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Alleviating Salt Stress in Tomatoes through Seed Priming with Polyethylene Glycol and Sodium Chloride Combination

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Abstract: Tomato cultivation grapples with salt stress, disrupting growth parameters and physiological processes. High salinity levels induce osmotic stress, impacting cellular integrity and hindering metabolic activities. Salt accumulation at the root zone alters key physiological attributes, compromising overall harvestable output. Seed priming emerges as a potential solution to enhance plant resilience. A research gap exists in understanding the combined influence of polyethylene glycol and sodium chloride as seed priming agents under salt stress conditions. The study occurred in the Greenhouse of Laboratory Horticultural Science at Tokyo University of Agriculture. Micro Tom seeds underwent a factorial randomized design, involving five salinity and four priming treatments. Replicated ten times, totaling 200 plants, seed priming used polyethylene glycol, inducing salinity stress with sodium chloride. Meticulous measurements of growth parameters, photosynthetic traits, yield attributes, and electrolyte leakage were conducted. Statistical analyses discerned treatment effects at a 5% significance level. Seed priming, especially with 'PEG plus NaCl', effectively mitigated salt stress effects on tomato plants. Under severe salt stress, primed plants exhibited increased plant height, trusses, leaves, and leaf area. Photosynthetic efficiency and yield attributes demonstrated significant improvements with seed priming. Electrolyte leakage, indicative of leaf damage, was notably reduced by seed priming treatments, with 'PEG plus NaCl' exhibiting the highest efficacy. These results offer valuable guidance for optimizing agricultural practices in saline environments, contributing to sustainable strategies for food security amidst escalating environmental challenges.

Keywords: growth; photosynthesis; salinity; seed priming; yield

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1. Introduction

Salt stress poses a significant challenge in the cultivation of tomatoes, impacting various growth parameters [1,2] and physiological processes within the plants [3–5]. High salinity levels can lead to osmotic stress, disrupting the normal physiology of plants leading to cellular damage [6] and hindering normal metabolic activities. The accumulation of salt at the root zone has the potential to significantly alter key physiological attributes in plants, such as the photosynthetic rate, transpiration rate, and stomatal conductance [7]. Elevated salt levels in the soil can induce various responses in plant physiology, disrupting the delicate balance of these essential processes [8]. Salt stress often leads to a reduction in photosynthetic rate, impacting the plant's ability to convert light energy into chemical energy through photosynthesis [9]. Additionally, increased salt concentration can disrupt the transpiration process, affecting water movement within the plant and potentially leading to water stress. Stomatal conductance, which regulates the exchange of gases and water vapor between the plant and its environment, is also influenced by salt accumulation, further impacting overall plant performance [10,11].

Salt stress exerts a notable influence on crop yield, constituting a critical factor in agricultural productivity [12]. The deleterious impact of elevated soil salinity on plant growth and development extends beyond physiological changes, significantly compromising the overall harvestable output. This adverse effect on yield is multifaceted, encompassing disruptions in reproductive processes, hampered nutrient uptake, and compromised cellular functions [13].

Seed priming is a pre-sowing technique that involves treating seeds to initiate the germination process before planting. This practice is designed to enhance seed performance and subsequently improve overall plant growth [14]. Several mechanisms contribute to the positive effects of seed priming on plant growth. Moreover, seed priming has been reported as an effective technique for influencing various parameters related to photosynthesis, a fundamental process in plant growth and development [15]. This includes promoting chlorophyll synthesis, activating enzymes crucial for carbon fixation, enhancing carbon assimilation, optimizing stomatal conductance, and positively impacting the overall photosynthetic rate. Additionally, seed priming has demonstrated the potential to improve water use efficiency and mitigate the impact of abiotic stresses on photosynthesis [16]. These combined effects contribute to a more robust and efficient photosynthetic system, ultimately enhancing plant growth, development, and resilience under varying environmental conditions [17].

Previous studies have investigated the varied impacts of salt stress on tomato plants. Seed priming with PEG6000 has been proven to efficiently induce salt tolerance in tomatoes [3,17]. Additionally, using sodium chloride as a priming reagent has shown effectiveness in reducing the negative effects of salt stress on tomato plants [18]. PEG6000 induces osmotic stress [19], while NaCl induces ionic stress due to sodium ions [20]. Both stress types can challenge seeds to produce seedlings that tolerate salt stress [21]. However, their combination may offer a more balanced osmotic adjustment and ionic balance within seed and seedling tissues, leading to better stress tolerance during germination and early growth stages. Furthermore, salinity stress triggers oxidative stress in plants due to the overproduction of reactive oxygen species (ROS) [22]. Both PEG6000 and NaCl can affect antioxidant enzyme activities [23], but combining these agents may result in a synergistic effect that enhances the antioxidant defense mechanism, thus reducing oxidative damage and improving salt tolerance. The novelty of this study lies in the fact that no prior research has explored the combination of PEG6000 and NaCl as a priming agent to improve salt tolerance in tomatoes.

2. Results

2.1. Growth Parameters

Salinity stress had a notable impact on plant height, resulting in a reduction that correlated with increasing salt concentrations. The most pronounced diminishment in plant height was observed at the higher salt concentrations of 150 mM and 200 mM sodium chloride. In contrast, there was no significant disparity in plant height between the control group and those subjected to 50 mM or 100 mM NaCl salt stress conditions. Interestingly, salt stress had a considerable suppressive effect on plant height, yet the application of seed priming proved effective in augmenting and elevating plant height. This positive influence was further accentuated by the presence of a significant interaction between salinity and seed priming, signifying the remarkable role of priming in counteracting the adverse effects of salt stress on plant height. Moreover, salt stress exerted a severe reduction in the number of trusses per plant, but this detrimental impact was substantially mitigated in primed plants when compared to their non-primed counterparts. Additionally, plants originating from non-primed seeds exhibited a notably lower number of leaves in comparison to those from primed seeds. Salinity, in this context, had a significantly negative effect on the number of leaves, while seed priming had a marked, positive influence on this parameter, as exemplified in Figure 1. Remarkably, the plants derived from primed seed using PEG plus NaCl produced broader leaves in contrast to those without priming. This observation underscores the effectiveness of seed priming in mitigating the harmful consequences of salt stress on leaf area, highlighting its potential for improving the overall health and performance of plants under challenging conditions. In general, the combined application of polyethylene glycol and sodium chloride as a seed priming treatment exhibited a profound influence on various growth parameters of tomato plants, including plant height, the number of trusses, the number of leaves, and leaf area, particularly when exposed to salt stress conditions. Notably, the effectiveness of PEG plus NaCl became most pronounced under severe salt stress conditions, specifically at salt concentrations of 150 mM and 200 mM NaCl, as illustrated in Figure 1.

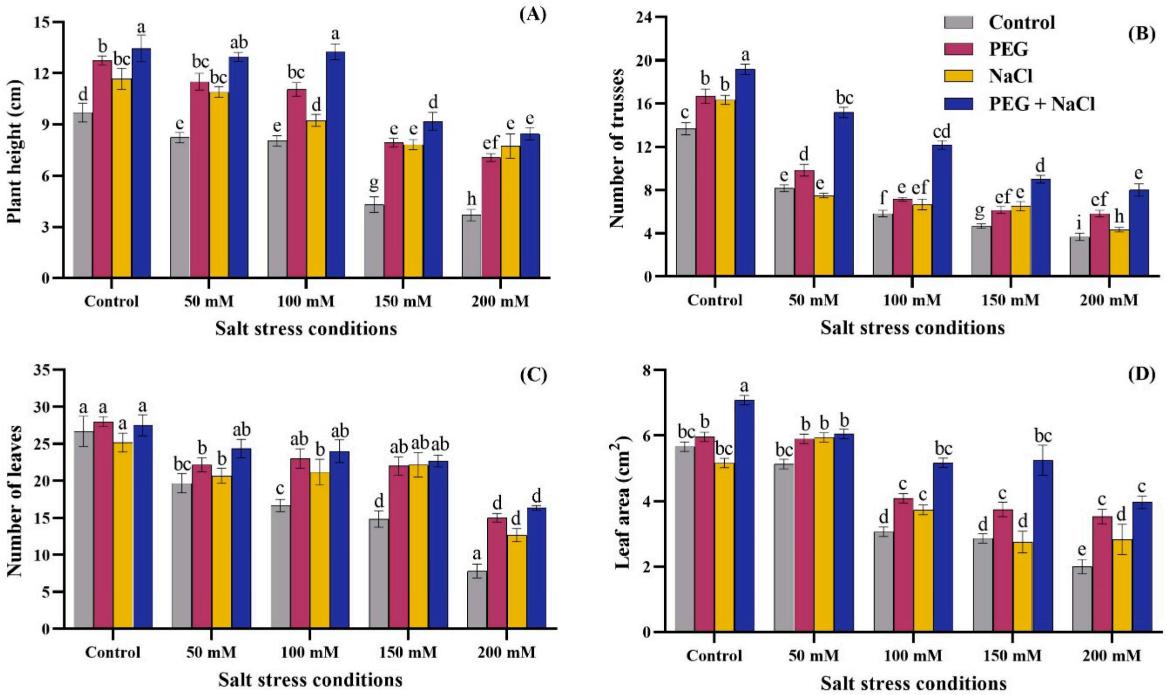

Figure 1. Impact of seed priming on plant height (**A**), number of trusses (**B**), number of leaves (**C**), and leaf area (**D**) of tomato plants subjected to varied salt stress conditions. The bars with the same alphabetical letters did not differ significantly, based on ANOVA followed by the Tukey test at 5%.

2.2. Photosynthetic Attributes

Photosynthetic rate, transpiration rate, stomatal conductance, and leaf surface temperature were meticulously assessed as key parameters related to photosynthesis. Based on Table 1, as the salinity levels escalated, there was a notable decline in the photosynthetic rate within tomato leaves. However, a promising reversal was observed with seed priming, showcasing a distinct improvement. The divergence between the control group and the seed priming treatments was particularly noteworthy. The transpiration rate, indicative of the efficient utilization of water for leaf cooling, faced adversity in the presence of salt stress. Remarkably, the application of seed priming treatments demonstrated a positive impact, fostering an increase in transpiration rate. Even in the face of severe salt stress, leaf stomata exhibited closure; however, plants subjected to seed priming treatments exhibited heightened activity and more open stomata compared to their control counterparts. This heightened stomatal activity potentially contributed to the increased transpiration rate in leaves derived from primed seeds. Under the duress of salt stress, leaf surface temperature witnessed a surge compared to ambient conditions. Conversely, under the influence of seed priming treatments, a contrary trend was evident, signifying a significant reduction in leaf surface temperature for tomato plants exposed to salt stress conditions (Figure 2). This outcome underscores the potential of seed priming as a strategic intervention to mitigate the adverse effects of salt stress on the physiological aspects of tomato plants, specifically in the context of photosynthesis and temperature regulation.

Table 1. Influence of seed priming on photosynthetic parameters of tomato plants under salt stress conditions.

Salinity	Priming	Pn (μmol CO_2 $m^{-2}s^{-1}$)	E (μmol CO_2 $m^{-2}s^{-1}$)	Gs (mol CO_2 $m^{-2}s^{-1}$)	LT (°C)
Control	Control	7.68 ± 0.15 ab	0.41 ± 0.024 c–e	0.37 ± 0.01 b	27.05 ± 1.05 c–e
	PEG	7.73 ± 0.54 ab	0.45 ± 0.023 bc	0.39 ± 0.014 b	20.46 ± 0.69 gh
	NaCl	5.38 ± 0.33 ef	0.44 ± 0.012 cd	0.36 ± 0.019 b	22.43 ± 0.68 f–h
	PEG plus NaCl	8.49 ± 0.44 a	0.52 ± 0.014 a	0.46 ± 0.011 a	19.97 ± 1.59 h
		***	***	**	***
50 mM	Control	6.06 ± 0.42 c–e	0.35 ± 0.012 fg	0.27 ± 0.015 cd	30.75 ± 1.05 bc
	PEG	6.48 ± 0.45 cd	0.41 ± 0.013 de	0.28 ± 0.006 c	24.33 ± 0.48 e–g
	NaCl	5.5 ± 0.35 d–f	0.38 ± 0.012 ef	0.26 ± 0.014 c–e	25.76 ± 0.68 d–f
	PEG plus NaCl	7.14 ± 0.38 bc	0.49 ± 0.024 ab	0.36 ± 0.016 b	22.52 ± 1.12 f–h
		***	***	***	***
100 mM	Control	4.57 ± 0.25 f–k	0.22 ± 0.02 hi	0.2 ± 0.013 fg	29.63 ± 0.85 b–d
	PEG	4.86 ± 0.59 f–i	0.25 ± 0.012 h	0.22 ± 0.009 d–g	24.07 ± 2.97 e–g
	NaCl	4.64 ± 0.19 f–k	0.23 ± 0.013 h	0.19 ± 0.013 fg	27.21 ± 1.2 c–e
	PEG plus NaCl	5.24 ± 0.35 e–h	0.34 ± 0.012 fg	0.27 ± 0.008 c	22.53 ± 2.11 f–h
		**	***	***	***
150 mM	Control	4.3 ± 0.33 g–k	0.19 ± 0.013 i–k	0.15 ± 0.018 hi	32.77 ± 1.41 ab
	PEG	4.74 ± 0.34 f–j	0.25 ± 0.014 h	0.18 ± 0.015 gh	25.32 ± 0.76 ef
	NaCl	4.06 ± 0.11 i–k	0.21 ± 0.015 h–j	0.15 ± 0.013 h–j	27.22 ± 0.9 c–e
	PEG plus NaCl	5.27 ± 0.24 e–g	0.32 ± 0.011 g	0.22 ± 0.017 e–g	23.2 ± 1.17 e–h
		**	***	***	***
200 mM	Control	3.56 ± 0.35 k	0.15 ± 0.022 k	0.09 ± 0.02 k	35.1 ± 1.72 a
	PEG	4.18 ± 0.15 h–k	0.18 ± 0.021 jk	0.13 ± 0.011 ij	24.5 ± 0.87 e–g
	NaCl	3.71 ± 0.27 jk	0.17 ± 0.011 jk	0.1 ± 0.023 jk	25.6 ± 1.21 d–f
	PEG plus NaCl	4.69 ± 0.35 f–j	0.24 ± 0.031 h	0.23 ± 0.014 d–f	23.3 ± 1.18 e–h
		***	**	***	***

Pn: photosynthetic rate, E: transpiration rate, Gs: stomatal conductance, and LT: leaf surface temperature. Data are expressed as mean ± SD of 10 replications (n = 10), and one plant was considered a replication. The values with the same alphabetical letters did not differ significantly, based on ANOVA followed by the Tukey test at 5%. *** for $p < 0.001$, and ** for $p < 0.01$.

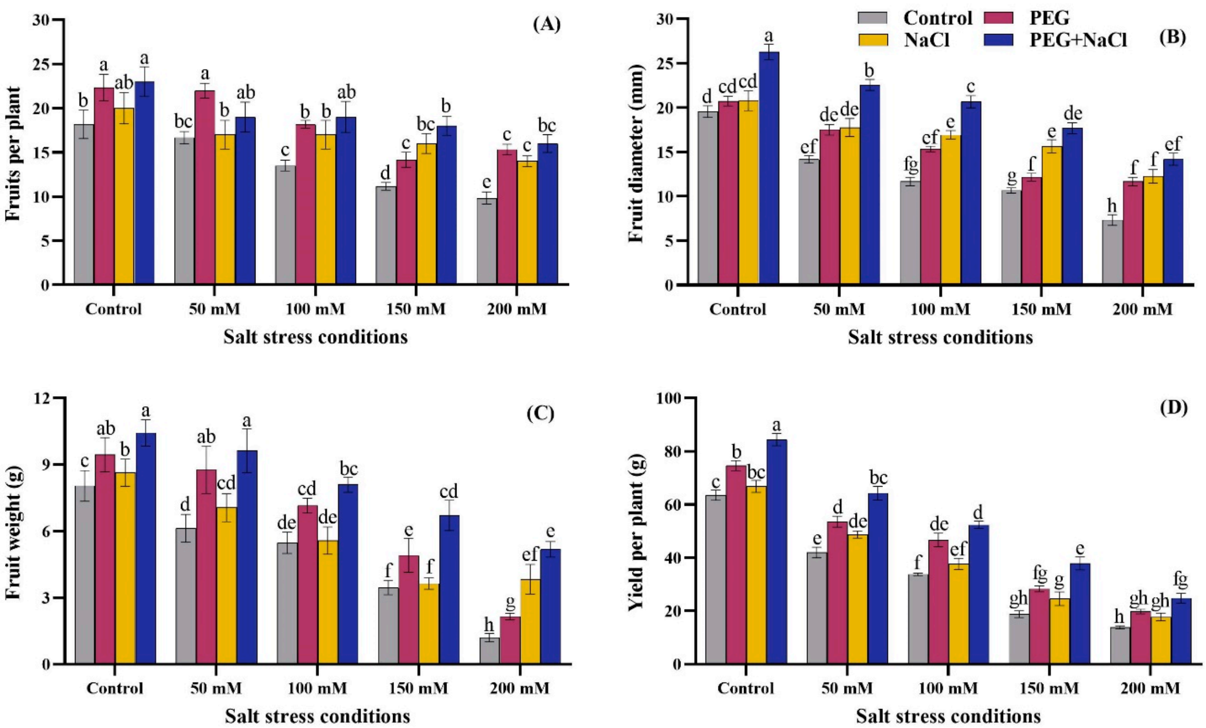

Figure 2. Influence of seed priming on fruits per plant (**A**), fruit diameter (**B**), fruit weight (**C**), and yield per plant (**D**). The bars with the same alphabetical letters did not differ significantly, based on ANOVA followed by the Tukey test at 5%.

Following the analysis of variance, the treatment labeled 'PEG plus NaCl' exhibited the highest rates of photosynthesis, transpiration, stomatal conductance, and leaf temperature. Subsequently, the 'PEG' and 'NaCl' treatments demonstrated superior performance compared to the control group. The recorded photosynthetic rates ranged from 3.56 to 8.49, with the lowest value associated with the highest salinity level without priming (3.56), and the highest value (8.49) observed under ambient conditions when the 'PEG plus NaCl' treatment was applied. Moreover, a noteworthy disparity in transpiration rates between the priming treatments and the control was observed, indicating that priming had a positive impact on water use efficiency in tomato leaves. The significant difference in stomatal conductance suggested that salt stress induced stomatal closure, resulting in a reduction in transpiration rates and an elevation in leaf temperature (Table 1).

2.3. Yield Attributes

The analysis of variance pertaining to yield parameters unveiled a significant decline in tomato yield attributes under the influence of salt stress. This decline was observed to intensify as salt concentration increased. However, an encouraging trend emerged with the application of seed priming, which notably bolstered the plant's vigor, leading to higher yields compared to the control group. Salt stress had a detrimental impact on the reproductive phase of tomato plants, leading to a reduction in various critical parameters, including the number of fruits per plant, fruit diameter, fruit weight, and overall plant yield. Notably, the adverse effects of salt stress were mitigated by seed priming techniques. Specifically, the number of fruits per plant was significantly higher in plants derived from primed seeds when compared to those that were not subjected to priming. The most remarkable increase in the number of fruits per plant was observed in the treatment utilizing a combination of polyethylene glycol and sodium chloride as priming agents. This underscores the effectiveness of this priming approach in bolstering fruit production. Moreover, it is worth noting that the growth rate of the primed plants outpaced that of the non-primed counterparts, resulting in larger-sized fruits. As salt concentrations escalated, fruit weight decreased; however, seed priming emerged as a potent method for enhancing fruit weight. Among the various priming treatments, polyethylene glycol and the combination of polyethylene glycol and sodium chloride proved to be the most effective in this regard. The significance of these findings becomes evident when considering that plants yielding a greater number of fruits and larger, heavier fruits ultimately contribute to a higher total yield. These desirable attributes were consistently observed in the plants subjected to seed priming treatments. Consequently, the plants undergoing priming treatment with PEG plus NaCl exhibited a substantially greater fruit yield compared to other treatments, as depicted in Figure 2A–D.

2.4. Electrolyte Leakage

Leaf electrolyte leakage exhibited an increase corresponding to higher salt concentrations, but seed priming treatments demonstrated a significant reduction in this phenomenon. Notably, the treatment labeled 'control' consistently registered the highest electrolyte leakage values across all salinity levels. Conversely, seed priming treatments consistently yielded lower electrolyte leakage values, with the most effective treatment being 'PEG plus NaCl'. Remarkably, the 'PEG plus NaCl' treatment exhibited a noteworthy reduction in electrolyte leakage, demonstrating reductions of 10%, 15%, 15%, 13%, and 10% at salinity levels of control, 50 mM, 100 mM, 150 mM, and 200 mM, respectively (Figure 3). This underscores the efficacy of seed priming, particularly with the 'PEG plus NaCl' treatment, in mitigating the adverse effects of salt-induced electrolyte leakage in the examined plant leaves.

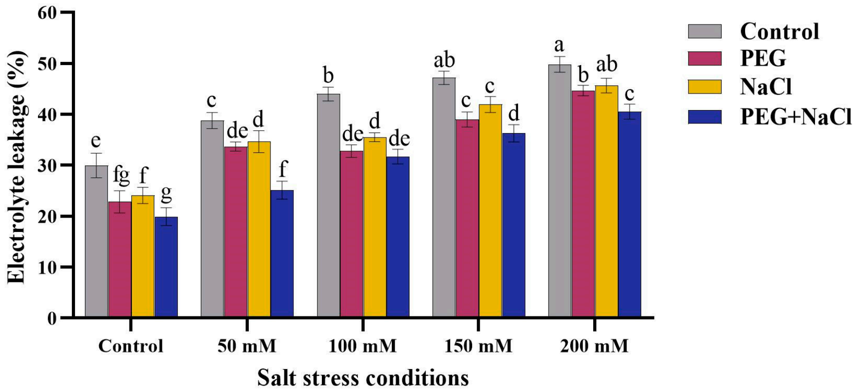

Figure 3. Effect of seed priming on leaf electrolyte leakage of tomato plants under salt stress conditions. The bars with the same alphabetical letters did not differ significantly, based on ANOVA followed by the Tukey test at 5%.

2.5. Correlation Anaylsis

The correlation analysis of growth and physiological parameters reveals a significant interrelation between leaf temperature and various growth parameters. Specifically, there is a substantial negative correlation between leaf temperature and essential growth indicators such as plant height (−0.85), number of trusses (−0.64), number of leaves (−0.67), and leaf area (−0.67). This implies that as leaf temperature increases, the plants tend to exhibit diminished height, fewer trusses, reduced leaf count, and smaller leaf sizes. The implication is clear: elevated leaf temperature adversely impacts plant growth metrics. Furthermore, the correlation between leaf temperature and electrolyte leakage is strongly positive (0.82), indicating that an escalation in leaf temperature coincides with an increase in electrolyte leakage. This connection underscores the sensitivity of electrolyte leakage to variations in leaf temperature. Interestingly, electrolyte leakage exhibits strong negative correlations with key physiological processes: photosynthetic rate (−0.81), transpiration rate (−0.87), and stomatal conductance (−0.92). In essence, an increase in electrolyte leakage corresponds to a decrease in these crucial physiological functions. This intricate relationship suggests that salt stress induces elevated leaf temperature and subsequent electrolyte leakage, resulting in reduced photosynthesis in leaves. However, the application of seed priming acts as a mitigating factor, reducing both leaf temperature and electrolyte leakage, thereby fostering enhanced plant performance (Figure 4).

The regression analysis examining fruit yield, photosynthetic rate, and electrolyte leakage highlights a strong positive correlation between fruit yield and photosynthetic rate, accompanied by a negative relationship with electrolyte leakage. As photosynthetic rate increases, there is a notable elevation in fruit yield. Conversely, an increase in electrolyte leakage is associated with a decrease in fruit yield. This intricate relationship underscores the pivotal role of photosynthetic activity in influencing fruit yield positively. A higher photosynthetic rate implies an increased production of energy and assimilates, contributing to enhanced fruit development and yield. Conversely, the negative correlation with electrolyte leakage suggests that a rise in cellular damage, as indicated by electrolyte leakage, is associated with a decline in fruit yield. In essence, the findings suggest that the physiological health of the plant, as reflected in photosynthetic efficiency and electrolyte leakage, directly impacts fruit yield. These insights are crucial for understanding and optimizing factors influencing fruit production, providing valuable information for agricultural practices aimed at enhancing crop yields (Figure 5).

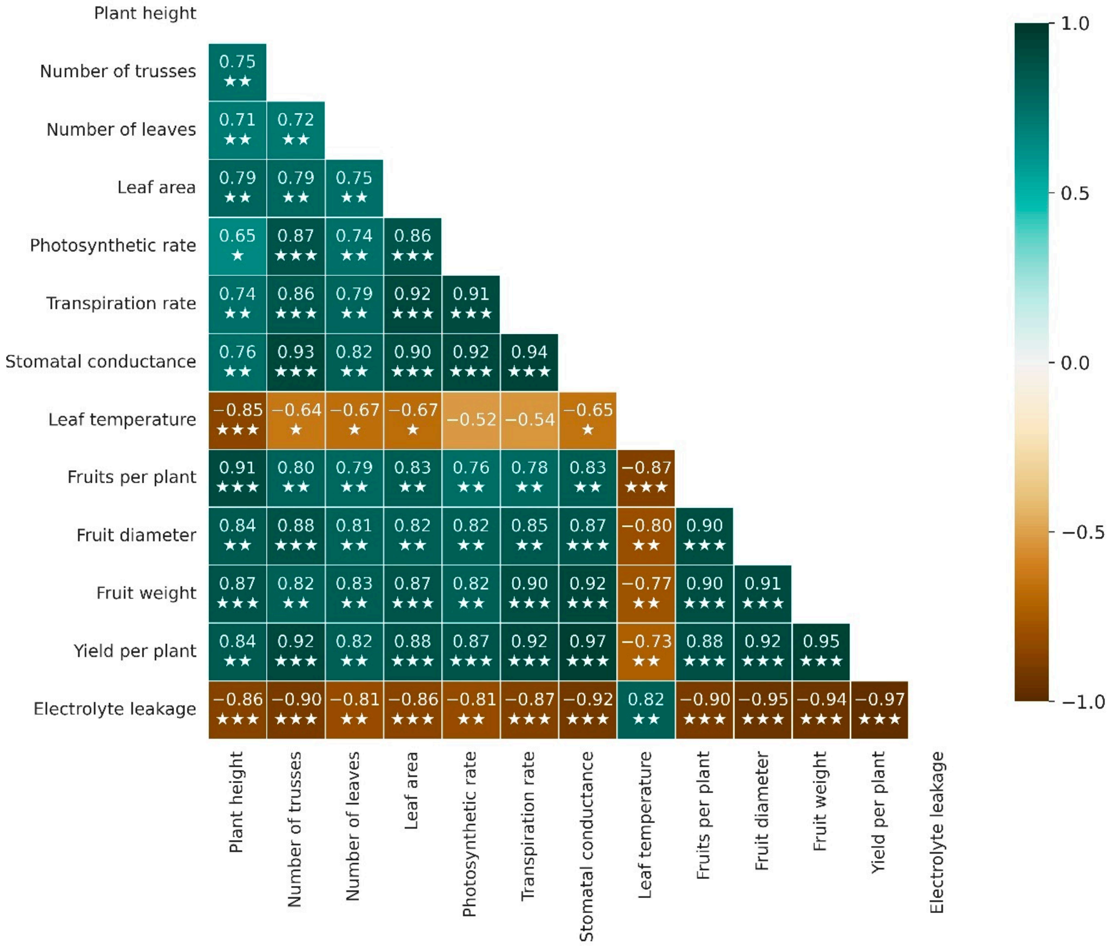

Figure 4. Correlation analysis of growth and physiological parameters. Stars show the significance level of the values. The stars represent significance level. *** for $p < 0.001$, ** for $p < 0.01$ and * for $p < 0.1$.

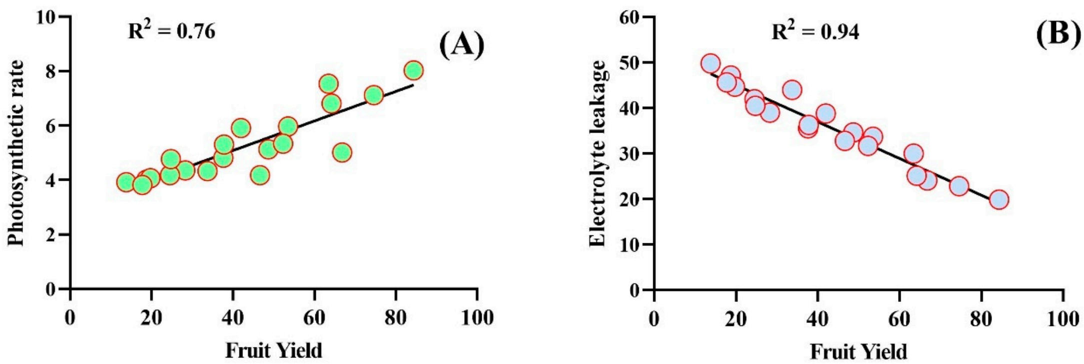

Figure 5. Regression analysis illustrates the relationship of fruit yield with photosynthetic rate using green circles (**A**), and fruit yield with electrolyte leakage using blue circles (**B**).

3. Discussion

Seed priming is indeed a powerful technique with wide-ranging benefits for plant growth and stress tolerance, especially in crops like tomatoes [24]. This method involves treating seeds with specific substances or conditions to initiate germination processes without fully germinating the seeds [25]. One of the key advantages of seed priming is its ability to enhance osmolyte accumulation within plant cells. Osmolytes such as proline, glycine betaine, and soluble sugars are like cellular superheroes, helping plants maintain water balance and structural integrity during stressful conditions like salinity [3,25]. When seeds are primed, they kickstart the production of these crucial compounds, essentially equipping plants with a built-in defense mechanism against water scarcity and osmotic stress. But that is not all—seed priming also triggers the activation of antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX) [26]. These enzymes are warriors against oxidative stress, neutralizing harmful reactive oxygen species (ROS) that can wreak havoc on plant cells, particularly in saline soils [22]. By bolstering these defense systems, primed seeds pave the way for healthier plants that can withstand environmental challenges more effectively [27]. Another fascinating aspect is how seed priming influences ion homeostasis through the modulation of ion transporters such as SOS1 and NHX. These molecular players help regulate sodium (Na^+) levels within cells, crucial for preventing salt toxicity, while also improving potassium and sodium ratio (K^+/Na^+) selectivity, which is vital for overall plant health and productivity [28]. In essence, seed priming is not just about jumpstarting germination; it is about arming plants with the tools they need to thrive in adverse conditions [29]. This approach holds immense promise for tomato production, offering a proactive solution to combat environmental stresses.

The present study was carried out to highlight the effects of seed priming with a combination of polyethylene glycol and sodium chloride on the growth and physiological attributes of Micro Tom tomato plants. In the present study, growth parameters such as plant height, number of trusses, number of leaves, leaf length, and leaf area significantly decreased with increasing salt concentration. Recently, Rahman et al. investigated the effect of NaCl-salinity on tomatoes in a pot experiment, and revealed that growth parameters such as average number of leaves per plant, average length of leaf, and average number of trusses simultaneously decreased under salt stress. Furthermore, it was revealed that the decrement in the parameters varied between species. Average number of leaves, average length of leaf, and average number of trusses showed to decrease under salt stress and a decrement of 50%, 30%, and 40%, respectively, was observed under severe salt stress [30]. Moreover, an investigation by Bacha et al. reported a significant decrease in leaf area of tomato plants after two weeks of exposure to salt stress. It was revealed that 150 mM sodium chloride treatment was severe and caused a 45% decrease in leaf area of stressed plants compared to those of the control group [31]. It has also been confirmed that salt stressed tomato plants are shorter in height compared to those of the control group [32]. The present study agrees with Rahman et al. that salinity decreases number of leaves, leaf length, and number of trusses per plant; however, the doses of salt stress were different and Micro Tom plants were shown to be sensitive to salinity treatments (50, 100, 150, and 200 mM sodium chloride), especially to 200 mM, where a difference of 70%, 75%, and 65% compared to ambient conditions was observed in number of trusses, number of leaves per plant, and leaf area. Moreover, the result of plant height agrees with Caro et al. and Rafiqu et al. and suggests that the decrement in plant fresh and dry biomass might be due to shorter plant height in stressed plants. The reason for the mentioned reduction might be the adaptive mechanism for survival, which allows plants to combat salt stress [33,34]. Salt stress might lead to decreased cell numbers in the meristem and a growth inhibition which impacts the plant's ability to absorb nutrients and water efficiently. Anyway, the present study revealed that seed priming with a combination of polyethylene glycol and sodium chloride (PEG plus NaCL) was the best treatment which could improve the resilience of tomato plants to salt stress compared to the control group. This treatment increased the plant height by 4 cm, 4.5 cm, 5 cm, 5 cm, and 4 cm in plants grown under control, 50 mM, 100 mM, 150 mM, and 200 mM salt stress, respectively. This improvement might be due to rapid growth in plants derived from primed seeds compared to the control group, which is parallel to Mirabi and Hassanabadi's result [25]. Additionally, PEG + NaCl treatment significantly increased the number of trusses per plant, number of leaves per plant, and leaf area. Pradhan et al. reported that seed priming with −0.5 MPa PEG increases tomato plant height compared to the control group and hydropriming, which varied between genotypes [35]. The present study confirms and suggest that if PEG is combined with sodium chloride for seed priming plant growth might be faster compared to PEG itself, because seed priming with sodium chloride gives a pre-sowing shock to seeds and this shock prepares the newly established seedling to tolerate salt stress. Additionally, Ali et al. [36] reported that seed priming with 150 mM NaCl and 4 °C of thermopriming had the highest leaf area among all of the treatments. In contrast, the results from the present study showed that the seed priming treatment with PEG + 200 NaCl had wider leaves compared to the control group. El-Saifi et al. reported that plants derived from primed seeds with PEG produce a greater number of leaves compared to the control group [24]. It was revealed that PEG increased the number of leaves per plant 15% compared to the control group, where the present study confirms it and adds that combining NaCl with PEG as a priming reagent creates better results. A significant increase in the number of leaves in 100 mM, 150 mM, and 200 mM NaCl salt stress was observed in plants derived from primed seeds with PEG + NaCl compared to other treatments.

Reports indicate that salt stress has a detrimental impact on yield [37]. For instance, Zhang et al. [38] demonstrated in tomato plants that salt stress significantly reduced both total yield and fruit number. The highest yields and fruit counts were achieved under control conditions, while the lowest values were recorded under severe salt stress conditions (EC = 2.0 dS m^{-1}). Although there are limited reports on the effects of seed priming on tomato fruit yield under salt stress, Cano et al. [39] noted that salt priming of seeds can increase fruit yield in tomatoes under salt stress, albeit with variations depending on the cultivar. Some tomato cultivars exhibited a roughly 20% increase in fruit yield with salt priming, while in others, the difference was less pronounced. Additionally, plants originating from salt-primed seeds tended to produce heavier fruits compared to the control group. The findings of our study corroborate those of Zhang et al. [38] and Alves et al. [40], highlighting the severe impact of salt stress on tomato fruit yield. However, contrary to Cano et al., our study did not find a significant difference in fruit yield with NaCl seed priming treatment. Nonetheless, fruits from the salt-primed treatment were heavier compared to those from the control group under 200 mM NaCl salt stress. Moreover, a significant increase in fruit yield was observed under ambient and all salinity levels in the PEG + NaCl treatment compared to the control. Specifically, this increase amounted to 25 g, 23 g, 20 g, 20 g, and 15 g under control conditions and 50 mM, 100 mM, 150 mM, and 200 mM salt stress conditions, respectively.

Physiological processes such as photosynthesis are also affected by salt stress, as discussed by Jakab et al. [41]. The authors of [42] reported that chemical seed priming improves stomatal conductance in Arabidopsis. Anwar et al. [43] investigated the benefits of seed priming to enhance growth, chlorophyll content, photosynthesis, and nutrient levels in cucumber seedlings. They found that seed priming with potassium nitrate (KNO_3 5%) significantly enhances photosynthesis attributes compared to the control. This enhancement was observed as a 40% increase in the photosynthetic rate, a 30% increase in stomatal conductance, a 25% increase in transpiration rate, and a 40% decrease in leaf surface temperature. Additionally, Jisha and Puthur [44] reported that seed priming with sodium chloride enhances photosynthetic pigments in *Vigna radiata* L. compared to the control, resulting in a higher photosynthetic rate. Limited research exists on how seed priming affects photosynthesis parameters in tomatoes under salt stress conditions, and there are no prior reports on the combined effects of PEG + NaCl. Therefore, the findings of the present study are novel. The results indicate that PEG + NaCl significantly enhances the photosynthetic rate. The highest photosynthetic rate (8.49 µmol CO_2 m^{-2} s^{-1}) was recorded in the PEG + NaCl treatment under ambient conditions, while the lowest (3.56 µmol CO_2 m^{-2} s^{-1}) was observed in the control (no priming) treatment under 200 mM NaCl salt stress conditions. This result is consistent with Anwar et al., who reported that KNO_3 induces photosynthesis. However, the current study suggests the combined use of PEG + NaCl to improve photosynthetic rate, stomatal conductance, transpiration rate, and decrease leaf surface temperature. The increase in photosynthetic rate may be attributed to stomatal regulation which avoids water loss and an increase in enzymatic antioxidants that target reactive oxygen species (ROS) and decrease cell damage, though further investigation is required. Moreover, leaf electrolyte leakage was measured to assess whether seed priming reduces cell damage and enhances the photosynthetic rate. It was found that leaf electrolyte leakage decreased in plants derived from primed seeds, and there was a significant negative correlation between photosynthetic rate and leaf electrolyte leakage (−0.81). Furthermore, regression analysis revealed a positive relationship between photosynthetic rate and fruit yield (R^2 = 0.76), while electrolyte leakage had a negative relationship with fruit yield (R^2 = −0.94). This suggests that seed priming mitigates harmful molecules (ROS), leading to lower cell wall damage (as indicated by electrolyte leakage), a higher photosynthetic rate, and ultimately higher fruit yield.

4. Materials and Methods

4.1. Experimental Design

This experiment was carried out within the controlled environment of the Greenhouse of Laboratory Horticultural Science at Tokyo University of Agriculture, located in Setagaya Campus, Tokyo, Japan. The plant material chosen for this investigation was Micro Tom (wild type) seeds. The experiment was structured as a factorial completely randomized design (CRD), encompassing five different salinity treatments and four priming treatments. Each unique combination was replicated ten times, with an individual plant considered to be one replication unit. In total, this research involved the cultivation and measurement of parameters in 200 plants. The details of greenhouse temperature and humidity are illustrated in Figure 6, which were both measured on a weekly basis for four months until harvest stage was completed.

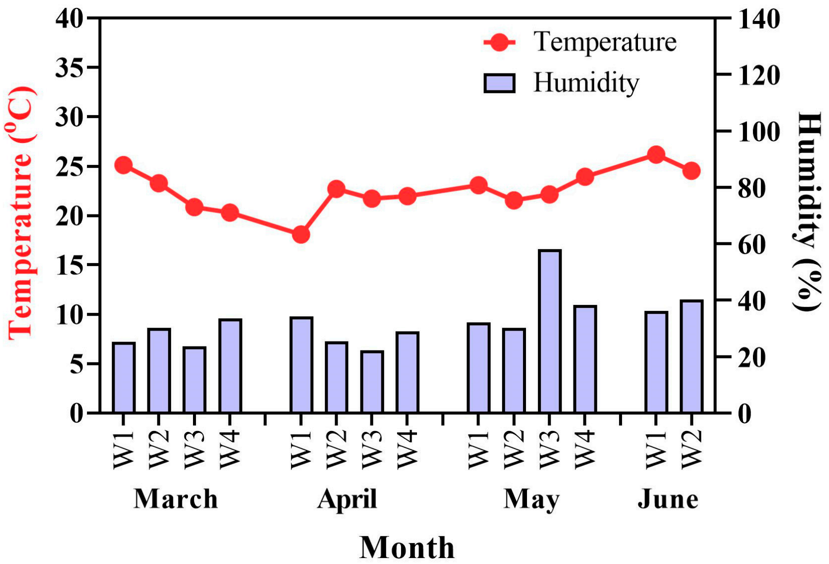

Figure 6. Average weekly temperature and humidity. Data are averaged from a daily basis dataset.

4.2. Cultivation and Application of Treatments

Polyethylene glycol (PEG6000) from Cica-Reagent in Tokyo, Japan, served as the priming agent for seeds in this study. The seeds underwent a priming process by soaking in the PEG6000 solution for a duration of 48 h. Following this period, the seeds underwent thorough drying, accomplished by washing them three times with clean water and subsequently allowing them to air-dry on a table for three hours, followed by air drying. The seeds were weighed to determine their approximate initial weight. The experiment encompassed four distinct priming treatments: control (no priming), PEG (−1.2 MPa), NaCl (200 mM), and PEG plus NaCl (−1.2 MPa plus 200 mM NaCl).

The concentrations of the seed priming reagents were determined based on previous research findings. The concentration of PEG6000 was selected according to the study by Habibi et al. [3], while for NaCl, Nakaune et al. demonstrated that a concentration of

300 mM can enhance seedling vigor and other characteristics in tomatoes [18]. However, for a combined treatment of seed priming reagents, 300 mM NaCl was a high dose. Therefore, a concentration of 200 mM NaCl was chosen as the seed priming reagent for this study. The treatment involving both PEG and NaCl was administered in a specific sequence. Initially, seeds were primed with PEG6000 for 24 h, followed by careful washing with distilled water to remove excess water from the seeds, a process that took 6 h in an open area. Subsequently, the seeds were primed with NaCl (200 mM) for an additional 24 h. This sequential priming procedure ensured the proper application of each reagent while allowing for adequate hydration and preparation of the seeds for subsequent treatments.

To ascertain the appropriate concentration of PEG6000 to be dissolved in pure water for creating the priming treatments, the researchers employed a formula outlined in the studies conducted by Garcia et al. [17] and Mechil and Kaufman [45]. This meticulous approach ensured precision in the priming process, laying the foundation for a comprehensive analysis of the ensuing experimental outcomes.

$$\mathrm{OP} = \left(-1.18 \times 10^{-2}\right) \times \mathrm{C} - \left(1.18 \times 10^{-4}\right) \times \mathrm{C} + \left(2.67 \times 10^{-4}\right) \times \mathrm{C} \times \mathrm{T} + \left(8.39 \times 10^{-7}\right) \times \mathrm{C}^2\mathrm{T} \quad (1)$$

In Equation (1), the variables are denoted as follows: OP represents osmotic pressure, T stands for temperature, and C signifies the concentration of polyethylene glycol (PEG).

To induce salinity stress, sodium chloride was employed in this study across five distinct concentrations: control (0 mM), 50 mM, 100 mM, 150 mM, and 200 mM. The experimental design encompasses a two-dimensional approach, considering both salinity stress and various priming treatments. The combination of these factors results in a total of 20 treatments, as detailed in Table 2. This comprehensive set of treatments allows for a thorough exploration of the interplay between salinity and priming effects on the experimental parameters.

Table 2. Combination of salinity and seed pre-sowing priming treatments.

Salt Stress Treatments	Priming Treatments	Amount
0 mM	Control	0 MPa
0 mM	PEG	−1.2 MPa
0 mM	NaCl	200 mM
0 mM	PEG + NaCl	−1.2 MPa plus 200 mM
50 mM	Control	0 MPa
50 mM	PEG	−1.2 MPa
50 mM	NaCl	200 mM
50 mM	PEG + NaCl	−1.2 MPa plus 200 mM
100 mM	Control	0 MPa
100 mM	PEG	−1.2 MPa
100 mM	NaCl	200 mM
100 mM	PEG + NaCl	−1.2 MPa plus 200 mM
150 mM	Control	0 MPa
150 mM	PEG	−1.2 MPa
150 mM	NaCl	200 mM
150 mM	PEG + NaCl	−1.2 MPa plus 200 mM
200 mM	Control	0 MPa
200 mM	PEG	−1.2 MPa
200 mM	NaCl	200 mM
200 mM	PEG + NaCl	−1.2 MPa plus 200 mM

The cultivation process commenced with the initial sowing of seeds in seed trays. After a month, when the seedlings reached an appropriate stage, meticulous transplantation into rockwool cubes took place. Salinity was introduced into the irrigation water during this transplantation phase, precisely when the seedlings attained the 3–4 leaf stage. These salinity treatments were consistently maintained throughout the entire growth cycle of the plants, extending up to the fruit harvest stage. The irrigation water, drawn from the tap, underwent pH adjustment to fall within the range of 5.8–6, achieved through a judicious combination of sodium hydroxide and hydrochloric acid. The pH adjustment was performed at the onset of each growth stage and the water solution was retained for subsequent irrigation times. To achieve the targeted salinity levels, sodium chloride (NaCl) was thoughtfully integrated into the irrigation water. An essential practice involved the preparation of fresh irrigation water for each cycle, mitigating potential salt concentration issues. This approach guaranteed that each set of plants within every treatment group received individualized and meticulously regulated irrigation, ensuring optimal conditions for their growth and development.

4.3. Growth Parameters

Among the growth parameters, plant height was assessed upon harvest using a standard ruler. The count of leaves, on the other hand, was undertaken three times throughout the plant's growth cycle: initially during the early growth stage, followed by a second count during flowering, and a final count during the fruit-bearing stage. The average of these three counts was then computed to represent the number of leaves per plant accurately. The measurement of leaf area involved a meticulous process. The leaves were scanned using a digital scanner, creating high-resolution digital images. Subsequently, ImageJ software v.154g "https://wsr.imagej.net/notes.html (accessed on 3 October 2022)" was employed to process these scanned images and accurately calculate the leaf area, ensuring precision in the evaluation of this growth parameter.

4.4. Photosynthetic Traits

To evaluate various photosynthetic indices, including the net photosynthetic rate (Pn), transpiration rate (E), and stomatal conductance (gs), measurements were conducted on the upper, middle, and lower fully expanded leaves. This assessment utilized a Portable Photosynthesis Measuring System, specifically the LCi-SD model manufactured by ADC Bioscientific in Hoddesdon, UK. The measurements were taken between 10:00 a.m. and 1:00 p.m. to ensure a consistent time frame. Throughout the measurement process, a constant light intensity of 1500 m^{-2} s^{-1} was maintained, the humidity level was set at 20%, and the temperature within the leaf chamber was regulated at 30 °C. To ensure comprehensive data collection, three leaves from each pot underwent a thorough examination. This rigorous approach guarantees a robust dataset for analyzing the photosynthetic performance of the plants under these controlled conditions.

4.5. Fruit Yield Attributes

Quantifying the number of fruits per plant involved counting from a sample of ten plants, and the resulting count was then averaged. To determine fruit diameter, we employed a caliper, measuring three fruits from each of ten different plants and calculating an average for this parameter. The weight of individual fruits was measured from a selection of ten different plants, with three fruits sampled from each plant, utilizing a digital balance. Subsequently, the yield per plant was computed by multiplying the number of fruits per plant by the weight of each fruit. This meticulous and comprehensive approach allowed for the precise and detailed collection of data concerning various attributes of tomato fruit yield.

4.6. Determination of Electrolyte Leakage

Electrolyte leakage, indicative of leaf damage, was assessed by determining the number of electrons leaking from the leaves [46]. In each treatment, ten random leaves were selected for measuring electrolyte leakage, treating each leaf as a replication. Leaf cuttings, made using a 1 cm diameter stainless steel cork-borer, were stored in pure water in 2 mL tubes under room temperature (25 ± 1 °C) for half an hour. The electric conductivity (EC) of these leaf cuttings was measured using an electrical conductivity meter (LAQUATWIN-S070, Horiba Scientific Ltd., Kyoto, Japan). This methodological approach ensures consistent and reliable assessment of electrolyte leakage, contributing to a comprehensive understanding of leaf health in response to various treatments.

4.7. Statistical Analysis

The data underwent analysis using ANOVA with the statistical software R 3.6.2. For visualizing the examined parameters, Python was employed. To discern treatment means at a 5% significance level, Tukey's test was applied. This meticulous statistical analysis provided a comprehensive evaluation of the dataset, enabling the differentiation of treatment effects with a high degree of confidence. This rigorous approach enhances the reliability of the study's findings and strengthens the overall validity of the statistical inferences drawn from the data.

5. Conclusions

The study reveals the significant benefits of seed priming, particularly with a combination of polyethylene glycol and sodium chloride, in mitigating the adverse effects of salt stress on tomato plants. This technique positively influences growth parameters, photosynthetic traits, fruit yield, and electrolyte leakage, particularly under severe salt stress conditions. Overall, seed priming emerges as a promising strategy to enhance tomato plant resilience in saline environments. This finding underscores the potential of innovative techniques like seed priming to optimize crop cultivation amidst global challenges such as climate change. By offering valuable insights, the study paves the way for further research and application of seed priming methods in diverse agricultural contexts to address salinity stress and improve crop productivity.

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