV6 were immersed for 5 min in 500 mL of the commercial product Azokop®, which guarantees a minimum rhizobacterial concentration of $2 \times 10^8\ CFU\ mL^{-1}$. Seeds not receiving the inoculant were immersed in distilled water for the same period to ensure moisture levels

comparable to those of the treated seeds. All seeds were then placed on paper towels to remove surface moisture.

The seeds were sown at a depth of 1 cm in lidded Gerbox-type acrylic boxes (11 × 11 × 3 cm) and lightly covered with 60 g of medium-grade vermiculite. Depending on the treatment, the vermiculite was moistened with either distilled water or the respective sodium chloride (NaCl) solution to maintain 100% water-holding capacity. The boxes were subsequently placed in biochemical oxygen demand (BOD) germination chambers at a constant temperature of 30 °C under a 16-h light and 8-h dark photoperiod (Silva, 2020).

Evaluations were performed daily by recording the number of normal seedlings until germination stabilized. The final evaluation was conducted 31 days after sowing (Morelli et al., 2021), when the numbers of normal seedlings, abnormal seedlings, ungerminated seeds, and dead seeds were recorded. Primary root and

shoot lengths (cm) were also measured in up to 10 seedlings per experimental unit using a millimeter ruler. Root and shoot dry masses (g) were determined after drying the samples in a forced-air oven at 70 °C until they reached constant mass. The samples were then weighed using a precision balance with a resolution of 0.001 g (Shimadzu®, model AY220).

Seedlings were considered normal when they had a root at least 2 cm long, a well-developed hypocotyl, and visible or well-formed leaflets without damage (Figure 1A). Seedlings originating from the same polyembryonic seed were evaluated as a single unit (Figure 1A). Seedlings that did not meet the criteria for normal seedlings but exhibited root emergence or hypocotyl deformation were classified as abnormal (Figure 1B). Ungerminated seeds were those that showed no signs of germination (Figure 1C). Seeds were considered dead when they were soft and/or showed evidence of microbial deterioration (Figure 1D).

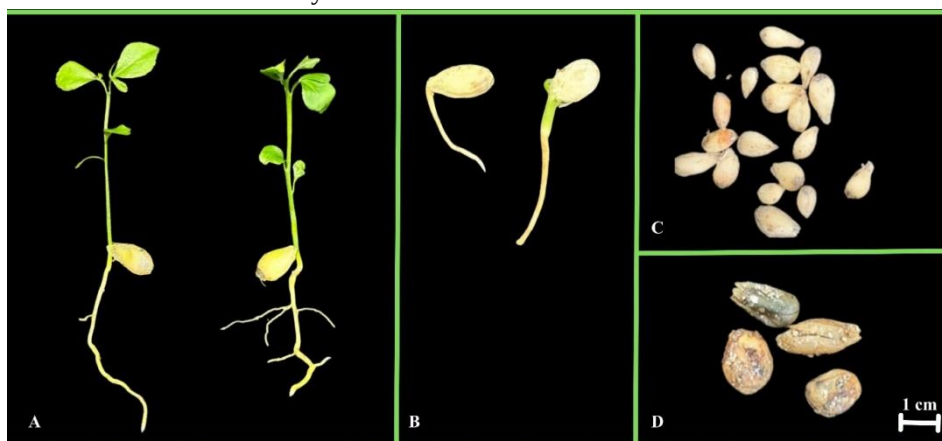


Figure 1. Examples of normal seedlings without and with polyembryony (A), abnormal seedlings (B), ungerminated seeds (C), and dead seeds (D) according to the criteria used in the germination test.

The following parameters were calculated from the collected data: germination percentage (%G); germination speed index (GSI), using the formula proposed by Maguire (1962) and described by Ferreira et al. (2021); mean germination time (MGT), using the formula proposed by Labouriau (1983) and also described by Ferreira et al. (2021); percentages of abnormal seedlings, viable ungerminated seeds, and dead seeds; and total dry mass, calculated as the sum of root and shoot dry mass.

Statistical analyses were performed using AgroEstat software (Barbosa and Maldonado Junior, 2015). When the interaction between salinity and *A. brasilense* inoculation was significant according to the F-test at the 5% probability level, means for the absence and presence of inoculation were compared using Tukey's test at the 5% probability level. When significant differences were detected among salinity levels, polynomial regression analysis was performed to

evaluate parameter responses to increasing salinity concentrations.

3. Results and Discussion

The interaction between salinity levels and *Azospirillum brasilense* inoculation was not significant for either the germination speed index (GSI) or mean germination time (MGT). Inoculation with *A. brasilense* did not affect either parameter, whereas salinity levels significantly affected both. A cubic regression model was fitted to GSI (Figure 2A), indicating that germination was fastest in the control treatment and slowed at NaCl concentrations of 30 mM and above. A linear regression model was fitted to MGT (Figure 2B), showing that mean germination time was 12 days in the control treatment and increased progressively with NaCl concentration up to 120 mM.

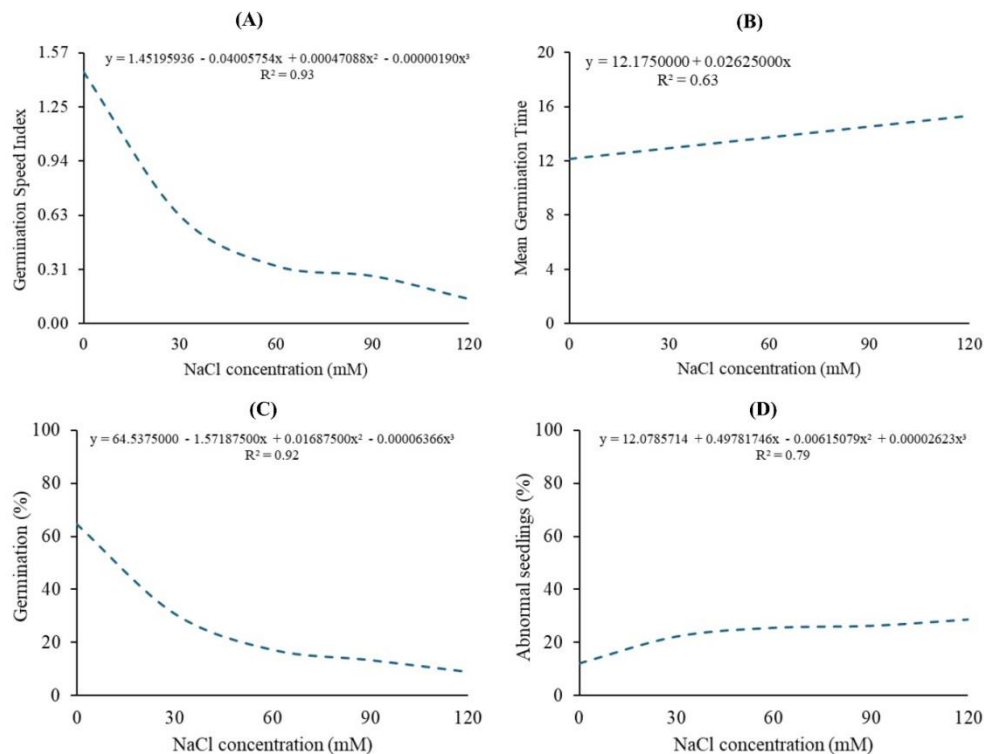


Figure 2. Germination speed index (A), mean germination time (B), germination percentage (C), and percentage of abnormal seedlings (D) of 'Swingle' citrumelo seeds sown in substrate under different NaCl concentrations, with or without prior inoculation with *Azospirillum brasilense*. Jaboticabal, São Paulo, Brazil, 2025.

The interaction between NaCl concentration and *A. brasilense* inoculation was not significant for either germination percentage, based on normal seedlings, or the percentage of abnormal seedlings. The highest germination percentage of 'Swingle' citrumelo seeds was 64.54% in the control treatment. Germination decreased progressively with increasing NaCl concentration, reaching 8.91% at 120 mM among seeds not inoculated with *A. brasilense* (Figure 2C). Similarly, Brito et al. (2018) reported that increasing irrigation-water salinity reduced seedling emergence in the citrus genotypes HTR-083, LVK × LCR-030, 'San Diego' citrandarin, TSKC × CTARG-019, TSKC × CTARG-036, and TSKC × CTSW-018.

Therefore, 'Swingle' citrumelo was not tolerant to salinity during seed germination. Salt stress can inactivate genes involved in gibberellin synthesis, and these phytohormones are essential for promoting germination and early seedling growth (Liu et al., 2018). This mechanism may explain the observed reductions in germination percentage and germination speed. By contrast, other citrus genotypes exhibit salinity tolerance, including 'Cravo Santa Cruz' Rangpur lime and trifoliolate hybrid 069 (Brito et al., 2014), as well as the hybrids TSKC × CTARG-019 (Brito et al., 2018) and TSKFL × CTTR-013 (Brito et al., 2021).

Inoculation with *A. brasilense* did not affect germination percentage or the percentage of abnormal seedlings, whereas both parameters differed among NaCl concentrations. Cubic regression models were fitted to germination percentage (Figure 2C) and the percentage of abnormal seedlings (Figure 2D). The percentage of abnormal seedlings increased progressively with NaCl concentration, reaching 30.3% at 120 mM among seeds not inoculated with *A. brasilense* (Figure 2D).

The interaction between NaCl concentration and *A. brasilense* inoculation was significant for the percentages of non-germinated and dead seeds. Regardless of inoculation, the lowest percentages of non-germinated seeds (Figure 3A) and dead seeds (Figure 3B) occurred in the control treatment.

Salts at different concentrations impair water uptake by seeds, restricting early seedling growth and causing metabolic changes similar to those observed under water deficit (Gomes et al., 2024). In 'Swingle' citrumelo, these effects impaired germination and early seedling establishment, as demonstrated by reductions in shoot and primary root lengths with increasing NaCl concentration in the substrate (Figure 4A). No significant interaction between NaCl concentration and *A. brasilense* inoculation was detected for either parameter.

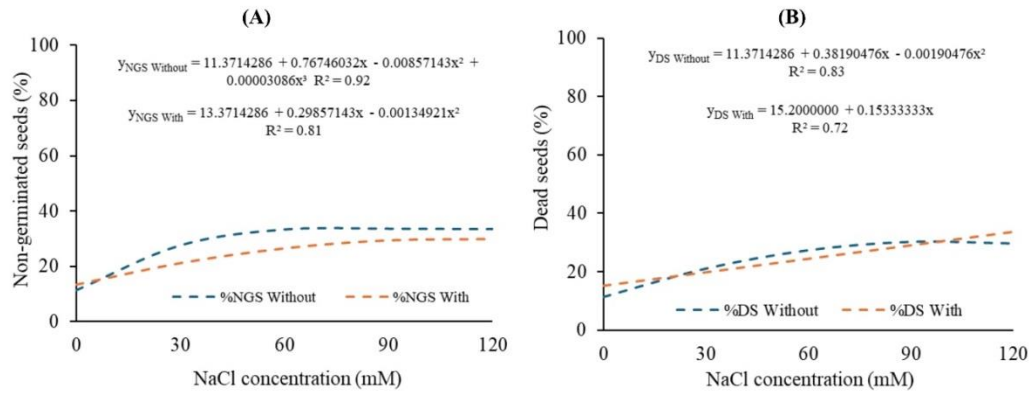


Figure 3. Percentages of non-germinated seeds (A) and dead seeds (B) of 'Swingle' citrumelo seeds sown in substrate under different NaCl concentrations, either previously inoculated with *Azospirillum brasilense* (with) or left uninoculated (without). Jaboticabal, São Paulo, Brazil, 2025.

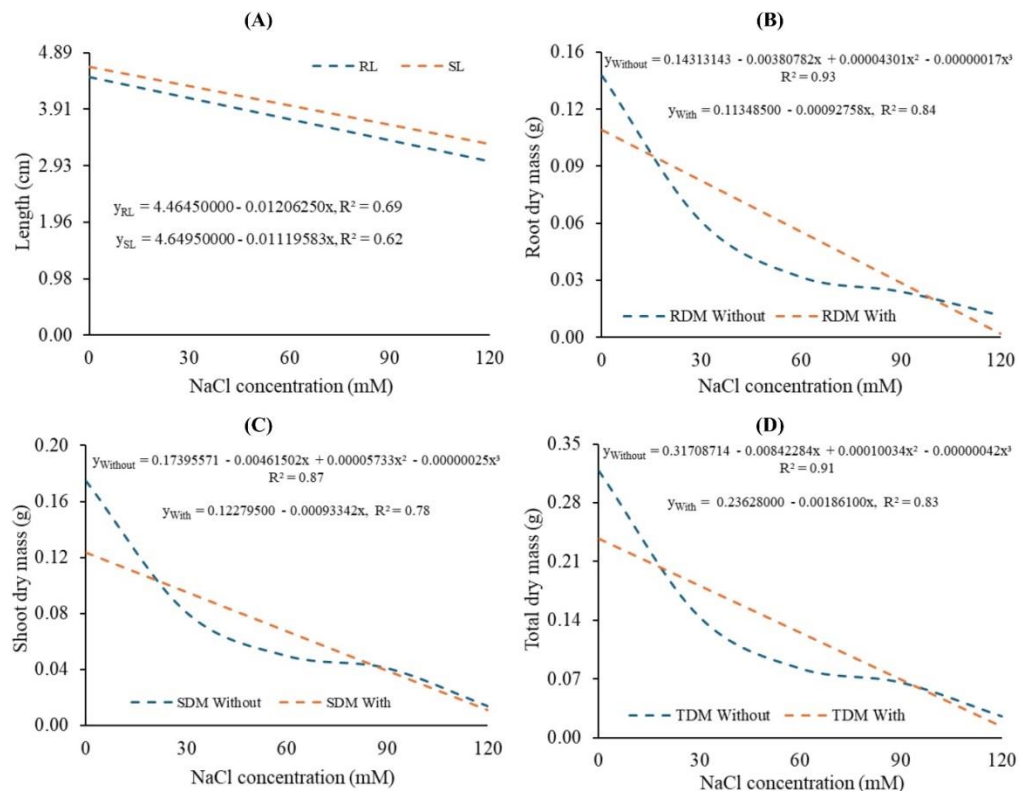


Figure 4. Primary root length (RL) and shoot length (SL) (A); root dry mass (B), shoot dry mass (C), and total dry mass (D) of 'Swingle' citrumelo seedlings grown in substrate under different NaCl concentrations and obtained from seeds previously inoculated with *Azospirillum brasilense* (with) or left uninoculated (without). Jaboticabal, São Paulo, Brazil, 2025.

A significant interaction between NaCl concentration and *A. brasilense* inoculation was detected for root dry mass (RDM), shoot dry mass (SDM), and total dry mass (TDM). Regardless of inoculation, the highest mean RDM (Figure 4B), SDM (Figure 4C), and TDM (Figure 4D) values were recorded in the control treatment and decreased progressively with increasing NaCl concentration. This response may be attributed to salt accumulation in the substrate, which impairs essential physiological processes, including root water uptake, meristematic activity, and cell elongation, thereby reducing plant growth (Santos et al., 2022). Severe salt stress may also induce excessive production of reactive oxygen species

in some bacteria (Liang et al., 2018), potentially limiting their beneficial effects on plant dry mass accumulation.

Salinity adversely affects microbial communities by reducing microbial biomass and the abundance of salt-sensitive functional groups (Zheng et al., 2021). It also interferes with plant nutrient uptake. Because citrus genotypes differ in their nutritional requirements, their responses to salt stress may also vary (Almeida et al., 2018b; Brito et al., 2021).

Plant growth-promoting bacteria have potential for use in salt-affected areas (Barros et al., 2025). These bacteria may mitigate salt stress by stimulating the expression of plant genes encoding antioxidant

enzymes, including superoxide dismutase, glutathione reductase, guaiacol peroxidase, and glutathione peroxidase, which are involved in plant defense mechanisms (Alves et al., 2018). Studies involving several plant species have shown promising responses to inoculation with these microorganisms under salt stress. For example, inoculation of wheat seedlings with bacteria of the genus *Azospirillum* increased biomass accumulation and seedling growth (Ilyas et al., 2020). Similarly, inoculation of chickpea plants with *Azospirillum lipoferum* increased the accumulation of soluble sugars, glycine betaine, proline, and proteins associated with salt stress tolerance (El-Esawi et al., 2018).

Our results therefore showed that 'Swingle' citrumelo was not tolerant to NaCl-induced salinity during seed germination. Chetto et al. (2025) evaluated the salinity tolerance of nine citrus rootstocks exposed to NaCl and found that 'Swingle' citrumelo and 'Changsa' mandarin were among the most sensitive genotypes. Eatshan et al. (2025) investigated the response of in vitro-grown 'Swingle' citrumelo shoots to NaCl-induced salt stress. The authors observed significant reductions in growth parameters, including shoot number, shoot length, and dry matter percentage, as NaCl concentration increased, further indicating the sensitivity of this rootstock to salt stress.

Treatment of 'Swingle' citrumelo seeds with the rhizobacterium *A. brasilense* was not fully effective in mitigating the adverse effects of NaCl-induced salinity. However, inoculation moderately mitigated the reductions in RDM, SDM, and TDM, particularly at NaCl concentrations ranging from 30 to 90 mM (Figures 4B, 4C, and 4D, respectively). Nevertheless, bacterial populations were not quantified in the seedlings, precluding confirmation of bacterial establishment and limiting the assessment of inoculation efficacy under salt stress.

The limited effectiveness of *A. brasilense* may be associated with factors such as the strain used, application method, environmental conditions during the experiment, particularly temperature and moisture, and interactions among the bacterium, plant species, and substrate (Campos et al., 2023). The factors affecting the balance and dynamics of *Azospirillum* spp. populations are numerous and complex, reflecting the complexity of the ecosystems inhabited by these microorganisms.

Abiotic factors—including temperature; the availability and quality of nutrient sources; medium pH; salinity; the presence and type of energy sources; and potentially toxic or inhibitory compounds—play a major role in the growth, survival, and metabolic activity of microbial populations (Schaefer et al., 2024). Because the germination test was conducted at 30 °C,

temperature may have affected the survival of the strains. According to Prando et al. (2022), bacteria have an optimal temperature range for survival. Temperatures below 15 °C can reduce bacterial activity or even inhibit bacterial growth, whereas temperatures above 30-35 °C may lead to a loss of bacterial viability.

High salt concentrations can alter plant metabolism, affecting carbohydrates, polysaccharides, and protein metabolism as well as oil content. However, physiological and biochemical parameters including osmolyte accumulation, carbohydrate and total soluble sugar contents, ionic balance, and antioxidant activity were not measured in this study, limiting the mechanistic interpretation of the observed responses. Thus, although the results suggest that seed inoculation with *A. brasilense* may mitigate salt stress, this inference should be interpreted with caution.

Moreover, the conclusions are limited to the germination stage and controlled laboratory conditions. Therefore, the results should not be extrapolated to later developmental stages or field conditions. These limitations underscore the need for further studies integrating physiological and biochemical approaches with evaluations under conditions more representative of commercial cultivation to provide a more comprehensive understanding of the responses observed.

4. Conclusions

'Swingle' citrumelo seeds were sensitive to NaCl-induced salinity during germination. Seed inoculation with the rhizobacterium *Azospirillum brasilense* strains AbV5 and AbV6 by 5-min immersion did not effectively mitigate the overall adverse effects of salt stress on germination and seedling vigor.

Authors' Contribution

Conceptualization and methodology: Kathia Fernandes Lopes Pivetta; Renata Aparecida de Andrade; data collection and curation: Carime Gibran; Alessandra da Silva Andrade; Gabriel Longuinhos Queiroz; André Caturelli Braga; Mariana Martins da Silveira; formal analysis: Antonio Maricélio Borges de Souza; Thiago Souza Campos; Carime Gibran; data interpretation: Antonio Maricélio Borges de Souza; Thiago Souza Campos; Carime Gibran; Kathia Fernandes Lopes Pivetta; project administration: Kathia Fernandes Lopes Pivetta; Renata Aparecida de Andrade; supervision: Kathia Fernandes Lopes Pivetta; Renata Aparecida de Andrade; preparation of the original draft: Carime Gibran; Alessandra da Silva Andrade; Gabriel Longuinhos Queiroz; André Caturelli Braga; Mariana Martins da Silveira; writing-revision and editing:

Antonio Maricélio Borges de Souza; Thiago Souza Campos; Kathia Fernandes Lopes Pivetta. All authors read and approved the final version of the manuscript.

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