Hormones mitigate salt stress in tomato (Solanum lycopersicum L.) plants during vegetative growth

Las hormonas mitigan el estrés salino en plantas de tomate (Solanum lycopersicum L.) durante el crecimiento vegetativo

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ABSTRACT

Tomato is one of the most important vegetables in Colombia. This crop is sensitive to salinity, so high salt concentrations in the soil can negatively affect its growth and development; tolerance levels vary among cultivars. A viable strategy used in other cultivated species is the application of phytohormones that help plants acclimate to variable environments. Since few studies report the influence of growth regulators that alleviate this type of stress in tomatoes, this research aimed to determine the effect of different naphthaleneacetic acid and gibberellic acid doses on some physiological and growth parameters in tomato plants subjected to saline stress. We implemented a randomized design with a 2×6 factorial scheme. The first factor corresponded to salinity with two levels (0 and 40 mM), and the second factor involved the individual application of hormones (auxins - naphthaleneacetic acid (NAA) and gibberellins – gibberellic acid (ProGibb SP®)) at doses of 50, 75, and 100 μM each, for a total of 12 treatments with six replicates. We evaluated growth variables such as plant height, number of leaves, leaf area, fresh biomass of the aerial part and roots, as well as physiological variables of chlorophyll content and stomatal conductance (g_s). The application of gibberellins at 100 µM demonstrated the ability to mitigate the deleterious effects of salinity on some growth parameters in tomato plants by improving leaf expansion and aerial fresh biomass.

Key words: plant hormones, naphthaleneacetic acid, gibberellic acid, abiotic stress.

RESUMEN

El tomate es una de las hortalizas más importantes en Colombia. Este cultivo es sensible a la salinidad, por lo que las altas concentraciones de sal en el suelo pueden afectar negativamente su crecimiento y desarrollo, con niveles de tolerancia que varían entre cultivares. Una estrategia viable en otras especies cultivadas es la aplicación de fitohormonas, las cuales permiten a las plantas aclimatarse a entornos variables. En este sentido y considerando que pocos estudios reportan la influencia de reguladores de crecimiento en el alivio de este tipo de estrés en tomate, la presente investigación buscó determinar el efecto de diferentes dosis de ácido naftalenacético y ácido giberélico sobre algunos parámetros fisiológicos y de crecimiento en plantas de tomate sometidas a estrés salino. Se realizó un diseño completamente al azar con un esquema factorial 2×6 . El primer factor correspondió a la salinidad con dos niveles (0 y 40 mM) y el segundo factor a la aplicación individual de hormonas (auxinas - ácido naftalenacético (NAA) y giberelinas - ácido giberélico (ProGibb SP®) en dosis de 50, 75 y 100 μM cada una, para un total de 12 tratamientos con 6 repeticiones. Se evaluaron variables de crecimiento como altura, número de hojas, área foliar, biomasa fresca de parte área y raíz, y variables fisiológicas como contenido de clorofila y conductancia estomática (g.). La aplicación de giberelinas en dosis de 100 µM demostró que puede mitigar el efecto deletéreo de la salinidad en algunos parámetros de crecimiento en plantas de tomate, mejorando la expansión foliar y la biomasa fresca de la parte aérea.

Palabras clave: hormonas vegetales, ácido naftalenacético, ácido giberélico, estrés abiótico.

Introduction

Salinity is the result of natural and anthropogenic processes, the anthropogenic mainly associated with inadequate irrigation and excessive chemical fertilization (Sing *et al.*, 2016). Agricultural soil salinity limits the productivity of various crops worldwide. About 34 million ha are

affected by salinity problems and annual loss in agricultural productivity caused by salinization amounts to US\$ 31 million (FAO, 2024). In Colombia, 46% of the continental and insular land area shows some degree of susceptibility to salinity (SIAC, 2025).

The accumulation of salts affects plant growth and development by inhibiting water absorption, reducing nutrient

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availability, and generating phytotoxicity. Osmotic imbalance in the soil due to overfertilization contributes to the accumulation of Na⁺ and Cl⁻ ions in the plants, leading to physiological and biochemical disorders. At the photosynthetic level, biochemical and photochemical limitations occur. An increase in the intracellular concentration of Na⁺ promotes a decrease in chlorophyll content, negatively affecting electron transport chains during the photochemical phase of photosynthesis (Fita *et al.*, 2017; Taiz *et al.*, 2017).

Salinity affects plant water uptake, inducing water stress and water availability for physiological processes; this condition limits CO₂ uptake of the leaf mesophyll due to reduced stomatal conductance in response to salinity. Consequently, biochemical limitations arise from a reduction in the carboxylation rates of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and the inhibition of enzymes such as ribulose-5-phosphate kinase and glyceraldehyde-3-phosphate dehydrogenase (GAPDH) (Acosta-Motos *et al.*, 2017).

In addition to these effects, oxidative stress impacts plant photosynthetic metabolism. The increase in reactive oxygen species (ROS) oxidizes molecules such as lipids, chlorophyll, and proteins essential for maintaining cellular homeostasis (Taïbi *et al.*, 2016). From the plant defense perspective, there are several mechanisms that enable coping with this type of stress. The first is the activation of the plant antioxidant system. Enzymes such as superoxide dismutase, catalase, peroxidase, and ascorbate peroxidase, among others, mitigate cellular oxidative damage caused by the increase in ROS (Kashyap *et al.*, 2021).

Another defense mechanism during stress is related to the role of plant hormones. These growth regulators for development, and nutrient allocation are essential for modulating the physiological responses that lead to salinity tolerance (Fahad *et al.*, 2015). Evidence of this can be seen in fluctuations of endogenous plant hormone levels like auxins that in conjunction with nitric oxide cooperate in different ways to mitigate abiotic stresses like salinity and heavy metals (Ahmad, 2024).

Different studies have shown that exogenous application of phytohormones increases plant tolerance to salinity stress (Iqbal *et al.*, 2012; Javid *et al.*, 2011); for example, the use of naphthaleneacetic acid (NAA) increases chlorophyll content, plant height, leaf area, spike length, and the number and weight of grains in oat plants (Abed Jeber & Khaeim, 2019; Jahan *et al.*, 2019). Similarly, exogenous applications

of gibberellic acid (GA₃) in maize plants under saline stress improve growth, reduce oxidative stress, increase the activity of antioxidant enzymes, and enhance potassium concentration (Shahzad *et al.*, 2021). Additionally, the interaction between arbuscular mycorrhizal fungi (AMF) and exogenous applications of gibberellic acid (GA₃) improve tomato growth under salinity conditions (Khalloufia *et al.*, 2017).

The tomato crop (*Solanum lycopersicum* L.) can be significantly affected by the excessive accumulation of salt in the soil; this impacts plant growth, physiology, and, ultimately, yield (Zhang & Sonnewald, 2017). Recognized as the most important fresh vegetable in the human diet and rich in vitamins, carbohydrates, proteins, and antioxidants such as lycopene, β -carotene, and lutein (Heuvelink, 2018; Singh *et al.*, 2016), tomato cultivation is considered one of the most important vegetables globally (even though botanically it is actually a fruit), with China being the largest producer in the world (FAOSTAT, 2019). Meanwhile, Colombia has approximately 7,135 ha planted under greenhouse conditions in the Colombian high tropics, with an average yield of 25.18 t ha⁻¹ (MinAgricultura, 2024).

Considering that few studies report the influence of growth regulators on alleviating this type of stress in tomatoes, our research aimed to determine the effect of different exogenous doses of naphthaleneacetic acid and gibberellic acid on the physiological characteristics of growth and development in tomato plants subjected to salinity stress.

Materials and methods

Location

The experiment was conducted in the greenhouse of the Universidad Pedagógica y Tecnológica de Colombia (UPTC), Tunja, Boyacá, Colombia (5°33'8.255" N; 73°21'21.164" W), altitude of 2,735 m a.s.l., and a maximum air temperature of 42.1°C.

Experimental design

A completely randomized design was used with a 2 x 6 factorial scheme. The first factor was salinity with two levels (0 and 40 mM), and the second factor was the individual application of hormones (auxins – naphthaleneacetic acid (NAA) (Quimicompany®) and gibberellins (GA $_3$) – gibberellic acid (ProGibb SP®, Bayer) at doses of 50, 75, and 100 μ M for each with a total of 12 treatments (Tab. 1) with 6 replicates, with 72 experimental units, each corresponding to one tomato plant.

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TABLE 1. Description of treatments.

Treatment	Dose of NaCl, mM	Hormone	Dose, µM
1	40	NAA	50
2	40	NAA	75
3	40	NAA	100
4	0	NAA	50
5	0	NAA	75
6	0	NAA	100
7	40	GA	50
8	40	GA	75
9	40	GA	100
10	0	GA	50
11	0	GA	75
12	0	GA	100

Application of treatments

We planted tomato var. Chonto seedlings at growth stage 1 (code 13–103 - third true leaf of the unfolded main stem) (Meier, 2001) in bags with a capacity of 1 L filled with soil from the La María experimental farm at the Universidad Pedagógica y Tecnológica de Colombia (UPTC). The soil used had a clay texture with a particle size distribution of 48.2% clay, 36.16% silt, and 15.64% sand, analyzed using the Bouyoucos method at the Soil Laboratory of the Universidad Pedagógica y Tecnológica de Colombia. The soil chemical properties were as follows: pH 5.7, organic matter (3.22%) determined by the Walkley-Black method, and phosphorus 97.37 mg kg-1 measured using Bray II -Colorimetry. Base saturation was 10.33 cmol kg⁻¹ soil, potassium: 0.75 cmol kg⁻¹ soil, calcium: 6.88 cmol kg⁻¹ soil, magnesium: 2.35 cmol kg⁻¹ soil determined with NH₄Ac extraction and atomic absorption spectroscopy. The cation exchange capacity (CEC) was 26.20 cmol kg⁻¹ soil, while the electrical conductivity was 0.31 dS m⁻¹, and base saturation percentage was 38.66%.

The seedlings were watered and fertilized with Nutriponic® (Walco S.A.S.) 1 cc L⁻¹ every 3 d for 15 d before starting the application of 100 ml d⁻¹ of water with NaCl. Application was performed once a week. On the first day of saline application, the doses of the two phytohormones were applied using manual sprayers with 25 ml applied per plant at the established doses as a single application.

Measurement of variables

After applying the hormone treatments, we measured the variables at 20 d and 30 d. The variables included the following: (1) relative chlorophyll content from the middle-third

leaves of the plant using the SPAD 502-Plus chlorophyll meter (Konica Minolta®, USA), (2) stomatal conductance (mmol $\rm H_2O~m^{-2}~s^{-1}$) measured by taking three measurements per plant with the SC-1 Porometer in the middle-third leaves between 9:00 am and 10:00 am, (3) plant height measured with a tape measure from the base of the stem on the soil surface to the apical bud, (4) stem diameter measured with a caliper, (5) leaf count, and (6) leaf area.

For the determination of fresh weights, we separated the plants into roots and aerial parts (stems + leaves) and weighed them using an Acculab VIC 612 electronic scale with a precision of 0.01 g. We placed the samples in paper bags with a 10 kg capacity properly labeled, according to the treatment and replicate.

Statistical analysis

We analyzed the data in the following manner: for variance homogeneity we used the Bartlett test, normality using the Shapiro-Wilk test, subsequently evaluated using an analysis of variance (ANOVA) with a significance of ($P \le 0.05$). The analyzed significant differences using a mean comparison test (the Tukey's test, $P \le 0.05$) for the factors of salt concentration, hormone types, and doses. We performed all analyses using the 'agricolae' package of the statistical software R Core Team (2022).

Results and discussion

Growth variables

The application of 40 mM NaCl to the soil affected ($P \le 0.05$) the height of the tomato plants compared to the treatment without salinity: stressed plants showed a 14% decrease in growth (Fig. 1). Plant growth is affected by exposure to salinity; one of the first symptoms is a reduction in cell elongation, which decreases plant growth, and reduces photosynthetic rate. This damage is produced due to programmed cell death (Iqbal, 2014). Soil salinity decreases the soil water potential, preventing proper water absorption by the plants; this in turn limits metabolic reactions, impedes nutrient transport, and hinders gas exchange, thus affecting photosynthetic rates, leading to a reduction in growth (Martínez Villavicencio *et al.*, 2011).

Although the tomato is a moderately salt-tolerant species (Saldaña *et al.*, 2017), the evaluated NaCl dose had a deleterious effect on plant height. However, studies like those of Murillo-Amador *et al.* (2017) report that only NaCl concentrations greater than 100 mM show significant variations in parameters such as stomatal conductance and

water relative content (WRC), important for plant growth. Rodríguez *et al.* (1997) indicate that hydraulic conductivity in plants subjected to salinity depends on the exposure time to the stressful conditions, soil type, and temperature, since the latter factor affects water flow. The same authors indicate that hydraulic conductivity in plants also depends on other hydraulic signals perceived by the roots, which communicate the soil's water status to the rest of the plant.

Several researchers have debated the possible involvement of plant hormones such as abscisic acid in this signaling (Kishor *et al.*, 2022; Taiz *et al.*, 2017). However, other studies report that auxins and gibberellins may participate in the hormonal balance that allows the plant to seek growth strategies according to the soil water status (Gornals, 2015; Omena-Garcia, 2019).

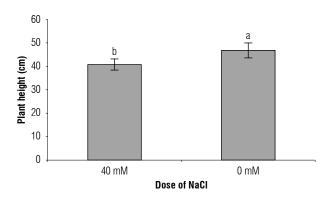


FIGURE 1. Height of tomato plants (*Solanum lycopersicum* L.) watered with 40 mM and 0 mM NaCl solution for 20 d. Different letters indicate significant differences between treatment means according to the Tukey's test ($P \le 0.05$); bars represent the standard error, n = 6.

According to our data, the plant height showed significant statistical differences ($P \le 0.05$) for the interaction of factors, dose, and type of hormones used for day 20 and day 30 post-application (Fig. 2A and 2B). These results agreed

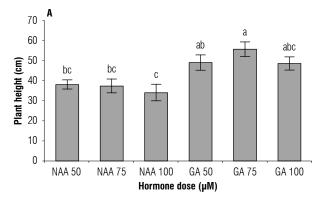
with the findings of Taiz *et al.* (2017), who indicated that plant height is related to several environmental factors and hormonal regulation.

The application of gibberellins increased plant height at all doses in our experiment, compared to auxin applications, especially at higher doses (75 and $100 \,\mu\text{M}$). The exogenous application of gibberellins increases endogenous levels, thus inducing the growth and expansion of new shoots (Bidadi *et al.*, 2010).

Gibberellins act as mobile molecules that can cross the plasma membrane for cell-to-cell transport (Gao *et al.*, 2017), which explains their effectiveness through exogenous applications, and the GA signal is perceived by the soluble receptor protein (GID1). Additionally, GAs promotes plant growth and development by facilitating the degradation of DELLA proteins, a family of nuclear growth repressors (Gao *et al.*, 2017); this could explain the results obtained in our research.

It is important to highlight studies such as Fu and Harberd (2003) and Oh *et al.* (2014) that show that there is synergy between auxins and gibberellins for cell elongation. Once the auxin movement increases, it destabilizes DELLA proteins that are recognized as transcriptional regulators responsible for repressing responses to GA (Boccaccini *et al.*, 2014).

In general, the number of leaves affected by the type of hormones were as follow: gibberellins promoted the highest leaf formation; auxins promoted greater root formation (Fig. 3A and B). De Smet *et al.* (2010) mention that auxins regulate a wide range of morphological responses and play an important role in the initiation of lateral roots, while gibberellins are recognized for their role in cell elongation,



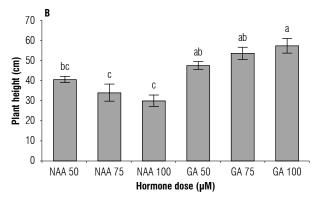


FIGURE 2. Height of tomato plants (*Solanum lycopersicum* L.) treated with 50, 75 or $100 \,\mu\text{M}$ of auxins – naphthaleneacetic acid (NAA) and gibberellins – gibberellic acid (GA₃) for 20 d (A) and 30 d (B). Different letters indicate significant differences between treatment means according to the Tukey's test ($P \le 0.05$); the bars represent the standard error; n = 6.

induction of floral and fruit development in some species, apical dominance, leaf expansion, and internode elongation. However, studies such as Fu and Harberd (2003) and Tong *et al.* (2014) demonstrate that, in tobacco and rice plants, stem elongation is coordinately regulated by auxins and gibberellins and brassinosteroids, and that gibberellininduced root elongation requires auxins because their activity in cellular expansion, as well as in tissue differentiation, overlaps.

The fresh root weight had statistically significant differences related to the factor of dose and hormones used (Fig. 3C). Doses of 50 and 75 μ M of naphthaleneacetic acid favored root growth in tomato plants compared to the same doses of gibberellic acid (Fig. 3C). Other studies show that high concentrations of auxins in plants, such as *Arabidopsis thaliana*, generate shorter roots but with more root hairs that increase the root volume and, consequently, the final root weight (Casanova-Sáez & Voß, 2019).

Research conducted on tomatoes with exogenous applications of gibberellins shows that the endogenous increase in GA after exogenous applications inhibits root growth (Bidadi *et al.*, 2010), similar to what we found in the present

study. These results can be explained because the roots present high contents of GA, and when exogenous applications are made. The GA reach such high concentrations that they inhibit root growth (Hedden & Sponsel, 2015).

Regarding the number of leaves and the amount of fresh biomass accumulated in the aerial part for the salinity-hormones-dose interaction, we found that gibberellins at the $100\,\mu\text{M}$ dose mitigated the detrimental effect of salinity on these two growth parameters compared to auxins (Fig. 3).

Salinity stress induces the synthesis of abscisic acid, leading to stomatal closure, which decreases water uptake, causing photoinhibition and oxidative stress (Silva *et al.*, 2022). The main effect of these physiological changes is the inhibition of cell expansion. Similar results are reported by Feng *et al.* (2023) in rice plants subjected to saline stress and by Li *et al.* (2022) in tomato plants.

For this reason, the exogenous application of GA can help mitigate these effects since gibberellins are involved in tolerance to biotic stress, since they are implicated in various physiological and metabolic changes: for example, in grapevine (*Vitis vinifera*) GA₃ sprays are applied shortly

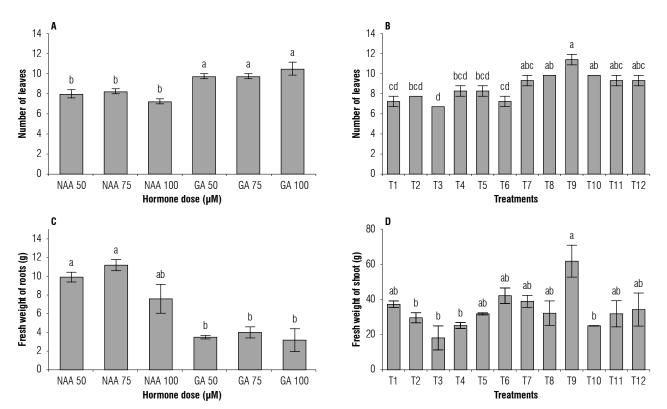


FIGURE 3. Number of leaves of tomato plants (Solanum lycopersicum L.) treated with 50, 75 or 100 μ M of auxins – naphthaleneacetic acid (NAA) and gibberellins – gibberellic acid (GA) (A and C) and fresh weights of roots and shoots of plants grown in soil under two concentrations of NaCl (B and D) for 30 d. Treatment descriptions (T1-T12) are as in Table 1. Different letters indicate significant differences between treatment means according to the Tukey's test ($P \le 0.05$); the bars represent the standard error, n=6.

before veraison to regulate fruit development and improve stress tolerance (Murcia *et al.*, 2017). Regarding osmotic stress caused by water deficit and/or salinity stress, GA levels are directly involved in tolerance in several plant species (Zawaski & Busov, 2014).

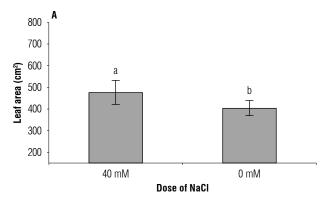
Gibberellins stimulate various physiological processes, including stem growth by elongation. The site of action of gibberellins is the intercalary meristem located at the base of the internode (Taiz *et al.*, 2017). While GA promotes internode elongation, the increase in the number of leaves observed in tomato plants may be associated with an overall enhancement of shoot development rather than a direct effect on leaf initiation.

Tomato plants whose leaf areas were subjected to salt stress presented significant statistical differences between treatments, with plants under stress showing a larger leaf area. Since the study did not include absolute control, we determined that the increase in this variable corresponds to the application of hormones that have a beneficial effect, even

when the plant is under stress (Fig. 4A). Additionally, the interaction of hormonal doses of auxins and gibberellins showed a significant statistical difference for the gibberellin treatment at 100 μ M (Fig. 4B). Gibberellic acid regulates leaf cell expansion primarily through the *SiDREB* gene, which is activated by abscisic acid (ABA) and decreases leaf expansion. Due to the GA/ABA antagonistic regulation under osmotic stress, this gene is suppressed, leading to greater leaf expansion and plant growth (Li *et al.*, 2012).

Chlorophyll contents (SPAD units) showed significant statistical differences for the hormone-dose interaction (Fig. 5A), with higher values in the 75 and 100 μ M auxin doses compared to all gibberellin doses studied. Gibberellins caused an increase in plant height that leads to a nitrogen "dilution effect", in contrast to plants with auxins that did not show an increase in plant height.

The hormone-salinity-dose interaction also showed significant statistical differences (Fig. 5B). The treatment with salinity and $100 \,\mu\text{M}$ gibberellins presented the lowest



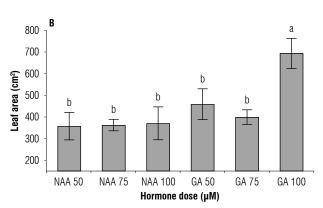
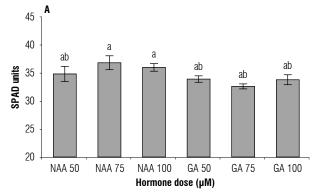


FIGURE 4. Leaf area of tomato plants (*Solanum lycopersicum* L.) grown in soil treated with two concentrations of NaCl (A) and with applications of 50, 75, or 100 μ M of auxins – naphthaleneacetic acid (NAA) and gibberellins – gibberellic acid (GA) (B) for 30 d. Different letters indicate significant differences between treatment means according to the Tukey's test ($P \le 0.05$); bars represent the standard error, n = 6.



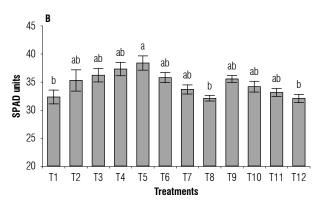


FIGURE 5. Relative chlorophyll content (SPAD units) in leaves of tomato plants (Solanum lycopersicum L.) treated with 50, 75, or $100 \,\mu\text{M}$ of auxins – naphthaleneacetic acid (NAA) and gibberellins - gibberellic acid (GA) (A) and grown under two concentrations of NaCl (B) for 30 d. Treatment description (T1-T12) as in Table 1. Different letters indicate significant differences between treatment means according to the Tukey´s test ($P \le 0.05$); the bars represent the standard error, n = 6.

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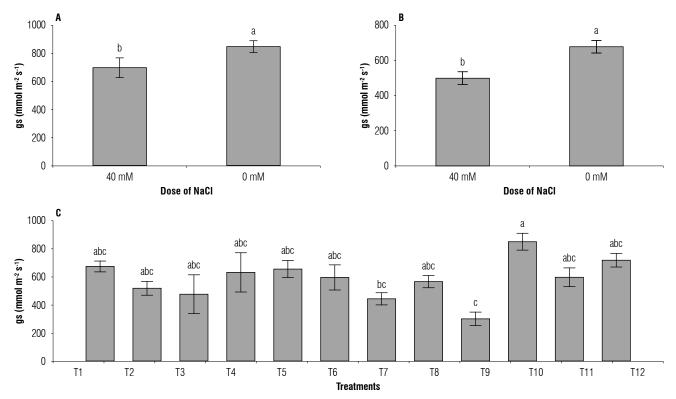


FIGURE 6. Stomatal conductance (g_s) in leaves of tomato plants (*Solanum lycopersicum* L.) grown in soil under two concentrations of NaCl at 20 d after application (A) and at 30 d (B), and g^s of tomato plants subjected to salinity and treated with 50, 75 or 100 μ M of auxins – naphthaleneacetic acid (NAA) and gibberellins – gibberellic acid (GA) (C). Treatment description (T1-T12) as in Table 1. Different letters indicate significant differences between treatment means according to the Tukey's test ($P \le 0.05$); the bars represent the standard error, n = 6.

SPAD values. Total nitrogen content in the leaves can be estimated indirectly through SPAD units, which measure leaf chlorophyll content as an indicator of nitrogen status (Anjum *et al.*, 2013). These results are similar to those of Florina *et al.* (2013), who find that salt stress affects chlorophyll content in tomato plants subjected to 200 and 400 mM NaCl solutions, decreasing chlorophyll concentration and SPAD values as salt concentration in the soil solution increases.

Stomatal conductance (g_s) presented significant differences in tomato plants subjected to salt stress (Fig. 6A and B). Plants exposed to 40 mM NaCl in the soil solution showed lower values than plants not subjected to salt stress at both evaluation times. These results are similar to those of Li *et al.* (2022), who evaluate the effect of sodium nitroprusside (SNP) on tomato plants subjected to 100 mM NaCl and find a decrease in plant growth and gas exchange, similar to the findings of the present study.

The application of GA at 75 μ M to plants cultivated in soil with 40 mM NaCl (Fig. 6) resulted in growth values similar to those of plants that were not subjected to stress (e.g., 0 mM NaCl, 75 μ M GA). Therefore, we suggest that

the application of this hormone under stress conditions may help maintain gas exchange. In tomato, DELLA proteins promote stomatal closure mediated by ABA (Nir *et al.*, 2017), and the authors postulate that this could be due to the antagonistic function of gibberellin. Recent studies find that endogenous GA levels control stomatal opening in steady-state conditions in *Arabidopsis* through the GID1 receptors in a mechanism involving the degradation of DELLA proteins (Sukiran *et al.*, 2020). However, future research should evaluate parameters such as transpiration, net photosynthesis, and water use efficiency.

Conclusions

The use of gibberellins is a viable option to reduce the negative effect of salinity and improve osmotic stress tolerance in tomato crops when concentrations of 40 mM NaCl are present in the soil solution. The use of this phytohormone improves stomatal conductance, bringing stressed plants closer to the g_s values observed in plants without saline stress. However, auxins at concentrations of 50 and 75 μ M NAA promote root growth and fresh weight of roots in plants not subjected to saline stress, making it a viable option to improve nutrient absorption in commercial crops.

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Conflict of interest statement

The authors declare that there is no conflict of interests regarding the publication of this article.

Author's contributions

ZCCR and HDRB designed the conceptual approach and objectives; ZCCR and HDRB carried out the field and laboratory experiments and elaborated visual representations of the data and results; ZCCR and HDRB designed and developed the research methodology, including methods of data collection, equipment and verified the accuracy and reliability of the research results through a validation process; ZCCR and HDRB wrote the initial draft. All authors participated in the critical review and approval of the final version of the manuscript.

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