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USE OF TREHALOSE TO ALLEVIATE SALINITY STRESS IN RICE AT THE REPRODUCTIVE STAGE

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ABSTRACT

Salinity affects the growth of rice at all growth stages and can reduce productivity around the world, while the use of phytoprotectants is used to alleviate salt stress in plants. The study aims to determine the effects of the use of exogenous trehalose on a variety of characteristics of three lowland rice cultivars, namely IN35, CNT1 and PT1, under salt stress. **Research Method:** Salinity was simulated by using sodium chloride (NaCl) and added to the rice from seedling to harvest stage. The effects of trehalose at four concentrations on rice under salt stress were evaluated by determining some physical and biochemical properties at the reproductive stage and agronomic traits at the harvest stage. The effects of trehalose supplementation in rice were observed only when chlorophyll (Chl) A was increased above 100 mM trehalose. Exogenous trehalose promoted increase in percentage of filled grains per panicle and grain yield per plant from 50 mM trehalose and harvest index from 100 mM trehalose. There were effects of variety on almost all characteristics, including relative water content (RWC), Chl A, Chl B, total Chl, proline content, soluble sugar and starch content in leaves, with IN35 having higher values than CNT1 and PT1. In addition, IN35 had higher values than CNT1 and PT1 for 6 out of 8 agronomic characteristics. The study is one of the few studies to report on the effect of appropriate concentrations of exogenous phytoprotactants on the growth of rice in the reproductive phase under saline conditions.

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INTRODUCTION

Food security is crucial for people all over the world. It is not just about having enough to eat, but also about getting good quality food. Paradoxically, the growing world population, estimated at 8.51 billion in 2030 and 9.69 billion in 2050 (United Nations Department of Economic and Social Affairs, Population Division, 2022), has led to a higher demand for food. For this reason, agricultural production will be accelerated to meet the enormous demand for food. Therefore, there is a high probability that inappropriate input will be used for agricultural production, e.g. the use of pesticides, herbicides and excessive use of inorganic fertilizers, etc. taking into account the negative impact on both the high costs and the health of farmers, consumers and the environment. Another obstacle to agricultural production today and in the future is the problem of climate change, which leads to an environment unsuitable for agriculture, both through the increase in problems caused by abiotic factors such as drought, saline soils, acidic soils, heat, etc., and biotic factors such as the appearance of many species and severe outbreaks of insects

and diseases, etc. (Cui *et al*., 2022). In crop production, the challenge for researchers is therefore to find a way to produce crops safely and cost-effectively with high productivity, i.e. to adapt cultivation accordingly and to find effective biological and chemical substances that can be used for crop cultivation in appropriate quantities and over an appropriate period of time. In terms of rice production, Thailand, with an export value of USD 4 billion (13.5 % of global export value) in 2022, will be one of the five largest rice exporting countries, alongside India (USD 10.8 billion, 36.8 %), followed by Vietnam (USD 2.5 billion, 8.6 %) and Pakistan (USD 2.4 billion, 8.0 %) and the United States (USD 1.7 billion, 5.8 %) (Workman, 2022). However, Thai rice production is influenced by both biotic and abiotic factors. Among the abiotic factors, drought and salinity are two major constraints today, both in coastal areas and other agricultural areas. Salinity starts above 4 dS m^{-1} and is caused by many factors such as climate change, irrigation and extreme fertilizer use (Chen *et al*., 2022). Rice (*Oryza sativa* L.) is a plant species that is sensitive to salinity at many growth stages, with the most sensitive stage being found in the seedlings and reproductive stage (Singh *et al*., 2021). Nevertheless, there is relatively little research on mitigating salt damage in rice plants at the reproductive stage compared to the seedling stage. Finding an alternative method to help rice plants survive under salt stress during the reproductive phase is therefore of interest to farmers as it is safe for the consumer and has less or no impact on the environment. Among the substances of interest for reducing salt stress in rice cultivation, trehalose, an osmoprotective and stabilizing molecule in plants, plays a role in protecting plants from unfavorable conditions that are not conducive to plant growth (Yang *et al*., 2022 a). However, the optimal use of this substance in rice during the reproductive phase, when it is confronted with salt stress, is still limited. For this reason, the objective of this study was to use trehalose to mitigate the effects of salinity during the reproductive phase in rice cultivation by evaluating some physical, biochemical and agronomic properties.

MATERIALS AND METHODS

Plant Material, Soil Properties and Study Site: Three non-photosensitive lowland rice varieties were used in this study, including two Thai varieties: Chai Nat 1 (CNT1) and Pathum Thani 1 (PT1), and varieties from Indonesia, such as Inpari 35 (IN35). PT1 and CNT1 are salt-sensitive varieties, while IN35 is a salt-tolerant variety. A sandy loam soil consisting of 70.97% sand, 20.43% silt, 8.60% clay and 0.93% organic matter was used for this study. The chemical properties of the soil included 5.18 mg kg^{-1} phosphorus (P), 83.09 mg kg^{-1} potassium (K), 88.31 mg kg^{-1} calcium (Ca) and 69.98 mg kg^{-1} magnesium (Mg). The physical properties of the soil included a pH of 6.39, an electrical conductivity of the saturated soil extract of 0.92 dS m^{-1} and a sodium adsorption ratio of 0.22. The study was conducted in an open field at the Faculty of Animal Sciences and Agricultural Technology, Silpakorn University, IT campus, Phetchaburi, Thailand. The location of the pot trial was 12.65245 north latitude and 99.88186 east longitude. The trial area has a tropical climate and is characterized by high temperatures and low rainfall during the study months of January to May 2020.

Simulating Salty levels, Trehalose Levels and Experimental Practices: Prepare the soil for salinity by using sodium chloride (NaCl) in four salinity levels (concentrations) as 0 mM (0 dS m^{-1}), 50 mM (5 dS m^{-1}), 100 mM (10 dS m-1) and 150 mM (15 dS m^{-1}), respectively. Four concentrations of exogenous trehalose were used in this study, namely 0 mM, 50 mM, 100 mM and 150 mM. Five seedlings were planted in a plastic pot 30 cm high × 30 cm in diameter containing the soil. After planting the seedlings, saline conditions were provided for the rice until harvest. Water management included providing normal water every two days and 150 ml of saline water once a week until harvest. When exogenous trehalose was used, one hundred milliliters of this solution were sprayed on the plants (in each pot) only once a week, depending on the treatment (at the heading stage; R3, partly panicle exserted) before flowering (at the anthesis stage; R4).

Physical and Biochemical Properties Determination: After a five-day application of trehalose, plant samples were taken to analyse the physical and biochemical properties. These properties, including relative water content (RWC) and chlorophyll content (Chl A, Chl B and total Chl) (Khaleghi *et al*., 2012), proline content (Bates et al., 1973), soluble sugar and starch content (Chow and Landhäuse, 2004), were determined in both leaves and stems. For agronomic characteristics, including plant height (PH), number of productive tillers per plant (PTP), panicle length (PL), percent of filled grains per panicle (FGP), 1000-grain weight (1000 GW), straw dry weight (SDW), harvest index (HI) and grain yield per plant (GYP), were evaluated at harvest stage.

The RWC was calculated using the following formula:

$$RWC(\%) = \frac{(Fresh\ weight - Dry\ weight)}{Turgid\ weight - Dry\ weight} x\ 100$$

HI was calculated using two values such as the GYP and the biological yield per plant, the sum of GYP and SDW, according to the following formula:

$$Harvest\ index = \frac{Grain\ yield\ per\ plant}{Biological\ yield\ per\ plant}$$

Experimental Design and Data Analysis: The 4 × 4 × 3 factorial completely randomized design with three replications was used in this study. Three factors were the four concentrations of NaCl to stimulate soil salinity, four trehalose concentrations, and three lowland rice varieties. One pot with five plants was designed in each replication. Analysis of variance (ANOVA) was used to analyses the data. Differences were considered significant at a probability level of <0.05 and the treatments were then compared using Duncan's new multiple range test. All traits were analyzed using the agricolae package in the R program, version 4.0.2 (R Core Team, 2020).

RESULTS AND DISCUSSION

Effects of Salinity, Trehalose and Variety on RWC: In this study, the RWC was only influenced significantly differently by one factor, the variety. The highest RWC value was observed in PT1 (93.37 %), followed by CNT1 (76.91 %) and IN35 (73.83 %). However, the interaction of variety × salinity was significantly different only for the interaction of these factors. A lower change in RWC, compared to 0 mM NaCl, was observed for PT1 (0-0.32 %) and IN35 (1.65-3.58 %) when plants were grown at soil salinity of 50-150 mM, and a higher negative change for CNT1 (-4.12 to -12.93 %) (Table 01). Salinity can trigger oxidative and osmotic stress in plants, causing both physiological and biochemical changes in many characteristics. The osmotic stress induced by salinity could be reflected in plants by measuring relative water potential and stomatal conductance (Arif *et al*., 2020). The result of the differences between the rice varieties in terms of RWC and the changes related to salinity is the consequence of the different genetics of the varieties. The change in RWC from low to high values, but taking into account the direction of change, indicates the different ability of the rice varieties to retain water for plant metabolism under salt stress. Rice is considered a salt-sensitive crop, but there are questions about the degree of sensitivity between different growth stages. The result of RWC in this study is a criterion to confirm the effects of salinity at the reproductive stage, which is very important because this stage determines grain yield. It has been reported that the reproductive stage (panicle initiation to flowering and fertilization) in RWC is more sensitive to salinity than the germination, active tillage and maturation stages (Sajid *et al*., 2017; Singh *et al*., 2021). Table 1: Mean and ANOVA data for relative water content (RWC) (%) at flowering stage in lowland rice varieties: Chai Nat 1 (CNT1), Pathum Thani 1 (PT1),and Inpari 35 (IN35) when plants were watered with different sodium chloride (NaCl) andtrehalose concentrations.

Effects of Salinity, Trehalose and Variety on Chl Contents: Chlorophyll (Chl) contents (e.g. Chl A, Chl B and total Chl) were significantly affected by the varieties. Trehalose only had a significant effect on Chl A. In the variety × salinity interaction, there was only one interaction between these factors, which showed a significant difference in Chl B and total Chl (Table 2). A higher Chl A content was observed in two rice varieties, namely IN35 (0.32 mg g^{-1}) and PT1 (0.31 mg g^{-1}), followed by CNT1 (0.27 mg g^{-1}). When trehalose was applied, a significant increase in Chl A content was observed at 100-150 mM trehalose, which was higher than that at 0 mM trehalose, which ranged from 7.14-14.29 % (Table 2 a). PT1 and IN35 also had a higher Chl B content of 3.26 mg g^{-1} and 3.35 mg g^{-1}, respectively, followed by CNT1 with 2.80 mg g^{-1}. The interaction between variety and salinity showed a continuous decrease in Chl B content with increasing salinity only for IN35 (-3.33 to -15 %), while lower value changes were observed for CNT1 (0-14.07 %) and PT1 (-5.78 to 2.74 %). Nevertheless, both IN35 and PT1 showed a higher Chl B content compared to CNT1 at all salinity levels (Table 2 b). The results of the study were consistent, both in the ranking of variety values and in the magnitude and direction of change between Chl B and total Chl (Table 2 b-c). A higher total Chl value was observed in PT1 (3.57 mg g^{-1}) and IN35 (3.67 mg g^{-1}), followed by CNT1 (3.08 mg g^{-1}). In addition, a greater decrease in the continuous value was observed in IN35 with increasing salinity (-3.81 to -14.72 %). Smaller changes in total Chl were observed in CNT1 (1.01–13.85 %) and PT1 (-5.29 to 2.51 %).

Table 1. Mean and ANOVA data for relative water content (RWC) (%) at flowering stage in lowland rice varieties: Chai Nat 1 (CNT1), Pathum Thani 1 (PT1),and Inpari 35 (IN35) when plants were watered with different sodium chloride (NaCl) andtrehalose concentrations

	Relative water content (RWC) (%) (% over control; 0 mM NaCl)				
Varieties	Salinity (NaCl) (mM)				
	0	50	100	150	Mean
CNT1	82.0 b	77.8 bc (-4.12 %)	71.4 e (-12.93 %)	76.5 cd (-6.71 %)	76.91 B
PT1	93.3 a	93.3 a (0 %)	93.2 a (0.10 %)	93.6 a (0.32 %)	93.37 A
IN35	72.6 de	73.8 dce (1.65 %)	73.8 cde (1.65 %)	75.2 cde (3.58 %)	73.83 C
Mean	82.63	81.61 (-1.23 %)	79.50 (-3.79 %)	81.75 (-1.06 %)	

Variety (V) = 2×10^{-16}**, Salinity (S) = 0.0974 NS, Trehalose (T) = 0.9755 NS, V × S = 0.0096**, V × T = 0.3080 N, S × T = 0.4805 NS, V× S × T = 0.3395 NS; *Note: ** = significant difference at 0.01 level of probability, NS = non-significant difference at 0.05 levels of probability, different letters (A, B, C or a, b, c) mean a significant difference at the 0.05 probability level.*

Table 2. Mean and ANOVA data for chlorophyll a (Chl A), chlorophyll b (Chl B) and total chlorophyll (total Chl) at flowering stage in lowland rice varieties: Chai Nat 1 (CNT1), Pathum Thani 1 (PT1),and Inpari 35 (IN35) when plants were watered with different sodium chloride (NaCl) and trehalose concentrations.

(a)

	Chlorophyll A (mg g^{-1}) (% over control; 0 mM trehalose)			
		Trehalose (mM)		
	0	50	100	150
Mean	0.28 b	0.29 b (3.57%)	0.32 a (14.29%)	0.30 ab (7.14%)
Varieties	CNT1 = 0.27 B	PT1 = 0.31 A	IN35 = 0.32 A	

Variety (V) = 0.0007**, Salinity (S) = 0.4609 NS, Trehalose (T) = 0.0257*, V × S = 0.7113 NS, V × T = 0.2648 NS, S × T = 0.2829 NS, V× S × T = 0.6054 NS; *Note: ** = significant difference at 0.01 and * = significant difference at 0.05 level of probability, NS = non-significant difference at 0.05 levels of probability, different letters (A, B, C or a, b, c) mean a significant difference at the 0.05 probability level.*

(b)

	Chlorophyll B (mg g^{-1}) (% over control; 0 mM NaCl)				
Varieties	Salinity (NaCl) (mM)				
	0	50	100	150	Mean
CNT1	2.70 c	2.74 c (1.48 %)	3.08 bc (14.07 %)	2.70 c (0 %)	2.80 B
PT1	3.29 ab	3.10 bc (-5.78 %)	3.27 ab (-0.61 %)	3.38 ab (2.74 %)	3.26 A
IN35	3.60 a	3.48 ab (-3.33 %)	3.29 ab (-8.61 %)	3.06 bc (-15.0%)	3.35 A
Mean	3.20	3.11 (-2.81 %)	3.21 (0.31 %)	3.05 (-4.69 %)	

Variety (V) = 7×10^{-8}**, Salinity (S) = 0.3888 NS, Trehalose (T) = 0.5239 NS, V × S = 0.0324, V × T = 0.0770 NS, S × T = 0.0698 NS, V× S × T = 0.6663 NS; *Note: ** = significant difference at 0.01 and * = significant difference at 0.05 level of probability, NS = non-significant difference at 0.05 levels of probability, different letters (A, B, C or a, b, c) mean a significant difference at the 0.05 probability level.*

(c)

	Total Chlorophyll (mg g^{-1}) (% over control; 0 mM NaCl)				
Varieties	Salinity (NaCl) (mM)				
	0	50	100	150	Mean
CNT1	2.96 c	3.00 c (1.35 %)	3.37 bc (13.85 %)	2.99 c (1.01 %)	3.08 B
PT1	3.59 ab	3.40 bc (-5.29 %)	3.59 ab (0 %)	3.68 ab (2.51 %)	3.57 A
IN35	3.94 a	3.79 ab (-3.81 %)	3.60 ab (-8.63 %)	3.36 bc (-14.72 %)	3.67 A
Mean	3.50	3.39 (-3.14 %)	3.52 (0.57 %)	3.34 (-4.57 %)	

Variety (V) = 5.53×10^{-8}**, Salinity (S) = 0.3853 NS, Trehalose (T) = 0.3926 NS, V × S = 0.0402*, V × T = 0.0827 NS, S × T = 0.0578 NS, V× S × T = 0.6185 NS ; *Note: ** = significant difference at 0.01 and * = significant difference at 0.05 level of probability, NS = non-significant difference at 0.05 levels of probability, different letters (A, B, C or a, b, c) mean a significant difference at the 0.05 probability level.*

In addition, IN35 and PT1 showed higher Chl B content than CNT1 at all salinity levels (Table 2 c). Table 2: Mean and ANOVA data for chlorophyll a (Chl A), chlorophyll b (Chl B) and total chlorophyll (total Chl) at flowering stage in lowland rice varieties: Chai Nat 1 (CNT1), Pathum Thani 1 (PT1),and Inpari 35 (IN35) when plants were watered with different sodium chloride (NaCl) and trehalose concentrations. The clear result was that the variety had a major influence on the accumulation of Chl content (Chl A, Chl B and total Chl), which was higher in IN35 and PT1 and lower in CNT1. Thus, the response to increasing salinity depends on genetics, as shown by the interaction of variety × salinity for Chl B and total Chl (Table 02 a-c). Although the percentage decrease in Chl content was higher in IN35 compared to CNT1 and PT1 with increasing salinity, higher Chl content was observed in IN35 at all salinity levels. These results will be considered along with other characteristics in this study before clarifying the resistance of IN35 to salinity. Similarly, the higher values with lower changes in Chl content of PT1 compared to CNT1 should be evaluated together with other characteristics to compare the resistance of the two Thai rice varieties to salinity. The influence of rice varieties on the differences in chlorophyll A, chlorophyll B and total chlorophyll was also reported by Ali *et al*. (2004). Although salinity had no significant effect on Chl A, Chl B and total Chl. However, Chl B and total Chl were affected by salinity via a variety-salinity interaction with negative changes observed in two out of three varieties (PT1 and IN35) when plants received salinity (Table 02). Therefore, it can be said that salinity still has a negative effect on phytosynthetic capacity, as Chl B plays a key role in the light-harvesting complexes in photosystem I and II in the photosynthetic process of plants (Tanaka and Tanaka, 2011; Yahia *et al*., 2019). However, it was found that not only the chlorophyll content, but also the size of the chlorophyll is influenced by salt stress (Ali *et al*., 2004). The highest percentage reduction of Chl B and total Chl (-15% and -14.72% at 150 mM NaCl) was observed at IN35, where the percentage reduction increased with increasing salinity after the rice had been grown under saline conditions for 30 days. The reduction in Chl content (Chl A, Chl B and total Chl) under salt stress in this study was less than the 32.89%, 18.44% and 24.04% reduction in Chl A, Chl B and total Chl reported by Ali *et al*. (2004) in rice grown for 90 days (after planting) at a salinity of 8.5 dS m^{-1}. Therefore, shorter or longer salt stress could not only lead to a different reduction in

Table 3: Mean and ANOVA data for proline contents in leaves and stems at flowering stage in lowland rice varieties: Chai Nat 1 (CNT1), Pathum Thani 1 (PT1),and Inpari 35 (IN35) when plants were watered with different sodium chloride (NaCl) and trehalose concentrations

(a)

	Proline contents (µmole g^{-1}) Varieties		
	CNT1	PT1	IN35
Leaves	1.56 b	1.66 b	2.01 a
Stems	0.82 B	1.22 A	1.11 A

(b)

	Proline contents (µmole g^{-1}) (% over control; 0 mM NaCl)			
	Salinity (NaCl) (mM)			
	0	50	100	150
Leaves	1.81	1.77 (-2.21 %)	1.64 (-9.39 %)	1.75 (-3.32 %)
Stem	1.26 a	0.98 b (-22.22%)	0.91 b (-27.78%)	1.05 ab (-16.67%)

Leave, Variety (V) = 0.0001**, Salinity (S) = 0.6007 NS, Trehalose (T) = 0.0611 NS, V × S = 0.1242 NS, V × T = 0.4257 NS, S × T = 0.8003 NS, V× S × T = 0.4852 NSStem, Variety (V) = 8.8 × 10^{-5}**, Salinity (S) = 0.0094**, Trehalose (T) = 0.3916 NS, V × S = 0.2683 NS, V × T = 0.9875 NS, S × T = 0.65 40 NS, V× S × T = 0.9993; *Note: ** = significant difference at 0.01 level of probability, NS = non-significant difference at p = 0.05, different letters (A, B or a, b) mean a significant difference in the same row at the 0.05 probability level.*

Table 4: Mean and ANOVA data for sugar contents in leaves and stems at flowering stage in lowland rice varieties: Chai Nat 1 (CNT1), Pathum Thani 1 (PT1),and Inpari 35 (IN35) when plants were watered with different sodium chloride (NaCl) and trehalose concentrations

	Sugar contents (mg g^{-1}) Varieties		
	CNT1	PT1	IN35
Leaves	61.46 a	58.61 ab	54.72 b
Stems	86.14 A	77.54 B	59.34 C

Leave, Variety (V) = 0.0056**, Salinity (S) = 0.7431 NS, Trehalose (T) = 0.3050 NS, V × S = 0.5836 NS, V × T = 0.5035 NS, S × T = 0.6414 NS, V× S × T = 0.2475, Stem, Variety (V) = 4.16 × 10^{-10}**, Salinity (S) = 0.1993 NS, Trehalose (T) = 0.0967 NS, V × S = 0.7393 NS, V × T = 0.7512 NS, S × T = 0.8566 NS, V× S × T = 0.8776; *Note: ** = significant difference at 0.01 level of probability, different letters (A, B, C or a, b) mean a significant difference in the same row at the 0.05 probability level.*

Table 5: Mean and ANOVA data for starch contents in leave and stem at flowering stage in lowland rice varieties: Chai Nat 1 (CNT1), Pathum Thani 1 (PT1),and Inpari 35 (IN35) when plants were watered with different sodium chloride (NaCl) and prolilne concentrations

	Sugar contents (mg g^{-1}) Varieties		
	CNT1	PT1	IN35
Leaves	10.01	10.92	11.00
Stems	55.24 b	59.88 ab	64.61 a

Leaves, Variety (V) = 0.475 NS, Salinity (S) = 0.810 NS, Trehalose (T) = 0.636 NS, V × S = 0.611 NS, V × T = 0.075 NS, S × T = 0.541 NS, V× S × T = 0.915 NS, Stem, Variety (V) = 0.0056 **, Salinity (S) = 0.0818 NS, Trehalose (T) = 0.6883 NS, V × S = 0.6908 NS, V × T = 0.8311 NS, S × T = 0.3142 NS, V× S × T = 0.9827 NS *Note: ** = significant difference at 0.01 level of probability, NS = non-significant difference at 0.05 levels of probability, different letters (a, b) mean a significant difference at the 0.05 probability level*

chlorophyll content in different rice varieties. In addition, different growth stages showed different sensitivity to plant chlorophyll content, with the flowering stage reported to be less sensitive to salt stress than other growth stages such as the seedling, tillering and panicle stages (Ali *et al*., 2004; Djanaguiraman and Ramadass, 2004). Although the use of trehalose could support the increase of Chl content only in Chl A, at higher concentrations (100-150 mM trehalose) (Table 2 a), Chl A plays an important role in the reaction centre associated with the photochemical process in the photosynthetic process of plants (Tanaka and Tanaka, 2011; Yahia *et al*., 2019). Therefore, the application of exogenous trehalose could promote the photosynthetic ability of plants. Exogenous trehalose has been reported to reduce chlorophyll damage and excess energy, improve the distribution of excess absorbed energy due to stress, increase the content of osmotic substances and promote trehlose metabolism to promote osmoprotective and stabilising molecules in plants (Yang *et al*., 2022 b).

Effects of Salinity, Trehalose and Variety on Proline Content: The proline content was not significantly affected by the application of exogenous trehalose and the interaction between the factor trehalose, salinity and variety (Table 3). However, proline content differed significantly between rice varieties, with IN35 having a higher proline content in leaves and stems than PT1 and CNT1. Proline appears to accumulate more in the leaves than in the stems. However, the proline content was only significantly reduced in the stems from 50 mM NaCl, the reduction in content at 50-150 mM NaCl was between -16.67% and -27.78% (Table 3). It was observed that proline as an osmotic protective substance in the plants increased when the plants were confronted with salinity. However, the different levels of proline accumulation under salt stress can be explained by the days within 3-10 days after stimulation by salt stress (Hakim *et al*., 2014; Nguyen *et al*., 2021). However, in this study, proline accumulation in the plant tissues was only analysed 30 days after salt stimulation. For this reason, the difference in proline accumulation in the leaves, the main plant tissues where the photosynthetic process takes place, was not recognised. Therefore, the change in proline accumulation under salt stress could be short-lived. The higher accumulation of proline content in the leaves than in the stems explains the energy requirements in the different plant tissues and the transport and utilisation mechanisms in these tissues (Liang *et al*., 2013). Trehalose is a non-reducing sugar and plays a role as an osmoprotectant that can mitigate abiotic stress, such as salinity. The role of exogenous trehalose application is associated with the accumulation of many osmolytes, including proline and soluble sugars, and the regulation of stress response genes (Hassan *et al*., 2023). Proline accumulation was not altered by the exogenous supply of trehalose in this study; however, the reduction in proline accumulation influenced by salinity was only observed in the stem but not in the leaves (Table 3). This could be due to the fact that trehalose was sprayed directly onto the leaves, which could keep proline accumulation in the leaf constant under salt stress. Furthermore, the higher proline accumulation in the

Table 6. Mean and ANOVA data for eight agronomic characteristics in lowland rice varieties, namely, Chai Nat 1 (CNT1), Pathum Thani 1 (PT1) and Inpari 35 (IN35), when plants were watered with different sodium chloride (NaCl) concentrations and sprayed with varying concentrations of trehalose at reproductive stage

Factors	PH (cm)	PTP	PL (cm)	FGP (%)	1000 GW (g)	SDW (g)	HI (%)	GYP (g)
Variety								
CNT1	93.2 X	8.0 Z	23.9 X	55.5 Y	25.3 Y	12.26 Z	36.54 Y	7.3 Y
PT1	92.1 Y	8.5 Y	23.9 X	48.3 Z	24.7 Z	14.05 Y	29.31 Z	6.2 Z
IN35	90.7 Y	9.8 X	21.6 Y	68.4 X	25.7 X	15.03 X	40.48 X	10.2 X
Salinity (NaCl)								
0 mM	95.3 a	10.4 a	23.5 a	74.2 a	25.4 a	17.36 a	38.06 a	10.6 a
50 mM	92.8 b (-2.62%)	8.8 b (-15.38%)	23.2 ab (-1.28%)	61.5 b (-17.12%)	25.3 b (-0.39%)	14.51 b (-16.42%)	37.97 a (-2.36%)	8.9 b (-16.04%)
100 mM	90.8 b (-4.72%)	8.2 c (-21.15%)	23.1 b (-1.70%)	52.2 c (-29.65%)	25.2 b (-0.78%)	12.41 c (-28.51%)	35.17 b (-7.59%)	6.9 c (-34.91%)
150 mM	88.1 c (-7.56%)	7.6 d (-26.92%)	22.8 b (-2.98%)	41.7 d (-43.80%)	25.1 c (-1.18%)	10.85 d (-37.50%)	30.58 c (-19.65%)	5.1 d (-51.89%)
Trehalose								
0 mM	91.4	8.8	22.9	55.6 C	25.2	13.62	34.64 B	7.6 C
50 mM	92.2 (+0.88%)	8.8 (0%)	23.1 (+0.87%)	56.7 B (+1.98%)	25.2 (0%)	13.95 (+2.42%)	34.94 B (+0.87%)	7.9 B (+3.95%)
100 mM	92.3 (+0.98%)	8.8 (0%)	23.2 (+1.31%)	58.2 A (+4.68%)	25.2 (0%)	13.71 (+0.66%)	35.80 AB (+3.35%)	8.0 B (+5.26%)
150 mM	92.1 (+0.77%)	8.6 (-2.27%)	23.4 (+2.18%)	59.1 A (+6.29%)	25.3 (+0.40%)	13.84 (+1.62%)	36.39 A (+5.05%)	8.2 A (+7.89%)
F-test								
Variety (V)	**	**	**	**	**	**	**	**
Salinity (S)	**	**	*	**	**	**	**	**
Trehalose (T)	NS	NS	NS	**	NS	NS	*	**
V × S	NS	**	NS	**	NS	**	**	**
V × T	NS	NS	NS	NS	NS	NS	NS	NS
S × T	NS	NS	NS	NS	NS	NS	NS	NS
V × S × T	NS	NS	NS	NS	NS	NS	NS	NS

*Note: PH = plant height, PTP = no. productive tillers per plant, 1000 GW = 1000 grains weight, FGP = percent of filled grains per panicle, SDW = straw dry weight, HI = harvest index, GYP = grain yield per plant, ** = significant difference at 0.01 and * = significant difference at 0.05 level of probability, NS = non-significant difference at 0.05 levels of probability, different letters (X, Y, Z or a, b, c or A, B, C) mean a significant difference at the 0.05 probability level.*

leaves could be explained by a higher accumulation in the source organs and a lower accumulation in the sink organs, which is related to proline translocation between the tissues. Proline translocation was caused by proline transporters reported to be the amino acid transporter family (ATF) and the amino acid/auxin permease (AAAP) gene family in all plant organs of rice plants (Lehmann *et al*., 2010). Table 3: Mean and ANOVA data for proline contents in leaves and stems at flowering stage in lowland rice varieties: Chai Nat 1 (CNT1), Pathum Thani 1 (PT1),and Inpari 35 (IN35) when plants were watered with different sodium chloride (NaCl) and trehalose concentrations.

Effects of Salinity, Trehalose and Variety on Sugar Content: The accumulation of sugar content in both leaves and stems was only significantly differentially affected by varieties, but not by trehalose and salinity and the interaction between all factors (Table 04). Both in leaves and stems, higher sugar content was found in CNT1, followed by PT1 and IN35, respectively. Although no significant difference in sugar content in leaves was affected by salinity, a higher percentage increase in sugar content was observed at 0 mM trehalose when salinity (50–150 mM NaCl) was increased compared to non-salinity (0 mM NaCl) in two Thai rice varieties; CNT1 at 16.37-55.43 %, PT1 at 7.28-16.41 % compared to IN35 at -9.74 to 12.54 %. When trehalose was applied, the direction of percentage change in sugar content was observed at 0 mM NaCl when trehalose (50-150 mM trehalose) was increased compared to no trehalose application in all rice varieties, but the percentage increase was higher in two Thai rice varieties (CNT1 and PT1); CNT1 with 18.15-45.98 %, PT1 with 7.06-33.16 % more than IN35 with -3.36 to 11.46 %. In non-saline soils, only CNT1 showed positive percentage of sugar content in the leaves when trehalose was applied. The positive change in percentage sugar content in stems was observed in CNT1 at elevated salinity (50-150 mM NaCl) compared to trehalose application; CNT1 at -9.07 to 2.52 %, PT1 at -19.67 to -23.01 % and IN35 at -32.52 to -43.32 %. When trehalose (50-150 mM trehalose) was applied without salinity (0 mM NaCl), a positive change in sugar content in the stem also was observed for CNT1; CNT1 at -9.33 to 7.78 %, PT1 at -4.42 to -28.00 % and IN35 at -13.62 to -34.16 % (data not shown).

Effects of Salinity, Trehalose and Variety on Starch Content: The starch content in leaves and stems was not significantly different for all factors and their interactions, except for the varieties in the stem. Higher starch content was observed in IN35 followed by PT1 and CNT1 in the stem (Table 5). With careful observation, the starch content in the leaves without trehalose application, expressed as a percentage compared to 0 mM NaCl without salinity, was observed with increasing salinity (50-150 mM NaCl) only at CNT1 (-1.72 to 40.53 %); PT1 at -3.43 to -31.46 % and IN35 at -3.91 to -10.96 %. When trehalose was administered with 0 mM NaCl, a positive percentage starch content was observed in the leaves of two rice varieties, including CNT1 and IN35, compared to 0 mM trehalose.

Although the interaction between all factors was not significant, the percentage starch content in the stems of all rice varieties increased slightly when either the salt content (50-150 mM NaCl) (CNT1 at 10.82 to15.01 %, PT1 at -1.24 to 13.13 % and IN35 at 7.56 to 25.91 %) or trehalose (50-150 mM) (CNT1 at -9.30 to 29.28 %, PT1 at -11.07 to 27.62 % and IN35 at 4.20 to 11.13 %) was applied to the plants. However, the percentage starch content of the stems in the rice varieties appears to increase from 100 mM trehalose. The results show that the salt concentration and the application of trehalose have an influence on the sugar and starch content in both the leaves and the stems although no significant statistics are available. Table 5 Mean and ANOVA data for starch contents in leave and stem at flowering stage in lowland rice varieties: Chai Nat 1 (CNT1), Pathum Thani 1 (PT1),and Inpari 35 (IN35) when plants were watered with different sodium chloride (NaCl) and prolilne concentrations. In photosynthesis and carbon translocation, both the types of products and the type of tissue in which the product is accumulated are associated with each other. Sucrose is the main product of photosynthesis, which can be converted into starch in the tissues, the leaves (source) and the stems (sink), which can determine the accumulation of these substances in the plants (Chaturvedi *et al*., 2017).

In this study, the sugar content in the leaves appeared to increase when the plants were exposed to salt stress (50-150 mM NaCl). In contrast to the stems, the sugar content decreased in all rice varieties under salt stress. The breakdown of sucrose to fructose and glucose is controlled by the enzyme sucrose synthase and invertase (Koch, 2004). The higher sugar content in the leaves serves the photosynthetic capacity of the plants under salt stress conditions. Sugar plays an important role in photosynthesis and plant metabolism and is therefore the most important storage and transport medium in plants (Koch, 2004). The decrease in starch content in the leaves was observed with an increase in salt content in the rice varieties. This result explains that the conversion of sucrose (in the swelling tissue parts) to starch (in the sinking parts) is impaired due to the limited activity of enzymes, i.e., starch phosphorylase and the enzyme that converts sucrose to starch, resulting in higher sucrose content in the swelling parts (Chaturvedi *et al*., 2017). At this time, the activity of sucrose synthesis enzymes such as sucrose synthase and sucrose phosphate synthase for sucrose production increases, allowing sucrose to serve as a photoprotectant (Das *et al*., 2016). In addition, high levels of soluble sugars in plants under stress conditions could increase the osmotic potential that stimulates enzymatic activities and protects the biomolecules in plants (Das *et al*., 2016; Kumar *et al*., 2021).

Plants that accumulate high amounts of starch in the plant play an important role in protecting against abiotic stress through the source-sink allocation of carbon. In this study, it was found that the accumulation of sugars and starch in both leaves and stems of CNT1 under salt concentrations. Sugar as osmoprotection, so the degradation of starch into sugar is a mechanism in plants to protect plants under unsuitable conditions. In addition, the storage of starch in the plant helps to promote the conversion of starch to sugar in the plant,when necessary, such as in the case of salinity problems, etc., which are considered unsuitable environmental factors (Dong and Beckles, 2019). Nevertheless, positive percentage changes in sugar and starch content were observed in both leaves and stems under salinity conditions only in CNT1. Similarly, the changes in PT1 and IN35 were similar under salinity conditions with a percentage increase in sugar content only in the leaf tissue, while the positive percentage change in starch content was only maintained in the stem. These results, which only concern the accumulation of sugars and starch in leaves and stems, indicate that CNT1 has a higher resilience because it was able to store higher photosynthetic products such as sugars and starch in both leaves (source) and stems (sink). However, the changes in agronomic traits will be analysed and compared between these varieties. Increased sugar accumulation in the leaves (source part) was observed in all three rice varieties, but a higher accumulation of starch in the leaves was observed in CNT1 and IN35 when exogenous trehalose was applied. Thus, trehalose application was able to promote plant survival under salt stress in all three rice varieties, with CNT1 and IN35 responding particularly favourably. Furthermore, an increase in sugar and starch accumulation in the stem tissue (sink) was only observed in CNT1. Thus, CNT1 seems to show a more positive adaptive response in terms of sugar and starch accumulation in Thai rice cultivars when confronted with both salinity and trehalose than PT1. The benefit of trehalose application by increasing the sugar content in the leaves was higher than in the stems at all trehalose concentrations. However, trehalose application resulted in a decrease in sugar content in leaves when plants were exposed to salinity, suggesting that salt stress in plants decreases, thus reducing the accumulation of sugar content. It can be caused by the conversion of sugars into other substances to take advantage of the reduction of salt stress in plants. In the rice varieties, an increase in the percentage sugar content in leaves and stems was only observed in IN35 when exogenous trehalose was applied at the highest salt concentration (150 mM NaCl). This could be an indication of the salt tolerance of IN35 when exposed to salinity even though it uses exogenous trehalose. For the application of exogenous sugar, Koch (1996) reported that photosynthesis in plants is restricted, which is related to the balance between consumption and production of sugar, i.e. that a lower sugar requirement in plants through the use of exogenous sugar leads to a restriction of photosynthesis. However, Eckstein *et al*. (2012) reported in Arabidopsis that exogenous sugars can support photosynthesis. Meanwhile, starch accumulation in both leaves and stems changed in a different direction when trehalose was supplied under saline conditions. The benefit of using exogenous sugar for photosynthesis therefore depends on many factors, such as the plant species, the type and concentration of sugar.

Effects of Salinity, Trehalose and Variety on Agronomic Traits

For eight agronomic traits, all traits were significantly reduced by starting salinity at 50 mM NaCl, with the exception of HI starting at 100 mM NaCl (Table 06). Exogenous trehalose had a significant effect on two traits, such as GYP and HI, starting at 50 mM and 100 mM trehalose, respectively. The rice varieties had significant effects on all traits. Higher values were observed for CNT1 for PH and for the Thai rice varieties CNT1 and PT1 for PL compared to IN35. However, IN35 showed higher values for other traits such as PTP, FGP, 100 GW, SDW, HI and GYP. Among Thai rice varieties, CNT1 and PT1 showed higher values for various traits, but higher HI and GYP were observed in CNT1.

The interaction of factors was found only for variety × salinity for five traits, including PTP, FGP, SDW, HI and GYP (Table 06). Both PTP and FGP were observed decreasing at 50 mM NaCl and above in all rice cultivars. However, a higher percentage decrease in both traits (PTP and FGP) –was observed in CNT1 (-14.32 to -37.80 % and -22.62 to -48.34 %) and PT1 (-18.29 to -32.57 % and -26.11 to -68.49 %) under salt stress (50-150 mM NaCl) than in IN35 (-12.27 to -13.74 % and -2.17 to -14.07 %).

The decrease in SDW and GYP properties was influenced by salinity (50-150 mM NaCl). At 50 mM NaCl and above, a higher percentage decrease in SDW and GYP was observed in CNT1 (-15.45 to -43.91% and -18.30 to -63.42%) and PT1 (-19.27 to -40.48% and -23.01 to -67.57%) and a lower one in IN35 (-14.36 to -28.82% and -7.73 to -30.18%). The effects of salinity on Thai rice varieties (CNT1 and PT1) and IN35 were almost double that of Thai rice varieties. The value of percentage reduction of IN35 for GYP at salinity (50–150 mM NaCl) appeared to be similar to that of SDW, but the reduction for GYP was higher in CNT1 and PT1. The percentage changes differed between rice varieties compared to 0 mM NaCl. IN35 increased at 50–100 mM NaCl (41.42-41.58, 4.41-48.15 %) and remained constant at 150 mM NaCl (39.25, -1.06 %), while it decreased continuously in CNT (30-38.83, -2.31 to -24.53 %) and PT1 (22.5-33.67, -3.11 to -35.25 %).

A decline in most agronomic traits affected by salinity begins at 50 mM NaCl, the lowest NaCl concentration in this study, suggesting that salinity is an important abiotic stress for plants, affecting both biochemical and physical traits, leading to a reduction in yield and other agronomic traits. In addition, the reproductive stage in rice is a stage that is also very sensitive to salinity, as the yield reduction in all rice cultivars ranged from -30.18% to -67.57% at 150 mM NaCl. Similar to that reported by Zheng *et al*. (2023), salinity could reduce both the quantity and quality of yield components and grain yield of rice. In addition, the percentage decrease in grain yield was more than 64.52% on average across many studies (58 studies). Considering the lowest percentage of reduction of GYP at all salinity levels (50-150 mM NaCl) in IN35, it seems to be more tolerant to salinity than the other two varieties, CNT1 and PT1. Among the Thai rice varieties, CNT1 showed higher salinity tolerance than PT1, as it had a lower percentage reduction of GYP than PT1 at 50 mM and 100 mM NaCl, with close percentages at 150 mM NaCl. In this study, a positive role of exogenous trehalose was observed, but not a significantly clear one in the physical and biochemical properties of the plants. However, the addition of trehalose clearly had positive effects on three agronomic traits: FGP, HI and GYP. For the percentage of filling grains as a secondary yield component developed at the panicle differentiation stage, the stage at which the number of grains per panicle develops (at the anthesis stage). This stage is associated with viable and fertilize pollen grains at the reproductive stage (Moldenhauer *et al*., 2013). Khatun and Flowers (1995) reported that pollen viability and stigma quality in the pollinating plant part and in the female plant part (infertile flowers) of rice (cultivar IR36) were also negatively affected when the plants were grown under NaCl stress (10-25 mol m-3). Thus, the application of trehalose at the reproductive stage, the heading stage, affects traits such as FGP, which occur at this stage, but not PH, PTP or 100 GW, which are formed before (at tillering stage) or after (grain filling stage) the heading stage, respectively.

CONCLUSION

Regarding the significant effect of rice variety on physical and biochemical traits (RWC, Chl A, Chl B, total Chl, proline, soluble sugar and starch content in leaves), rice variety IN35 showed the highest value in all these traits, except sugar content, ahead of CNT1 and PT1.Salinity had a negative effect on physiological and biochemical traits, single effect on proline content in stem and interaction with variety including RWC, Chl B and total Chl. However, varieties responded differently to salinity levels (50-150 mM NaCl). The accumulated proline content appeared to be higher in the leaves than in the stems. In contrast, a greater decrease in proline content was observed in the stems (-16.67 to -27.78%) than in the leaves (-2.21 to -9.39%) when the plants were treated with salt. Although salinity had no significant effect, it could cause an increase in sugar content in the leaves or a decrease in stems.The exogenous application of trehalose (100-150 mM) at the reproductive stage was only able to induce Chl A. However, starch content in both leaves and stems appeared to be induced by trehalose application in CNT1 and IN35, which was compared with the value without salt stress (0 mM NaCl).Salinity showed significant negative effects on all eight agronomic traits above 50 mM NaCl, with the exception of HI, which starts at 100 mM NaCl. However, a greater negative decrease in percentage affected by salinity was observed for productive tillers per plant (-15.38 to -26.92 %), percentage filled grains per panicle (-17.12 to -43.80 %), straw dry weight (-16.42 to -37.50 %) and grain yield per plant (-16.04 to -51.89 %). IN35 had higher values for 6 in 8 characteristics, except for plant height and panicle length. In addition, IN35 showed higher salt tolerance at 50-150 mM NaCl with less reduction in grain yield per plant than Thai rice varieties CNT1 and PT1 (-7.73 to -30.18 %, -18.30 to -63.42 % and -23.01 to -67.57 %, respectively).However, the application of exogenous trehalose had a positive significant effect on HI (3.35-5.05 %) at 100 mM trehalose and the percentage of filled grains per panicle (1.98-6.29 %) and grain yield (3.95-7.89 %) at 50 mM trehalose. Explain the benefit of using exogenous trehalose on filled grains per panicle as a secondary yield component since this trait was formed at the reproductive, heading stage.

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