Antitranspirant modulates Na$^+$ enrichment and yield in indica rice under salt stress

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Abstract Rising salinity in agricultural land is a major barrier limiting yields of crops like rice, which has been reported as a salt-sensitive plant. An improvement in salt tolerant ability of rice has been achieved by obstructing the sodium (Na) transpiration flow via apoplastic route. Here we assess the potential of an antitranspirant (AT) in modulating Na enrichment and yield in rice under salt stress. Sodium concentration in flag leaf was enriched in relation to the salt exposure time and significantly decreased in plants grown under 0.2% AT foliar application. Free proline accumulation in salt-stressed plants was increased by 15.3 folds over the control, whereas it was stable in plants grown under 0.2% AT foliar application. Chlorophyll *a*, chlorophyll *b*, total chlorophyll, total carotenoids, photon yield of photosystem II (PSII), net photosynthetic rate, transpiration rate, and stomatal conductance in salt-stressed plants were lower than the control with the exogenous foliar spray of 0.2% AT. Positive relationships between total chlorophyll and photon yield of PSII, photon yield of PSII and net photosynthetic rate, and net photosynthetic rate and fertile seed were also evident. Number of seeds per panicle in salt-stressed plants was significantly enhanced by 0.2% AT foliar application, whereas other yield attributes declined. Antitranspirants could be a promising option to improve the growth and yield of rice cultivated on salt-affected soils.

Keywords Antitranspirant · Free proline · Net photosynthetic rate · Sodium ion · Transpiration rate · Yield traits

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1 Introduction

Soil salinity is a major abiotic constraint regulated by global climate change (Corwin 2021), which negatively affects plant growth and development and reduces crop yield (Shahid et al. 2018; Sahab et al. 2021). Salt-affected area in the arid and semi-arid regions is gradually and steadily increasing (Kılıc et al. 2022; Singh 2022). A soil is saline due to the presence of high-concentrated salts, such as sodium chloride (NaCl), sodium sulfate (Na$_2$SO$_4$) and magnesium sulfate (MgSO$_4$) (Kumar and Sharma 2020; Hopmans et al. 2021) In halophytic species, adaptive

mechanisms, *i.e.*, Na$^+$ homeostasis, compartmentalization, secretion, osmoregulation, antioxidant production, and hormonal regulation provide tolerance to high salt concentration (Loconsole et al. 2019; Rahman et al. 2021; Islam et al. 2022). In contrast, glycophytic plants, including many cultivated crop species, are very sensitive to high soil salinity, due to the lack of key salt-defense mechanisms (Hasegawa et al. 2000; Hasegawa 2013).

Rice (*Oryza sativa* L.) is a staple food crop for more than half of the world's population, especially for 3.5 billion people in Asia (Devkota et al. 2019). It is a major source of carbohydrate, antioxidants, oils, fiber, minerals, and vitamins, which also help against metabolic disorders and cardiovascular diseases (Khush 2005; Sen et al. 2020; Behl et al. 2021). Rice has been reported as a salt-susceptible crop and salt stress leads to the inhibition of plant growth, development, and crop yield (Fahad et al. 2019; Schneider and Asch 2020). In general, sodium (Na) is a dominant cation, which is accumulated in large amounts in the root tissues (restriction) of rice (Plett and Møller 2010; Chakraborty et al. 2019) and bypass flow or apoplastic route to translocate Na from root to other organs (Faiyue et al. 2010, 2012) via transpiration stream (Hasanuzzaman et al. 2018), thereby reducing photosynthetic efficiency (Gadelha et al. 2021). Moreover, the application of abscisic acid (ABA), a plant hormone, which controls the stomatal closure, has been reported to limit the Na movement via transpiration flow (Parveen et al. 2021; Sharmin et al. 2021).

Antitranspirants have been widely applied for enhancing abiotic defense mechanisms in various crops grown under drought (AbdAlla et al. 2019), salt stress (Boari et al. 2016), high temperature stress (Cirillo et al. 2021), and ozone pollution (Francini et al. 2011), and are constituted by three classes, such as metabolic (*s*-ABA, chitosan, fulvic acid), reflective (kaolin, $CaCO_3$, CaO), and film-forming (di-1-*p*-menthene, poly-1-*p*-menthene, acrylic polymers) (Mphande et al. 2020). The performance of the application of antitranspirants is highly dependent on plant species, developmental stage, and plant density (Morsy and Mehanna 2022; Mphande et al. 2022). Antitranspirant (AT)-induced negative effects have also been reported, including stomatal closure to limit CO_2 assimilation, leaf temperature increase, and sunburn (Rodriguez et al. 2019). Pathumthani 1

rice genotype has been reported as a salt-susceptible species, exhibiting reduced plant growth and development when subjected to high salt treatment (Cha-um et al. 2009). It was hypothesized that the foliar spray of AT on the leaf tissues of Pathumthani 1 might limit transpiration, which in turn could reduce Na translocation from root to shoot and alleviate Na toxicity in terms of osmotic adjustment, photosynthetic pigment stabilization, photosynthetic capacity, and yield stability. The objective of this study was to evaluate the potential of an AT in modulating crop growth and yield in rice under salt stress.

2 Material and methods

2.1 Plant material, antitranspirant, and salt treatments

Seeds of *indica* rice (*Oryza sativa* L. ssp. *indica* cv. Pathumthani 1) were collected from the Pathum Thani Rice Research Center, Rice Department, Ministry of Agriculture and Cooperatives, Thailand. The seeds were surfaced sterilized by 20% Clorox$^®$ [8.25% *ai* sodium hypochlorite (*w/v*), Clorox, CA, USA] for 15 min, primed in the water for 12 h, and sowed in the water-saturated soil (EC = 2.69 dS m^{-1}, pH = 5.7, organic matter = 12.26%, total nitrogen = 0.30%, total phosphorus = 578 mg kg^{-1}, total potassium = 3073 mg kg^{-1}, calcium = 7020 mg kg^{-1}, and magnesium = 1034 mg kg^{-1}). Four weeks after seed germination, individual rice seedling was directly transplanted into clay pots (ϕ 15 cm and 30 cm in height) containing soil. Fertilizer (16-16-16: N-P-K) was applied three times after 15 days (initial establishment stage), 45 days (vegetative stage), and 90 days (booting stage) of transplanting, based on the recommendation of Rice Department, Ministry of Agriculture and Cooperatives, Thailand. At booting stage, 50 mL per plant of 0.0% and 0.2% AT [Gustec-S$^®$, 25.2% ai (*w/v*) sucrose esters of fatty acids, BIOSAFFER Co., Ltd., Thailand] were applied as a foliar spray using a hand-held sprayer. Then, 0 and 200 mM NaCl solution were applied to the pots, representing the control and salt stress treatments, respectively. Concentrations of Na$^+$, K$^+$, and Ca^{2+} were determined in the flag leaf collected at 1, 3, 5, 7, and 14 days after NaCl treatments. Biochemical and physiological data were also collected 14 days after

NaCl treatments. Yield attributes were recorded at harvesting stage in each treatment.

2.2 Na^+, K^+, and Ca^{2+} assay

Na^+, K^+, and Ca^{2+} concentrations [mg g^{-1} dry mass (DM)] were assayed following the modified method of Tanaka et al. (1999) and Hossain et al. (2006). Flag leaf tissue of rice was washed by deionized water to remove excess ions on the surface of each leaf. Plant samples were dried at 80 °C for 3 days, ground into powder using mortar with liquid nitrogen, and then dissolved by deionized water. The ions in plant tissues were extracted after boiling in water for 15 min and centrifuged at $10,000 \times g$ for 10 min. Supernatant was then diluted into 100 times and filtered through a 0.45 μm-filter membrane (VertiPure™, Vertical®, Thailand). Fifty μL of solution was applied into WATER IC-PACK™ ion exclusion column. The column was equipped with high-performance liquid chromatography (HPLC) system (e595 Alliance, Waters Associates, Milford, MA, USA) and 432-Conductivity Detector (Waters Associates, Milford, MA, USA). A mobile phase of 3 mM nitric acid and 0.1 mM EDTA was supplied with a flow rate at 1 mL min^{-1}. Concentrations of Na^+, K^+, and Ca^{2+} were determined, based on standard curve of each ion (Sigma®, MA, USA).

2.3 Biochemical and physiological traits

Free proline concentration [μmol g^{-1} fresh mass (FM)] in the flag leaf was estimated according to the method of Bates et al. (1973). In brief, 50 mg of fresh samples were ground in a mortar with liquid nitrogen. One mL of aqueous sulfosalicylic acid (3%, *w/v*) was added into the homogenate powder and then filtered through a filter paper (Whatman™ #1). The supernatant was reacted with an equal volume of glacial acetic acid and ninhydrin reagent (1.25 mg ninhydrin in 30 mL glacial acetic acid and 20 mL 6 M H_3PO_4) and boiled at 95 °C in water bath for 1 h. Then, the reaction was stopped by incubating the reaction mixture in an ice bath. The reaction mixture was mixed vigorously with 2 mL of toluene. After cooling at 25 °C, the chromophore (pink color) was collected and measured at 520 nm using UV–VIS spectrophotometer (HACH DR/4000; HACH Company, Loveland,

CO, USA). L-proline ($0 - 20$ μmol mL^{-1}) standard was validated as the calibration standard.

Chlorophyll a (Chl_a), chlorophyll b (Chl_b), total chlorophyll (TChl), and total carotenoid (C_{x+c}) concentrations in the flag leaf were measured according to the method of Shabala et al. (1998). In brief, 100 mg of leaf tissues were chopped and transferred to glass vials containing 10 mL of 99.5% acetone and blended using a homogenizer. The glass vials were sealed with Parafilm® (Sigma-Aldrich, USA) to prevent acetone evaporation, and kept at 4 °C in the darkness for 48 h. Chl_a, Chl_b, and C_{x+c} concentrations [μg g^{-1} fresh mass (FM)] were measured at 662 nm, 644 nm, and 470 nm, respectively, using UV–VIS spectrophotometer against acetone (99.5%) as a blank.

Chlorophyll a fluorescence in the flag leaf was measured using a fluorescence monitoring system (FMS 2; Hansatech Instruments Ltd., Norfolk, UK) with the pulse amplitude modulation mode (Loggini et al. 1999). In brief, a dark-adapted leaf kept for 30 min was subsequently exposed to the modulated measuring beam of far-red light (LED source) with a typical peak at wavelength 735 nm. Initial fluorescence (F_0) and maximum fluorescence (F_m) yields were measured under weakly-modulated red light (< 85 μmol m^{-2} s^{-1}) with 1.6 s pulse of saturating light ($> 1,500$ μmol m^{-2} s^{-1} photosynthetic photon flux density) and calculated using FMS software for Windows®. The variable fluorescence yield (F_v) was calculated by the equation: $F_v = F_m - F_0$. The ratio of variable to maximum fluorescence (F_v/F_m) was calculated as the maximum quantum yield of PSII photochemistry. The photon yield of PSII (Φ_{PSII}) in the light was calculated as: $\Phi_{PSII} = (F_m' - F)/F_m'$ after 45 s of illumination when steady state was achieved (Maxwell and Johnson 2000), where F is a steady-state yield and F_m' is a maximum fluorescence yield.

Net photosynthetic rate (P_n; μmol CO_2 m^{-2} s^{-1}), stomatal conductance (g_s; mmol H_2O m^{-2} s^{-1}), and transpiration rate (E; mmol H_2O m^{-2} s^{-1}) in the flag leaf were recorded using a portable photosynthesis system fitted with an infra-red gas analyzer (LI 6400XT, LI-COR, Lincoln, NE, USA), following the method of Cha-um et al. (2007). The g_s and E were auto-calculated by monitoring the H_2O of air entering and exiting the infra-red gas analyzer head space chamber. The flow rate of air in sample line and micro-chamber temperature was

set at 500 μmol m^{-2} s^{-1} and 27 ± 1 °C block temperature, respectively. The light intensity was set at 1,000 μmol m^{-2} s^{-1} photosynthetic photon flux density by 6400-02B red-blue light emitting diode (LED) light source.

2.4 Yield attributes

Panicle mass, panicle length, number of panicles per plant, number of seeds per panicle, fertile seed percentage, and one-hundred grain mass in each treatment were recorded (IRRI 2002).

2.5 Experimental layout and data analysis

The experiment was arranged in 2×2 factorials in completely randomized design with four replications. The data were subjected to a two-way analysis of variance (ANOVA) and were analyzed using Statistical Package for the Social Sciences (SPSS) software (version 11.5 for Window®). The mean values obtained from four treatment combinations, from either antitranspirant or NaCl, were compared using Tukey's honest significant difference test at $p \leq 0.05$.

3 Results

3.1 Morphology and biochemical changes

Leaf burning, leaf rolling, and leaf chlorosis in salt-stressed plants without the application of AT (0.0%) were observed, whereas the toxic damages were reduced by 0.2% AT foliar application (Fig. 1). Under 200 mM NaCl, Na$^+$ concentration in older leaf (third from the top) without AT was the maximal at 31.1 mg g^{-1} DM, causing leaf chlorosis. A reduction of Na$^+$ in the leaf tissues was observed (19.6 mg g^{-1} DM) when sprayed with 0.2% AT (Fig. S1). In flag leaf, Na$^+$ was significantly increased in relation to NaCl exposure period, whereas the increment was comparatively slower under 0.2% AT application (Fig. 2a). In contrast, K$^+$ concentration in plants under salt stress was significantly declined irrespective of AT applications when compared with the

Fig. 1 Morphological characteristics of Pathumthani 1 rice genotype treated with or without antitranspirant (AT) and subsequently exposed to 0 and 200 mM NaCl for 14 days
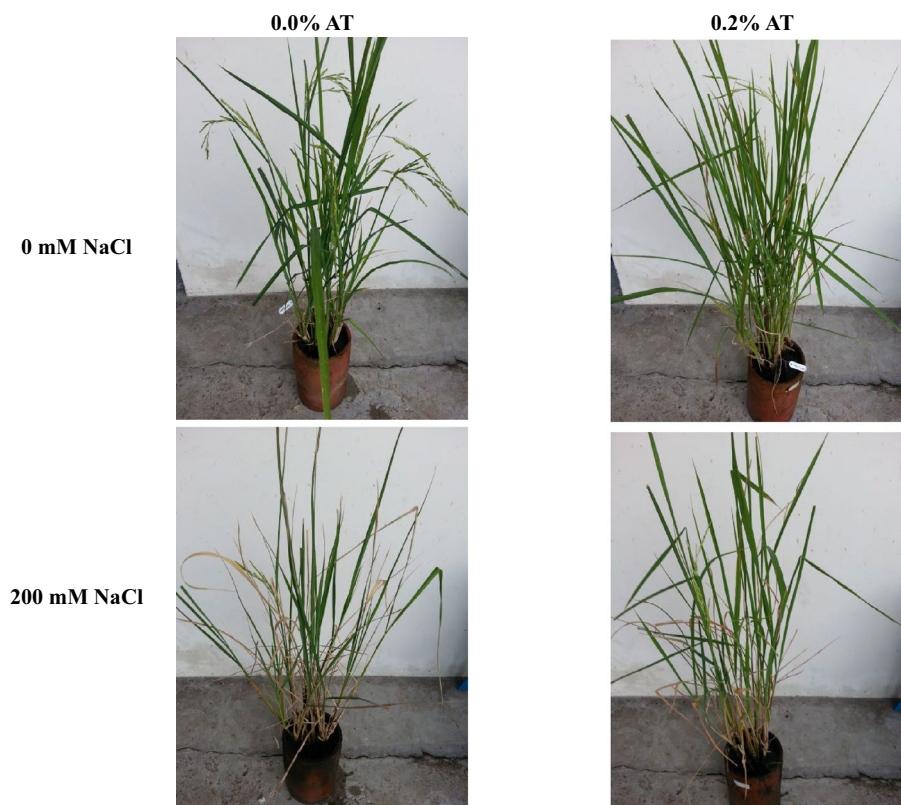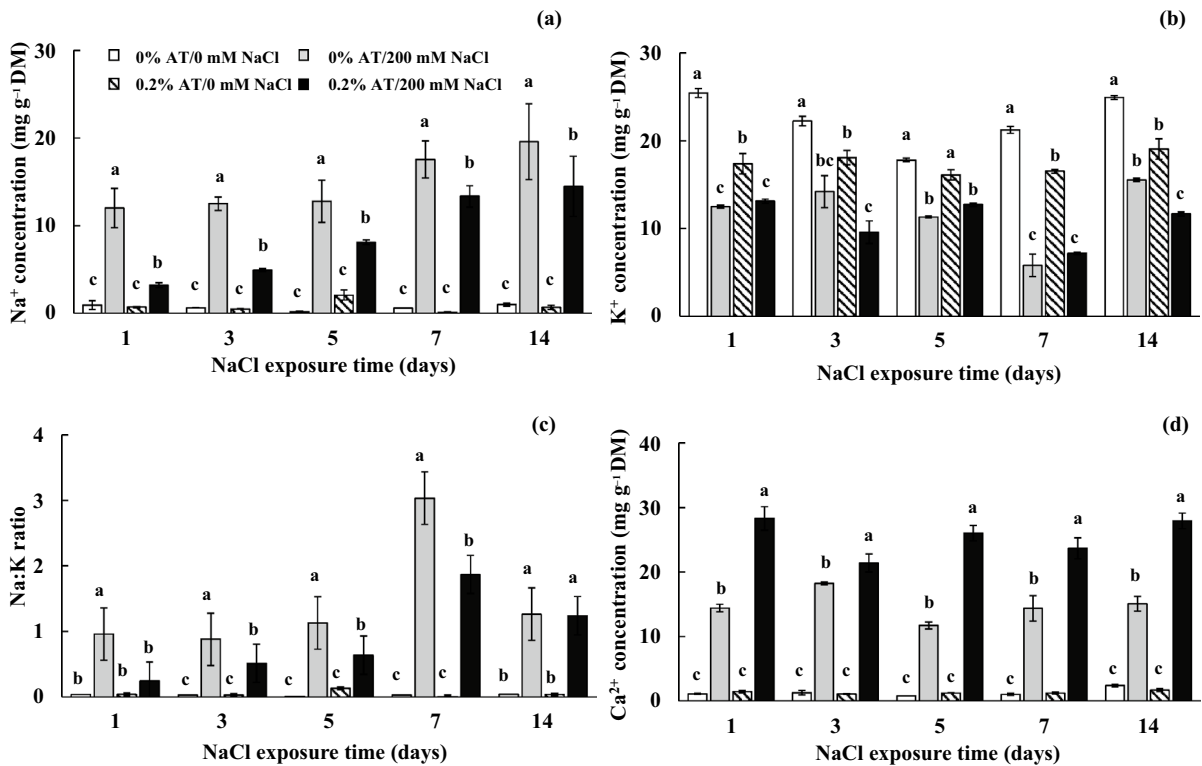
Fig. 2 Sodium (Na$^+$; a), potassium (K$^+$; b), sodium:potassium ratio (Na$^+$:K$^+$; c), and calcium (Ca.$^{2+}$; d) concentrations in flag leaf tissues of Pathumthani 1 rice genotype treated with or without antitranspirant (AT) and subsequently exposed to 0 and 200 mM NaCl for 1, 3, 5, 7, and 14 days. Data are presented as means of four replications ± standard errors. Different letters in a bar represent significant difference based on Tukey's honest significant difference test at $p \leq 0.05$

control (Fig. 2b). Na:K ratio was also the maximal in plants without foliar application of AT when exposed to 200 mM NaCl for 14 days (Fig. 2c). Likewise, Ca^{2+} concentration was also increased in salt-stressed plants and it was the highest in 0.2% AT-treated plants under salt stress. Free proline accumulation in flag leaf tissues of salt-stressed plants without AT was the maximal at 3.98 μmol g^{-1} FM and it was reduced to 1.08 μmol g^{-1} FM in 0.2% AT-treated plants (Table 1).

3.2 Physiological changes

Chl$_a$, Chl$_b$, and C$_{x+c}$ concentrations in the salt-stressed plants without AT were significantly decreased by 50.43%, 49.13%, and 80.16% over the control, respectively. Interestingly, in the salt-stressed plants with 0.2% AT, these parameters were reduced by 33.21%, 47.29%, and 68.61%, respectively, compared with the control (Table 1). Total chlorophyll (TChl)

concentration in the leaf tissues of salt-stressed plants without AT was significantly declined by 49.83% over the control and TChl of salt-stressed plants with 0.2% AT was also degraded by 39.65% over the control without NaCl (Fig. 3a). A negative relationship between Na$^+$ enrichment and TChl concentration was demonstrated (Fig. 3b; $R^2 = 0.87$). F$_v$/F$_m$ did not vary significantly among the treatments (Fig. S2a), whereas Φ$_{PSII}$ in the salt-stressed plants without AT and 0.2% AT was significantly diminished by 17.15% and 9.53% over the control, respectively (Fig. 3c). A positive relationship between TChl concentration and Φ$_{PSII}$ was evident (Fig. 3d; $R^2 = 0.57$). Consequently, P$_n$ in the salt-stressed plants without AT and 0.2% AT was sharply dropped by 93.94% and 75.14% over the control, respectively (Fig. 4a). Moreover, g$_s$ and E in the salt-stressed plants were also decreased (Fig. S2b; $R^2 = 0.80$) in plants without AT (50.0% and 85.71% reduction over the control, respectively) (Table 1). A positive relationship between Φ$_{PSII}$ and P$_n$ (Fig. 4b;

Table 1 Free proline, chlorophyll a (Chl_a), chlorophyll b (Chl_b), total carotenoids (C_{x+c}), stomatal conductance (g_s), and transpiration rate (E) of Pathumthani 1 rice genotype treated with or without antitranspirant (AT) and subsequently exposed to 0 and 200 mM NaCl for 14 days. Data are presented as means of four replications ± standard errors

Antitranspirant (%)	NaCl (mM)	Free proline (μmol g^{-1} FM)	Chl_a (μg g^{-1} FM)	Chl_b (μg g^{-1} FM)	C_{x+c} (μg g^{-1} FM)	g_s (mmol H$_2$O m^{-2} s^{-1})	E (mmol H$_2$O m^{-2} s^{-1})
0	0	0.26 ± 0.07c	293.3 ± 11.8a	231.0 ± 15.5a	24.7 ± 1.0a	0.02 ± 0.003a	0.77 ± 0.06a
	200	3.98 ± 0.26a	145.4 ± 7.9b	117.5 ± 14.8b	4.9 ± 0.8b	0.01 ± 0.001b	0.11 ± 0.02b
0.2	0	0.69 ± 0.08bc	290.0 ± 12.2a	250.8 ± 6.06a	25.8 ± 6.4a	0.03 ± 0.005a	0.72 ± 0.08a
	200	1.08 ± 0.08b	193.7 ± 17.8b	132.2 ± 21.9b	8.1 ± 0.6b	0.01 ± 0.001b	0.31 ± 0.03b
Significance level							
AT		**	ns	ns	ns	ns	ns
NaCl		**	**	**	**	**	**
AT × NaCl		**	**	**	**	**	**

Mean values followed by different letters in a column indicate significant difference based on Tukey's honest significant difference test at $p \leq 0.05$; ns and ** represent not significant and significant at $p \leq 0.01$, respectively
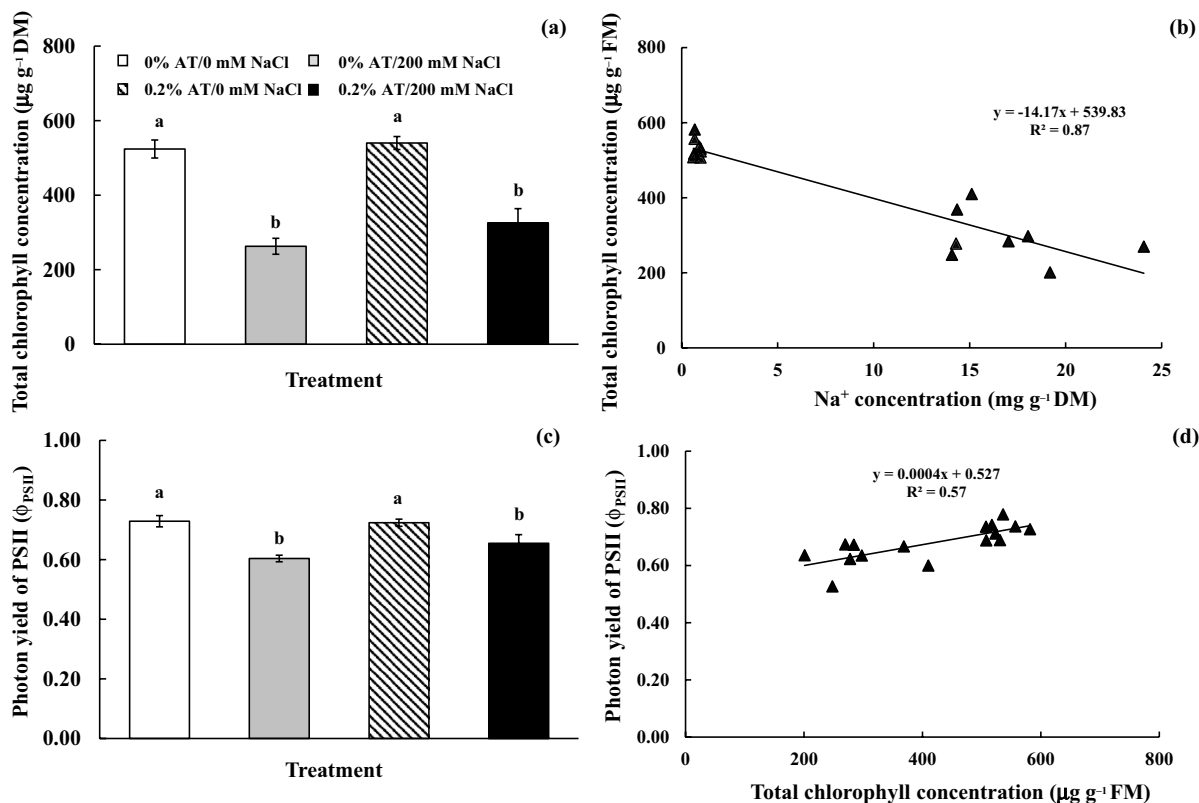

Fig. 3 Total chlorophyll concentration (**a**), relationship between sodium concentration and total chlorophyll concentration (**b**), photon yield of PSII (**c**), and relationship between total chlorophyll concentration and photon yield of PSII (**d**) in flag leaf tissues of Pathumthani 1 rice genotype treated with or without antitranspirant (AT) and subsequently exposed to 0 and 200 mM NaCl for 14 days. Data are presented as means of four replications ± standard errors. Different letters in a bar represent significant difference based on Tukey's honest significant difference test at $p \leq 0.05$
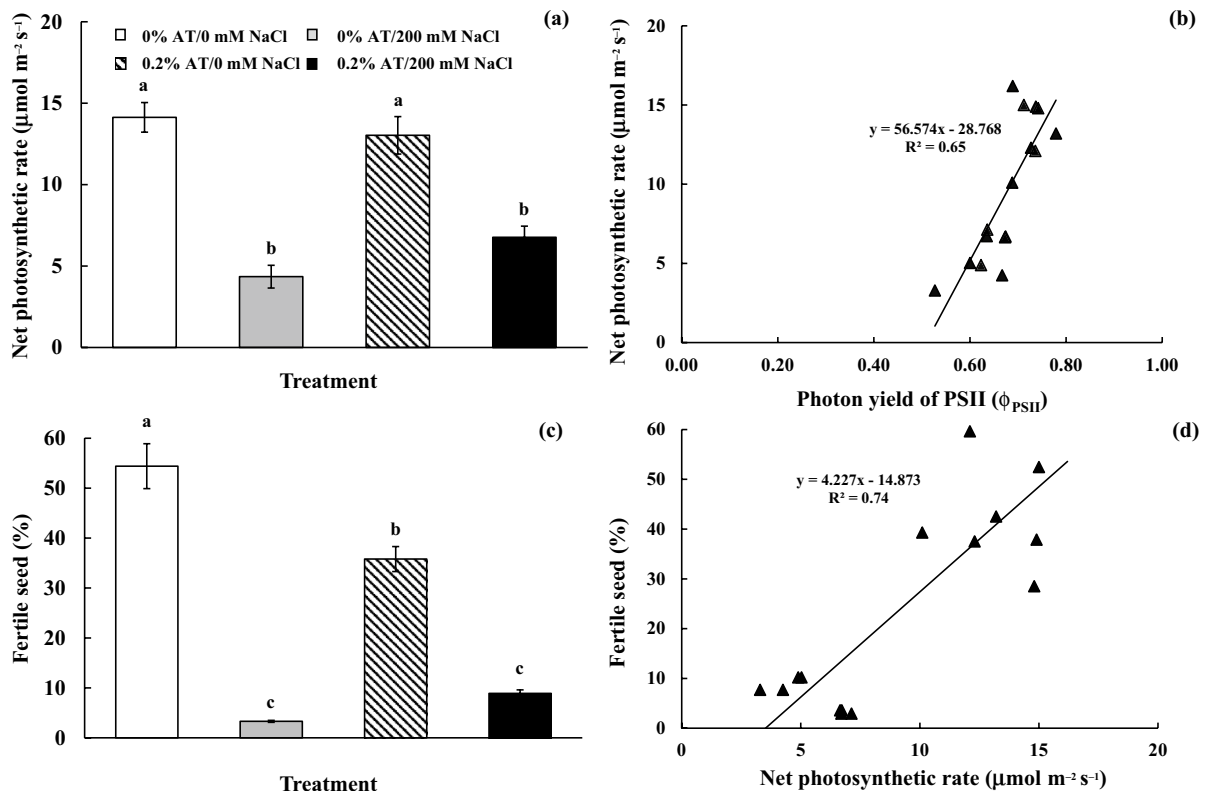
Fig. 4 Net photosynthetic rate - P_n (**a**), relationship between photon yield of PSII and net photosynthetic rate - P_n (**b**), fertile seed (**c**), and relationship between net photosynthetic rate - P_n and fertile seed (**d**) in flag leaf tissues of Pathumthani 1 rice genotype treated with or without antitranspirant (AT) and sub-sequently exposed to 0 and 200 mM NaCl for 14 days. Data are presented as means of four replications ± standard errors. Different letters in a bar represent significant difference based on Tukey's honest significant difference test at $p \leq 0.05$

$R^2 = 0.65$) and P_n and fertile seed percentage of rice grain was demonstrated (Fig. 4d; $R^2 = 0.74$).

3.3 Yield attributes

Fertile seed percentage in salt-stressed plants with and without AT was significantly decreased by 75.14% and 93.94% over the control, respectively (Fig. 4c). Under 200 mM NaCl, panicle mass, panicle length, number of panicles per plant, number of seeds per panicle, and one-hundred grain mass were sharply declined by 81.70%, 39.92%, 91.67%, 71.15%, and 43.50% in plants without AT over the control, respectively. On the other hand, panicle mass, number of panicles per plant, and number of seeds per panicle in AT-treated plants were significantly dropped by 48.08%, 25.0%, and 31.23% over the control, respectively. Number of seeds per panicle of AT-treated plants under salt stress was retained. Moreover, yield attributes under salt stress were increased with the application of 0.2% AT (Table 2).

4 Discussion

Pathumthani 1 rice genotype exhibited leaf rolling, chlorosis, and leaf burn when plants were exposed to 200 mM NaCl. Previously, growth performance, including number of leaves, plant fresh mass, plant dry mass, and root length, of seedlings of Pathumthani 1 rice genotype under 342 mM NaCl has been reported to significantly decline (Cha-um et al. 2009). Similarly, tip burn and leaf chlorosis in 21-day-old seedlings of Pathumthani 1 genotype under hydroponic culture with 10 dS m^{-1} or 68 mM NaCl have been reported (Pongprayoon et al. 2019).

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Table 2 Panicle mass (PM), panicle length (PL), number of panicles per plant (NP), number of seeds per panicle (NS), and one-hundred grain mass (OHM) of Pathumthani 1 rice geno-type treated with or without antitranspirant (AT) and subsequently exposed to 0 and 200 mM NaCl for 14 days. Data are presented as means of four replications ± standard errors

Antitranspirant (%)	NaCl (mM)	PM (g)	PL (cm)	NP	NS	OHM (g)
0	0	1.04 ± 0.07a	23.8 ± 0.5a	12 ± 1.2a	65.0 ± 4.5a	2.23 ± 0.09a
	200	0.19 ± 0.02c	14.3 ± 1.8b	1 ± 0.1d	15.5 ± 1.3c	1.26 ± 0.04c
0.2	0	0.54 ± 0.10b	20.4 ± 1.2a	9 ± 0.4b	44.7 ± 7.7b	2.09 ± 0.03a
	200	0.23 ± 0.01c	15.3 ± 1.0b	5 ± 0.6c	31.8 ± 3.4bc	1.56 ± 0.03b
Significance level						
AT		**	ns	**	**	**
NaCl		**	**	**	**	**
AT × NaCl		**	**	**	**	**

Mean values followed by different letters in a column indicate significant difference based on Tukey's honest significant difference test at $p \leq 0.05$; ns and ** represent not significant and significant at $p \leq 0.01$, respectively

The overall performance of rice crop under salt stress was markedly improved by 0.2% AT foliar application. Plant canopy and height of 6% kaolin (a member of antitranspirants) pretreated sesame (*Sesamum indicum* L.) under 2.3 dS m^{-1} NaCl salt stress have been reported to significantly improve over the control without AT (Gaballah et al. 2007). Likewise, the aboveground traits of tomato (*Solanum lycopersicum* L.) under salt stress have been observed to be slightly improved by kaolin application (Boari et al. 2016). The concentration of Na in the older leaves and flag leaf at the booting stage of rice under salt stress was the maximal. In IR2153-26–3-5–2 rice genotype, the maximal Na concentration (0.513 mmol g^{-1} DM) has been reported in old leaf (first from the base), whereas it has been observed as the lowest (0.170 mmol g^{-1} DM) in young leaf (fifth from the base) (Yeo et al. 1985). At the reproductive stage, Na concentration has been recorded in the order root > stem > middle leaf > flag leaf of Pokkali and Chettiviruppu rice genotypes under 8 dS m^{-1} NaCl for 4 weeks (Chakraborty et al. 2019).

An enrichment of Na and a decrement of K in antagonism have been well established in several rice genotypes grown under salt stress, leading to increased Na:K ratio (Sriskantharajah et al. 2020; Yong et al. 2020). However, the increase depends on the degree of salt concentration (Sriskantharajah et al. 2022), salt exposure period (Chakraborty et al. 2020; Gadelha et al. 2021), and environmental variations (Yong et al. 2020). Potassium has been reported as a macronutrient that controls the movement of Na in relation to transpiration rate, especially in K-starved plants (Quintero et al. 2007). In general, Na is directly absorbed by root tissues and translocated to other organs by apoplastic route (Yeo et al. 1987; Ochiai and Matoh 2002; Foster and Miklavcic 2017) and is closely related with transpiration stream (Naito et al. 1994; Quintero et al. 2008; Nomiyama et al. 2013; Hasanuzzaman et al. 2018). Abscisic acid (ABA) is one of signaling hormones induced by NaCl-mediated salt stress, which controls stomatal closure to limit the Na transpiration flow (Park et al. 2020; Parveen et al. 2021; Sharmin et al. 2021; Xue et al. 2021). Suppression of transpiration rate using polyethylene glycol, exogenous glycinebetaine, and proline has been reported as an effective way to limit transpiration rate, Na uptake, and apoplastic flow in rice crops (Ochiai and Matoh 2004; Sobahan et al. 2009).

Enrichment of Ca in epidermal cells near stomata plays a key role in stomatal closure, especially under environmental stress conditions (Fricke 2004). Alternatively, free proline accumulation is an important indicator of salt toxicity as it is a major osmolyte (Chakraborty et al. 2020; Sriskantharajah et al. 2022) due to increased Δ^1-pyrroline-5-carboxylate synthetase and ornithine-δ-aminotransferase activities (Irakoze et al. 2022). An exogenous foliar spray of AT (chitosan) has been reported to strongly restrict Na concentration in the leaf tissues, stabilize photosynthetic pigments, and regulate enzymatic antioxidants (Attia et al. 2021; Zhang et al. 2021).

Chlorophyll degradation in salt-stressed rice without AT was observed, leading to diminished Φ_{PSII}, reduced P_n, and impaired stomatal functions (declined g_s and E). The photosynthetic abilities of

0.2% AT-treated plants grown under 200 mM NaCl were improved. In African rice (*Oryza glaberima* L.), Chl_a, Chl_b, and C_{x+c} in the leaves of seedlings under 50 mM NaCl for 15 days have been observed to be significantly degraded, causing diminished Φ_{PSII} and decreased P_n (Prodjinoto et al. 2021). In addition, chlorophyll degradation and Φ_{PSII} diminution in *indica* rice genotypes have been reported as sensitive parameters under salt stress (Tsai et al. 2019; Chakraborty et al. 2020; Gadelha et al. 2021). Stomatal closure in salt-stressed rice is a primary adaptation response of plants, leading to decreased P_n, g_s, and E (Fu et al. 2018; Prodjinoto et al. 2021), which is regulated by large amount of endogenous ABA synthesis (Park et al. 2020; Xue et al. 2021). A positive relationship between TChl concentration and Φ_{PSII} ($R^2 = 0.72$), Φ_{PSII} and P_n ($R^2 = 0.84$), and P_n and plant dry mass ($R^2 = 0.61$) in Pathumthani 1 rice seedlings under salt stress has been reported in a previous study (Cha-um et al. 2009). A key function of antitranspirants in salt-stressed plant is to limit transpiration rate and Na translocation from root to shoot (Malash and Flowers 1984; Oddo et al. 2019).

Yield attributes of a crop species are very important criteria while considering salt tolerance improvement using antitranspirants. Increased percent sterility and reduced grain yield in rice crop grown under saline soil have been previously reported (Chakraborty et al. 2019). In the present study, the overall yield traits of salt-stressed Pathumthani 1 rice genotype were sustained by 0.2% AT foliar application. The harvest index and biological yield of wheat (*Triticum aestivum* L.) plants under salt stress have been reported to be retained by AT foliar spray (Gaballah and Moursy 2004). In tomato, the fruit yield traits have been reported to be strongly improved due to the application of AT even when exposed to salt stress (Boari et al. 2016; Ullah et al. 2020). Moreover, seed yield and oil percentage in sunflower (*Helianthus annuus* L.) grown under salt stress have been significantly improved by foliar application of AT (Bakhoum et al. 2020).

In conclusion, Na translocation from root to shoot via bypass flow (apoplastic route) in salt-stressed plants at the booting stage of Pathumthani 1 rice genotype was reduced by foliar application of antitranspirant, depending on stomatal closure. Photosynthetic pigments, photon yield of PSII, and net photosynthetic rate in salt-stressed plants with AT application were better retained than the control, thus maintaining grain yield attributes. Based on the present study, it can be concluded that the foliar application of antitranspirant in rice crop grown in saline soils is beneficial. However, studies are required to validate these findings under field conditions.

Declarations

Conflict of interests The authors declare no conflict of interest.

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